

Radiotelemetric Study of Habitat Use by the Arboreal Snake *Hoplocephalus stephensii* (Elapidae) in Eastern Australia

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Simply classifying a species as “arboreal” may tell us little about the ways that it uses above-ground habitats. For example, some species of arboreal snakes select exposed positions on branches, others lie among foliage, and yet others exploit crevices within the trunk. These different structural niches may involve fundamentally different patterns not only of habitat selection criteria but also of morphological, behavioral, and ecological traits. We implanted miniature radio-transmitters in 16 adult Stephens’ banded snakes (*Hoplocephalus stephensii*) in a forest managed for timber production in northeastern New South Wales, and relocated these snakes regularly over a two-year period to clarify their patterns of habitat use. Unlike the vast majority of Australian elapid species, *H. stephensii* are primarily arboreal. Radio-tracked snakes were in trees on > 80% of observations, generally hidden within hollows. The snakes remained inactive in trees for three to five months during winter each year. Snakes in wet sclerophyll forest sometimes foraged in tall sedges, whereas snakes in rain forest spent little time on the ground. Attributes of 139 trees used by the snakes were compared with those of 1437 trees in randomly selected plots. Snakes selected old, large trees with many hollows or extensive vine cover. Except for being above ground, the retreat sites used by these arboreal elapids were structurally similar to those used by their terrestrial relatives. The tree attributes important to *H. stephensii* thus differ profoundly from those important to many other species of arboreal snakes.

BROAD classifications of habitat types often fail to capture the subtlety with which animals actually use those habitats. Even in cases of closely related sympatric taxa, detailed studies generally identify significant interspecific differences in actual patterns of habitat use (Reinert, 1984). Presumably for logistical reasons, terrestrial habitats have generally attracted more scientific attention in this respect than have aquatic or arboreal systems (Bell et al., 1991). Nonetheless, even a cursory examination of available data suggests that there is immense interspecific and intraspecific diversity in the ways in which organisms exploit any given category of habitats. The use of arboreal habitats by snakes offers a good example of this diversity.

The phylogenetic distribution of arboreal species among living snakes indicates that there have been multiple evolutionary invasions of above-ground habitats within snake phylogeny. Indeed, most major snake lineages include at least some arboreal species (Lillywhite and Henderson, 1993); even scolecophidians have been reported many meters above-ground (Swanson, 1981). These independent phylogenetic shifts have been accompanied by striking convergences in many aspects of morphology, ecology, and behavior (e.g., Henderson and Binder, 1980; Lillywhite and Henderson, 1993). Presumably,

such convergences reflect similar selective pressures on snakes using above-ground habitats.

Despite these examples, however, there is enormous diversity among arboreal snakes. The most obvious dimension of this diversity involves morphology: arboreal snakes range from large heavy-bodied taxa (especially boids, pythons and viperids) to extremely small, elongate species (such as typhlopids, many colubrids and elapids). However, the diversity also extends to numerous facets of behavior and ecology. Many tree-dwelling snakes feed on arboreal prey, but others simply use their above-ground positions as ambush-sites from which to seize terrestrial prey (Shine et al., 1996). One obvious axis of variation involves the structural attributes of trees used by snakes. Some elongate well-camouflaged taxa (especially elongate “vine snakes”: Henderson and Binder, 1980) occupy foliage, whereas more heavy-bodied species lie outstretched (e.g., *Gloydus*; Li, 1995) or when resting, coiled (e.g., *Corallus*; Henderson and Winstel, 1995; Henderson et al., 1998; *Chondropython*; Murphy et al., 1976) along branches. Yet other arboreal taxa may avoid such exposed sites, relying instead on secure retreat sites such as crevices or thick vine cover. Although they are above-ground, these latter retreat sites may resemble those occupied by terrestrial snakes.

If we are to understand the ways in which

snakes use arboreal habitats, we will need detailed information on topics such as the types of trees that are used, and the particular sites that are occupied within those trees. Of particular interest in this regard are arboreal species that belong to predominantly terrestrial lineages. If arboreality has evolved independently within such a group, patterns of habitat use provide phylogenetically (and hence, statistically) independent information on the ways in which the attributes of terrestrial snakes have become modified in the course of an adaptive shift to exploit novel habitats.

We have studied such a system. Although elapid snakes dominate the Australian snake fauna, the vast majority of species are terrestrial or fossorial (Greer, 1997). Only a single genus, *Hoplocephalus*, is frequently reported to use arboreal habitats (Shine, 1983, 1991; Greer, 1997) and displays morphological adaptations to tree-climbing (e.g., slender body form, distinct keel on ventral scales; Wilson and Knowles, 1988; Greer, 1997). Because this genus has arisen from within a clade of terrestrial taxa (Wallach, 1985; Keogh et al., 2000), information on habitat use by *Hoplocephalus* may clarify the degree to which this taxon has diverged from its terrestrial relatives.

MATERIALS AND METHODS

Study species.—Stephens' banded snakes (*Hoplocephalus stephensii*) are medium-sized (to 1.0 m total length, 250 g; Wilson and Knowles, 1988, Fitzgerald, 2001) slender snakes. They are distributed discontinuously along the eastern part of the Great Dividing Range from the central coast of New South Wales to Krombit Tops in southeastern Queensland (Longmore, 1986). These snakes feed on a wide array of vertebrate taxa, especially lizards and small mammals (Shine, 1983). Females bear a litter of two to nine live young (Fitzgerald, 2001) but reproduce on a less-than-annual schedule (Shine, 1983).

Study area.—We worked in Whian Whian State Forest (WWSF) 30 km northeast of Lismore in northeastern New South Wales (see Fig. 1). WWSF (5212 ha) is located on a low plateau contiguous with a large (4945 ha) conservation reserve, Nightcap National Park. The plateau consists of low ridges and gullies with localised rhyolite cliffs along the northern and eastern rim. Geology is volcanic, with basaltic soils overcapping rhyolite at higher elevations. The climate is mild with mean daily maximum tem-

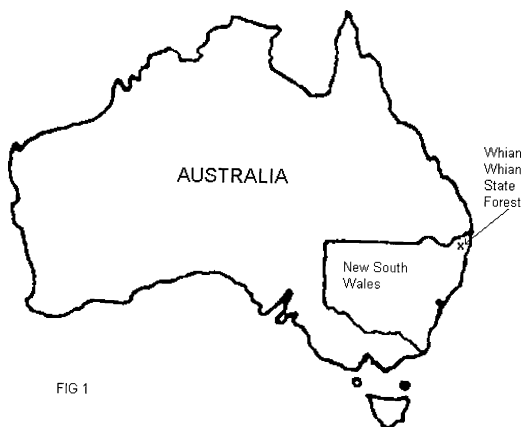


Fig. 1. Map of Australia showing the location of the study area (Whian Whian State Forest).

peratures of 17.7 C for June and 26.5 C for December.

Snakes were monitored at three sites, each approximately 1 km apart: Blue Fig Road (BFRd; three snakes), Mango Bark Road (MBRd; 5 snakes) and Rummery Road (RRd; eight snakes; see Table 1). The vegetation of WWSF is predominantly wet sclerophyll forest and rainforest with small areas of drier open forest and heath. All study areas were forested, although roads, tracks and log dumps produced variable canopy gaps. Minor variations in elevation at BFRd greatly influenced vegetation (especially the sedges *Lepidosperma clipeicola* and *Gahnia* spp.) and resulted in "island" stands of inland brush box *Lophostemon confertus* surrounded by turpentine *Syncarpia glomulifera* and blackbutt *Eucalyptus pilularis* communities. Disturbance regimes affected tree sizes and spacing differently in different sites. In short, vegetation at our study sites was complex and heterogeneous at the spatial scale likely to be of most importance to snakes, that is, tree attributes and spatial arrangement of trees.

Methods for capture and telemetry.—Snakes were mainly captured by driving roads at night when they were encountered crossing roads or crawling along roadside edges. Some animals were also captured in the vicinity of telemetered snakes during reproductive activity. Sixteen adult snakes (6 M:10 F) were surgically implanted with miniature temperature-sensitive radiotransmitters (Holohil, Canada; BD-GT1, PD-2T and SB-2T models) and released at the point of capture within 48 h of implantation (Appendix 1). Snakes collected on roads were released near the capture site in adjacent forest. Surgical procedures followed Reinert (1992) and Webb

TABLE 1. ATTRIBUTES OF THE THREE STUDY SITES. "Forest types" refer to the State Forests of New South Wales (SFNSW) forest typing system where numbered types are named for the occurrence of indicator species which dominate a stand (Forestry Commission of New South Wales, Sydney, NSW, Australia, 1989 unpubl.). 1 = Booyong *Heritiera actinophylla* and *Heritiera trifoliata*; 13 = Water Gum-Coachwood *Tristaniopsis laurina* and *Tristaniopsis collina* with *Ceratopetalum apetalum*; 23 = Myrtle, various species of Myrtaceae; 36 = Moist Blackbutt *Eucalyptus pilularis*; 49 = Turpentine *Syncarpia glomulifera*; 53 = Inland Brush Box *Lophostemon confertus*.

	Rummery Road	Blue Fig Road	Mango Bark Road
Forest Types	1, 53, 23, 36, 13	36, 49, 1, 53	36, 1
Topography	Upper slopes	Plateau, incised	Low ridges and gullies,
Catchment	Heads of gullies	3rd order streams	2nd and 3rd order streams
attributes	1st order streams		
Elevation (m)	360 to 590 asl	300 to 350 asl	350 to 400 asl
SFNW Cpt #s	72, 74	94	75
Disturbance	Selective logging	Selective logging	Selective logging
history	1962–1994	1955–1975	1962–1985
	Management fire	Ring-barking	Management fire
	Jan 1968	1955–1996 & 1974	May 1964
			Plantation 1974
			Ring-barking 1964

and Shine (1997a,b). Transmitters were enclosed in waterproofing with sleeved antenna, weighed from 2.3–5.8 g and constituted < 5% of the mass of the snake (mean = 3.3%, SD = 1.07). In the field, snakes were located using a Regal 2000 receiver and 3-stage Yagi antenna (Title Electronics, Ballina, NSW).

Data on habitat selection and behaviour were gathered from one-week postrelease to avoid disturbance artifacts. Snakes were located two to three times per week during the active season from September to May and less frequently during the sedentary overwintering period. Where snakes were found active, they were followed until they disappeared from view. However, this represents < 2% of overall observations. Locations were flagged with dated and labeled tape identifying the snake to which the location referred. Ambiguous observations were excluded from analysis. For three snakes observations were limited to use of a single overwinter tree (F082), use of two trees before entering the overwinter tree (F796), and use of three trees before predation (M330). Trees used by these snakes were included in "use tree" analysis; however shelter site use by two of these snakes was not included for analysis because of the small sample sizes (F082 $n = 18$; M330 $n = 9$).

Analysis of tree use by radio-tracked snakes.—In total, the 16 telemetered snakes used 162 trees. All trees used by snakes were flagged and 139 of these later measured and scored for possession of a series of structural features. Twenty-three of the WWSF use trees were not sampled because of difficulties in relocating them or to

ambiguity about which tree was used (flagging was removed by animals on several occasions).

Tree attributes that might influence snakes' use of trees were selected for more detailed analysis. Tree height and diameter at breast height were measured, and percent canopy cover was estimated by comparison with a sample sheet (McDonald et al., 1990). Where possible, we measured diameter above buttresses; however in many cases it was only possible to measure over buttresses. Other attributes were assigned categorical scores as follows. (1) Bole shape: 0 = round, 1 = oval or buttressed in cross section, 2 = extreme development of buttresses. (2) Bark texture: 0 = smooth/glassy, 1 = as 0 but with short fibrous stocking, 2 = finely grainy, 3 = coarse or fibrous, 4 = strongly coarse fissured or ridged, or 1 or 2 with *Pothos longipes* (a climbing fern) covering. (3) Basal crevice: providing access to interior cavity: 0 = absent, 1 = present. (4) Hollow-bearing stage: nine stage key to the forms of hollow-bearing trees based on successional stages: 0 = no hollows, 1 = live tree with hollows, 2 = live tree with dead or broken top, 3 = dead tree with most branches intact, 4 = dead tree with 0–25% of the top broken off, 5 = dead tree with top 25–50% lost, 6 = dead tree with top 50 to 75% lost, 7 = dead tree with > 75% of top lost, 8 = hollow stump (modified from Smith and Lindenmayer, 1988). (5) Growth stage: 0 = immature, 1 = mature, 2 = late mature/senescent, 3 = stag. (6) Tree position: 0 = subcanopy, 1 = canopy level, 2 = emergent. (7) Interconnectedness: 0 = isolated, 1 = connected to adjacent tree canopy, 2 = strong structural links with ad-

jacent trees by vines, crown overlap. (8) Trunk hollow: 0 = absent, 1 = present, 2 = continuous hollow from base to tree crown (especially as in strangler figs). (9) Branch hollow: 0 = absent, 1 = one branch hollow present, 2 = > one branch hollow present. (10) Termitarium: 0 = absent, 1 = present and intact, 2 = present with holes or cracks providing access to the interior. (11) Epiphytes: 0 = absent, 1 = some epiphytes present, 2 = large (> 1 m²) well-developed epiphyte clumps present. (12) Vines: 0 = absent, 1 = vines extending into the tree canopy, 2 = large (> 1 m²) well-developed vine masses present. (13) Fire scar: 0 = absent, 1 = present on lower bark, 2 = extending to the crown, 3 = penetrating to heartwood.

Random plot trees.—To determine whether snakes were actively selecting trees or using trees at random, data on 1437 trees were collected from 17 plots (0.1 hectare; usually 50 m × 20 m) at randomly selected locations within areas used by the 16 telemetered snakes. All plants > 10 cm dbh (alive or dead) within the plot were flagged, identified to species level where possible, measured and scored for structural attributes.

Comparison between used trees and random plot trees.—To compare the 139 WWSF use trees to the 1437 random plot trees, we counted the number of observations in each attribute category and compared the use tree sample with the random plot samples.

We used contingency table analysis (*G* test of independence, Biomstat 3.2) to compare the distribution of scores for attribute categories between the two samples. Where cell values were < 5, attribute categories were pooled. Our null hypothesis was that use trees were no different from random plot trees in the attributes that we measured.

Multivariate analyses.—There are two statistical difficulties in interpreting patterns from the tests reported above. First, many of these tree attributes are themselves highly intercorrelated; for example, tree position is correlated with height and with growth-stage. Second, a series of tests on multiple variables raises the problem of spuriously “significant” results via multiple testing. To reduce the number of variables and remove problems of intercorrelation among traits, we carried out a principal components analysis (PCA) on the combined data set (i.e., all trees, both used and random plot). Raw data were subjected to factor analysis using Statview 5. An orthogonal transformation of the initial

factor solution was performed to produce an oblique solution reference structure. We retained roots > 1 to identify principal components. The factor loadings for these components were then used as independent variables in a logistic regression with tree usage by snakes as the dependent variable.

RESULTS

Radiotracking effort.—Overall, snakes were radiotracked on 1221 days (mean observations per snake = 76.31, SD = 45.80, *n* = 16 snakes). The number of discrete locations where snakes were observed varied from 13–67 per snake (mean = 34.38, SD 17.3, *n* = 447 locations, for 13 snakes). Net monitoring periods varied from 41–635 days (exclusive of intervals for reimplantation of new transmitters, mean = 288.20 days, SD = 72.77 for 16 snakes). Additional effort spent measuring trees, conducting random plot surveys, mapping locations, collecting snakes and implanting snakes with transmitters is summarised elsewhere (Fitzgerald, 2002).

Macrohabitat use.—Snakes tracked in WWSF remained in forest at all times and were located in arboreal positions on 82% of all observations. Although rock outcrops were present at RRd, they were not used by telemetered snakes. When in terrestrial locations (18% of all observations), snakes were most often (46% of observations) found in tall sedges (principally *Lepidosperma clipeicola*), on the ground (37%), or on or beneath logs (17%). Snakes in wet sclerophyll forest were often encountered basking or asleep perched near the upper surface of sedge clumps.

Forest type.—At MBRd where moist blackbutt predominated, rainforest was mainly present in narrow riparian strips. Although four of the five snakes at this site largely remained in the blackbutt, the other animal used riparian rain forest (57% of observations) more than blackbutt (43%).

Forest type heterogeneity was greatest at BFRd, and the three snakes at this site exploited this vegetation in different ways. A male used blackbutt (55% of observations) and turpentine forest (38%) as well as rain forest (2%) and inland brush box (4%). A female used turpentine (65%) and rain forest (31%) and ventured into blackbutt rarely (4%). The third snake, a large female, exclusively used blackbutt forest.

The RRd site included areas of moist blackbutt adjoining rain forest. Four snakes remained exclusively in rain forest and inland

TABLE 2. TREES USED AS OVERWINTERING SITES BY RADIO-TRACKED STEPHENS' BANDED SNAKES. dbh = diameter at breast height. See text for listing of growth stages, hollow-bearing stages, and tree position categories.

Species	dbh (cm)	ht (m)	Growth stage	Hollow stage	Tree position	Study site	Used by snake #
<i>Lophostemon confertus</i>	51.8	35	1	1	1	rrd	F978
<i>Heritiera trifoliata</i>	60.0	45	1	0 ^a	2	rrd	M938
<i>Allocasuarina torulosa</i>	65.5	30	2	1	1	mbrd	F141
<i>Heritiera actinophylla</i>	72.4	68	1	0	2	rrd	F190
<i>Eucalyptus grandis</i>	129	12	3	7	0	rrd	M351
<i>Syncarpia glomulifera</i>	151.6	20	3	7	0	bfrd	F299
<i>Eucalyptus pilularis</i>	170	41	3	3	2	mbrd	F200
<i>Eucalyptus pilularis</i>	172.7	43	2	2	1	mbrd	F796
<i>Syncarpia glomulifera</i>	175.0	26	3	4	1	bfrd	F299 & ^b M919
<i>Eucalyptus pilularis</i>	234	62	2	2	2	mbrd	F338
<i>Ficus watkinsiana</i>	304.6	42	2	1	2	rrd	M938
<i>Eucalyptus pilularis</i>	196	50	2	2	2	rrd	M057
<i>Eucalyptus pilularis</i>	292.6	19	3	6	1	rrd	F082
Mean values	159.63	37.15					
SD	84.21	17.67					

^aNo hollows were seen in the complex canopy of this live tree but may have been present.

^bOverwintering was normally solitary. It is likely that the shared use of this tree resulted from capture and implantation of F299 late in May after M919 had apparently displaced here from this tree. They occupied different parts of the tree during winter.

brush box over rain forest while three remained in blackbutt forest. Home range boundaries for these snakes approximately coincided with the rain forest/blackbutt forest ecotone (Fitzgerald, 2001). Forest type use was not established for one snake monitored only during winter in a single tree.

Overwinter trees.—Microhabitat use varied seasonally. All snakes in both years overwintered in large trees (n = 13; mean dbh = 159.63 cm, SD = 84.21, and mean tree height = 37.15 m, SD = 17.67; Table 2) for periods from 69 to 170

days. Snakes entered overwinter trees in May or June and generally left these trees between late August and November. Snakes overwintered in tree hollows, with one possible exception. Most overwinter trees (78%) were late mature or stags and 50% were in emergent positions.

Shelter sites.—Telemetered snakes spent most of their time sequestered in refuges. Shelter sites used by snakes were determined on 668 occasions (55% of all observations; Table 3). Snakes M330 and F082 were excluded from this table as too few records exist for this analysis. Tree

TABLE 3. OVERALL PATTERNS OF USAGE OF THE DIFFERENT KINDS OF SHELTER SITES IN WHICH RADIO-TRACKED SNAKES WERE RECORDED.

Snake	Tree hollow	Termitarium	Vines	Foliage	Sedge	Log	Litter
F121	3	0	0	3	2	2	0
F200	50	0	13	10	7	4	10
F019	0	0	14	6	3	1	0
F141	5	1	1	0	5	0	4
F190	1	3	3	2	0	1	8
F978	15	0	53	5	20	6	14
F299	63	1	1	1	2	0	6
F796	31	0	0	0	0	0	0
F338	30	2	0	0	6	1	1
M919	53	0	4	1	12	1	0
M271	6	0	11	0	6	1	0
M938	2	0	1	5	0	0	1
M057	22	43	2	0	10	5	7
M351	47	0	6	0	1	0	1
TOTALS	328	50	109	33	74	22	52
%	49.1	7.49	16.32	4.94	11.08	3.29	7.78

hollows were by far the most important category of retreat sites recorded (49%). Only 39 (28%) of the trees used by snakes lacked identifiable hollows. All but two of these trees had vines or epiphytes. The exceptions were two forest oaks (*Allocauarina torulosa*) where shelter sites used were a termitarium and a thick layer of accumulated cladodes (photosynthetic stems). When in trees lacking hollows, snakes were recorded in the following shelter sites: vines 11, foliage 2, litter platform 1, termitarium 1, epiphyte 1. On five other occasions snakes were not seen but were probably in vines.

Tree hollows used by snakes could not usually be examined without destructive sampling. However when transmitters failed, we examined shelter locations while retrieving the snake. One shelter site was 6 m above-ground within the spherical leaf nest of a small mammal (*Antechinus* or *Acrobates*) behind a panel of rotting wood in a vertical trough-shaped hollow in a live crab-apple (*Schizomeria ovata*), 7.3 m in height, dbh = 43.5 cm, which was covered in a dense curtain of thorny vines and creepers. The hollow was 2.6 m high and 7–20 cm wide.

Another shelter site was within a spherical leaf-nest 1.5 m above-ground in a narrow hollow in a blackbutt stump, 3 m in height, dbh = 122.5 cm. This tree had been cut for timber before the 1950s, as evidenced by board notches. A panel cut to expose this retreat revealed a narrow vertical hollow (2–3 cm deep, 60 cm × 45 cm) with access from the interior of the stump. A telemetered snake seen ascending a blackbutt stag was later seen coiled beneath an adherent flake of timber on the underside of a horizontal upturned trough-shaped hollow branch 22 m from the ground.

A fourth shelter site, which was repeatedly used, was a hole in the middle of a large defunct termitarium on the bole of a large blackbutt stag. Sacred kingfishers (*Todirhamphus sancta*) bore a narrow cylindrical hole into live arboreal termitaria and hollow out a spherical chamber in the middle (Beruldsen, 1980). One telemetered snake repeatedly sheltered within two such termitaria, occasionally basking with part of the body exposed. Another snake also used this shelter site. Finally, one telemetered female snake was observed active within the vertical crevice of a blackbutt stag in a space no wider than her body.

Comparison between used trees and random plot trees.—For all of the variables that we measured, use trees differed significantly from the random plot sample (for histograms and statistical tests, see Figs. 2–4). Compared to the randomly se-

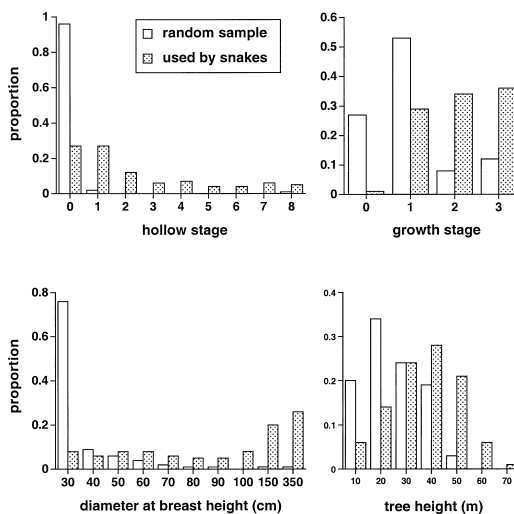


Fig. 2. Comparisons between trees used by Stephens' banded snakes and a random sample of available trees, in terms of the attributes hollow stage, growth stage, diameter at breast height, and tree height. Use trees differed significantly from random plot trees ($P < 0.001$) in hollow stage [$G(W) = 359.29$], growth stage [$G(W) = 141.74$], in diameter at breast height [$G(W) = 385.30$], and in height [$G(W) = 126.81$].

lected trees, use trees displayed later hollow-bearing and growth stages (Fig. 2) and were taller and thicker (Fig. 2). Use trees had more trunk hollows (Fig. 3), branch hollows (Fig. 3), more buttress development (Fig. 3), rougher bark (Fig. 3), more basal crevices (Fig. 3), and more fire scars (Fig. 3).

Random plot trees generally exhibited intermediate levels of canopy cover, whereas use trees disproportionately comprised either extreme in this respect (Fig. 4). The low canopy cover trees were primarily stags, whereas the highest canopy-cover trees were umbrageous rain-forest species or had dense vines. More use trees were in emergent rather than subcanopy positions (Fig. 4) and were highly connected to other trees (Fig. 4). The trees selected by snakes had more termitaria (Fig. 4), epiphytes (Fig. 4), and vines (Fig. 4).

Use trees included 32 species (Table 4) and the random plot sample included 78 species. The use tree sample contained five species that were not found in the random plots. Comparison of the proportion of the five most frequently used tree species against the proportion of each species in the random plot sample indicates a preference by snakes for blackbutt (*Eucalyptus pilulari*; 23.7% of use trees vs 15.7% of plot trees, $G = 5.51$; $P = 0.019$) and turpentine

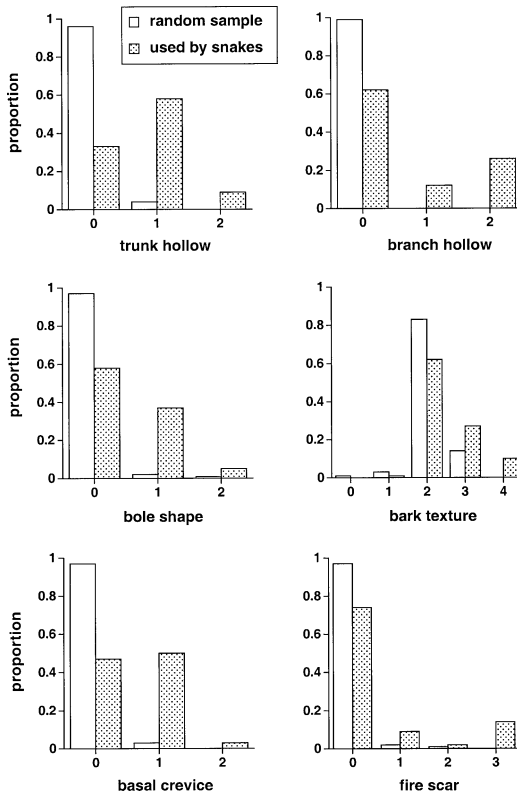


Fig. 3. Comparisons between trees used by Stephens' banded snakes and a random sample of available trees, in terms of the attributes trunk hollow, branch hollow, bole shape, bark texture, basal crevice and fire scar (see text for definition). Use trees differed significantly from random plot trees ($P < 0.001$) in trunk hollow [$G(W) = 326.70$], branch hollow [$G(W) = 210.33$], in bole shape [$G(W) = 177.03$], in bark texture [$G(W) = 39.69$], in basal crevice [$G(W) = 235.17$], and in fire scar [$G(W) = 90.33$].

(*Syncarpia glomulifera*; 17.3 vs 1.3%, $G = 66.01$; $P < 0.001$), and an avoidance of the nightcap wattle (*Acacia orites*; 4.3 vs 17.3%, $G = 20.30$; $P < 0.001$). The remaining two species were neither avoided nor preferentially used.

The analyses above (and note statistical tests reported in figure legends) show that the trees used by *H. stephensii* differed strongly from the random plot trees in a wide variety of attributes. The multivariate analysis identified five principal components that summarise these diverse axes of variation. The component describing the highest amount of variation (28%) corresponded to age of the tree, with higher scores on this axis for trees that contained many hollows, basal crevices and fire scars and were thick at the base (Table 5). The second axis (14.2%) described tree height and tree position. The

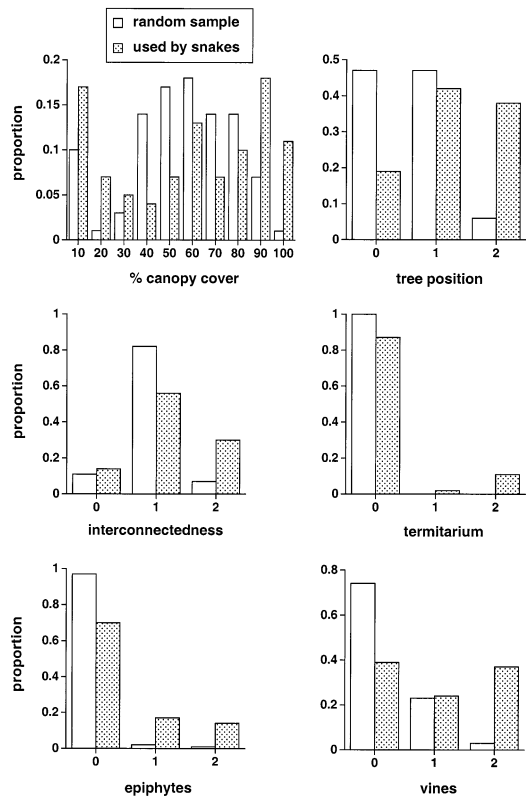


Fig. 4. Comparisons between trees used by Stephens' banded snakes, and a random sample of available trees, in terms of the attributes percent canopy cover, tree position, interconnectedness, termitarium, epiphytes and vines (see text for definition). Use trees differed significantly from random plot trees ($P < 0.001$) in percent canopy cover [$G(W) = 96.77$], tree position [$G(W) = 116.25$], interconnectedness [$G(W) = 60.29$], termitarium [$G(W) = 56.24$], epiphyte [$G(W) = 100.37$], and vines [$G(W) = 153.55$].

third axis (9.2%) described complexity of canopy structure. Remaining axes incorporated information on bole shape and epiphytes (7.5%) and on dead standing trees (6.7%, Table 5).

To avoid the problem of multiple nonindependent tests, we incorporated the factor loadings for each tree into a logistic regression analysis. The dependent variable was whether the tree had been used by a snake, and the independent variables were the factor loadings for each of the five components identified by our PCA. The clear result was to support the independent ANOVAs; whether a snake used the tree was affected by all five components entered into the analysis (in each case, $P < 0.0001$ in a log-likelihood table). Thus, we concluded that the trees used by *H. stephensii* did indeed constitute a highly non-random sample of those available.

TABLE 4. SPECIES OF TREES USED AS SHELTER SITES BY STEPHEN'S BANDED SNAKES THAT WERE RADIO-TRACKED IN WHIAN WHIAN STATE FOREST. Data are given separately by site.

Tree species	BFRd	MBRd	RRd.	Total
<i>Acacia orites</i>	2	0	3	5
<i>Allocasuarina torulosa</i>	1	3	1	5
<i>Archontophoenix cunninghamiana</i>	1	0	0	1
<i>Anthocarapa nitidula</i>	0	0	1	1
<i>Alphitonia excelsa</i>	0	1	0	1
<i>Baloghia inophylla</i>	0	0	1	1
<i>Callicoma serratifolia</i>	1	0	0	1
<i>Cinnamomum oliveri</i>	2	2	0	4
<i>Corymbia intermedia</i>	2	1	1	4
<i>Canarium australasicum</i>	0	0	1	1
<i>Caldcluvia paniculosa</i>	0	0	1	1
<i>Doryphora sassafras</i>	0	0	1	1
<i>Dysoxylum mollissimum</i>	0	0	1	1
<i>Eucalyptus pilularis</i>	12	13	8	33
<i>Eucalyptus</i> sp.	2	0	1	3
<i>Eucalyptus grandis</i>	0	0	2	2
<i>Eucalyptus microcorys</i>	0	0	1	1
<i>Endiandra muelleri</i>	0	0	1	1
<i>Ficus fraseri</i>	0	0	1	1
<i>Ficus watkinsiana</i>	0	0	13	13
<i>Geissois benthami</i>	0	0	3	3
<i>Gmelina leichardti</i>	0	0	1	1
<i>Heritiera actinophylla</i>	0	0	5	5
<i>Heritiera trifoliata</i>	0	0	5	5
<i>Lophostemon confertus</i>	0	1	3	4
<i>Polyscias murrayi</i>	0	0	1	1
<i>Sarcopterys stipata</i>	0	0	2	2
<i>Schizomeria ovata</i>	3	1	4	8
<i>Sloanea australis</i>	0	0	2	2
Species unknown	0	0	2	2
<i>Syncarpia glomulifera</i>	17	6	1	24
<i>Tristaniopsis laurina</i>	1	0	0	1
Number of species	11	8	27	32
Total trees	44	28	67	139

We used a similar set of methods to compare the trees used by male snakes to those used by females. In this case, we carried out PCA on the data for use trees only. This PCA generated five components, broadly similar to the first five components above. These factor loadings served as independent variables in a multiple logistic regression with the sex of the snake as the dependent variable (trees used by both sexes were deleted from the analysis). Males sheltered in tall emergent trees with high canopy cover and many epiphytes and vines more frequently than did females (log-likelihood ratio test, $\chi^2 = 6.64$, $df = 1$, $P = 0.01$).

DISCUSSION

Our data on 16 radio-tracked *H. stephensii* revealed that these snakes are highly arboreal, in

support of many previous anecdotal observations (Worrell, 1970; Gow, 1976; Ehmann, 1992). Juvenile *H. stephensii* are probably arboreal also; for example, a neonate was located beneath the exfoliating bark of a live burnt blackbutt in Mt. Belmore State Forest.

Given that the trees used by snakes were distinctive in several ways (see Figs. 2–4), which of these attributes actually played a functional role in tree selection? There are several possible answers to this question:

Availability of shelter-sites.—Most attributes of use trees can be readily interpreted in the light of retreat-site availability. Some of the traits we measured directly assessed shelter availability, whereas others were correlated with it. The presence of trunk hollows was highly correlated with dbh ($R = 0.71$) and basal crevices ($R =$

TABLE 5. THE OBLIQUE SOLUTION REFERENCE STRUCTURE FROM A PRINCIPAL COMPONENTS ANALYSIS ON ATTRIBUTES OF TREES IN WHIAN WHIAN STATE FOREST. This analysis was based on the entire sample of trees measured during the study, including random plot trees as well as trees that were used by radio-tracked snakes.

Major characteristics	Factor 1 Age	Factor 2 Height, emergence	Factor 3 Canopy complexity	Factor 4 Bole epiphytes	Factor 5 Stags
height	.024	.897	-.006	.047	-.057
dbh	.540	.376	.098	.167	.071
% c/c	.095	.042	.291	-.012	-.726
bole	.047	.106	.008	.733	.055
bark	.035	.237	.346	-.604	.278
bascrev	.645	.026	.100	.163	-.003
grosta	.110	.002	.128	-.052	.717
trepos	-.014	.893	.024	-.015	-.014
intcon	-.001	-.008	.691	-.210	-.151
holsta	.606	-.212	-.030	.051	.241
truhol	.684	.026	.140	.165	.070
brahol	.662	.128	-.029	-.250	-.093
termitar	.548	.019	-.218	-.105	-.203
epiphyte	-.145	.299	.485	.377	.163
vines	.008	-.025	.788	-3.05E-5	.020
firescar	.637	-.108	-.100	-.080	3.17E-6

0.61), whereas the presence of branch hollows was correlated with growth stage ($R = 0.36$), all of which are functions of tree age.

Trees that offered shelter sites may often have also been easier to climb. These snakes use surface irregularities to gain a secure grip on the tree. The presence of rough bark, basal crevices, vines and dense climbing fern (*Pothos longipes*) further enhance the climbability of trees. Smooth-barked trees may be inaccessible for snakes, as they are for squirrel gliders *Petaurus norfolcensis* (Rowston, 1998). The presence of vines also influences activity in trees for at least one prey species: the fawn-footed melomys *Melomys cervinipes* (Wood, 1971).

Our radio-tracked snakes spent virtually all of their time within retreat sites when in trees, strongly suggesting that retreat-site availability was a crucial criterion for tree selection. Most trees within the forest did not provide the kinds of shelter sites that were such a consistent feature of the snakes' locations. Although 72% of use trees had hollows, these were seen in only 0.04% of random plot trees.

Many of the attributes of trees selected by snakes are related to the age of the tree. In 40 m stand height forest, blackbutt need to grow for about 150–200 yr before they form hollows suitable for occupation by arboreal marsupials (Mackowski, 1987). Although there are variations according to tree species and to other factors (damage, fire), hollows that are accessible to animals usually appear late in tree development. Crabapple (*Schizomeria ovata*) in WWSF

formed trunk hollows earlier than other trees. The smallest hollow-bearing use tree was a crabapple 15 m in height with dbh = 21.4 cm.

Availability of thermoregulatory opportunities.—By selecting emergent trees, snakes were often (53 of 139 trees) in sites above the main canopy and, hence, were exposed to basking opportunities not offered by lower trees. Also, snakes frequently used standing dead trees (stags) with many hollows and greater exposure to sunlight. Of 50 stags used by snakes, 58% were at or above canopy level. Canopy cover in stags was usually lower than in live trees (mean percent in stags = 23.72, SD = 24.78; in live trees, = 72.7, SD = 18.87).

Nonetheless, our observations both in the field and in captivity indicate that direct basking by *H. stephensii* is rare and of brief duration (pers. obs.). Radiotelemetric monitoring of body temperatures did not reveal maintenance of high, constant body temperatures even under conditions that would facilitate protected basking (Fitzgerald, 2002). We do not doubt that thermal criteria play a role in site selection, but they are unlikely to be primary determinants of snake locations. Maintaining stable and high levels of relative humidity might also be easiest in tree-hollows (Sedgely, 2001), but we doubt that humidity is a major problem in our high-rainfall study area.

Availability of food.—A seasonal pattern of terrestrial foraging in sedge beds at all sites dem-

onstrates that some prey are located on the ground. Given the long periods of time that telemetered snakes remained in trees without descending to the ground, however, snakes must obtain much of their prey in trees. In keeping with this inference, most prey items reported for *H. stephensii* belong to taxa that can be found in arboreal sites (Fitzgerald, 2002). It is important to note that the most likely microhabitat in which to find these small mammals would be crevices or hollows (Ward, 1990; Braithwaite, 1995; Woodside, 1995). Indeed, two of the hollows we excavated to recover snakes contained mammal nests (above). Thus, even if prey is an important attraction for the snakes, the result is that the animals will select trees with appropriate hollows.

Protection from predators.—Potential predators for snakes in WWSF include feral dogs and dingos (*Canis familiaris*), feral cats (*Felis catus*), quolls (*Dasyurus maculatus*), kookaburras (*Dacelo novaeguineae*), goshawks (*Accipiter fasciatus* and *Accipiter novaehollandiae*), blacksnakes (*Pseudechis porphyriacus*), and lace monitors (*Varanus varius*). Juvenile snakes may also be vulnerable to frogmouths (*Podargus strigoides* and *Podargus ocellatus*) and small-eyed snakes (*Rhinoplocephalus nigrescens*). As is the case for prey availability, however, the sites that provide the best protection will be those that provide the most secure retreat sites. Thus, hollows and dense vines are likely to be important in this respect as well.

Future research could usefully examine the proximate mechanisms by which snakes select trees. Olfactory cues associated with prey items or potential predators might be important in this respect. Snakes inspect tree bases during terrestrial movements by tongue-flicking before choosing a tree to climb. The frequent reuse of specific trees by individual snakes suggests that the animals may preferentially return to "suitable" trees, and hence their subsequent selection may be driven by memory rather than by any current visual or olfactory stimuli associated with prey or predation.

In summary, our data show that arboreality in Stephens' banded snakes is strongly linked to the utilisation of secure retreat sites, typically tree-hollows and dense vines. In this respect, the arboreal habitats used by *H. stephensii* differ from those of other arboreal snake taxa in our study area. For example, radio-tracked carpet pythons (*Morelia spilota mcdowelli*) selected trees with a dense covering of vines but did not use tree hollows (Shine and Fitzgerald, 1996). Common tree snakes (*Dendrelaphis punctulatus*) and brown tree snakes (*Boiga irregularis*) forage in

foliage and on the ground (Wilson and Knowles, 1988; Ehmann, 1992; Cogger, 1996; pers. obs.) and in water (*Dendrelaphis*, pers. obs.). They use tree hollows but also are often found on branches and among foliage, as well as in termitaria, buildings, and rock crevices. These snakes are frequently seen in small as well as large trees (pers. obs.).

These differences between *H. stephensii* on the one hand and sympatric arboreal colubrids and pythons on the other are interesting in light of the differing patterns of arboreality in the lineages involved. Arboreality is rare in Australian elapids (Shine, 1983, 1991) and occurs less frequently in elapid snakes than in some other macrostomatan families (Shine, 1983, 1991; Lillywhite and Henderson, 1993). In contrast, many colubrids and pythons live in the trees (e.g., Cogger et al., 1983). Our observations suggest that arboreality in Stephens' banded snakes is linked to the presence of enclosed cavities in trees. Most Australian elapid snakes are cryptic and avoid exposure, generally remaining sequestered in holes or crevices (pers. obs.). In this respect, *H. stephensii* has retained the retreat-site selection behavior of their terrestrial relatives. The same phenomenon has been reported in typhlopids snakes, where using a vertical hollow filled with rotting wood may be little different than using the same kind of shelter object on the ground (Swanson, 1981). It is notable, however, that although *H. stephensii* occasionally foraged in and beneath hollow logs, once a hollow tree had fallen it was no longer used as a shelter site by our radio-tracked snakes.

We thus conclude that the evolution of arboreality in Australian elapid snakes has not involved as profound a shift in habitat selection as might be suggested by intuition. Stephens' banded snakes are indeed highly arboreal, but the kinds of places in which they spend their time are similar in many ways to the secure retreat sites favored by their terrestrial counterparts. The congeneric broad-headed snake (*H. bungaroides*) also preferentially exploits large hollow-bearing trees during the summer months, although it is restricted to rocky crevices during the rest of the year (Webb and Shine, 1997a,b). However, *H. bungaroides* avoided turpentine (*Syncarpia glomulifera*) (Webb and Shine, 1997b), whereas *H. stephensii* actively selected this tree.

Our results highlight the importance of hollow-bearing trees as refuges for snakes and the scarcity of this resource in the snakes' habitat. The wide range of tree species used by snakes suggests that trees are selected because of struc-

tural attributes, although these are also to some extent taxonomically determined. Snakes depend upon large hollow-bearing trees for overwintering and for shelter sites during most of the active season. Although trees with vines, epiphytes and termitaria are also used, the importance of hollows as shelter sites is a key aspect of the ecology of Stephens' banded snakes.

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