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Why don't small snakes bask? Juvenile broad-headed snakes trade thermal benefits for safety

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Previous studies have suggested that most small Australian elapid snakes are nocturnal and rarely bask in the open because of the risk of predation by diurnal predatory birds. Because the physiology and behaviour of reptiles is temperature dependent, staying in refuges by day can entail high thermoregulatory costs, particularly for juveniles that must grow rapidly to maximise their chances of survival. We investigated whether the risk of predation deters juveniles of the endangered broad-headed snake (*Hoplocephalus bungaroides*) from basking, and if so, whether there are thermal costs associated with refuge use. To estimate avian attack rates on snakes, we placed 900 plasticine snake replicas in sunny locations and underneath small stones on three sandstone plateaus for 72 h. At the same time we quantified the thermal benefits of basking vs refuge use. On sunny days, juveniles could maintain preferred body temperatures for 4.7 h by basking but only for 2.0 h if they remained inside refuges. Our predation experiment showed that basking has high costs for juvenile snakes. Predators attacked a significantly higher proportion of exposed models (13.3%) than models under rocks (1.6%). Birds were the major predators of exposed models (75% of attacks), and avian predation did not vary across the landscape. By trading heat for safety, juvenile *H. bungaroides* decreased the potential time period that they could maintain preferred body temperatures by 57%. Thermal costs of refuge use may therefore contribute to the slow growth and late maturation of this endangered species. Our results support the hypothesis that nocturnal activity in elapid snakes has evolved to minimise the risk of avian predation.

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Most animals modify their behaviour and reduce their activity levels in the presence of predators (Lima and Dill 1990). One widely used predator avoidance strategy is to avoid activity during time periods when predators are most active. For example, freshwater and oceanic zooplankton often migrate vertically at night to avoid fish predators (Gliwicz 1986, Hays 1995). In several groups of mammals and insects, predation risk from diurnal birds may prevent activity during daylight hours (Speakman 1995, Halle 2000). For example, most species of insectivorous bats hunt during the night, even though prey abundance is much higher during the day (Rydell and Speakman 1995, Rydell et al. 1996). Although it is plausible, the predation-risk hypothesis is difficult to test because predation is rarely observed in nature, and most nocturnal organisms show little variation in their activity patterns. Ideally, to determine whether predation risk constrains diurnal activity, we need to study nocturnal species with plastic activity patterns, in systems where alternative hypotheses can be tested simultaneously (Speakman and Rydell 2000).

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Australian snakes in the family Elapidae are good model organisms for investigating whether predation risk constrains diurnal activity. Of the 75 species of Australian elapids, most small-bodied species are crepuscular or nocturnal, and only the largest species are strictly diurnal (Greer 1997). Because the risk of predation in reptiles is size-dependent (Ferguson and Fox 1984, Forsman 1993), small elapids may have responded to predation risk by avoiding activity during daylight hours (Shine 1991, Greer 1997). Most small elapids rarely bask in the open, but spend the day sequestered in refuges (Shine 1991). Staying within a refuge can minimise the risk of predation, but it entails several costs, including lost opportunities for foraging, reproduction, and thermoregulation (Lima and Dill 1990, Martin and Lopez 1999a, b). Because the behavioural and physiological processes of reptiles are temperature dependent (Huey 1982), juveniles that spend long time periods in thermally suboptimal refuges could suffer significant decreases in energy assimilation, growth rates and future survival (Martin and Lopez 1999a, b). In viviparous snakes from temperate climates, neonates are born in late summer and early autumn. Thus, the physiological costs of refuge use will be most important for juveniles during autumn, when neonates begin feeding (Greer 1997). Previous studies on snakes show that food intake early in life can dramatically influence subsequent survival, growth rates, and body sizes (Forsman 1993, Madsen and Shine 2000). Even in species that hibernate, energy assimilated during autumn may influence lipid reserves, which in turn can influence over-winter survival (Bauwens 1981, Martin 1992). Clearly, the decision to bask or shelter in refuges can have important consequences for juvenile snakes.

Theory suggests that reptiles should only bask when the benefits of thermoregulation outweigh the costs associated with this activity (Huey and Slatkin 1976). There are obvious benefits of thermoregulation for juvenile snakes. Individuals that thermoregulate for long time periods can grow faster, and because body size limits the size of prey that can be ingested, faster growing individuals have higher survival rates than smaller conspecifics (Forsman 1993). Nonetheless, juveniles may not bask if they can thermoregulate for long time periods within refuges (there are no additional benefits of basking), or if the movements associated with basking (e.g. tracking small sunlit patches in a shaded forest) increases the risk of predation (basking has high costs, Huey and Slatkin 1976). Thus, to understand whether avian predation risk constrains basking in snakes, it is necessary to estimate both environmental and predator-imposed constraints on thermoregulation – two factors that are rarely investigated simultaneously in a single study (Huey et al. 1989).

We investigated whether predation risk constrains thermoregulation in the nocturnal broad-headed snake *Hoplocephalus bungaroides*. This species displays size-dependent activity patterns: juveniles rarely bask or move by day, whereas some adults are active by day and bask in the open (Webb and Shine 1998a). We tested the hypothesis that juvenile *H. bungaroides* forgo basking because it increases the risk of avian predation. Our approach was twofold. First, we measured the snakes' thermal environment (underneath rocks and in the open), to quantify the additional physiological benefits that juveniles would gain by basking beside refuges. Because predation on juvenile snakes is rarely observed, even in long term field studies (Lourdais et al. 2002), we placed plasticine snake replicas in exposed locations to estimate the frequency of avian predation. Although it seems obvious that stones should protect snakes from avian predators, at our study sites we have witnessed superb lyrebirds (*Menura novaehollandiae*) turning stones in search of prey. This chicken-sized bird forages intensively by raking leaf litter and turning cover items (logs, bark and rocks), and because it can turn stones up to 2 kg in mass (Adamson et al. 1983) it may also prey on juvenile snakes. Thus, to estimate the frequency of lyrebird predation on inactive snakes, we also placed snake replicas under small rocks. To determine whether avian attack rates on snakes varied across the landscape, we replicated our experiment on three sandstone plateaus where the broad-headed snake occurs.

Methods

Study species

The endangered broad-headed snake *Hoplocephalus bungaroides* is a small (<90 cm total length), viviparous, nocturnal elapid that is restricted to sandstone habitats within a 250 km radius of Sydney, NSW, Australia (Shine et al. 1998). The study population in Morton National Park, 160 km south of Sydney, has been the subject of a long term (1992–present) mark–recapture study (Webb et al. 2003). Neonates are born in late March and shelter under small stones during autumn, winter and spring. Juveniles (<2 yr old) have lower survival (54.7%) than adults (81.6%, Webb et al. 2002). During a three-year mark–recapture and radio-telemetry study, only adult snakes were observed moving by day or basking in the open (Webb and Shine 1997, 1998a). In laboratory thermal gradients free of constraints, the snakes' mean preferred body temperature (T_p) is 29.1°C, while their T_p range (temperatures bounded by the upper and lower quartiles of T_p) is 28.1–31.1°C. In the laboratory, strike speed, prey-capture success, anti-predator behaviours and locomotor performance of *H. bungaroides* are maximised at 30°C

(Webb and Shine 1998a, Llewelyn 2003), and like most reptiles, their peak physiological performance probably also occurs within the T_p range (Huey 1982).

Temperatures available to snakes under rocks and in the open

To measure environmental temperatures available to snakes (Bakken 1992), we placed miniature temperature loggers (thermochron iButton, Dallas Semiconductor, Dallas, USA; diameter 15 mm, height 6 mm) underneath 20 rocks within the size range of rocks used by juveniles (<150 mm thick) during autumn. Rock temperatures closely approximate the body temperatures (T_bs) of snakes sheltering underneath them ($r^2 = 0.96$, $n = 5$ snakes, Webb and Shine 1998a,b). Because snakes have access to both shaded and exposed rocks (Pringle et al. 2003), we measured rock temperatures at an exposed area 5 m from the cliffs and at a heavily shaded area 30 m from the cliffs, at a study site where there is long term data on snake demography. Because rock thickness can influence rock temperatures (Huey et al. 1989), we selected 10 pairs of rocks (each pair was similar in size and thickness) and placed half of these rocks at the exposed site and half at the shaded site. At both locations, the physical dimensions of rocks ranged from 115–585 mm long, 16–100 mm thick, and 0.2–25.0 kg in mass. At each location, we glued a thermochron to the middle underside of each rock, and placed the rocks flush onto a flat 3 × 3 m area of rock substratum. All thermochrons recorded the temperature at 15 min intervals over three days (30 March 2003–1 April 2003). To estimate T_bs of basking snakes, we placed 5 copper models (220 mm long, 8 mm diameter, painted black, with thermocouple suspended in the middle and with sealed ends, and with flattened ventral surface to maximise contact with the substrate) connected to data loggers (Hobotemp, Onset Corporation, USA) beside five rocks at the exposed location. We placed each model flush onto the rock substrate along a north–south axis in the open so it would receive direct sun during daylight hours. A previous study confirmed that exposed black copper models accurately estimated T_bs of basking broad-headed snakes (Webb and Shine 1998a).

Using the thermal data from exposed rocks ($n = 10$) and copper models ($n = 5$), we calculated the cumulative time that snakes could potentially spend in their T_p range during the 24 h day by remaining hidden underneath rocks or by behaviourally thermoregulating (i.e. basking beside rocks in the morning and shuttling between rocks and sun later in the day). We did this for each of the three days that our plasticine snake replicas were exposed to potential predators in the field. We used a repeated-measures ANOVA to compare the potential time that basking and non-basking snakes could spend in their T_p range during the two sunny days of the study (30 March 2003 and 1 April 2003).

Plasticine snake replicas and location of experimental transects

We made snake replicas from black plasticine (Rainbow modelling clay, Newbound Pty Ltd, Rydalmere, NSW). The plasticine was pre-packaged in 500 g blocks, separable into individual pieces (5 mm in diameter), closely approximating the dimensions of a juvenile *H. bungaroides*. We made all models 275 mm long, the average total length of a hatchling broad-headed snake (Webb et al. 2003). For each model, we smoothed out any inconsistencies in the plasticine, expanded one end to resemble a snake's head, and tapered the opposite end to resemble a tail (Fig. 1).

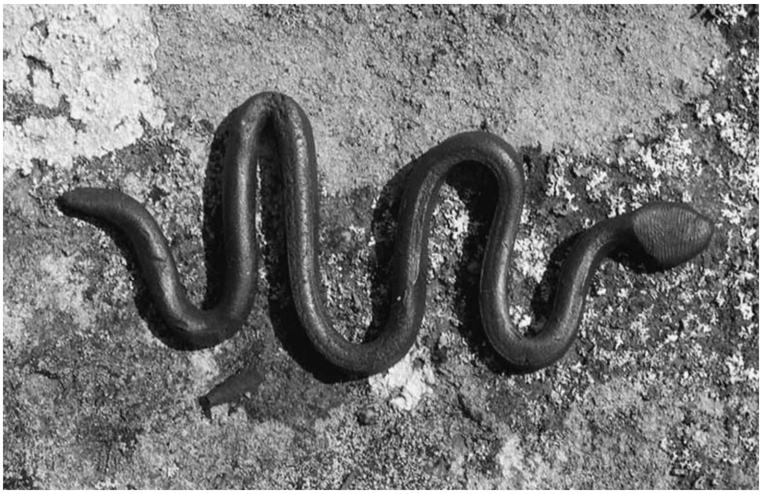

Fig. 1. Black plasticine replica of a juvenile broad-headed snake *Hoplocephalus bungaroides*. All replicas were approximately 275 mm long, the mean total length of a hatchling *H. bungaroides*, and had a well-defined head and a narrow tapering tail.

To investigate whether avian predation risk varied across the landscape, we selected three geographically isolated plateaus (approx. 2.5 km apart) where *H. bungaroides* occurs. At each plateau, we selected three sites (all >450 m apart) to ensure adequate spatial replication. On each site, we walked a 500 m transect parallel to the cliffs, keeping within 50 m of the cliffs to ensure that models were placed in habitats favoured by *H. bungaroides* (open areas of bare rock). Thus, experimental transects were not straight, but deviated depending on the local geology of the site. On each transect we drew straws to determine the placement of the first model (underneath a rock versus exposed), and thereafter we randomly selected models from a box and placed them at 5 m intervals in alternate sequence. A total of 100 models were placed on each transect, 50 in exposed locations on bare rock (to simulate basking snakes) and 50 hidden beneath small rocks lying flush on rock substrates (to simulate non-basking snakes). We positioned all models in an identical S-shape and firmly pressed them onto the rock substrate (Fig. 1). For hidden models, we randomly selected flat stones large enough to conceal a small snake (mean diameter = 158 mm, range 85–260 mm, mean thickness = 32 mm, range 10–70 mm, sub-sample of 112 rocks). We placed 900 models in the field between 28 and 30 March 2003, and scored them after 72 h.

We filmed each model with predation marks with a digital video camera, and retained a subset of models with identical imprints for later comparison with marks made by known predators. The location of predation imprints on the snake replica (head, mid-body and tail) was also recorded. Published species lists for Morton National Park (Fox 1988) were used to determine the predatory mammals likely to occur on the study sites, and predation marks on plasticine replicas were compared with the imprints left by skulls of these species.

Results

Thermal environment available to snakes

Temperatures underneath rocks showed significant diel and temporal variation (Fig. 2). On overcast days temperatures under rocks showed little variation, whereas during fine, sunny days rock temperatures were highest between 1500 and 1700 h (Fig. 2). Shaded rocks were significantly cooler than exposed rocks (repeated-measure ANOVAs: mean temperature as dependent variable, exposure $F_{1,17} = 66.91$, $p < 0.0001$, time $F_{2,34} = 334.90$, $p < 0.0001$, time × exposure $F_{2,34} = 31.31$, $p < 0.0001$; for maximum temperature, exposure $F_{1,17} = 38.52$, $p < 0.0001$, time $F_{2,34} = 257.25$, $p < 0.0001$, time × exposure $F_{2,34} = 10.80$, $p < 0.001$; Fig. 2). The physical characteristics of rocks (size, thickness, or mass) did not influence mean or maximum temperatures underneath shaded rocks (all correlations were non-significant), but there were significant negative correlations between rock thickness and maximum temperatures underneath exposed rocks (day 1, $r^2 = 0.74$, $p = 0.003$; day 2, $r^2 = 0.90$, $p = 0.003$; day 3: $r^2 = 0.77$, $p = 0.01$, $n = 10$ rocks).

Temperatures under shaded rocks never reached the snake's T_p range, whereas temperatures underneath exposed rocks were within the T_p range on two of the three days of the thermal study (Fig. 2). Thermoregulatory behaviour (basking versus not basking) significantly influenced the time that snakes could potentially spend within their T_p range (repeated measures ANOVA: thermoregulatory behaviour, $F_{1,13} = 72.6$, $p < 0.001$; time, $F_{1,13} = 8.51$, $p = 0.01$, behaviour × time, $F_{1,13} = 3.39$, $p = 0.09$). On sunny days, basking snakes could attain preferred body temperatures for significantly

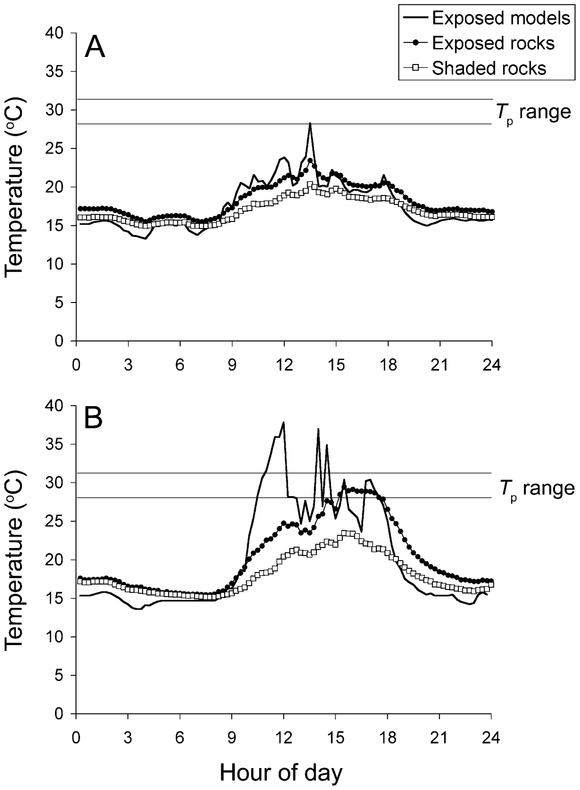

Fig. 2. Temperatures available to juvenile broad-headed snakes *Hoplocephalus bungaroides* during autumn in exposed locations and underneath exposed and shaded rocks of similar size (115–585 mm long) and thickness (16–100 mm thick). The two horizontal lines show the snake's preferred body temperature (T_p) range in a thermal gradient. The ability of snakes to achieve body temperatures within their T_p range depends on the snake's choice of retreat site, their behaviour (basking versus non-basking), and local weather conditions. During cold overcast days (A), snakes could not achieve T_ps in any habitat. By contrast, on fine sunny days (B), snakes could potentially achieve T_ps for up to 5.7 h by basking in the morning and sheltering under rocks in the afternoon.

longer time-periods than non-basking snakes (means of 4.7 vs 2.0 h respectively).

Predation on snake models

Bird attacks on plasticine replicas were identifiable by the presence of a pair of V- or U-shaped marks on opposite sides of the replica (Fig. 3a, b). Most birds attacked the head or tail region of the replicas, and the head often bore multiple stab wounds (Fig. 3c). In some cases, birds had torn the replicas in two or had displaced them several metres. Potential snake predators that were observed on the study sites included pied currawongs (*Strepera graculina*), kookaburras (*Dacelo gigas*), superb lyrebirds (*Menura novaehollandiae*), whistling kites (*Milvus sphenurus*) and brown falcons (*Falco subniger*). However, we could not assign particular beak marks to any of these species because of the similarity in beak sizes among some species. Mammal predatory attempts on plasticine models were characterised by the presence of a pair of incisor marks on the dorsal surface (Fig. 3d, e) or by the presence of multiple tooth marks (Fig. 3f).

We recorded 60 predatory attacks on exposed models and 7 on models under small rocks. Predators attacked significantly higher numbers of exposed models than models under rocks (two factor ANOVA, $F_{1,12} = 49.28$, $p < 0.001$), and this pattern was consistent across the three sandstone plateaus ($F_{1,12} = 0.33$, $p = 0.72$; plateau × exposure: $F_{2,12} = 0.23$, $p = 0.80$, Fig. 4). Birds were the major predators of exposed models (75.0% of attacks), followed by mammals (16.7%) and unidentified predators (8.3%). Of 7 models hidden under rocks, five were attacked by the small dasyurid marsupial *Antechinus agilis*, one was attacked by a superb lyrebird (*Menura novaehollandiae*) that had displaced the rock, and one was bitten by a native bush rat *Rattus fuscipes*. The models that *A. agilis* attacked had been pulled out from underneath the rock, bitten multiple times on the head, neck and mid-body, and torn into multiple pieces. In all of these attacks, the models were visible to a predator foraging at ground level because there were spaces (25–30 mm) under the rocks.

Discussion

Previous long term studies on temperate snake species have reported that juveniles are secretive and rarely bask during the day (Webb and Shine 1998b, Madsen et al. 1999, Lourdais et al. 2002). Why do juveniles forgo basking? Juvenile snakes may not bask because of a high risk of avian predation, or because there are no additional thermal benefits gained from basking (i.e. juveniles can thermoregulate inside their refuges). Clearly, the net benefits of thermoregulation will vary with season, habitat, and the species in question (Huey and Slatkin 1976), so that the question of why juvenile snakes are cryptic must be framed within an ecological and seasonal context. Most obviously, during summer, juveniles of most temperate snake species can thermoregulate for long periods under cover (Peterson et al. 1993), and there are no additional thermal benefits gained from basking. By contrast, during autumn, when our study was carried out, temperatures are cooler, and juveniles of species that feed year-round (as does *H. bungaroides*, Webb and Shine 1998c) could benefit from basking and maintaining preferred body temperatures for long periods (below).

Our thermal data show that juvenile broad-headed snakes could increase the time period spent maintaining preferred body temperatures (T_ps) by 135% by basking beside rocks in the morning and retreating underneath them later in the day. Sunny patches were readily available on the exposed rock outcrops, so that there are no energetic costs associated with thermoregulation: juvenile *H. bungaroides* could easily bask by moving

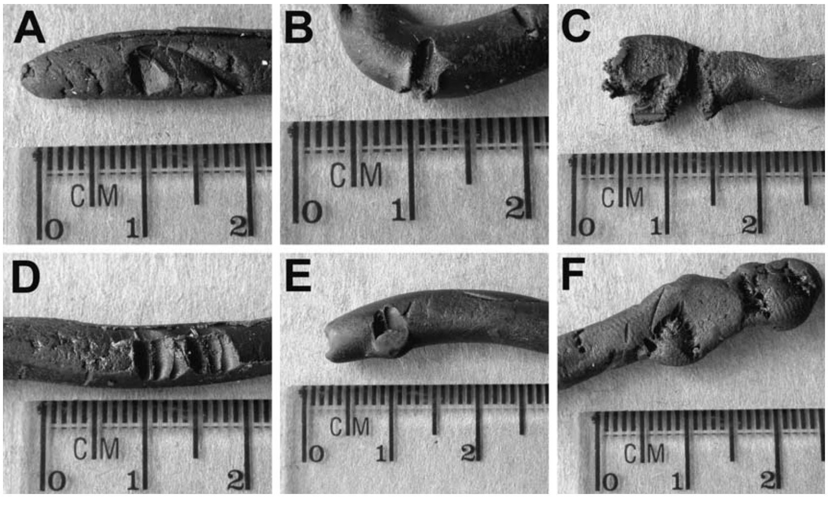

Fig. 3. Photographs of imprints left by predatory attacks on plasticine snake models in the field. Figure shows (A) U-shaped bill mark from a bird; (B) bill mark from a large bird; (C) head of a replica that has been torn apart by a bird; (D and E) incisor marks from a large rodent (probably the native bush rat *Rattus fuscipes*); (F) tooth marks from the dasyurid marsupial *Antechinus agilis*.

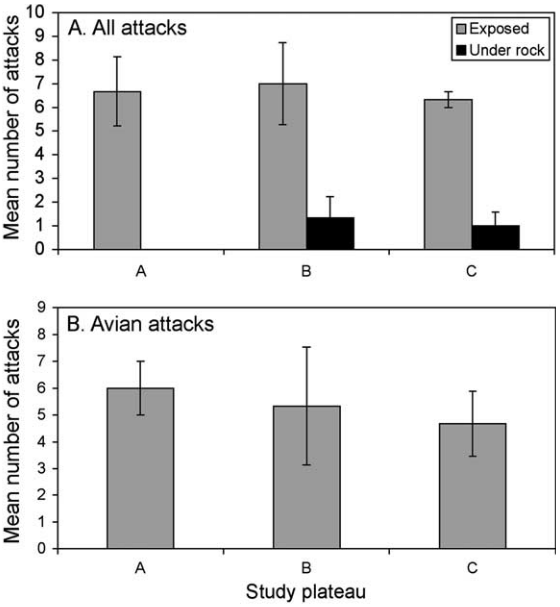

Fig. 4. Variation in predatory attacks on 900 plasticine snake models from nine transects on three geographically isolated sandstone plateaus in Morton National Park, NSW, Australia. Exposed snake models were attacked significantly more often than were models hidden underneath small rocks (A), but the frequency of avian attacks on exposed models was similar across the study plateaus (B).

several centimetres from their refuges. Reptiles that maintain T_ps for longer time-periods can maximise their rates of energy acquisition and can grow faster, mature earlier, and achieve higher reproductive output (Dunham et al. 1989, Autumn and DeNardo 1995, Angilletta 2001). In some snakes, rates of energy assimilation early in life can dramatically influence subsequent survival, growth rates, and body sizes (Forsman 1993, Madsen and Shine 2000). In *H. bungaroides*, juveniles feed throughout autumn and winter (Webb and Shine 1998c), and larger individuals have higher survival rates than do smaller conspecfics (Webb et al. 2002). Clearly, doubling the time period maintaining T_ps would have positive benefits for juvenile *H. bungaroides*, but at a cost: our predation experiment demonstrated that birds attacked exposed plasticine snake models. Thus, a juvenile's best survival strategy is to remain hidden in refuges during the day and thereby trade off thermal benefits for safety.

Sheltering in refuges has important life history and ecological consequences for *H. bungaroides*. Juvenile broad-headed snakes shelter under rocks during autumn, winter and spring (Webb and Shine 1998b), and because they do not bask in the open, they cannot maintain preferred body temperatures for long time periods (Fig. 2). Laboratory studies show that ectotherms that maintain T_ps for longer time periods assimilate more energy, and grow faster than do conspecifics with limited opportunities for thermoregulation (Sinervo and Adolph 1989, Autumn and DeNardo 1995). Moreover, biophysical models of ectotherm life histories predict that a reduction in the time spent maintaining T_ps can cause slow growth and delayed maturity (Adolph and Porter 1996). As predicted, juvenile *H. bungaroides* have slower growth rates, and mature much later in life (at age 6 yr, Webb et al. 2003) than the sympatric, heliothermic elapid snake *Demansia psammophis* that basks in the open (at 2 yr, Shine 1980). However, because the rate of prey capture limits the rate of energy assimilation, the broad-headed snake's reliance on ambush foraging may also contribute to its' slow growth (Webb et al. 2003). Future laboratory and field experiments could investigate whether temperature, prey availability, or genetic factors contribute to the slow growth rates of juveniles (Ford and Seigel 1994, Niewiarowski 2001).

Previous authors have suggested that birds are the primary predators of Australian elapid snakes, but there is little quantitative data on the frequency of avian predation for most species (Greer 1997). In our study, birds attacked 10% of black plasticine snake replicas during a 72 h period in autumn. However, because we used plasticine snake models that are immobile, we may have overestimated the true frequency of avian predation on juvenile snakes. Nonetheless, we believe that our results are biologically relevant for three reasons. First, our estimate of avian predation is similar to that reported by Brodie (1993) for brown replicas placed in tropical rainforests in Costa Rica (16%) for 72 h. The fact that birds from both studies attacked the head or tail regions of the replicas (Fig. 3c) suggests that they treated the replicas as if they were real snakes (Smith 1973, Brodie 1993) and were not merely 'tasting' the plasticine as some rodents do (Madsen 1987). Second, broad-headed snakes use crypsis to avoid detection, so that plasticine models may provide reasonable estimates of attack rates on immobile snakes. Third, the plasticine replica technique controls for variation in snake anti-predator behaviour that result from differences in body temperatures that could influence the outcome of an avian attack (Christian and Tracy 1981).

Previous studies on retreat-site selection have emphasised that reptiles should choose retreats that allow them to maintain T_ps for long time periods (Huey et al. 1989, Webb and Shine 1998b, Pringle et al. 2003). Our results suggest that predation risk also influences retreat-site selection by *H. bungaroides*. Although it seems obvious that stones should protect snakes from bird attacks, our most interesting finding was that several predators (including the superb lyrebird) attacked plasticine snake replicas hidden under stones, albeit at much lower frequencies (1.6 vs 13.3%) than replicas in the open (Fig. 4a). On several transects, sandstone antechinus (*A. agilis*) attacked plasticine snake replicas hidden under small stones with wide crevices. *Antechinus agilis* are generalist predators that eat lizards and snakes (Strahan 1983), and this species may be an important predator of juvenile *H. bungaroides*. Likewise, the superb lyrebird *Menura novaehollandiae,* a chicken-sized bird that forages by raking litter and overturning rocks, may also be an important snake predator. Although lyrebird predation on snake models was rare in this 72 h study, during a longer six-week study lyrebirds displaced 7.1% of small stones on our transects and attacked 40% of snake models under disturbed rocks (J. K. Webb and M. J. Whiting, unpubl.). Thus, the risk of predation may not only exert strong selection on snakes to avoid basking, but also to avoid rocks with large crevices or small rocks that are easily overturned or that do not fully conceal them from predators.

In summary, our field results suggest that juvenile broad-headed snakes do not bask during autumn because of the high risk of avian predation associated with this activity. More generally, our results support the hypothesis that the risk of diurnal avian predation has shaped the activity patterns of Australian elapid snakes (Shine 1991, Greer 1997). Indeed, of the 75 species of Australian elapid snakes, only the larger bodied species are strictly diurnal, whereas most small bodied species are nocturnal or crepuscular (Greer 1997). Thus, predation risk imposed by diurnal birds may not only have selected against activity during daylight hours in some groups of mammals and insects (Speakman 1995, Halle 2000), but also in some of the world's most successful predators – the snakes.

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