

Life history attributes of the threatened Australian snake (Stephen's banded snake *Hoplocephalus stephensii*, Elapidae)

Mark Fitzgerald^a, Richard Shine^{a,*}, Francis Lemckert^b

^a School of Biological Sciences A08, University of Sydney, Sydney, NSW 2006, Australia

^b Research Division, State Forests of New South Wales, P.O. Box 100 Beecroft, NSW 2119, Australia

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Abstract

Whether or not a species is threatened by habitat change is influenced by its life-history traits as well as by the nature and severity of the threatening process. Detailed studies of declining taxa can clarify reasons for their vulnerability, both in proximate terms (e.g., taxa with slow growth, delayed maturation, low fecundity and infrequent reproduction will be poorly suited to withstand increases in adult mortality rates) and in an evolutionary perspective (i.e., what attributes of the environment have favoured the evolution of certain life history traits?). We obtained data on life history traits during an intensive radio-tracking study on the threatened arboreal elapid snake *Hoplocephalus stephensii* from forest habitats of eastern Australia. Based on 39 field-collected specimens, these long, slender snakes (mean adult snout–vent length 73 cm, mass 114 g) feed predominantly on mammalian prey such as Bush Rats (*Rattus fuscipes*) and Pygmy-possums (*Cercartetus nanus*); but juveniles also take lizards. Foraging modes are diverse, from active searching through to ambush. Gape-limitation prevents snakes from ingesting adults of the most abundant local rodent (*R. fuscipes*), limiting the snakes to specialise on sub-adult rats which are only seasonally available. Rates of feeding, growth and reproduction are low; for example, none of 21 wild-caught females was reproductive. However, snakes given access to abundant prey in captivity, rapidly gained in body condition, grew significantly, and subsequently reproduced. Litters consisted of a few (1–9), relatively large (25 cm snout–vent length, 7.5 g) offspring. The “slow” life-history traits that have contributed to endangerment of this taxon may include proximate as well as evolutionary responses to the low temperatures and limited prey availability in the forest habitat of *H. stephensii*.

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1. Introduction

Understanding the factors that have caused a species to become threatened is the critical first step towards developing strategies for effective conservation. Such factors include not only the threatening processes such as habitat destruction or fragmentation, disease, invasion of feral predators or competitor, but also characteristics of the species. Frequently, a single disturbance causes a severe decline in abundance and/or geographic range in some taxa, but related taxa thrive and increase in numbers (Webb et al., 2002). Understanding the

processes that drive a species towards extinction requires information not only on the causes of mortality, but also on the attributes of a species that render it vulnerable to these causes (e.g., Burgman and Lindenmayer, 1998). This truism has stimulated a wide body of research that attempts to identify generalities in the kinds of traits that make a species vulnerable to extinction. Many such factors have been proposed including large body sizes (Richman et al., 1988; Gaston and Blackburn, 1996), small population sizes (Dickman, 1996; Burgman and Lindenmayer, 1998), slow growth rates, late maturation (Brown, 1991; Webb et al., 2002), low fecundity (Greene and Campbell, 1992), habitat and/or dietary specialisation (Greene and Campbell, 1992; Foufopoulos and Ives, 1999), restriction to islands, and poor dispersal capacity (Richman et al., 1988; Wilson, 1991). However,

* Corresponding author. Tel.: +61-2-9351-3772; fax: +61-2-9351-5609.

E-mail address: rics@bio.usyd.edu.au (R. Shine).

the generality of most of these factors is limited; particular features may be consistently associated with vulnerability to endangerment in some lineages but not others. For example, a specific foraging mode (reliance upon ambush) has been associated with vulnerability to endangerment in Australian snakes, but not for several other types of organisms (Reed and Shine, 2002).

Given the lack of phylogenetic generality in factors that predispose a species towards endangerment, there is no substitute for detailed natural-history studies on specific threatened species. Indeed, Caughley (1994) argued that intensive natural-history studies on specific systems have generally provided a more robust means of identifying and reversing threatening processes than have more theory-based approaches such as conservation genetics. Ideally, both kinds of studies in unison provide a stronger basis for identifying causes for decline. We have conducted a detailed ecological study of an arboreal snake species from forested habitats of eastern Australia. This species has declined dramatically over much of its historical range, apparently due to destruction and fragmentation of forest habitat (Cogger et al., 1993). Genetic analyses suggest that the resulting fragmentation has occurred so recently that there has been little divergence or loss of heterozygosity in isolated populations (Keogh et al., 2003), so that causes for decline are likely to have been ecological rather than genetical. In this paper we describe general life-history traits of the species, discuss their relevance to its threatened conservation status, and speculate on the evolutionary and ecological factors that have favoured this suite of “slow” life-history traits.

2. Materials and methods

2.1. Study species

Stephen's banded snakes (*Hoplocephalus stephensii*) are slender-bodied, arboreal, venomous snakes, restricted to forest habitats in north-eastern New South Wales and south-eastern Queensland (Wilson and Knowles, 1988; Cogger, 1996). Continuous over coastal and near-coastal regions at the time of European arrival 200 years ago, most of these forests have been cleared or highly modified for agriculture, silviculture or urban development (Hobbs and Hopkins, 1990; Lunney, 1991). On the basis of recent records available for this species, *H. stephensii* apparently persist only in remnant forest patches >5000 ha in extent (Fitzgerald, 2003).

Adult *H. stephensii* grow to 1 m in length and 250 g in mass. This species is a tree hollow specialist; radio-tracking reveals long sequestration periods in tree hollows and infrequent moves between suitable large hollow-bearing trees (Fitzgerald et al., 2002a,b). Adult snakes

occupy large home ranges (mean = 20.2 ha for males; 5.4 ha for females: Fitzgerald et al., 2002b).

2.2. Study site and field methods

We radio-tracked 16 adult *H. stephensii* over a two-year period in Whian Whian State Forest, an area managed principally for timber production 30 km northeast of the city of Lismore in northeastern New South Wales. Details of topography, climate, vegetation and radiotelemetry methods have been described elsewhere (Fitzgerald et al., 2002a). The study site is part of an 11 000 ha forest block surrounded by a mosaic of agricultural lands and small regenerating forest patches. Snakes were captured by driving along forest roads at night; additional specimens were found by monitoring the vicinity of telemetered animals. Snakes were weighed and measured at capture, and at irregular intervals thereafter (we avoided handling unless transmitters needed to be replaced). We palpated freshly-captured snakes to obtain regurgitated prey or faeces; prey remains in either case were identified by microscopic examination (e.g., Brunner and Coman, 1974). Radio-tracked snakes were usually located during the day, 2–3 times per week in the active season (September–May), and less frequently during winter when snakes were sequestered and inactive in overwinter trees. From April 1997 to April 1999, we made >1200 observations of these radio-tracked snakes, but on most occasions the snakes were hidden within arboreal shelter sites (tree hollows, vines, epiphytes and perforated termitaria). Snakes were occasionally located close to the ground in tall sedges (Fitzgerald et al., 2002a).

In addition to the 23 snakes captured in Whian Whian State Forest, we also obtained records on 38 captive-born offspring, as well as on 45 snakes from other areas (mostly from other biologists). Many of these latter records were restricted to time, date and locality of sightings, but data on diet, activity and body sizes were also obtained for some of these animals.

2.3. Observations of captive snakes

Because radio-tracked snakes were generally sequestered in hidden shelter sites more than 20 m above the ground, we maintained several *H. stephensii* in captivity in order to observe their behaviour directly. The duration of captive observation ranged from less than 1 month (for seven radio-tracked snakes retained between transmitter replacement or removal), to longer periods (12–36 months) for 12 snakes held to investigate reproductive behaviour. Fifteen captive-bred neonates were retained to clarify growth rates, time to sexual maturity and patterns of sequestration and emergence behaviour. All snakes were maintained at natural photoperiods. Neonates were housed individually in round

plastic tubs 13 cm × 21 cm. Older snakes were maintained individually in cages measuring 30 × 30 × 60 cm and 50 × 90 × 90 cm, or in groups of up to three animals in the larger cages. Each cage contained a shelter and a heat source; water was provided weekly. Snakes were fed thawed skinks and later, mice or sub-adult rats, every 10 days. We avoided handling these animals (as above), so that snout–vent lengths and weights were recorded only once per six months. At the end of the study, all wild-caught snakes were released at their original sites of capture.

3. Results

3.1. Body sizes

All snakes found during our fieldwork at Whian Whian State Forest were adults, averaging 74.7 cm snout–vent length (SVL) ($n = 23$, $SD = 9.1$). Males ($n = 7$, mean $SVL = 75.8 \pm 7.3$ cm; range 67.0–88.0 cm) averaged slightly but not significantly larger than females ($n = 16$, mean $SVL = 74.2 \pm 10.0$ cm, range 55.0–92.0 cm; $F_{1,21} = 0.16$, $P = 0.70$). Combining samples from all areas, males and females ($n = 21$ for each sex) did not differ significantly either in mean SVL (70.59 vs 74.57 cm; $F_{1,40} = 2.38$, $P = 0.13$) or mean mass (113.85 vs 115.01 g; $F_{1,40} = 0.01$, $P = 0.94$). However, ANCOVA revealed that males generally weighed more than females at the same body length (slopes, $F_{1,38} = 0.30$, $P = 0.58$; intercepts, $F_{1,39} = 6.18$, $P < 0.02$). Captive-born neonates averaged 24.8 ± 26.2 cm SVL (range 19.5–28.5 cm, $n = 23$). In five litters, mean neonatal SVL averaged 30% of maternal SVL ($SD = 2\%$, range 27–34%).

3.2. Growth rates

Body masses of nine radio-tracked snakes were measured at mean intervals of 234 days ($SD = 132$, $n = 18$). Seven of these snakes lost mass during tracking (mean % mass loss/month = $0.012 \pm 0.01\%$, range 0.001–0.02%) whereas the other two increased in mass (mean % mass gain/month = $0.013 \pm 0.013\%$, range 0.024–0.04%). Of nine adult snakes captured in the field and held in captivity, all increased in mass over this period. Thus, snakes gained mass more often in captivity than while monitored in the field (mass increase in 9 of 9 vs 2 of 9, $\chi^2 = 8.42$, $df = 1$, $P < 0.005$).

Snakes that were born and raised in captivity also increased rapidly both in body length and body mass, growing from a mean of 25 cm snout–vent length (7.5 g) at birth to approximately 36 cm snout–vent length (16 g) at 12 months, and 46 cm (29 g) at 24 months. Thus under favourable conditions, males might attain sexual maturity (>47.9 cm; from dissections by Shine, 1983) in

their third year and females might attain sexual maturity (>56.5 cm: Shine, 1983) in their fourth year of life (i.e., 43–44 months after being born). Adult snakes also grew appreciably in captivity. Three long-term captive adult females increased body mass, respectively, from 101 to 199 g (87% over 17 months), from 81 to 149 g (84% over 7 months), and from 101 to 233 g (83% over 3 years).

3.3. Body condition

The body condition of wild-caught snakes was similar in our main study site (Whian Whian State Forest) as in other areas (ANCOVA with 'other' vs Whian Whian State Forest snakes as the factor, \ln snout–vent length as covariate and \ln mass as the dependent variable; $F_{1,37} = 0.25$, $P = 0.62$). However, female snakes held in captivity averaged heavier relative to snout–vent length than did wild-caught animals (the former after >6 months in captivity, the latter at their time of first capture: ANCOVA with captive vs wild as the factor, \ln snout–vent length as covariate and \ln mass as the dependent variable; $F_{1,22} = 4.35$, $P < 0.05$). Males did not increase significantly in condition when taken from the wild and held in captivity (same design as ANCOVA above; $F_{1,18} = 0.01$, $P = 0.92$; note that each snake is represented only once in each of these analyses). These results reflect the fact that field-captured females were more emaciated than any other group (captive females, or males either in the field or captivity).

3.4. Reproduction

Of the 21 adult-size female *H. stephensii* collected from the wild during our study and available for palpation (15 from Whian Whian State Forest, six from other sites), none was reproductive (gravid or with enlarged ovarian follicles evident during palpation). In keeping with this low incidence of reproduction, few neonates or subadults were seen (zero from Whian Whian State Forest out of 23 snakes; one neonate and three subadults from other areas, out of 45 animals).

Courtship and copulation were observed in captive snakes during September and October (the Austral spring), although detailed observation was not possible because snakes were generally partially hidden inside shelters at these times. Although captive mixed-sex groups were maintained in autumn (March–May), no sexual interactions were observed except in spring. Following active pursuit by courting males, three adult females exhibited a stereotyped posture that apparently functioned to prevent copulation: a tightly stacked coil with the vent in the centre of the uppermost coil (pers. obs.).

Captive snakes produced 10 litters, four in February and six in March (see Table 1). One long-term (16-year) captive female produced three litters, but two of them

Table 1
Records of reproduction by captive Stephen's banded snakes, *Hoplocephalus stephensii*

| Female ID# and SVL (cm) | Litter size | Live neonates | Stillborn neonates | Infertile oocytes | Relative clutch mass and Date |
|-------------------------|-------------|---------------|--------------------|-------------------|-------------------------------|
| #1 and 82 | 9 | 9 | 0 | 0 | 0.37 and 25 February 2001 |
| #20 and 75 | 4 | 4 | 0 | 0 | 0.52 and 10 March 1999 |
| #37 and 78 | 4 | 2 | 2 | 0 | 0.22 and 24 February 2000 |
| #32 and 85 | 7 | 7 | 0 | 0 | 0.31 and 26 February 2000 |
| #19 and 65 | 2 | 2 | 0 | 0 | 0.32 and 4 March 2000 |
| #38 and 76 | 4 | 2 | 1 | 1 | 0.31 and 21 March 2000 |
| #9 and 63 | 4 | 0 | 3 | 1 | 0.30 and 27 March 2000 |
| #39 and 92 | 4 | 4 | 0 | 0 | 0.27 and 6 March 2001 |
| Statistics mean | 4.8 | 3.8 | 0.5 | 0.3 | 0.33 |
| SD | 2.4 | 3.0 | 1.1 | 0.5 | 0.1 |
| Range | 2–9 | 0–9 | 0–3 | 0–1 | 0.22–0.52 |
| <i>n</i> | 8 | 8 | 8 | 2 | 8 |

Table shows maternal snout–vent length (SVL), date of parturition, the numbers of live and stillborn neonates and infertile oocytes, and relative clutch mass (=litter mass divided by maternal postpartum mass).

each comprised four infertile oocytes + one dead neonate. To avoid problems of pseudoreplication, only one clutch from this female (of nine live young) was included in the following analysis. Mean maternal snout–vent length was 77 ± 9.7 cm ($n = 8$) and was not significantly correlated with number of offspring ($r = 0.54$, $P = 0.16$, $df = 6$), total clutch mass ($r = 0.60$, $P = 0.12$, $df = 6$), or mean mass of individual live neonates ($r = -0.60$, $P = 0.16$, $df = 5$).

3.5. Dietary composition and foraging strategy

Of 20 prey items that we identified, 16 (80%) were mammalian (mostly rats, but including pygmy-possums and a Feathertail Glider also: see Table 2). Many of the rats were small, clearly juveniles or subadults, and may have been taken in maternal nests. At least one (18 g) was well below the body size at which these rats first begin to leave their mother's nest to forage independently (Watts and Aslin, 1981). The only other prey types were the agamid lizard *Hypsilurus spinipes* (recorded from two sub-adult snakes) and undetermined lizard scales from two scats. Forest Dragons also have been found as prey in *H. stephensii* from Urbenville

(D. Milledge, pers. commun.) and the Watagans (T. Tasoulis, pers. commun.). Despite our small sample size, the mean snout–vent length of snakes containing lizards was lower than that of snakes containing mammalian prey (mean snout–vent length 55 ± 14.1 cm, $n = 4$, range = 36–70 cm vs 78.89 ± 6.78 cm, $n = 15$, range = 66–88 cm; $F_{1,17} = 24.73$, $P = 0.0001$). The proportion of snakes containing identifiable prey remains was similar in males (11 of 34 = 32%) and females (8 of 31 = 26%; $\chi^2 = 0.10$, $df = 1$, $P = 0.76$).

We were unable to observe predation by radio-tracked *H. stephensii*, because the snakes fed infrequently and obtained prey in enclosed cavities or vine tangles in trees or beneath dense sedges (*Lepidosperma clipeicola*). However, our radio-tracking data suggest that these snakes use a range of foraging strategies. Some observations suggest active searching and pursuit of prey:

- (1) A radio-tracked female snake (78 cm snout–vent length, 185 g) was located foraging in cloudy cool conditions at 10:30 h on 5 February 1999 (body temperature 22.1 °C, ambient temperature 20.0 °C). She was stretched out on the trunk of a live Blackbutt (*Eucalyptus pilularis*) 2 m above the ground with

Table 2
Dietary composition of free-ranging Stephen's banded snakes, *Hoplocephalus stephensii*

| Month/number of samples | Prey species | Common name | Number |
|-------------------------|----------------------------|-------------------------------|--------|
| January/1 | <i>Antechinus stuartii</i> | Brown Antechinus | 1 |
| February/4 | <i>Cercartetus nanus</i> | Eastern Pygmy-possum | 2 |
| March/4 | <i>Acrobates pygmaeus</i> | Pygmy Feathertail Glider | 1 |
| April/6 | <i>Rattus fuscipes</i> | Bush Rat | 4 |
| October/1 | <i>Rattus sp.</i> | Rat = most likely Bush Rat | 5 |
| November/1 | <i>Melomys cervinipes</i> | Fawn-footed Mosaic-tailed Rat | 3 |
| December/2 | <i>Hypsilurus spinipes</i> | Forest Dragon | 2 |
| | | Reptile scales | 2 |

Dietary analysis was based on 18 scats, 1 palpation, 1 direct observation, and comes from 16 adult snakes; 11 scats are from 9 radio-tracked snakes. Scat samples were obtained in February (5), March (4), April (6), October (1), November (1) and December (1).

her head and neck unseen in a vertical crevice in the tree. An adult Brown Antechinus (probably *Antechinus stuartii*: a small [to 35 g] dasyurid marsupial) was present on the tree; the snake struck at unseen prey within the crevice and later crawled in.

- (2) Two radio-tracked snakes located while moving through sedges at night were found to have consumed subadult (newly-weaned) bush rats (*Rattus fuscipes*) when collected the following morning.
- (3) We heard repeated alarm calls by rodents on three additional occasions in the near vicinity of radio-tracked snakes found moving through dense ground-layer vegetation with log and sedge tangles at night.
- (4) Nocturnal pursuit of an active frog was observed in the southern part of the species range (C. Slatyer, pers. commun.).

All of the above records suggest active searching, but ambush predation also occurs. For example:

- (1) Radio-tracked snakes frequently sheltered for days or weeks at a time inside the arboreal nests of prey species (e.g., *Melomys*, *Cercartetus*, *Acrobates*: Fitzgerald et al., 2002a).
- (2) Three snakes were observed to increase body mass during these long arboreal sequestration periods, demonstrating that prey are taken in trees by sedentary snakes.

4. Discussion

Our data paint a picture of a large, elongate snake feeding infrequently on a diverse prey range (mostly lizards in juvenile snakes, mammals in adult snakes) using a combination of ambush foraging and active searching. Predation upon newly-weaned rats (*R. fuscipes*) may be an important facet of this species' ecology. Low feeding rates result in snakes in the field being thin, growing slowly and reproducing infrequently; the proximate role of food intake appears to be supported by the observation that well-fed captives put on mass rapidly, gain in body condition, grow rapidly, and subsequently reproduce earlier than their field counterparts. Thus, energy-limitation is a critical aspect of the species' ecology based on the result that snakes from other areas were as slender-bodied at capture as were those at Whian Whian State Forest. A "slow" life-history may have been a feature of the species' ecology over evolutionary time, as evidenced by a low Relative Clutch Mass and large size of neonates, both correlates of taxa with high adult survival rates and low reproductive output (Webb et al., 2002, 2003). Below, we first compare our data with that previously published for this species and its relatives, then consider broader aspects of the life-history traits of *H. stephensii* within the ecological context of its forest habitat.

Our results are broadly consistent with anecdotal information from earlier studies. For example, the mean adult body sizes and magnitude of sexual size dimorphism that we found are similar to those reported by Shine (1983). *H. stephensii* is thus the largest of the three *Hoplocephalus* species, but the direction and degree of sexual size dimorphism are relatively conservative within this genus (Shine, 1994). Among Australian elapid snakes in general, smaller species (and juveniles within larger species) tend to specialise on lizards as prey whereas larger snakes take a higher proportion of mammals (Shine, 1994). *Hoplocephalus* fits this trend well; the smallest taxon (*H. bitorquatus*; mean adult snout–vent length 49.2 cm; Shine, 1994) specialises on frogs (Shine, 1983, 1994), the intermediate-sized *H. bungaroides* (mean adult snout–vent length 55.8 cm; Shine, 1994) eats mostly lizards but with some mammals in adult diets (Webb and Shine, 1998), and the largest taxon (*H. stephensii*; mean adult snout–vent length 74.7 cm) eats mostly mammals but takes lizards during juvenile life (this study). Our data on diet composition support previous reports of a diverse diet in *H. stephensii* (Shine, 1983, 1994); microchiropteran bats may also be taken (Ehmann, 1992), many of which live in tree hollows.

Growth rates of our captive-born neonates suggest that sexual maturation could be attained in about three to four years, similar to the estimate by Shine (1983) from seasonal body-size distributions of museum specimens of *H. bitorquatus*. Differences in feeding rates and body condition however, suggest that growth would be slower in the wild than in captivity (as is often the case: e.g., Foley, 1998). Even at three to four years of age, maturation in our captive *H. stephensii* was later than in other large elapids such as *Pseudonaja nuchalis* (Maryan and Bush, 1996) or *Notechis scutatus* (Fearn, 1993). Mark-recapture studies on the congeneric *H. bungaroides* have reported slow growth and late maturation in this species also, compared to sympatric elapid species (Webb et al., 2003).

Shine's (1983) inference of less-than-annual reproductive frequencies in female *H. stephensii* (based on dissection of museum specimens) is strongly supported by our data. Litter sizes from our study bracket those from previous reports (3–8 in Shine, 1983; a single litter of 8 live + 1 stillborn young by Wells et al., 1988). Neonatal body sizes from our captive-born litters (25 cm snout–vent length) are slightly larger than previous reports (20 cm: Shine, 1983; 20.5 cm: Wells et al., 1988), and larger than those of related taxa with similar adult body sizes. For example, 15 species of Australian elapid snakes have longer mean adult snout–vent lengths than does *H. stephensii*, but mean neonate snout–vent length (this study) is greater in only four species (Shine, 1994). In combination with the large relative head size in this species, the large neonatal size means that some newborn snakes are capable of ingest-

ing “pinkie” mice as their first meal (M. Fitzgerald, pers. obs.). Few Australian elapids can do this, relying instead on ectothermic prey for the first few months or years of their life (Maryan and Bush, 1996; M. Fitzgerald, pers. obs.).

Mean adult body size is a primary determinant of many facets of a species’ ecology (Gaston and Blackburn, 1996; Richman et al., 1988), and Australian snakes show many tight linkages between body size and traits such as diets and reproductive biology (Shine, 1994; Greer and Shine, 2000). Thus, the large body size of *H. stephensii* has strong implications for its life-history. This species ranks among the largest (longest) 25% of Australian elapids in terms of mean adult snout–vent length. Size may be important for arboreality, because a longer body facilitates climbing by allowing the snakes to bridge gaps between successive points of contact. In keeping with this interpretation, most arboreal snakes are relatively long (e.g., Henderson and Binder, 1980; Lillywhite and Henderson, 1993; Spawls and Branch, 1995), and arboreal taxa of three families (*Morelia*, *Hoplocephalus*, *Tropidechis*, *Boiga*, *Dendrelaphis*) within the snake fauna of our study site (Whian Whian State Forest) attain greater body lengths than do the majority of terrestrial species (e.g., *Cryptophis*, *Cacophis*, *Hemiaspis*, *Ramphotyphlops*).

Large body size is a two-edged sword, however. Although it facilitates arboreality (and thus provides access to secure shelters and arboreal prey), it also increases metabolic costs. Based on relationships between size and diet in other Australian elapid snakes (Shine, 1994), adult *H. stephensii* are too large to subsist on lizards. Although Bush Rats (*R. fuscipes*) are abundant in Whian Whian State Forest, they may be difficult to capture and to subdue, and adult rats are too large for even the largest *H. stephensii* to physically ingest. Adult *R. fuscipes* weigh up to 225 g (Lunney, 1995), whereas our captive snakes are unable to swallow a rodent >50 g (M. Fitzgerald, pers. obs.). Because other small mammal species are less abundant at Whian Whian State Forest than *R. fuscipes*, *H. stephensii* may be forced to specialise on sub-adult, (and thus, ingestible-sized) rats. These animals are available only following breeding in late spring and summer (Watts and Aslin, 1981) and only when climatic conditions are favourable (Lunney, 1995), thus substantially reducing foraging opportunities for the snakes. Bush Rat populations are also adversely influenced by fire (Lunney, 1995) and by a combination of fire and grazing (Tasker, 2002). In grazed and burnt sites, periodic local extinction and recolonisation of Bush Rats may occur. Cool conditions at foraging times may further reduce snake foraging success.

Reliance upon restricted seasonal “windows” of prey availability, with lower feeding rates through the intervening period, may characterise many ectothermic pre-

dators. Island populations of several snake taxa exploit brief seasonal availability of migratory birds (e.g., *Bothrops insularis*, Duarte et al., 1995; *Gloydus shedaoensis*, Sun et al., 2002). Adult tiger snakes (*Notechis scutatus*) on islands off southern Australia feed exclusively on the chicks of seabirds, ingestible only briefly because their high growth rates post-hatching soon render them too large to swallow (Worrell, 1966; Schwaner, 1985). Similarly, newly-hatched water pythons (*Liasis fuscus*) in tropical Australia are too small to ingest adult rats, and the juvenile snakes starve in years when juvenile rats are not available (Madsen and Shine, 2002). We suggest that *H. stephensii* ecology is influenced by a similar seasonal window of feeding opportunity.

The low temperatures and low and seasonal prey availability of Whian Whian State Forest may be responsible for a series of the distinctive traits of *H. stephensii*, both as direct proximate effects and as evolutionary pressures:

- (1) *Morphology* – a long slender body with a large head, maximising arboreal performance and ingestion of large prey but reducing metabolic costs.
- (2) *Spatial ecology* – large home ranges (to 40 ha) give access to thinly-spread prey resources, and frequent periods of inactivity (Fitzgerald et al., 2002b) further reduce metabolic costs and exposure to predators.
- (3) *Diet composition and foraging tactics* – these snakes appear to be generalist, opportunist feeders that consume prey either by active searching or ambush, and in the trees as well as on the ground.
- (4) *Low rates of growth and reproduction* – observations of captive snakes suggest that these low rates are direct proximate responses to low food availability.

However, the low relative clutch mass and large neonatal size of *H. stephensii* may represent evolutionary responses to low and stochastic prey availability, generating selection to maximise survival rates (of neonates as well as adults) rather than high reproductive output. The end result has been a distinctive constellation of traits that has ultimately reduced the ability of this taxon to persist in the face of additional mortality sources, and thus has made *H. stephensii* vulnerable to anthropogenic habitat alterations.

Therefore, conservation effort should be directed to areas where suitable ecological parameters prevail, and to ameliorating processes that adversely affect prey availability. Stephen’s banded snakes are unlikely to be conserved in fragmented remnant or regenerating forests. Populations present in larger forest blocks are seldom likely to produce surplus recruits to colonise ‘new’ areas or to replace adults lost through disturbance processes. Ongoing disturbances (logging, fire, grazing) throughout the species’ range in New South Wales are likely to directly affect the snake

and its prey species. Loss of adults through anthropogenic sources of mortality (e.g., logging, reduction of obligatory shelter sites by fire, firewood collection and by roadkills) is potentially of critical importance at the population scale, because of the species low reproductive rate and thus slow and inelastic capacity to recover from disturbance.

All three species within the genus *Hoplocephalus* exhibit similar life history patterns, and all are listed as threatened in New South Wales under the *Threatened Species Conservation Act* 1995. Our study suggests that this kind of life-history has evolved in response to a suite of ecological and evolutionary circumstances within eastern Australian forests. A broad correlational analysis by Reed and Shine (2002) identified ambush-foraging elapid snakes as particularly vulnerable to anthropogenic habitat change, and suggested two possible pathways for such an effect: (1) reliance on terrestrial ambush sites with specific types of ground cover that are disrupted by anthropogenic activities, and (2) “slow” life-history traits. The threatened status of the highly arboreal *H. stephensii* is consistent with the latter but not the former hypothesis, reinforcing the idea that the “slow” energy-limited life history patterns of the three *Hoplocephalus* species render them vulnerable to the scale and rate of contemporary disturbance processes.

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