

Ecological characteristics of a threatened snake species, *Hoplocephalus bungaroides* (Serpentes, Elapidae)

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Abstract

Species with ecological (habitat, dietary) specialization and low reproductive output may be at particular risk from anthropogenic habitat disturbance. We studied growth, reproduction and diet of the threatened broad-headed snake (*Hoplocephalus bungaroides*), a small nocturnal elapid from sandstone habitats in south-eastern Australia. Our data suggest that the life-history traits and diets of broad-headed snakes contribute to their vulnerability. Rather than searching actively for prey (like most sympatric elapids), broad-headed snakes wait under rocks to ambush prey. In consequence, these snakes feed infrequently, grow slowly, mature late and reproduce infrequently (compared with other sympatric snake species). Because of an ontogenetic shift in food habits, populations of broad-headed snakes require access to high densities of velvet geckos (in rock outcrops) as well as small mammals (in adjacent woodland). The specialized diet, reliance upon two distinctive habitats, low rate of growth, delayed maturation and low reproductive output may have exacerbated the vulnerability of broad-headed snakes to habitat destruction. All of these traits may be due to the species' reliance upon ambush predation rather than active foraging. A broader analysis supports the hypothesis that foraging mode may contribute to endangerment: a disproportionate number of 'threatened' species of Australian elapid snakes rely on ambush predation.

INTRODUCTION

The determinants of a species' vulnerability to extinction are obviously a central facet of conservation biology, and have attracted considerable scientific interest (e.g. Pimm, Lee Jones & Diamond, 1988; Harrison, 1991; Caughley & Gunn, 1995; Hanski, Moilanen & Gyllenberg, 1996). Nonetheless, available data on the ecological attributes of endangered species are strongly biased towards particular taxonomic groups (notably birds and mammals: Mittermeier *et al.*, 1992; Caughley & Gunn, 1995) in particular parts of the world (notably North America and Europe: e.g. Thomas, 1994). Even for these relatively well-studied systems, many puzzles remain. For example, even where the nature of the threatening process is clear, it is often difficult to understand why species differ so strongly in their vulnerability to that process. Commonly, only one or two taxa from a given habitat type will be severely affected by anthropogenic disturbance, while other (and, sometimes, closely related) taxa will be far more resilient (e.g. Caughley & Gunn, 1995).

Why is this so? Ecological theory identifies a series of species characteristics which may reduce a taxon's

ability to cope with disturbance. Clearly, some of these traits depend on the nature of the threatening process itself (e.g. high levels of social interaction within a species may facilitate the spread of disease: Thompson & Hall, 1993), but many are relatively general. In the case of species' vulnerability due to habitat destruction or modification (the largest single cause of decreasing biodiversity: e.g. Wilcove, McLellan & Dobson, 1986), the most important contributors to endangerment may include the following:

(i) small geographic range or population size, such that even a local impact threatens the continued existence of the entire taxon (e.g. Pimm *et al.*, 1988; Simberloff, 1994);

(ii) ecological specialization, such that the taxon relies heavily upon a particular habitat type or prey species, or some combination of these resources, and is unable to shift across to use alternative resources when the original ones are removed or degraded (e.g. Gaston, 1994; Simberloff, 1994; Thomas, 1994);

(iii) low vagility or high site fidelity, so that the taxon is unlikely to colonize available habitat patches unless they are easily accessible to existing populations (e.g. Wiens, Rotenberry & Van Horne, 1986; Warren, 1987; Bierregaard *et al.*, 1992; Belettsky & Orians, 1994; Wiens, 1994); and

(iv) low recruitment rates, so that the population is unable to maintain its numbers in the face of additional sources of mortality (e.g. Glazier, 1980; Pimm *et al.*, 1988).

Although it is straightforward to list such processes, evaluating their importance in actual case studies of endangerment is a much more difficult task. The difficulty is exacerbated by the fact that the correlates of rarity (and hence, potential contributors to endangerment) may differ substantially among major taxa (Gaston, 1994). In the case of reptiles, we have very little information on this topic. The best-studied reptilian systems in this respect have been turtles, where it seems that the low recruitment rates of many aquatic and terrestrial turtles have been a crucial factor in rendering these animals vulnerable to anthropogenic disturbance (e.g. Congdon, Dunham & Van Loben Sels, 1993, 1994). Unfortunately, so little is known about the general biology of most snake species that we often cannot even identify the cause of population declines (Dodd, 1993), let alone evaluate the reasons why the declines have differentially affected some species rather than others. Recent work has suggested that availability of particular habitat features (rather than food supply, etc) is the crucial determinant of endangerment of some python populations (Shine & Fitzgerald, 1996).

In south-eastern Australia, the broad-headed snake (*Hoplocephalus bungaroides*) has shown a drastic decline in numbers since European settlement (Krefft, 1869; Hersey, 1980; Shine & Fitzgerald, 1989). This small brightly coloured nocturnal snake is restricted to sandstone habitats within a 150 km radius from Sydney (Cogger, 1992). It was once found in inner suburbs of Sydney (Krefft, 1869), but has not been recorded in the Sydney metropolitan area for over 30 years (Australian Museum records). In contrast, other snake taxa are still commonly collected in the Sydney region (pers. obs.; Australian Museum accession records). The extent of the broad-headed snakes' decline can be estimated from our recent survey work (Shine *et al.*, 1998), where we examined all known sites from which broad-headed snakes have ever been reliably recorded (i.e. as represented by preserved specimens in museum collections). Of the total of 71 preserved specimens with locality data, 28 (39%) came from sites that no longer contained any suitable habitat (and thus, no snakes). A further 26 specimens (37%) came from a single small area close to Sydney, now substantially degraded by human activities including rock removal. Extensive surveys in 1994 revealed the presence of broad-headed snakes in only seven of the sites from which it had once been recorded (Shine *et al.*, 1998). In conjunction with this survey work, our radio-telemetric monitoring of broad-headed snakes provided extensive data on the ecology of these animals. One central theme to emerge from the work was the snakes' reliance on thin exfoliated sandstone boulders for diurnal retreat sites, especially during the cooler months of the year (Webb, 1996; Webb & Shine, 1997a,b, 1998a,b). The radio-tracked snakes were remarkably sedentary, often remaining under the same

rocks for weeks at a time (Webb & Shine, 1997a). Although the snakes showed little overt thermoregulatory behaviour (such as basking), they clearly based their selection of diurnal retreats on thermal characteristics, and hence showed strong seasonal (thermally driven) shifts in habitat type (Webb & Shine, 1997b, 1998a,b).

The broad-headed snakes' reliance on sandstone rocks for shelter sites during the cooler months makes them potentially vulnerable to habitat disturbance, especially the collection of sandstone boulders ('bush-rock') for Sydney gardens (Krefft, 1869; Hersey, 1980; Shine & Fitzgerald, 1989; Webb, 1996; Shine *et al.*, 1998). Bush-rock collection still occurs in many of the areas where the broad-headed snake is currently found, and at present there are no restrictions on the sale of bush-rock in New South Wales. However, it is unclear why the broad-headed snake appears to be so susceptible to rock removal, because (1) other favoured retreat sites of this species (crevices) are unaffected by this process; and (2) other sympatric snake species (e.g. *Rhinoplocephalus nigrescens*, *Demansia psammophis*) that also are often found under bush-rock, have maintained their numbers more successfully than has the broad-headed snake (pers. obs.; Australian Museum accession records; and see Slip & Shine, 1988b).

Our detailed ecological studies on the broad-headed snake have provided a partial answer to this question. The exfoliated sandstone rocks prized by bush-rock collectors offer distinctive microenvironments, and these rocks appear to play a more important role in the thermal ecology of the broad-headed snake than for other snake species (Webb, 1996; Webb & Shine, 1997a, 1998a,b). Also, our mark-recapture data suggest that neonatal broad-headed snakes disperse only relatively short distances (< 1 km) from their sites of birth and, thus, the species may have limited ability to recolonize suitable habitat (Webb, 1996; Webb & Shine, 1997a). Our studies have also provided data with which we can evaluate the other potential contributors to endangerment listed above. In particular, we can examine the dietary habits of this species, and the life-history traits that influence its maximal potential rate of population increase (and thus its ability to tolerate, and recover from, any additional sources of mortality).

METHODS

This study was part of a four-year (1992–1996) mark-recapture and three-year (1992–1995) radio-tracking project that was carried out in Morton National Park, 160 km south of Sydney, New South Wales, Australia. Snakes were marked by interperitoneal implantation of miniature PIT tags or harmonic radar diodes. In both cases the tags weighed < 3% of the snake's mass (see Webb, 1996 for details). Detailed information on study sites and tracking techniques is provided elsewhere (Webb, 1996; Webb & Shine, 1997a,b, 1998a,b). Dietary information was obtained from freshly collected snakes and by occasional capture of radio-tracked specimens. To find snakes, we turned over all suitable rocks in our

study areas at two-weekly intervals throughout autumn (March–May), winter (June–August) and spring (September–November). Most snakes move to adjacent forests in summer (December–February: Webb & Shine, 1997a,b), so were more difficult to collect at this time of year. The snakes mate from autumn through to spring, with females ovulating in late spring and giving birth in summer.

For all snakes we recorded snout–vent length (SVL), mass, head length (HL), head width (HW), sex and reproductive status. We palpated snakes to check whether they had fed recently, and collected faecal samples whenever possible. Juvenile snakes (< 35 cm SVL) with large bulges in their stomachs were placed in clear plastic containers (24 cm × 24 cm wide × 8 cm high) fitted with mesh lids and were kept at ‘field hut’ temperature (< 25 °C) for two days. Juveniles kept in this manner voluntarily regurgitated prey items after one to two days. We thereby minimized the possibility of injuring small snakes via forcible regurgitation. To reduce disturbance to telemetered snakes, we collected faecal samples rather than forcing them to regurgitate large prey items. However, during summer we were unable to sample most telemetered snakes because they sheltered in tree hollows at this time (Webb & Shine, 1997b). We occasionally managed to capture the snakes on the ground while they were moving between trees, but we have few dietary samples for adult snakes during summer.

Faecal material from broad-headed snakes usually contained scales or hairs. We identified excreted scales to the species level by comparing them to a reference collection of scales from lizards found on our study sites. During four years of fieldwork, only eight species of lizards were recorded on the exposed rock outcrops. These included velvet geckos (*Oedura lesueurii*) and seven species of skinks (*Cryptoblepharus virgatus*, *Ctenotus taeniolatus*, *Egernia cunninghami*, *Eulamprus quoyii*, *Lampropholis delicata*, *L. guichenoti* and *Bassiana platynota*). Of these species, *O. lesueurii* and *C. virgatus* were frequently found under rocks, *E. quoyii* was usually observed near crevices and *L. delicata* was commonly encountered in leaf litter. Mammalian fur was identified to species level using the field guide of Brunner & Coman (1974).

Recapture records (up to June 1996) of individually marked snakes were used to estimate growth rates. Growth rate (mm day⁻¹) was calculated as the increment in SVL between two captures divided by the time elapsed between captures. The four coldest months (June–September) were excluded from the calculation,

because no measurable growth occurred over that period (despite continued feeding by some snakes). Because of the small size of the study population (< 150 individuals), measurements from individuals captured more than once were included in the analysis, provided the period between recaptures was > 1 year. Our criterion for sexual maturity (> 50 cm SVL) was based on Shine’s (1983) dissection data. All adult-size females were palpated when captured, so that we could distinguish reproductive animals (with enlarged ovarian follicles or oviductal embryos) from non-reproductive specimens. Gravid females collected close to parturition were maintained in captivity so that we could quantify offspring sizes and litter sizes.

RESULTS

Body size

Table 1 presents data on sample sizes of adult broad-headed snakes, their body lengths and sexual size dimorphism. Adult females attained larger sizes than males, and mean SVL of females was significantly greater than that of males (one-factor ANOVA, $F_{1,49} = 4.89$, $P = 0.03$). Not surprisingly, larger snakes had longer and wider heads (for head length *versus* SVL: $r^2 = 0.95$, 1,57 d.f., $P < 0.0001$; for head width *versus* SVL: $r^2 = 0.88$, 1,57 d.f., $P < 0.0001$), but there were no significant differences between the sexes for these two variables (one-factor ANCOVAs with sex as the factor, SVL as the covariate, and head dimensions as the dependent variables — for head length: slopes, $F_{1,44} = 2.10$, $P = 0.15$, intercepts $F_{1,45} = 0.29$, $P = 0.59$; for head width: slopes $F_{1,44} = 0.22$, $P = 0.64$, intercepts $F_{1,45} = 0.02$, $P = 0.89$).

Foraging strategy

Radio-telemetric monitoring showed that the snakes remained sedentary, under rocks, for long periods of time (mean = 6.3 days between successive displacements: Webb & Shine, 1997a). We never observed broad-headed snakes actively searching for prey, despite many hours of observation both by day and by night. Continuous body temperature records of radio-tracked snakes (monitored by automatic data loggers) confirmed that the snakes remain inside their crevices for days or weeks at a time, and do not move even short distances. Instead, the snakes wait in their retreat sites until a potential prey item appears, and then seize the item. On several occasions, snakes that we knew to have remained

Table 1. Body sizes of broad-headed snakes, *Hoplocephalus bungaroides*

	Adult males				Adult females			
	<i>n</i>	Mean	SD	Range	<i>n</i>	Mean	SD	Range
SVL (cm)	35	54.5	5.1	45.3–66.5	16	58.8	6.2	46.5–68.0
HL (mm)	16	22.0	1.9	19.0–25.7	13	22.9	2.2	18.8–26.8
HW (mm)	16	18.0	1.7	13.8–21.6	13	19.1	2.5	15.9–24.1

SVL = snout-vent length, HL = head length, HW = head width.

sedentary for several days, contained freshly ingested prey items when they were captured and examined at the end of this period (pers. obs.). Hence, it is clear that these snakes rely upon ambush ('sit-and-wait') predation rather than active foraging, at least during the times of year when they remain on the rock outcrops. The snakes are more difficult to observe during summer, when most adult specimens migrate into the adjacent forests (Webb & Shine, 1997b). Nonetheless, the relatively long periods of time spent sedentary in tree hollows at this time also suggest a reliance on ambush predation (Webb & Shine, 1997b). Velvet geckos (the primary prey of juvenile broad-headed snakes, see below) strongly avoid the scent of these snakes, providing a plausible reason why the snakes benefit from remaining immobile within suitable retreat sites (Downes & Shine, 1998). 'Sit-and-wait' foraging has also been reported in captive broad-headed snakes (Wells, 1981).

Types of prey eaten

A total of 56 prey items was recorded from 50 individual snakes (Table 2). Two of these snakes were captured twice and contained prey on both occasions. Most snakes had ingested a single prey item, but two juveniles (SVLs of 27 and 30 cm) had each eaten a velvet gecko and an unidentified skink, while one subadult snake (SVL = 44 cm) had eaten a mouse, a velvet gecko and an unidentified skink. Body size strongly influenced the types of prey eaten by broad-headed snakes (Table 2). We divided snakes into three size classes: juveniles (SVL < 35 cm), subadults (35 cm < SVL < 45 cm) and adults (SVL > 45 cm). Juvenile snakes fed entirely on small lizards (geckos and skinks) while larger snakes fed on lizards and small mammals. Of 33 prey items recovered from juvenile snakes, 23 (70%) were velvet geckos. The relative importance of *O. lesueurii* in the diet of the broad-headed snake decreased as snakes grew larger. Velvet geckos comprised only 27% of the prey items consumed by adult snakes, significantly less than in juveniles ($\chi^2 = 6.78, 1 \text{ d.f.}, P < 0.05$).

Table 2. Prey items recorded from stomachs or faeces of 50 individual broad-headed snakes, *Hoplocephalus bungaroides*

	Number of snakes		
	Juveniles	Subadults	Adults
Reptiles			
Gekkonidae			
<i>Oedura lesueurii</i>	23	4	4
Scincidae			
<i>Cryptoblepharus virgatus</i>	1	–	–
<i>Eulamprus quoyii</i>	–	–	6
<i>Lampropholis delicata</i>	2	–	–
Unidentified skinks	7	2	1
Mammals			
Dasyuridae			
<i>Antechinus stuartii</i>	–	–	1
Muridae			
<i>Mus domesticus</i>	–	1	1
Unidentified	–	–	2

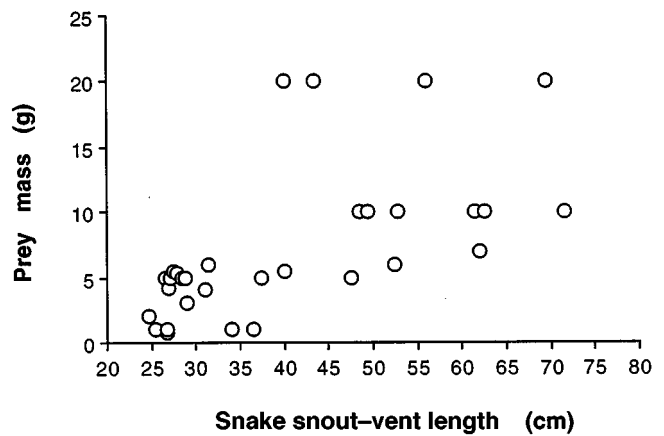


Fig. 1. Estimated masses of prey items recorded from free-ranging broad-headed snakes (*H. bungaroides*), compared to the size of the snake that had consumed them. Masses of small mammals were estimated to be 20 g, the weight of a small mouse that could be easily ingested by broad-headed snakes in captivity. A mass of 10 g was estimated for the six adult *Eulamprus quoyii* present in stomach contents.

A comparison of prey ingested by juvenile broad-headed snakes in late winter and spring compared to available prey under rocks at this time suggests that snakes were not selective with respect to prey type. Of 22 prey items consumed by juveniles during this period, 17 were *O. lesueurii* and five were skinks. The proportions of these two prey types were not significantly different to those in samples of lizards found under rocks at this time of year ($\chi^2 = 0.55, 1 \text{ d.f.}, P > 0.05$).

Predator-prey size relationships

This topic is relevant to our analysis, because gape limitation (if present) may constrain the size (and thus the total amount) of prey items consumed by snakes of different size classes. Feeding rates may in turn determine growth rates and ages at maturation. Our data show that larger snakes fed on larger prey items (Fig. 1), but continued to take relatively small items (skinks and geckos). There was a significant positive relationship between snake SVL and prey mass ($r^2 = 0.33, 1,30 \text{ d.f.}, P < 0.001$). This ontogenetic shift in prey size may be due to the inability of small snakes to swallow large prey. Adult snakes had significantly longer and wider heads than did subadults or juveniles (one-factor ANOVAs comparing the three snake size classes, for head length: $F_{2,56} = 176.3, P < 0.0001$; for head width: $F_{2,56} = 176.3, P < 0.0001$). Nonetheless, some of the gravid female geckos consumed by juvenile snakes were very large relative to the snake that ate them, weighing up to 86% of the snake's body mass ($n = 6, \text{ mean} = 69\% \text{ snake mass, SD} = 12\%$).

Proportion of fed snakes

Only 48 of 192 snakes (25%) contained freshly ingested prey when captured. The proportion of snakes with food in their stomachs was significantly higher in juveniles than

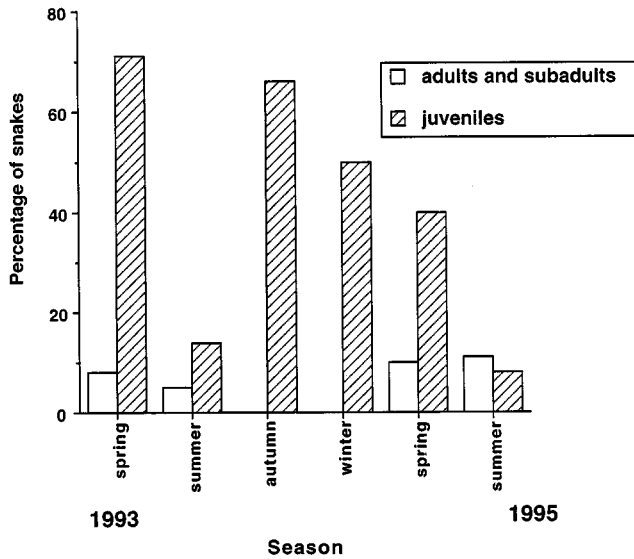


Fig. 2. Percentages of subadult and adult (snout-vent length > 45 cm) and juvenile (SVL < 35 cm) broad-headed snakes with food in their stomachs from spring 1993 to summer 1995.

in adults and subadults combined (42 versus 14%; $\chi^2 = 18.32$, 2 d.f., $P < 0.01$), and this trend was seen both during spring ($\chi^2 = 10.85$, 1 d.f., $P < 0.01$) and during autumn and winter ($\chi^2 = 5.64$, 1 d.f., $P < 0.05$; see Fig. 2). We could not compare the proportions of juveniles and adults that fed during summer, due to the difficulty of sampling both groups at this time. Juvenile snakes continued to feed year round (see Fig. 2), and there were no significant differences between the proportions of juvenile snakes containing food in the warmer months (spring and autumn) compared with winter ($\chi^2 = 1.59$, 1 d.f., $P > 0.05$).

Growth rates

Small juvenile snakes (< 32 cm SVL) grew very slowly during their first year of life (Fig. 3). Because very slow growth of young animals has not been reported in previous studies on other snake species (Parker & Plummer, 1987), we tested to see if it might be an artifact of our marking techniques. The low growth rate of neonatal broad-headed snakes does not appear to be due to a negative effect of implanted harmonic radar diodes or PIT tags, because very small untagged snakes were captured during late spring (9 months after birth, see Fig. 4; see also Keck, 1994). Hence, at least some unmarked snakes must have been growing just as slowly as our marked individuals. Also, our analysis did not reveal any significant difference between growth rates of snakes implanted with miniature PIT tags versus the larger diodes (one-factor ANCOVA with tag type as the factor, mean SVL over the recapture interval as the covariate, and growth rate as the dependent variable: slopes $F_{1,26} = 0.20$, $P = 0.66$, intercepts $F_{1,27} = 0.39$, $P = 0.54$).

Once snakes had grown past 32 cm SVL, their growth rates were high, and thereafter decreased with increasing snake size (Fig. 3). Males and females grew at similar rates, but females continued to grow past 55 cm

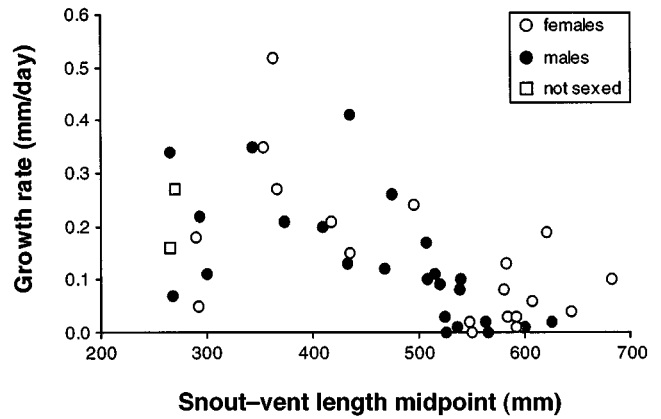


Fig. 3. Growth rates of male and female broad-headed snakes, *H. bungaroides*. The graph shows growth rates per growing day (i.e. SVL increment between recaptures, divided by the number of non-winter days between recaptures), plotted against the mean SVL of the snake over that recapture interval. Two small snakes were not sexed.

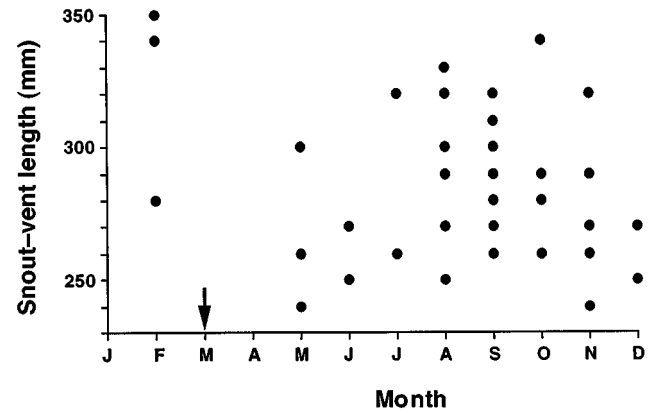


Fig. 4. Body sizes (snout-vent length = SVL) of untagged juvenile broad-headed snakes (< 350 mm SVL) captured on our study sites during four years of field work. Note that snakes similar in size to neonates (around 250 mm SVL) were captured during summer, some 10 months after birth. The arrow marks the mean offspring size and time of birth in this population.

SVL, whereas males did not (one-factor ANCOVA with sex as the factor, mean SVL over the recapture interval as the covariate, and growth rate as the dependent variable: slopes $F_{1,33} = 0.60$, $P = 0.45$, intercepts $F_{1,34} = 4.23$, $P = 0.047$). Reconstructing the overall growth trajectory (using mean growth rates), males probably mature at four years of age, whereas females mature at five years of age and give birth for the first time when they are six years old. Even if we use the maximum recorded growth rates in Fig. 3 for this calculation, females are still predicted to delay maturity until they are three years of age, and produce their first offspring at four years.

Reproduction

Generally, proportions of females reproducing in a given year were extremely low. Three out of seven females

were gravid in 1992, one out of five females was gravid in 1993, one out of five females was gravid in 1994, and two out of eight females were gravid in 1995. Although these data suggest that many adult females do not reproduce each year, it is difficult to estimate the exact reproductive frequency because of the possibility that gravid females modify their behaviour in ways that affect their probability of capture (e.g. Luiselli, Capula & Shine, 1996). Indeed, gravid female broad-headed snakes are more sedentary than non-reproductive animals, but also bask more frequently (Webb, 1996; Webb & Shine, 1997a). Both of these changes may affect their probability of capture. Long-term recapture records for individual females show that one animal was non-reproductive in four successive years, four animals were non-reproductive in two successive years, and three animals were non-reproductive when captured in the springs of both 1993 and 1995. We did not record more than one litter from any female over our four-year study. These records are consistent with intervals of about four years between successive litters, as suggested by the proportion of females that were reproductive in the year they were captured (7 out of 25 = 28%).

Another way to estimate reproductive frequencies is to compare the numbers of neonatal snakes captured at our study sites each year with the numbers of adult females. Given a mean litter size of 3.3 live offspring (for an average-sized female of 58.8 cm SVL (Table 1), based on the regression equation predicting litter size from maternal SVL, see below), we would expect the population to contain an average of 3.3 neonates per adult female if every female reproduced every year. In practice, this ratio ranged from 0.40 to 1.13 over the four years of the study (grand mean = 0.82, SD = 0.32), again suggesting that adult females reproduce, on average, once every four years. This estimate would be biased if recapture probabilities for neonates were different from those of adult snakes, but our data show that recapture probabilities were similar for adults (0.25) and juveniles (0.27).

We obtained detailed data on reproductive output for only a few snakes. Three gravid females captured during 1994 (one from our study sites, two 10 km from our sites) gave birth in the laboratory on 9 February 1995 and 6 March 1995. The smallest female (SVL = 54.5 cm) produced one offspring and four unfertilized oocytes, and the other females (SVLs = 71.5 and 76.0 cm) each gave birth to seven offspring. One of these females also produced an infertile oocyte. Relative clutch mass (RCM) was defined as maternal mass loss at parturition divided by maternal post-parturition mass (Shine, 1980). RCMs were high for the two large females (0.64 and 0.59), but (because infertile oocytes weigh much less than full-term young) was low for the small female (0.33). Offspring of all three females were large, ranging in size from 22.0 to 24.8 cm SVL (mean = 23.2 cm, SD = 0.83) and in mass from 4.9 to 6.2 g (mean = 5.5 g, SD = 0.34). Additional data on reproductive output came from a Blue Mountains (Mount Banks) female of 68.5 cm SVL, that gave birth to four live off-

spring (mean SVL = 22.2 cm, mean mass = 5.27 g) and two infertile oocytes on 3 April 1989 (RCM = 0.45). Combining these data with previous reports (Shine, 1983; Shine & Fitzgerald, 1989) reveals a significant positive correlation between female SVL and litter size ($r^2 = 0.57$, 1, 5 d.f., $P = 0.05$).

DISCUSSION

Our data considerably expand available information on the feeding habits and life-history traits of *Hoplocephalus bungaroides*. Previous reports on the diet of broad-headed snakes have been anecdotal in nature (e.g. Worrell, 1963; Cogger, 1992), or else have been based on small numbers of museum specimens (Shine, 1983) or captive animals (Wells, 1981). Our data thus enable us to examine whether the decline in numbers of broad-headed snakes over the last 200 years is related to dietary and life-history characteristics, as well as to behavioural traits (habitat specificity and limited dispersal) identified by our previous analyses (Webb, 1996; Webb & Shine, 1997a,b). To do this, we need to compare broad-headed snakes with other species that occur sympatrically, but have not experienced such severe declines (e.g. Glazier, 1980; Gaston, 1994). Candidates for such comparisons (i.e. snakes that occur in broadly similar habitats, within the geographic range of the broad-headed snake) include one blindsnake (*Ramphotyphlops nigrescens*, Typhlopidae), one python (*Morelia spilota*, Pythonidae), and 13 venomous snakes (Family Elapidae: *Acanthophis antarcticus*; *Austrelaps ramsayi*; *Cacophis squamulosus*; *Demansia psammophis*; *Drysdalia rhodogaster*; *Furina diadema*; *Hemiaspis signata*; *Notechis scutatus*; *Rhinoplocephalus nigrescens*; *Pseudechis porphyriacus*; *Pseudonaja textilis*; *Suta spectabilis*; *Vermicella annulata*: Swan, 1990). Clearly, the strongest comparisons are of broad-headed snakes with other Australian venomous (elapid) species, because many ecologically significant traits are phylogenetically conservative (e.g. blindsnakes feed only on invertebrates, a type of prey rarely taken by other Australian snakes: e.g. Shine, 1991).

The body sizes of elapids that are sympatric with broad-headed snakes range from much smaller to much larger than broad-headed snakes, and the dietary habits and life-history traits of these taxa are diverse also. Below, we compare *H. bungaroides* to the other taxa, to see if broad-headed snakes are unusual in these respects. For ecological data on the other species, we rely upon reviews by Shine (1991, 1994), plus unpublished data.

(i) *Dietary composition*. In broad outline, the diet of the broad-headed snake is similar to that of its con-familial species. Australian elapids the size of broad-headed snakes typically eat mostly lizards: almost exclusively scincids, of a wide taxonomic array (Shine, 1994). In contrast, 60% of the lizards eaten by broad-headed snakes were geckos of a single species (*Oedura lesueurii*). Frogs are also common prey items for medium-sized elapids, but were not recorded in the diet of broad-headed snakes (Table 2). The strong ontogenetic

shift in prey types and foraging habitats in broad-headed snakes (Table 2) also offers a contrast to most other elapid species. An ontogenetic shift from lizards to mammals is usually seen only in larger species of elapids, probably because these are the species that have a large range in absolute body sizes (e.g. Shine, 1989). The only other similarly sized elapid that regularly eats mammals is another ambush predator, the death adder (*A. antarcticus*: Shine, 1977a, 1983, 1991).

(ii) *Foraging tactics*. The specialization of juvenile broad-headed snakes on velvet geckos is probably a function of three factors: the abundance of the geckos, the foraging tactics of the snakes, and the inability of juvenile broad-heads to consume larger prey types. If juveniles were active foragers, then we might expect a higher proportion of non-saxicolous skinks (such as *Lampropholis* spp.) in their diet. At our sites small-eyed snakes (*Rhinoplocephalus nigrescens*) also sheltered under rocks, yet fed entirely on small skinks which they presumably located at night (Shine, 1984; Webb, 1996; Webb & Shine, unpubl. data). The absence of large prey from the diets of juvenile broad-headed snakes is probably a result of gape limitation. However, juveniles may also remain for most of the year on the rock outcrops, rather than penetrating deep into the woodland as adults do (Webb, 1996; Webb & Shine, 1997a, 1998a,b). The ontogenetic shift in habitat use may expose adults and juveniles to different prey spectra.

With the exception of the death adder, all of the venomous snakes (elapids) sympatric with the broad-headed snake are active searchers rather than ambush foragers (e.g. Shine, 1977a). The diamond python (*Morelia spilota*) also relies on ambushing its prey, but takes very different kinds of food items (possums, rats) than does the broad-headed snake (Slip & Shine, 1988a). Ambush foraging may enhance survival (because ambush predators are not exposed while foraging) but rates of food intake tend to be low, because of the reliance on prey movements (Shine, 1980). Thus, ambush-foraging snakes tend to have slow growth, delayed maturation and low reproductive frequencies (e.g. the death adder, *Acanthophis*: Shine, 1980). This putative link between foraging tactics and life-history attributes is supported by our data on the broad-headed snake.

(iii) *Age at maturity*. Australian elapids generally grow faster and mature earlier than do many other snake species in other parts of the world; for example, even the largest sympatric elapids (copperheads *Austrelaps ramsayi*, tigersnakes *Notechis scutatus*, blacksnakes *Pseudechis porphyriacus*, brownsnakes *Pseudonaja textilis*) mature at earlier ages than do broad-headed snakes (Shine, 1978). Slow growth in the smallest size classes of juveniles, as seen in our broad-headed snakes, has not been documented in similarly sized elapids (or other snakes: Parker & Plummer, 1987). Our dietary data (Table 2), combined with observations on captive broad-headed snakes, suggest that small snakes may not be able to consume or subdue the types of prey (e.g. mice, or the large skink *Eulamprus*) that are eaten by larger conspecifics (Webb & Shine, 1993). The ability of neonate

snakes to subdue and swallow prey may therefore influence energy acquisition, growth rates and survival in natural populations (Jayne & Bennett, 1990; Forsman, 1994), but detailed laboratory studies are needed to examine the putative link between head size and the ability to capture and swallow prey (e.g. Pough & Groves, 1983; Webb & Shine, 1993).

Low growth rates of juveniles may thus reflect gape limitation, as well as the sit-and-wait foraging strategy used by the broad-headed snake. These snakes may be less able to increase rates of prey encounter, or the size spectrum of potential prey that they find, than are active foragers. Thus, selection to overpower and ingest even large prey items, might have contributed to the evolution of large offspring size, a wide gape (broad head) and potent venom in this taxon.

(iv) *Reproductive output*. Litter sizes of broad-headed snakes are similar to those produced by similarly sized elapid species (see regressions in Shine, 1994) but the offspring are much larger than are those of any of the sympatric elapids, including species with much larger adult body sizes (Shine, 1991, 1994). As a result, relative clutch masses (RCMs) of broad-headed snakes are higher than for most other elapids, yet are remarkably similar to those of viviparous viperids that ambush prey (Seigel & Fitch, 1984). Ecological theory predicts that ambush predators should have higher RCMs than active searchers, because of the lesser importance of maternal mobility for foraging or from escape from predators; this pattern has been documented within lizards (e.g. Vitt & Congdon, 1978) but not in snakes (Seigel & Fitch, 1984). Our data for broad-headed snakes fit this prediction from theory.

(v) *Reproductive frequency*. Despite its importance in snake demography, the frequency of reproduction by adult females remains poorly known for most species (Seigel & Ford, 1987). Studies on five elapid species from montane habitats in northern New South Wales revealed reproductive frequencies (proportions of females that were reproductive in the year they were collected) of 84–93% (Shine 1977b). Other studies on south-eastern Australian elapids have reported reproductive frequencies from 55 to 93% (e.g. Shine, 1981). All of these estimates are considerably higher than we found in broad-headed snakes, suggesting that *H. bungaroides* is indeed unusual in this respect, at least among sympatric elapids. At our sites adult broad-headed snakes appear to have fed infrequently, and gravid females had high RCMs. Thus, females may be unable to obtain enough energy to reproduce every year (e.g. Bull & Shine, 1979; Andren & Nilson, 1983; Seigel & Fitch, 1985). Low frequencies of female reproduction seem to be more common in snake species that rely on ambush predation than in those that use active foraging (Shine, 1980).

In summary, broad-headed snakes may differ in substantial ways from most of the other snake species with which they are sympatric, such that broad-headed snakes are less well-suited to coping with anthropogenic habitat disturbance than are the other taxa. The central

feature of the biology of the broad-headed snake that is responsible for their ecological specialization and low reproductive output is their foraging mode — especially, their reliance on remaining sedentary for days or weeks under a rock, waiting to ambush a prey item. This sedentary behaviour may enhance survivorship (because the snake is able to remain hidden from predators) but is unlikely to allow high feeding rates. In consequence, the snakes grow slowly, mature late and reproduce infrequently. These characteristics militate against a rapid recolonization of habitat following disturbance, and enhance the probability of local extinctions of broad-headed snakes in areas where the food (i.e. velvet gecko) supply has been severely reduced by bush-rock removal. The snakes' reliance on a prey species that is particularly vulnerable to habitat disturbance (Schlesinger & Shine, 1994; Shine *et al.*, 1998) compounds this vulnerability.

Although adult broad-headed snakes shift to larger prey, the almost exclusive reliance of juvenile snakes on velvet geckos (Table 1) means that successful recruitment to the adult population cannot occur without an abundant supply of geckos. Thus, populations of broad-headed snakes may be able to persist only in areas that offer two distinctive prey types, in adjacent habitats. This combination of prey resources will occur more rarely than either of its components alone. In an ambush predator that relies on prey movements to obtain its food, even a modest reduction in prey abundance may significantly reduce feeding opportunities. Unlike an active searching forager (which can compensate for lower prey abundance by increasing foraging effort), ambush foragers like the broad-headed snake may have little control over their rates of prey encounter. Even limited movements in the immediate vicinity of an ambush site might leave scent trails that would frighten away potential prey items (Downes & Shine, 1998).

In combination with our other data (see Webb, 1996; Webb & Shine, 1997*a,b*, 1998*a,b*; Shine *et al.*, 1998), the present analysis helps to clarify the processes that have caused broad-headed snakes to decline in numbers since the European invasion of Australia. In particular, our analysis suggests a central importance for foraging mode. Ambush predation is associated with a set of other ecological traits that, in combination, predispose the species to endangerment in the face of anthropogenic habitat modifications. An analysis of published data on other Australian elapid snakes suggests that foraging mode may be consistently related to conservation status. Of the 17 elapid species identified as 'threatened' by a recent quantitative analysis (Cogger *et al.*, 1993), six (35%) are believed to rely on ambush predation (on the basis of dietary habits, body shape, and/or detailed information on congeneric species: see references in Shine, 1991). In contrast, ambush predators comprise only two of the other 62 'non-threatened' elapid taxa for which we have ecological data (3%). The difference in proportions is highly significant ($\chi^2 = 11.8$, 1 d.f., $P < 0.001$). Even if we are in error in classifying foraging modes in some of these taxa, the result is robust

(i.e. $P < 0.05$ even if five additional 'non-threatened' species are reclassified as ambush predators). This association suggests that life-history traits associated with ambush predation may render ambush-foraging species particularly vulnerable to anthropogenic habitat modification.

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