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OUT ON A LIMB: CONSERVATION IMPLICATIONS OF TREE-HOLLOW USE BY A THREATENED SNAKE SPECIES (*Hoplocephalus bungaroides*: SERPENTES, ELAPIDAE)

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Abstract

Habitat requirements of arboreal reptiles may determine their vulnerability to anthropogenic disturbance, but have attracted little research. We studied habitat use by the broad-headed snake Hoplocephalus bungaroides, *a threatened species from southeastern Australia. Intensive radio-tracking of 22 broad-headed snakes (from 1992 to 1995 in Morton National Park, 160 km south of Sydney) provided detailed information on the habitat requirements of these animals. During spring, broad-headed snakes were sedentary and used rocks and crevices on exposed cliff edges as diurnal retreat sites. These results are consistent with the widespread view that this species is restricted to rocky outcrops. However, >80% of our telemetered snakes moved away from the rock outcrops to open woodland during the summer. Radio-tracked snakes used one to nine trees each summer and spent long periods (up to 48 days) sequestered inside tree-hollows. Tree use was highly non-random; the snakes actively selected dead rather than live trees, large rather than small trees and trees with many branches and hollows. The selection of trees with hollow branches may reflect the thermo-regulatory opportunities provided by this microhabitat, and/or the abundance of potential prey (arboreal mammals) in tree-hollows. Our radio-tracked snakes actively selected grey gums* Eucalyptus punctata *and Sydney peppermints* E. piperita, *but avoided the most common tree species on our study sites (turpentine* Syncarpia glomulifera*). Our study shows that persistence of broad-headed snakes in an area may depend crucially not only on suitable rocky habitat, but on adjacent forests. Hence, forestry practices should be designed to ensure that suitable 'habitat trees' are retained in forested areas near rocky cliffs. © 1997 Elsevier Science Ltd*

Keywords: arboreality, Australia, Elapidae, forest, habitat selection, *Hoplocephalus bungaroides*, Serpentes, snake.

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INTRODUCTION

Many kinds of animals utilise tree-hollows as sleeping or nesting sites (Saunders *et al.*, 1982; Lunney *et al.*, 1988; Lindenmayer *et al.*, 1990; Dickman, 1991), and the availability of tree-hollows may limit some populations of arboreal mammals (Meredith, 1984; Lindenmayer *et al.*, 1991). The potential vulnerability of arboreal taxa to commercial forestry activities (especially, tree removal) is obvious. For example, clear-felling on 80–120 year rotation in montane ash forests in Victoria does not allow trees to reach an age suitable for hollow formation, and may seriously affect arboreal marsupials (Smith & Lindenmayer, 1988; Lindenmayer *et al.*, 1991; Lindenmayer & Possingham, 1995). Removal or burning of dead or 'over-mature' trees to enhance commercial timber production may also reduce the numbers of hollow-dependent arboreal mammals (e.g. Meredith, 1984). More generally, logging operations have been implicated as important causal factors in the decline of many endangered species (Losos *et al.*, 1995).

Although mammalian and avian use of tree-hollows has been well-studied (e.g. Smith & Lindenmayer, 1988; Inions *et al.*, 1989; Thomas *et al.*, 1990; Murphy & Noon, 1992; Buchanan *et al.*, 1995), arboreal reptiles have attracted far less attention in this respect (Lillywhite & Henderson, 1993). Available studies of tree-hollow use by reptiles are few and are generally anecdotal in nature (e.g. Stebbins & Barwick, 1968; Wilson & Knowles, 1988; Cogger, 1992; but see How & Kitchener, 1983). This situation is unfortunate because information on this topic may be directly relevant to conservation planning. For example, one of the criteria used to allocate logging licences in New South Wales concerns habitat requirements of any endangered fauna that are likely to be present (NSW Threatened Species Conservation Act, 1995). A wide variety of taxa should be taken into account when making such decisions, because of inter-specific differences in the types of hollows that are needed. Even closely-related species may differ significantly in the types of tree-hollow they use (e.g. Saunders *et al.*, 1982). Hollows used by birds and mammals may not necessarily be suitable for arboreal reptiles; for example, thermo-regulatory requirements may be more important for the latter group. Hence, research on the habitat requirements of arboreal reptiles can be of significant value for conservation planning.

Two species of arboreal snakes are currently listed as 'threatened' in New South Wales, but virtually nothing is known about the habitat requirements of either species (Cogger, 1992). To address this problem, we studied habitat use by one of these species, the broad-headed snake *Hoplocephalus bungaroides*. This small, brightly-coloured nocturnal elapid snake is restricted to rocky habitats within a 200 km radius of Sydney, where it shelters in crevices or under sandstone rocks during the day (Hersey, 1980; Shine, 1983; Shine & Fitzgerald, 1989). Populations in some areas have declined dramatically since the European invasion of Australia (Krefft, 1869; Cogger, 1992). Several authors have suggested that broad-headed snakes are threatened primarily by the removal of sandstone rock for use as garden ornaments (e.g. Hersey, 1980; Shine & Fitzgerald, 1989). However, our studies have shown that broad-headed snakes are less exclusively saxicolous than had previously been thought; these snakes leave rock outcrops and become arboreal during late spring and summer. Hence, *H. bungaroides* may be threatened by modification of forest habitat (such as the removal of trees during forestry operations) as well as by physical disturbance to rock outcrops. In this paper we describe tree use by *H. bungaroides*, and explore possible threats to this taxon posed by forestry operations.

STUDY AREA, MATERIALS AND METHODS

Study area

Our study sites were located in Morton National Park, 160 km south of Sydney. In this area the mean daily maximum air temperatures range from 25·9°C in January (mid-summer) to 15·8°C in July (mid-winter), while the mean daily minimum air temperatures for these months are 15·9 and 6·0°C, respectively (Bureau of Meteorology, 1988). Four study sites were used for a mark-and-recapture study, but we only radio-tracked snakes at three sites (each approximately 3 km apart) on the western side of a sandstone plateau of 400 m elevation. The plateau is covered by open woodland forest except for the exposed western cliff edge (10–30 m wide), where small rocks have weathered from the underlying sandstone. During winter and spring, broad-headed snakes are found under these rocks or in crevices along the sandstone cliffs. These cliffs are 20–30 m high and are deeply dissected by numerous horizontal crevices. The vegetation of the general area has been described elsewhere (Black, 1988); at our sites, the open woodland was dominated by turpentines *Syncarpia glomulifera*, red bloodwoods *Eucalyptus gummifera* and blue-leaf stringy barks *E. agglomerata*.

Transmitters and surgical techniques

We used miniature temperature-sensitive radio-transmitters (Holohil Systems, Woodlawn, Ontario, BD-2G TI slow-pulsing transmitters, 18×9×5 mm) with a flexible 15 cm long whip antenna and a battery life of approximately 6 months. Transmitters weighed 2·2 g (< 5% of the snakes' body mass: mean adult mass = 50 g, range 37–72 g) and were waterproofed with a thin layer of Dow Corning 100% flowable silicon sealant. Each whip antenna was placed inside a silastic medical grade tube (Dow Corning Australasia, Sydney, NSW, medical grade tubing, No. 602–175) and the end was sealed with flowable silicon sealant so that the wire antennae could not puncture any of the snake's internal organs. Placement of the antennae in these smooth tubes also facilitated subsequent removal of transmitters from the snake's body.

Prior to surgery, we sterilised transmitters and surgical instruments in 75% ethanol for 4 h. Each snake was placed inside a perspex tube and anaesthetised using a Fluotech 3 anaesthetic machine, with an oxygen–nitrous oxide mixture followed by halothane. We inserted the transmitter through a small incision (three body scales long) between the second row of body scales one-third of the way along the body anteriorly from the vent. The transmitter was then massaged 2–3 cm above the incision so that it would not press against the wound, and the antenna was inserted into the body cavity posteriorly. The incision was made on the left side of the snake to minimise the risk of damaging the lung, which lies along the right-hand side of the body. Following implantation, the incision was closed with Ethicon 5–0 (metric) coated vicryl, a dissolving suture. The wound was sealed with a few drops of medical glue to minimise the risk of infection. Most snakes recovered full mobility < 20 min after cessation of halothane inhalation. We kept snakes in clean cages after surgery for 1–2 weeks prior to release in the field. No snakes died during surgery or prior to release.

Radio-tracking

Eleven broad-headed snakes were radio-tracked from spring 1992 and in 1993. However, during 1994 one snake was radio-tracked from autumn, seven from spring and a further three from summer. Hence, the timing of release of telemetered snakes varied slightly each year (Table 1), mainly because we had difficulty finding snakes during the final year. Because of predation and early transmitter failure, only 10 snakes were radio-tracked during summer in the second field season (1993–1994) and only six snakes were radio-tracked during summer in the final field season (1994–1995; see Table 1). Hence, we gathered a total of 27 snake-summers of data over the 3 years. Five of these snakes were tracked in 2 years, so we have data on summer habitat use for a total of 22 individual broad-headed snakes (14 adult males, eight adult females). Mean snout-vent length (SVL) of these snakes was 56·5 cm (range 50·5–67 cm).

We released the implanted snakes at the point of capture, and commenced radio-tracking them immediately after release. Snakes were located daily during each field-trip and we usually conducted two field trips (each lasting 5–10 days) per month. Initial monitoring showed that telemetered snakes rarely moved from their diurnal retreat sites during daylight hours (movements between retreat sites occurred around dusk), so there was little point in carrying out multiple locations within a single day. Once this was established, we located each snake's retreat site daily and flagged it with fluorescent tape. Habitat variables were recorded after the snake had left the retreat site, to avoid disturbing the animal.

Measurement of trees

Trees used by telemetered broad-headed snakes were identified to species level using field guides (Cronin, 1988; Brooker & Kleinig, 1990). Tree height, numbers of hollow branches and stem holes were assessed visually, and diameter at breast height (dbh) was measured with a tape measure. In order to compare the characteristics of these trees with others available to the snakes, but unused, we also measured the same physical characteristics of the first five trees encountered on each of four transects running east, west, north and south from each tree occupied by a radio-tracked snake. Each transect was 2 m wide and up to 20 m in length.

Assessment of the impact of forestry activities

Because *H. bungaroides* has a very restricted geographic distribution and is frequently arboreal (see below), the species is potentially vulnerable to forestry operations. However, it is impossible to assess the likely impact of forestry activities on *H. bungaroides* without information on the distribution of this species within state forests and the nature of forestry activities within these areas. Thus, we compiled a list of state forests where *H. bungaroides* is likely to occur, using topographic maps, museum records and both published and unpublished fauna surveys. To identify the nature of officially-sanctioned forestry activities in each of these areas, we used management plans prepared by the Forestry Commission of NSW (1982, 1986–1988). Because of the possibility that such official prescriptions may not always be followed in practice, we also obtained more direct information by quantifying the impact of logging

Table 1. Broad-headed snakes, *Hoplocephalus bungaroides*, studied using radiotelemetry in this project

Year	Site	Snake no.	SVL[a] (cm)	Sex	Mass (g)	Date captured	Date released	Tracking duration (days)
1992	1	1DB5AFE	54·0	F	40	23/9/92	12/10/92	87
1992	1	13268F2	58·0	F (g)	53	31/8/92	22/9/92	121
1992	1	1E9B1A	52·5	M	40	31/8/92	22/9/92	87
1992	1	144935	61·0	M	43	31/8/92	22/9/92	118
1992	2	D32A8	54·5	F (g)	51	1/9/92	22/9/92	127
1992	2	1181	58·5	F (g)	53	12/10/92	9/11/92	105[b]
1992	2	1273	50·5	M	38	22/9/92	12/10/92	104
1992	2	1151	51·5	M	41	22/9/92	12/10/92	105
1992	2	D89C2	53·5	M	45	1/9/92	22/9/92	86
1992	2	14597E	56·0	M	47	10/11/92	26/11/92	76
1992	2	469	56·0	M	49	1/9/92	22/9/92	127
1993	1	D533D	57·5	M	59	12/5/93	15/6/93	133[b]
1993	1	144935	61·0	M	46	21/9/93	20/9/93	98
1993	2	D32A8	55·0	F	41	18/8/93	20/9/93	175
1993	2	D428D	55·0	F	44	18/8/93	20/9/93	124
1993	2	D56DB	59·0	F	47	3/6/93	15/6/93	182
1993	2	D89C2	53·7	M	50	3/6/93	15/6/93	168
1993	2	D3C5F	54·5	M	53	23/8/93	20/9/93	124
1993	2	14597E	56·5	M	46	17/8/93	20/9/93	84
1993	4	4DECAE	63·5	F	59	11/8/93	20/9/93	129
1993	4	144A26	52·0	M	39	23/8/93	20/9/93	132
1993	4	861	59·0	M	62	16/6/93	22/7/93	142[b]
1994	1	13268F2	58·8	F	51	31/8/94	20/9/94	38[c]
1994	1	1339F7B	67·0	F	70	28/7/94	20/9/94	122
1994	1	1BBE713	54·0	M	40	10/11/94	5/12/94	71
1994	1	1E9B1A	55·5	M	42	6/12/94	13/12/94	36[c]
1994	1	144935	61·0	M	48	25/1/94	3/3/94	184
1994	1	1341AE1	61·5	M	57	28/7/94	20/9/94	78
1994	2	D56DB	59·0	F	44	26/7/94	20/9/94	105
1994	2	A4597E	56·5	M	54	26/8/94	20/9/94	77
1994	4	1BBF261	52·0	M	40	28/7/94	20/9/94	122
1994	4	1DA64AD	62·5	M	60	9/11/94	5/12/94	36[c]
1994	4	D51AA	63·0	M	72	25/10/94	7/11/94	12[c]

[a]SVL, snout–vent length.
[b]The snake was killed by a predator.
[c]The transmitter failed much earlier than expected.

activities on habitat availability in one recently-logged site. Several months after logging, we measured unfelled and felled trees at a site (compartment 1004) in Yalwal State Forest, less than 15 km from our study area. At this time, we allocated all trees to one of three categories: (i) trees removed during logging (the size of which could be ascertained from their stumps); (ii) 'habitat' trees, intentionally left by the loggers (identifiable because they has been paint-marked with an 'H' prior to logging); and (iii) other live trees left by the loggers, presumably because their removal was judged not to be economically viable. We randomly selected six sites, each > 300 m apart, and within each site we randomly selected five 20×20 m quadrats and recorded: (i) dbh and species of felled trees; and (ii) dbh, species, number of stem holes, and number of hollow branches of 'habitat trees' and other standing trees. These measurements allowed us to assess the number of habitat trees retained per hectare, and the 'quality' of these trees in terms of their suitability for *H. bungaroides*.

RESULTS

During early spring, our radio-tracked broad-headed snakes used sandstone rocks or crevices as diurnal retreat sites. During late spring and summer, however, when temperatures under rocks became too hot for broad-headed snakes to tolerate, most of the telemetered snakes moved long distances (up to 780 m) away from sandstone cliffs and were located high up in tree-hollows.

Number of snakes using trees

Seventy-one trees were used as retreat sites by 22 telemetered broad-headed snakes during the 3 years of our study. Four of these snakes were tracked for two successive summers during the study, so we have data for 18 individual snakes that used trees. The number of snakes using trees varied among the 3 years of our study (Table 2), but not significantly ($\chi^2 = 4.61$, 2 d.f., $p = 0.10$). During the first year, three of our radio-tracked snakes were gravid females, and these remained in the sandstone habitat where they moved infrequently within small home ranges (mean home range size = 0·05 ha, Webb & Shine, 1997). Of the remaining eight non-reproductive snakes, seven used trees. During the second year, all 10 telemetered snakes were non-reproductive and all used tree-hollows as retreat sites during summer. In the final year, five of six snakes radio-tracked during summer used trees. Thus, almost all of the non-gravid snakes that we tracked used tree-hollows during summer.

Number of trees used by individual snakes

The mean number of trees used by individual snakes per summer was 3·2, and ranged from 1 to 9 (see Table 2). Two snakes returned to the same trees after long absences. One male used a blue-leaf stringybark in October 1993 and returned to this tree 46 days later during December. One female used a red bloodwood in November 1993 and returned to this tree 57 days later during January 1994.

Duration of stays in tree-hollows

During the first 2 years of the study, telemetered snakes spent long periods of time inactive while sequestered in tree-hollows (Table 2). The longest period of time spent by a snake in the same tree was 48 days during the first year and 34 days during the second year (Table 2). In the final year of the study, however, radio-tracked snakes spent less time inactive in trees: the longest period a telemetered snake remained in the same tree was 9 days (Table 2). Overall, our broad-headed snakes remained inactive in trees for an average of 7·0 days (SD = 10·5) over the 3 years of the study.

Home ranges and movements of snakes

Movements and home range sizes of broad-headed snakes are described elsewhere (Webb & Shine, 1997),

Table 2. Summary of habitat use by radio-tracked broad-headed snakes *H. bungaroides*

This table shows the numbers of snakes radio-tracked each summer, numbers using tree-hollows in forest above and below the cliffs, mean duration of periods spent inside tree-hollows, the total number of trees used in each year by snakes and the mean number of trees used by each radio-tracked snake that used tree-hollows.

	Year		
	1992–1993	1993–1994	1994–1995
Number of snakes			
Radio-tracked	11	10	6
Using tree-hollows	7	10	5
Using trees above cliffs	6	4	2
Using trees in gorges	1	6	3
Days in same tree			
Mean (SD)	10·6 (17·2)	7·0 (6·0)	2·0 (0·7)
Range	1–48	1–34	1–9
Number of trees used			
Total trees	15	34	22
Mean (SD)/snake	2·1 (1·5)	3·4 (2·1)	4·4 (2·8)
Range	1–5	1–8	2–9

but aspects related to tree use are briefly reviewed here. The maximum straight-line distance between a telemetered snake in forest and the nearest sandstone cliff was 780 m. The mean home range size of non-gravid snakes in woodland habitat was 3·43 ha (SD = 2·86, $n = 18$, range 0·94–11·43). Radio-tracked snakes used a mean of 1·75 trees/ha (SD = 1·68, $n = 18$, range 0·25–5·56), with no significant correlation between home range size and the number of trees used ($r^2 = 0{\cdot}16$, 1, 16 d.f., $p > 0{\cdot}05$). That is, snakes with larger home ranges did not necessarily use more trees.

Type of forest used by snakes

Forests on the sandstone plateaux of the Nowra region are less suitable for saw-log production than are those found below cliffs or in moist gullies (Forestry Commission of NSW, 1982). Thus, the type of forest used by broad-headed snakes (especially, whether it is above or below the cliffs) has implications for forest management. During the first year of our study, most of the radio-tracked snakes used trees on the plateau. In contrast, most of the snakes tracked during the second and third years used trees below the sandstone cliffs (Table 2). However, the year-to-year variation in relative usage of trees above and below the cliffs fell short of statistical significance ($\chi^2 = 4{\cdot}02$, 2 d.f., $p = 0{\cdot}13$).

Characteristics of trees selected by broad-headed snakes

Our radio-tracked snakes did not use trees randomly. Instead, they were highly selective with respect to several characteristics.

Live versus dead trees

Dead, standing trees constitute only about 10% of all available trees in the forest, but 35% of the trees used by the radio-tracked snakes (Table 3). A χ^2-test showed that the broad-headed snakes' use of dead rather than live trees was significantly different from that expected under the null hypothesis that snakes use dead trees in proportion to their availability ($\chi^2 = 58{\cdot}53$, 1 d.f., $p < 0{\cdot}0001$). 'Stags' (standing dead trees containing hollows) were used by 12 individual broad-headed snakes on 25 occasions (Table 3). One male snake used only stags ($n = 8$ trees), despite the abundance of adjacent live trees with hollows.

Species of trees used by broad-headed snakes

Eight species of trees were used by telemetered snakes over the three summers of the study (Table 3). Of live trees, grey gums *E. punctata* and red bloodwoods were used most often by broad-headed snakes (Table 3). Most broad-headed snakes used only a few tree species (mean = 2·2, range 1–4). Our 'random' transect counts enabled us to calculate the availability of different types of trees in the forest and, hence, to assess whether snakes were selecting particular species of trees or simply using trees according to their availability. Using each observation of a snake in a tree as a data point ($n = 71$), a contingency-table test revealed that snakes were highly selective in their usage of tree species (omitting dead trees and unidentified taxa; $\chi^2 = 58{\cdot}65$, 12 d.f., $p < 0{\cdot}0001$). Specifically, snakes used grey gums and Sydney peppermints *E. piperita* much more often than would be expected by chance, based on availability of these species of trees. Broad-headed snakes were never recorded using turpentines, the most common tree species on our study sites (Table 3).

Sizes of trees used by broad-headed snakes

Most of the trees on our study sites were considerably smaller than were the trees used by telemetered snakes. This pattern was evident among both live and dead trees (Fig. 1). We analysed these data using two-factor ANOVAs, where the factors were tree status (live vs dead)

Table 3. Abundance of trees as recorded from transect data compared with the usage of trees by radio-tracked broad-headed snakes
A total of 1116 trees was measured during the study, and data from the three study sites have been pooled. *N*, number of each species recorded; %, percentage occurrence; *n*, number of individual snakes using each tree species.

Common name	Species	Available trees		Trees used by snakes		
		N	%	*N*	%	*n*
Wattle	*Acacia* spp·	27	2·4	0	0	0
Banksia	*Banksia* spp·	8	0·7	0	0	0
Rough barked apple	*Angophora floribunda*	9	0·8	1	1·4	1
Oak	*Casuarina* spp·	32	2·9	0	0	0
Blue leaf stringybark	*E. agglomerata*	143	12·8	9	12·7	5
Red bloodwood	*E. gummifera*	185	16·6	12	16·9	8
Ironbark	*E. paniculata*	56	5·0	3	4·2	3
Sydney peppermint	*E. piperita*	36	3·2	7	9·9	5
Grey gum	*E. punctata*	73	6·5	11	15·5	7
Narrow leaved peppermint	*E. radiata*	78	7·0	0	0	0
Scribbly gum	*E. rossii*	4	0·4	1	1·4	1
Silver top ash	*E. sieberi*	6	0·5	2	2·8	2
Turpentine	*Syncarpia glomulifera*	330	29·6	0	0	0
Stags		101	9·1	25	35·2	12
Unidentified		28	2·5	0	0	0

and usage (whether or not radio-tracked snakes used the tree), and the dependent variables were measures of the size of the trees (i.e. height, or diameter at breast height). These analyses revealed that dead trees were significantly shorter than live trees ($F_{1,1182}=52{\cdot}62$, $p<0{\cdot}0001$) but were similar in mean diameter at breast height ($F_{1,1182}=1{\cdot}08$, $p=0{\cdot}30$). This difference reflects the higher frequency with which the uppermost branches of dead trees were lost, presumably during storms. The analyses also showed a highly significant size difference between trees which were available compared with those that were used by the snakes (for diameter, $F_{1,1183}=133{\cdot}27$, $p<0{\cdot}0001$; for height, $F_{1,1182}=62{\cdot}44$, $p<0{\cdot}0001$). Significant interaction terms between the two factors were also evident (for height, $F_{1,1182}=9{\cdot}22$, $p<0{\cdot}003$; for diameter, $F_{1,1183}=15{\cdot}18$, $p<0{\cdot}0001$). These interaction terms reflect the fact that only the largest live trees were used, whereas dead trees of a wider range of sizes were acceptable to snakes (Fig. 1). Overall, the snakes actively selected large trees, regardless of whether the tree was dead or alive.

Numbers of hollows in trees used by broad-headed snakes

A possible reason for the snakes to select larger trees was the fact that these trees were more likely to contain hollows. Pooling data for the eight species of *Eucalyptus* measured in our study, larger trees (greater dbh) contained more hollows ($r=0{\cdot}74$, 1, 579 d.f., $p<0{\cdot}001$). Do snakes choose trees based on the numbers of hollows they provide, rather than (or as well as) tree size *per se*? Tree hollows occur in two main forms: stem hollows and hollow branches. Because telemetered broad-headed snakes were usually located high up in trees, we were rarely able to determine which types of hollows were used as retreat sites. We suspect that most telemetered snakes were sheltering in hollow branches rather than stem hollows, for the following reasons.

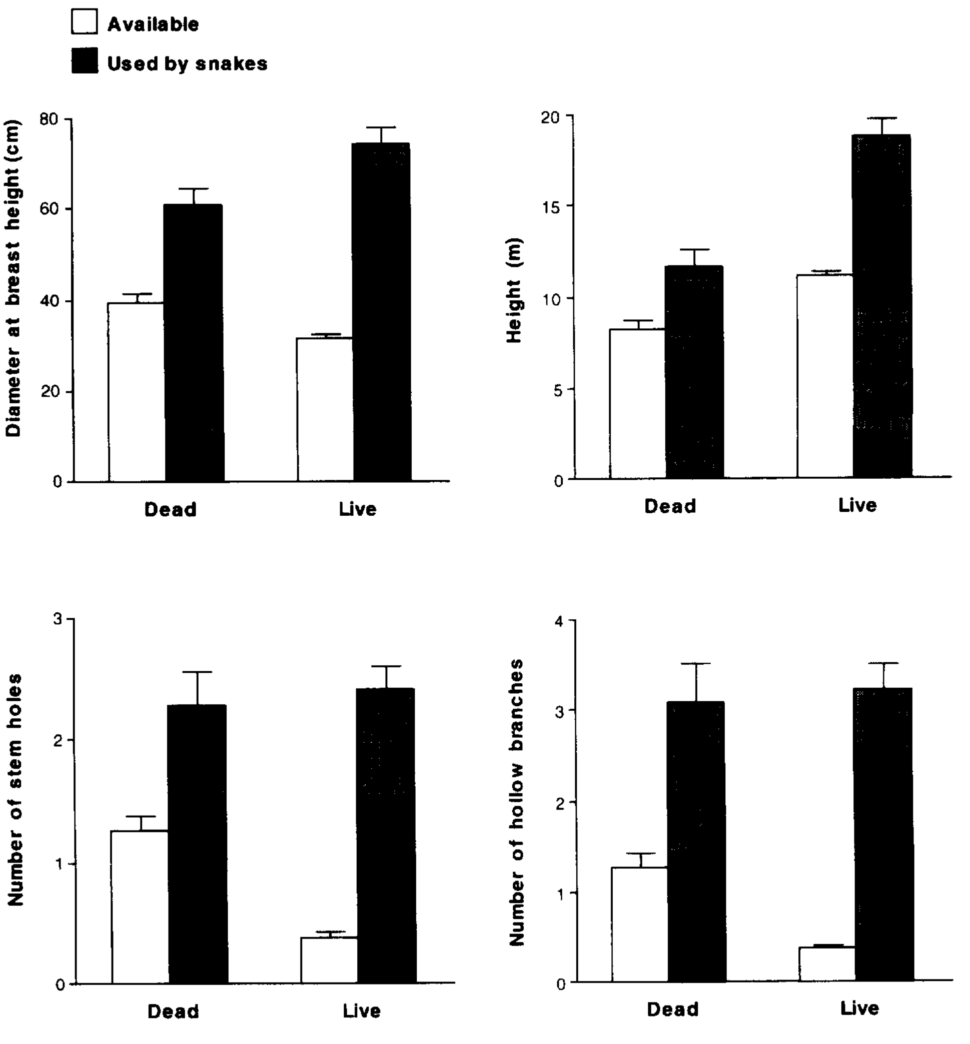

Fig. 1. Characteristics of trees selected by radio-tracked broad-headed snakes compared with available trees in the same area. The histograms show mean values and associated 95% confidence limits for dead standing trees ('stags') and live trees, separately. Open histograms represent 'available' trees and filled histograms represent the trees used by radio-tracked snakes. See text for results of statistical analyses of these data.

Direct observations
We observed two snakes entering the ends of dead horizontal branches 2–3 m long, with entrance holes 10–20 cm in diameter. Also, virtually all records of arboreality by radio-tracked snakes involved trees containing hollow branches, and the direction of the telemetry signals suggested that the animals were inside these hollows. In contrast, we have only one definite record of a snake inside a stem hollow. This snake spent 1 day at a height of approximately 2 m in a red bloodwood stem hollow before moving to another tree. In three other instances, telemetered snakes were found in trees (senescent stags) that did not contain hollow branches.

Thermal data
Hollow branches may provide better opportunities for behavioural thermo-regulation by the snakes. Observations of one radio-tracked snake that used a hollow branch in a Sydney peppermint tree as a retreat site for 48 days in 1992 support this idea. We were able to determine the position of the snake accurately by placing a radio receiver (without an aerial) next to the branch. This snake was able to regulate its body temperature fairly precisely by moving inside the hollow branch during the day in such a way that it remained inside those parts of the branch that were in direct sunlight. For example, between 14:00 h and 18:00 h (sunset) on 13 October 1992 this snake maintained a mean body temperature of 32·1°C (SD = 1·1, range 30·4–34·4°C) by means of these movements.

Our data on the numbers of hollow branches and stem hollows in trees enable us to test whether trees with these characteristics were actively selected by *H. bungaroides*. Overall, snakes chose trees with high numbers of both types of hollows (Fig. 1). A two-factor ANOVA (factors: live vs dead tree; used vs not used by snakes) showed that dead trees have more stem hollows than live trees ($F_{1,1183} = 7{\cdot}52$, $p < 0{\cdot}0001$), and that snakes prefer trees with more stem hollows ($F_{1,1183} = 128{\cdot}68$, $p < 0{\cdot}0001$), with a significant interaction between these two factors ($F_{1,1183} = 13{\cdot}98$, $p < 0{\cdot}0002$). The interaction term reflects the fact that most dead trees had many stem hollows, so that within the category of 'trees that were not used by snakes', the dead trees had more stem hollows than the live ones. The numbers of stem hollows in trees that were used by the snakes, however, did not differ between dead and live trees. In other words: (i) snakes selected trees with large numbers of stem hollows; and (ii) these constituted only a small fraction of all live trees, but a significant proportion of dead trees (Fig. 1).

Analysis of the number of hollow branches per tree showed exactly the same pattern as for stem hollows: dead trees had more hollow branches ($F_{1,1183} = 8{\cdot}09$, $p < 0{\cdot}013$), snakes preferred trees with more hollow branches ($F_{1,1183} = 233{\cdot}32$, $p < 0{\cdot}0001$), and there was a significant interaction term ($F_{1,1183} = 14{\cdot}93$, $p < 0{\cdot}0008$). As for stem hollows, the interaction term for hollow branches was due to the fact that even unused dead trees had many hollow branches, whereas unused live trees had very few. In trees that were used by snakes, the number of hollow branches per tree was similarly high for both dead and live trees (Fig. 1). In combination, these analyses show that broad-headed snakes actively selected trees with many hollows (in both stems and branches) as retreat sites.

Which tree characteristics are actually selected?
Above, we have shown that broad-headed snakes select: (i) large rather than small trees; (ii) dead rather than live trees; and (iii) trees with many hollows. However, all of these characteristics are correlated. For example, hollows are most common in large trees and more common in dead rather than live trees. Thus, the apparent selection for these three characteristics may be due to intercorrelation rather than causal relationship: snakes may select trees based on only one of these criteria. If this is true, the snakes' apparent preference for trees with many hollows may simply be an epiphenomenon of selection for large trees. Alternatively, the reverse may be true. To test this possibility, we calculated residual scores from the general linear regression of one trait against the other. For example, residual scores for numbers of hollows regressed against tree size (dbh) provide an index of the numbers of hollows relative to that expected from a tree of that size. Similarly, residual scores from the regression of dbh against the number of hollows provide an index of the diameter of the tree (dbh) relative to that expected from a tree with that number of hollows. Note that these two types of residual scores are negatively correlated, but not so strongly ($r^2 < 0{\cdot}50$) that it would be meaningless to use them as separate measures of tree dimensions. If the snakes use the number of hollows *as well as* tree size as criteria in selecting retreat sites, we expect that both of these residual scores will differ between selected vs unused trees. Our analyses support the proposition that the trees used by snakes are distinctive in several respects rather than just one:

1. *Numbers of hollows*: trees selected by snakes had more stem hollows relative to tree diameter ($F_{1,1183} = 15{\cdot}21$, $p < 0{\cdot}0001$) and more hollow branches relative to tree diameter ($F_{1,1183} = 73{\cdot}75$, $p < 0{\cdot}0001$). Not surprisingly, dead trees also had more hollows than live trees of the same diameter (for stem hollows, $F_{1,1183} = 20{\cdot}96$, $p < 0{\cdot}0001$; for hollow branches, $F_{1,1183} = 15{\cdot}81$, $p < 0{\cdot}0001$). Interaction terms were not significant ($p > 0{\cdot}20$) in either of these analyses. Thus, broad-headed snakes consistently chose trees with many hollows, independent of tree diameter (Fig. 2).
2. *Size of tree*: trees selected by snakes were larger (greater diameter at breast height) relative to their number of stem hollows ($F_{1,1183} = 23{\cdot}96$, $p < 0{\cdot}0001$) and number of hollow branches ($F_{1,1183} = 6{\cdot}07$, $p < 0{\cdot}015$). Dead trees also were smaller (in dbh) than were live trees with the same number of

hollows (for stem hollows, $F_{1,1183} = 14{\cdot}80$, $p < 0{\cdot}0001$; for hollow branches, $F_{1,1183} = 10{\cdot}39$, $p < 0{\cdot}0015$). The interaction term was not significant ($p > 0{\cdot}05$) in the first of these analyses, but was significant in the latter ($p < 0{\cdot}03$; snakes apparently were not selective among dead trees in terms of dbh relative to the number of hollow branches, but were selective in live trees; see Fig. 2). Thus, broad-headed snakes used relatively large trees, independent of the availability of hollows (Fig. 2). The snakes' selection of larger-than-average trees was also apparent when we restricted the analysis to habitat choice within a particular tree species. To do this, we compared the sizes of available trees with those used by snakes for each of the three species most commonly used by broad-headed snakes. The snakes consistently chose larger-than-average trees (Fig. 3). In all cases, the trees selected by broad-headed snakes were significantly larger than would be expected based on the size distribution of available trees (unpaired t-tests: red bloodwoods $t = -5{\cdot}42$, 195 d.f., $p < 0{\cdot}001$, grey gums $t = -3{\cdot}89$, 82 d.f., $p < 0{\cdot}001$, blue leaf stringybarks $t = -5{\cdot}36$, 150 d.f., $p < 0{\cdot}001$). Hence, the overall selection of large trees by the snakes was not a consequence of a preference for a particular taxon which was coincidentally a large species.

3. *Live vs dead*: to determine if snakes preferred to use dead trees rather than live trees with the same general characteristics, we restricted analysis to trees that were very large or had many hollows, and compared usage vs availability of dead vs live trees within these categories. These analyses showed that dead trees were actively selected among all large trees ($\geqslant$80 cm dbh: snakes used 5 of 7 dead trees, vs 17 of 53 live trees of the same size, $\chi^2 = 4{\cdot}12$, 1 d.f., $p < 0{\cdot}05$). However, we detected no preference for dead vs live trees among all trees with many hollows (for more than three stem holes per tree, snakes used 15 of 43 dead trees, vs 32 of 126 live trees, $\chi^2 = 1{\cdot}66$, 1 d.f., $p = 0{\cdot}20$: for more than three hollow branches per tree, snakes used 14 of 27 dead trees, vs 28 of 73 live trees, $\chi^2 = 1{\cdot}47$, 1 d.f., $p = 0{\cdot}22$). Thus, the selection of dead trees by the snakes may be due primarily to the greater number of hollows within these trees, rather than any other factor.

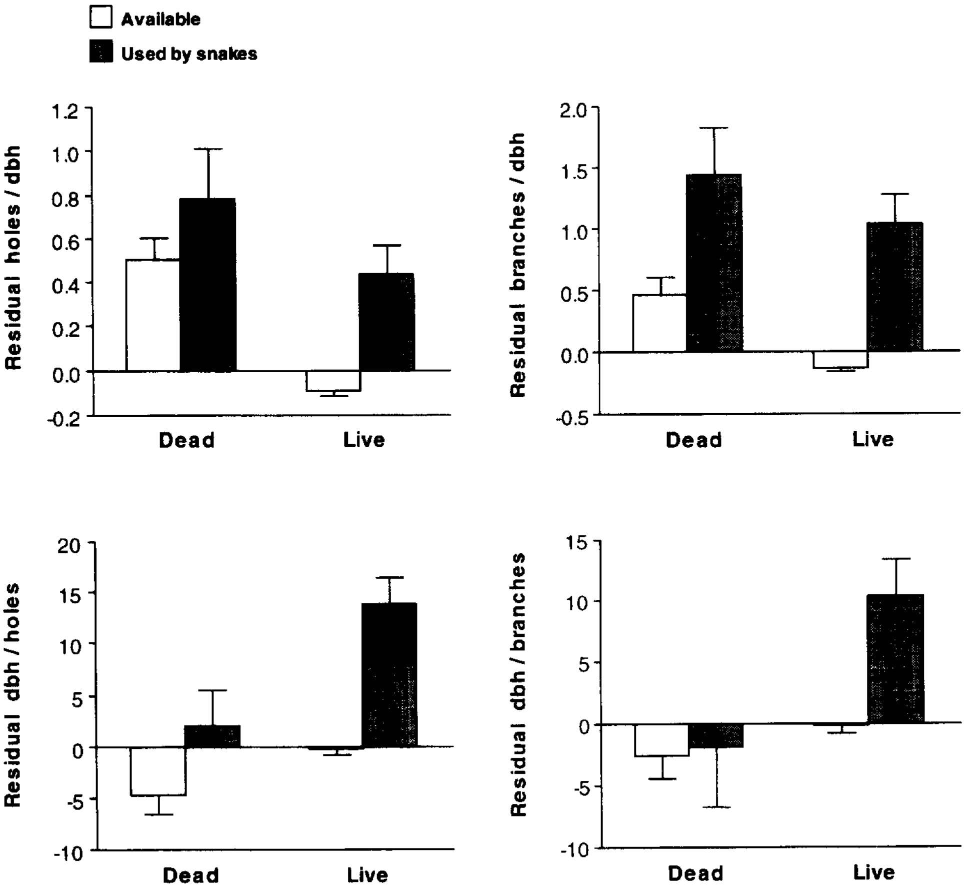

Fig. 2. Characteristics of trees selected by radio-tracked broad-headed snakes compared with available trees in the same area. The histograms show mean values and associated 95% confidence limits for dead standing trees ('stags') and live trees, separately. Open histograms represent 'available' trees and filled histograms represent the trees used by radio-tracked snakes. The variables used for these histograms are residual values from the general linear regression of one trait on another. Thus, for example, the 'residual holes/dbh' provides an index of the number of stem holes in a tree relative to the number expected from a tree of that dbh (diameter at breast height). See text for explanation and for statistical analyses of these data.

Impact of logging on broad-headed snakes

Our surveys of habitat characteristics suggest that 18 state forests contain habitat suitable for *H. bungaroides*, although we have definite records of *H. bungaroides* from only three of these areas (Table 4). Thus, it is clearly of interest to examine potential effects of commercial forestry operations on habitat availability for *H. bungaroides*.

Our most direct evidence comes from the recently-logged compartment at Yalwal State Forest, where we measured a total of 469 trees at six sites. Of these trees, 56 had been recently logged. Of the remainder, three were dead standing trees, 20 were marked as 'habitat trees', and another 390 were live trees left untouched by forestry operations. In this particular forest, spotted gums *Eucalyptus maculata* were the most commonly logged species (40 of 56 trees), although some blue-leaf stringybarks, grey gums and ironbarks *E. paniculata* were also logged. A one-factor ANOVA revealed significant size differences among the three categories of trees ($F_{2,463} = 245{\cdot}4$, $p < 0{\cdot}001$). Habitat trees were the largest (mean dbh = 63·2 cm, SD = 14·9), logged trees were intermediate in size (mean dbh = 53·0 cm, SD = 10·4) and the remaining 'unwanted' trees were relatively small (mean dbh = 22·1 cm, SD = 12·3).

The impact of logging activities on habitat availability for *H. bungaroides* will depend primarily on how similar the 'habitat trees' selected by foresters are to the trees selected by broad-headed snakes. To answer this question, we compared characteristics (dbh, and number of hollow branches and stem hollows) of 20 habitat trees selected by foresters to those of 25 trees used by our radio-tracked snakes. We restricted the sample of 'snake' trees to those on slopes below cliffs, so that habitat was broadly similar to that in the logged compartment. The 'habitat trees' selected by foresters were smaller (mean dbh = 63·2 vs 75·0 cm), and contained fewer hollow branches (mean = 2·2 vs 3·2) and stem holes (mean = 2·0 vs 2·4) than did the trees selected by broad-headed snakes. Although these differences were not statistically significant (one-factor ANOVAs, 1, 43 d.f., $p > 0{\cdot}05$ in all cases), some of the habitat trees selected by foresters were unlikely to be used by broad-headed snakes. For example, over 80% of the trees selected by our radio-tracked *H. bungaroides* contained more than one hollow branch (and usually, many hollow branches). In contrast, two of the 20 'habitat' trees selected by foresters had no hollow branches, while a further nine contained only one hollow branch. On average, only 1·5 trees with >1 hollow branch were retained per site (range 0–3), so that overall 7·5 such trees were retained per hectare. These trees were relatively evenly spaced in the post-logging habitat.

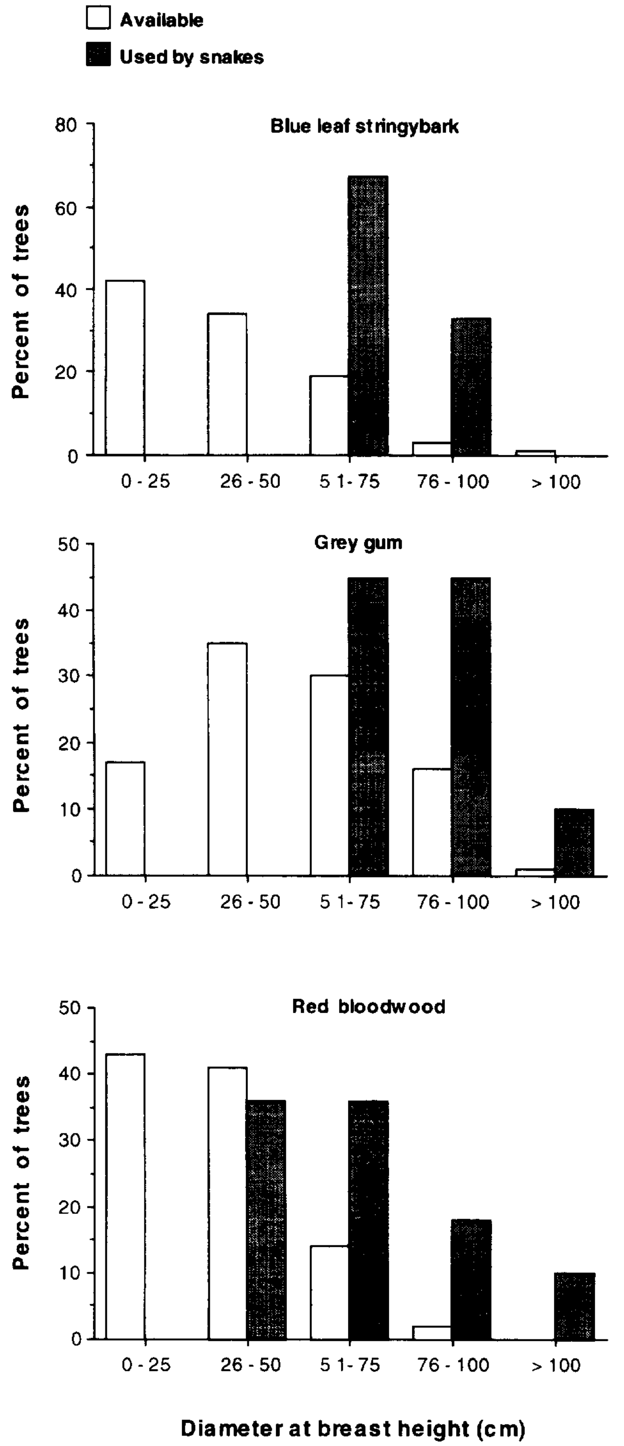

Fig. 3. Broad-headed snakes selected larger trees, even if comparison is restricted to within a single tree species. Open histograms represent 'available' trees and filled histograms represent the trees used by radio-tracked snakes. See text for statistical analyses.

DISCUSSION

Our results are of interest in two respects; what they tell us about the ways in which broad-headed snakes use the forested habitats adjacent to rocky outcrops, and the implications of these patterns for planning to conserve this threatened taxon.

Tree selection by broad-headed snakes

Although our analysis detected strong and consistently non-random patterns of tree selection by our radio-tracked snakes, we remain ignorant of either the ultimate or proximate causal factors that have generated these patterns. The overwhelming result from our study is that snakes generally used trees that offer many retreat-sites; that is, dead trees, large trees, trees of particular species and trees with high numbers of hollows. Arboreal marsupials also tend to select trees with many hollows (Lindenmayer *et al.*, 1990). In terms of the classification of Smith and Lindenmayer (1988), most of the trees used by broad-headed snakes were of the form 1, 2 or 3. That is, live trees were mature (form 1) or had dead tops (form 2), and dead trees had most branches still intact (form 3: Smith & Lindenmayer, 1988). The snakes' preference for hollow-bearing trees may explain their avoidance of the most common tree species on our study sites (turpentine), because turpentines seldom contain horizontal or 'bayonet type' (Mackowski, 1984) branches. Overall, our results suggest that broad-headed snakes will use any tree containing suitable hollows. Thus, other species of trees not listed in our study may be used by *H. bungaroides* in areas with different vegetation types.

Plausible advantages of tree-hollow occupancy include protection from predators, facilitation of behavioural thermo-regulation and availability of prey species (especially, birds and mammals) which use such retreat sites for nesting or resting. In practice, all three of these advantages may be important, and (since all depend upon the same kinds of physical characteristics of the tree) attempts to discriminate among them may be pointless. On a proximate level, a similar ambiguity remains. The trees selected by snakes are distinctive in several characteristics (especially, species, size and number of hollows), but intercorrelations among variables make it difficult to disentangle causation. Indeed, there may well be other cues, not measured in our study, that are the actual basis on which broad-headed snakes select trees. One likely possibility involves scent trails from potential prey items. For example, small mammals (e.g. *Antechinus stuartii* or *Mus domesticus*: Dickman, 1991; Cockburn & Lazenby-Cohen, 1992) may choose nesting trees based on their size and the availability of hollows, and snakes may choose trees based solely on the scent of these mammals. This scenario would result in the kinds of habitat-selection patterns we have documented in our radio-tracked snakes, even if the actual tree characteristics we measured (species, size and number of hollows) were completely irrelevant to any 'decisions' made by the snakes. The only way to tease this issue apart would be to conduct experimental investigations whereby alternative possible cues are manipulated and the animals' response recorded (e.g. Schlesinger & Shine, 1994*a*).

Implications for conservation

Our results confirm that broad-headed snakes depend on sandstone rocks for diurnal shelter sites, and so are likely to be negatively affected by the removal of boulders for garden ornamentation (as has been suggested previously: e.g. Hersey, 1980; Shine & Fitzgerald, 1989; Schlesinger & Shine, 1994*b*). To date, the focus of conservation efforts for broad-headed snakes has been on the rock outcrops themselves, because this is the only habitat in which the snakes can be regularly captured. Thus, conventional wisdom has been that snakes are largely restricted to this habitat (e.g. Hersey, 1980; Cogger, 1992), despite the arboreal habits of congeneric taxa (Shine, 1983; Wilson & Knowles, 1988) and occasional anecdotal observations of tree use by *H. bungaroides* (Worrell, 1963). Our data show that this apparently narrow habitat specialisation is an artefact of observability. Broad-headed snakes are easy to find

Table 4. Forests with habitat suitable for *H. bungaroides*, including forests where *H. bungaroides* has been recorded
Data on sizes of forests were obtained from management plans (Forestry Commission of NSW, 1982, 1986–1988).

Management area	State forest	Area (ha)	*H. bungaroides* recorded?	Reference
Nowra	Colymea	1690	Yes	J. Webb (unpublished data)
	Yalwal	2804	Yes	J. Webb (unpublished data)
	Yerriyong	11 078		
Moss Vale	Meryla	4197		
	Wingello	5249		
	Yarrawa	878		
Bathurst	Banshea	2165		
	Ben Bullen	8579		
	Capertee	2733		
	Jenolan	8583		
	Mt Werong	5093		
	Newnes	29 393	Yes	Shine *et al.* (in prep.)
	Sunny Corner	20 535		
	Wolgan	1454		
Cessnock	Corrabare	5082		
	Comleroy	2531		
	Putty	21 297		
	Yango	647		

when they are concentrated under sandstone rocks in the cooler months of the year, but are much more difficult to observe in summer when they are widely scattered through the woodland, and often inactive inside hollow branches. One of the major advantages of radiotelemetry is to overcome these kinds of massive biases in observability among habitats (e.g. Weatherhead & Charland, 1985). Our findings have significant implications for forest management.

Need for surveys
Because broad-headed snakes use forests as well as rock outcrops, effective conservation of this taxon must consider trees as well as rocks. In New South Wales, state forests have the dual role of providing timber while maintaining habitat suitable for wildlife. Thus, we need to identify the forest areas potentially important for broad-headed snakes, and to manage all of these forests carefully. There is an urgent need for faunal surveys in the areas where *H. bungaroides* is likely to occur (Table 4). This information is crucial if broad-headed snakes are to be maintained within state forests of southeastern New South Wales.

Retention of 'habitat trees'
Forestry management practices need to maintain suitable habitat for this threatened species. In particular, it is important to keep reasonable numbers of large hollow-bearing trees both above and below the sandstone cliffs used by *H. bungaroides*. Fortunately, the kinds of trees that are needed by the snakes are similar to those that have already been identified as valuable for other fauna (e.g. Meredith, 1984). The spacing and location of these retained 'habitat trees' may also be important. In many unlogged native forests, trees with hollows are regularly spaced (e.g. Ambrose, 1982; Lindenmayer *et al.*, 1990). Many species of arboreal marsupial are territorial (e.g. How, 1981; Henry & Craig, 1984; Kehl & Borsboom, 1984) and co-occupancy of trees is rare, so that behavioural interactions may lead to monopolisation of habitat trees by one species or colony in areas where trees are clumped (Lindenmayer *et al.*, 1990). Unfortunately, we have no equivalent data for arboreal reptiles. Habitat trees were evenly spaced in our study sites, and home ranges of telemetered snakes were usually non-overlapping (Webb & Shine, 1997). Therefore, in order to maintain habitat for a diversity of fauna (including *H. bungaroides*) we suggest that a minimum of five evenly-spaced 'habitat trees' per hectare should be retained. These trees should be located both on ridge tops and on slopes, not just near watercourses.

Existing forestry management plans do not fully accord with these recommendations. Management plans for different forest areas within the range of *H. bungaroides* differ substantially in their prescriptions for the number of habitat trees to be retained per hectare, the location of these trees and their spacing. For example, plans for the Bathurst and Moss Vale Management Areas simply state that 'sufficient habitat trees' should be retained (Forestry Commission of NSW, 1986, 1987), whereas prescriptions for the Nowra Management Area require that 'up to five mature or overmature trees' be retained per hectare. The spacing and location of retained habitat trees is not discussed in either of these management plans (Forestry Commission of NSW, 1982, 1986, 1987). Prescriptions for the Cessnock Management Area state that 'one to five habitat trees' should be retained per hectare, but 'preferably in groups, and preferably near watercourses' (Forestry Commission of NSW, 1988). Hence, the current management recommendations for forestry activities are likely to have a negative impact on broad-headed snake populations either because too few habitat trees are retained (all listed management areas) or because habitat trees are clumped or inappropriately located (Cessnock Management Area). Fortunately, in the one case where we quantified the effects of logging activities on habitat availability (Yalwal State Forest), a larger number of trees was left, in the appropriate locations and with suitable spacing.

Burning after saw-log extraction
Another aspect of forestry practice that deserves further study is post-logging burning. The recently logged areas that we examined lacked any understorey or leaf litter, and logs on the ground had been burnt so that they were no longer hollow. Logs on the ground are used as retreat sites by many small mammals and reptiles (e.g. Dickman, 1991; Wilson & Knowles, 1988; Cogger, 1992), including *H. bungaroides* (Webb & Shine, unpublished data). Hence, post-logging burning may have a negative impact on several animal species.

Conifer plantations
Exotic conifers (*Pinus* spp.) planted on plateaux relatively close to sandstone cliffs (as in Meryla State Forest and Newnes State Forest: Forestry Commission of NSW, 1986, 1988) pose another potential problem. Pine trees do not form hollows, and hence are unlikely to be of any value to the broad-headed snake. Extensive plantings of conifers close to ridge tops should be avoided.

Relevance to other threatened fauna
Tree-hollow use may be more widespread among arboreal reptiles than has previously been thought. The current lack of information on habitat requirements of arboreal reptiles precludes well-informed management decisions and further research is clearly required. Priority should be given to threatened species that may be directly affected by forestry activities. In New South Wales, one such species is the threatened Stephen's banded snake *Hoplocephalus stephensii*. This arboreal snake is entirely restricted to coastal forests, many of which are subject to logging (Cogger, 1992). We suspect that *H. stephensii* has similar habitat requirements to *H. bungaroides*, and work to investigate this possibility would be of significant value.

More generally, our study demonstrates the feasibility of radiotelemetric monitoring of habitat use by arboreal reptiles, and the potential usefulness of such research for conservation planning. Detailed natural history studies like ours may provide an essential basis from which to plan the conservation of threatened species. Although this 'natural history' approach lacks the sophisticated mathematical underpinning of some other areas of conservation biology, the pragmatic truth seems to be that a knowledge of the organism's natural history is an important first step towards identifying successful conservation strategies (e.g. Caughley & Sinclair, 1994; Simberloff, 1994). The need for these natural history studies is particularly great in the case of organisms that have attracted relatively little prior scientific attention. Traditionally, the vast majority of funding for conservation research has been allocated to studies of the 'charismatic' birds and mammals, to the neglect of equally threatened species from other vertebrate and invertebrate lineages (Mittermeier *et al.*, 1992). One heartening result from our own study has been to suggest that policies implemented to conserve arboreal mammals (notably, retention of 'habitat' trees in areas subject to logging) may also be well-suited to the conservation of at least one species of threatened reptile.

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