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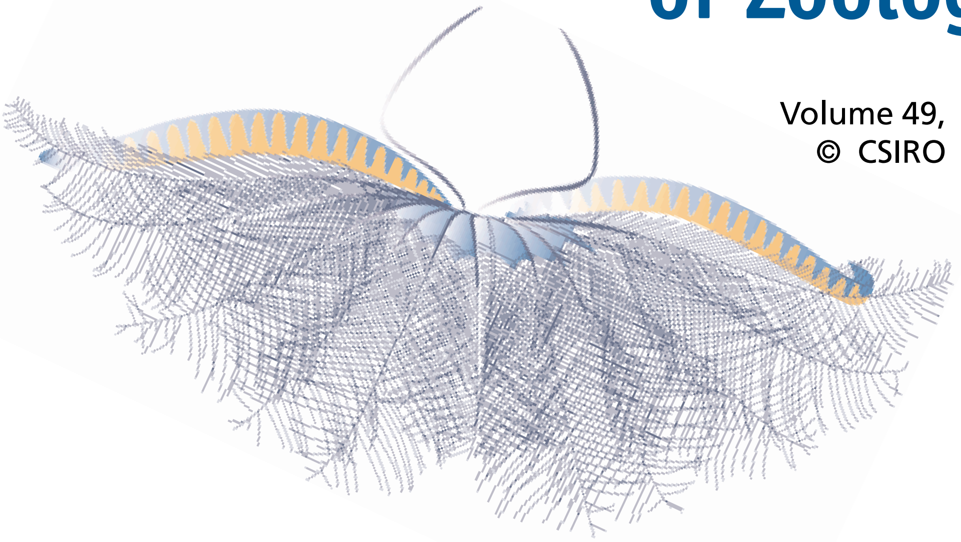
Volume 49, 2001



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Australian Journal of Zoology, 2001, **49**, 223–233

Activity times and body temperature in Australian copperheads (Serpentes : Elapidae)

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Abstract

Local climatic conditions influence the way in which ectotherms regulate their body temperature and activity. We examined correlations between local climatic conditions, body temperature and activity in adult, basking lowland copperheads (*Austrelaps superbus*) from two localities (warm-temperate *versus* cool-temperate) in south-eastern Australia. We also collected data from highland copperheads (*Austrelaps ramsayi*) at a locality with cold-temperate climate. We found that across the active season, mean body temperatures were similar among localities (approximately 27°C) irrespective of species. In contrast, activity times differed. Cool-temperate *A. superbus* emerged earlier in spring and in the morning and retreated earlier in the evening and in autumn than their conspecifics from the warm-temperate locality. Spring emergence was correlated with yearly fluctuations in thermal conditions, suggesting that activity times depend on environmental temperatures. Predator–prey interactions influenced body temperature and activity to some extent in spring when warm-temperate *A. superbus* with relatively low body temperatures (as low as 18.5°C) were captured around ponds in which they had been foraging for frogs. *Austrelaps ramsayi* from the cold-temperate locality not only displayed a later emergence in spring and reduced daily activity times compared with warm and cool-temperate *A. superbus* but also compared with *A. ramsayi*, as reported from a warmer locality in eastern Australia. These data indicate that activity times vary on a geographic basis while snake body temperatures largely remain inflexible. The surprising exception was that cold-temperate *A. ramsayi* retreated later in autumn than cool-temperate *A. superbus*, and at that time they showed body temperatures as low as 12.5°C, well below those we had recorded for *A. superbus*. We suggest that *A. ramsayi* retreat later in autumn because they need to extend their reproductive season and that this is mediated via adaptive changes in the critical minimum body temperature, as has been reported for other snakes.

Introduction

Local climatic conditions influence the way in which ectotherms regulate their body temperature and activity. At one extreme (i.e. in deserts), high environmental temperatures limit the time that ectotherms can stay actively on the surface without the risk of overheating. This affects daily activity times and resource utilisation and can lead to small energy budgets and slow growth (Beaupre 1995*a*, 1996; Bradshaw 1997). At the other extreme (i.e. in high-latitude and high-altitude environments), low environmental temperatures restrict the time of surface activity because it is rarely warm enough to reach a preferred body temperature. As a consequence, ectotherms in cold environments often experience short annual and daily activity periods, slow growth rates, and long intervals between reproductive events (Atkinson 1994; Partridge and French 1996; Rohr 1997).

Despite these examples, ectotherms are by no means restricted to passive responses to local climatic conditions. For example, many lizards and turtles inhabiting high-altitude environments display lower field body temperatures than at lower altitudes (e.g. Van Damme *et al.* 1989; Ellner and Karasov 1993; Hertz *et al.* 1993; Mathies and Andrews 1995). In this way they can avoid a reduction in their daily and annual activity times (Christian *et al.* 1983), thus reducing or ameliorating the negative effects of reduced activity on energy budgets (Ellner and Karasov 1993; Sinervo and Adolph 1994; Adolph and Porter 1996).

10.1071/ZO01018 0004-959X/01/030223

The evidence we have so far for snakes is that behavioural variation is common among snakes that inhabit climatically different habitats. In particular, there are many examples in which snakes that inhabit high-latitude and high-altitude environments are active for shorter periods during the day or active season and where they shift basking to relatively open habitats compared with snakes in low-latitude and low-altitude environments (Klauber 1972; Gregory 1984; Blem and Blem 1990; Brown 1992; Martin 1992, 1993; Sexton *et al.* 1992; see also Beaupre 1995*b*). At the same time, most studies on snake body temperatures described preferred body temperatures in the field and laboratory of approximately 27–35°C (Duguy 1972; Lillywhite 1980, 1987; Rosen 1991; Beck 1995; Brown and Weatherhead 2000). This could indicate that snakes primarily use behavioural means in order to respond to variation in proximate environmental conditions. However, studies that have examined correlations between body temperature and behaviour in snakes are still scarce. There are few examples of Australian elapid snakes (Shine 1977*a*, 1977*b*, 1979; Schwaner 1989; Shine and Lambeck 1990) in which body temperature and activity have been studied in the field (Greer 1997).

We examined correlations between local climatic conditions and behaviour in lowland copperheads (*Austrelaps superbus* Günther 1858), a viviparous and highly venomous elapid snake, in south-eastern Australia. We collected snakes at a locality near sea level in a warm-temperate climate, and at another localtity at 600–750 m above sea level in a cool-temperate climate (at the altitudinal limit of the species' distribution). We also sampled a population of highland copperheads (*Austrelaps ramsayi* Krefft 1964) at a localtity at 800–950 m above sea level in a cold-temperate climate. *A. ramsayi* is regarded as a high-altitude species closely related to *A. superbus*, and reports of sympatry are lacking (Rawlinson 1991). Shine (1977*a*, 1977*b*, 1979) studied field behavioural and ecological traits in a population of *A. ramsayi* in New South Wales; there are no such data for *A. superbus* (Greer 1997).

We collated evidence that the three localities differed in local climatic conditions (temperature and rainfall), which are thought to be the driving force of associations between the thermal quality of the environment and variation in thermoregulatory traits in ectotherms (e.g. Adolph and Porter 1996). We then tested two possible scenarios: (1) the 'constant temperature scenario', in which snakes show similar body temperatures during activity regardless of locality and perhaps species (as a consequence, they incur shorter daily and seasonal activity times as local environmental temperature decreases), or (2) the 'variable temperature scenario', in which snakes show different body temperatures during activity depending on locality and perhaps species (this may lead to snakes in cold environments having similar daily and seasonal activity times as snakes from warm environments). We then compared our data with others available for *A. ramsayi* and discuss evidence that the two species may differ in their behavioural responses to local environmental conditions.

Materials and Methods

Description of the study sites

The three localities were in south-eastern Australia, near Melbourne, Victoria. The low-altitude *A. superbus* population (near sea level) from Western Port was situated in the coastal sunkland of the Western Port catchment (38°13′S, 145°29′E). Sampling was conducted mainly in the vicinity of the township of Koo Wee Rup but also on the outskirts of Pakenham and Tooradin. The other population of *A. superbus*, on the eastern aspect of Mt Disappointment, was located 650–750 m above sea level on the low-altitude plateau and slope country of the Great Dividing Ranges, which rise suddenly from the flat plains extending from the Western Port area (37°25′S, 145°11′E). *A. superbus* is distributed throughout the area separating the two localities, and movement of snakes from the low-lying plains to the forested areas of Mt Disappointment

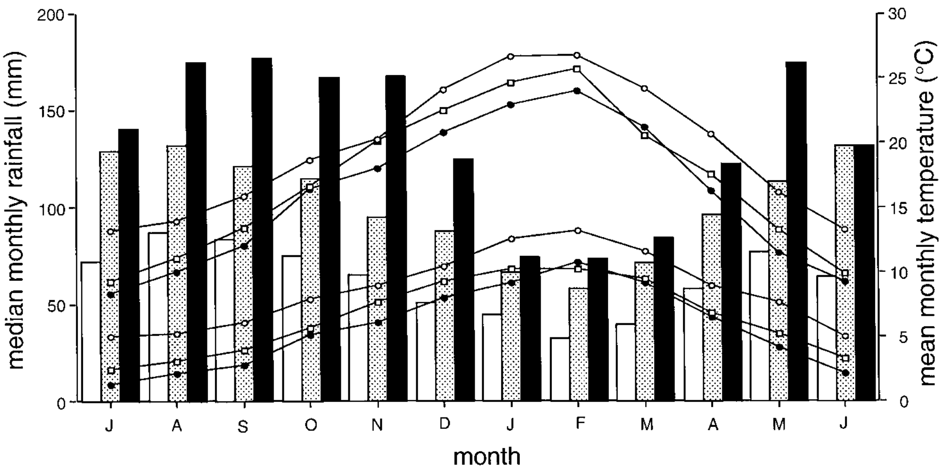

Fig. 1. Long-term rainfall and temperature averages for Western Port (open columns, open circles), Mt Disappointment (dotted columns, open squares) and Mt Baw Baw (solid columns, solid circles). For Western Port, cumulative long-term median rainfall data (1957–96) were recorded by Melbourne Water at Koo Wee Rup, and mean minimum and maximum monthly temperatures (1967–93) by the Bureau of Meteorology, Melbourne, at Frankston, about 25 km west of Koo Wee Rup, at an elevation of 25 m above sea level. Both cumulative median rainfall data (1885–1995) and mean minimum and maximum monthly temperatures (1979–96) were recorded by Melbourne Water in the Wallaby Creek catchment (600 m above sea level). Long-term averages (1942–71) of temperature and rainfall data for the Mt Baw Baw locality were taken from data collected by the Bureau of Meteorology (1988) at Tanjil Bren, approximately 6 km south-east of the study site and 838 m above sea level.

has been recorded (unpublished records). For *A. ramsayi*, a population was sampled about 16 km north-west of Mt Baw Baw (37°46′S, 146°22′E) at 800–950 m above sea level. The high-country environment at this locality is characterised by near-permanent snow cover in winter, and alpine vegetation starts at 1200 m altitude. Aerial distances between the localities are: Western Port to Mt Disappointment 85 km, Western Port to Mt Baw Baw 90 km, Mt Disappointment to Mt Baw Baw 70 km. Approximate areas of the sites sampled at each locality (determined from geographic maps and including all habitat types) were estimated at 0.8 km^2 for Western Port, 14.9 km^2 for Mt Disappointment and 3.5 km^2 for Mt Baw Baw. The three localities differed in terms of rainfall and environmental temperature (Fig. 1), with Western Port being the warmest with the least rainfall, and Mt Baw Baw the coldest with the most rainfall.

Sampling regime and data collection

Main sampling commenced in November 1994 and ended in February 1997. Care was taken to sample all localities in spring, autumn and winter in order to evaluate the length of the active season (the time between emergence in spring and retreat in autumn). For sampling during the active season, it was necessary to bias sampling effort to some extent towards periods of high activity and/or easy catchability in order to obtain sufficient samples with which to conduct a comparison of life-history traits among localities. The same bias applied to some extent to the duration of daily sampling, which was adapted to local and seasonal variation in activity and/or catchability. For example, sampling at Western Port was conducted between 0600 and 2000 hours in summer with a lengthy break during the hottest hours of the day whereas at Mt Baw Baw we sampled continuously between 1000 and 1800 hours in late summer and autumn. At frequent intervals we interrupted such sampling patterns to see whether snakes were detectable at other times. Within localities, we sampled randomly along transects that were determined by the perimeters of natural habitat features such as canals, tracks or forest edges. However, at each visit we also searched for snakes in areas away from the habitat perimeters and made sure that all types of habitat (e.g. swamps, grassland, forest) were sampled.

Sites were searched at a slow walking pace. Snakes were caught by hand or with a pinning stick. Some snakes were discovered under objects such as wooden logs or rocks. Others were retrieved from mammal burrows into which they had escaped. Some 'trapping' (which involved laying out sheets of corrugated iron at selected places at the three study sites) was carried out. At each capture, we noted the date and the time of day. From the 1995/96 field season onwards, we measured the body temperature of each snake with a digital thermometer (Checkmate 2: Hanna Instruments) within 1 min of capture by inserting a temperature probe approximately 5 cm into the cloaca while the snake was restrained head-first in a clear perspex tube. The size of the temperature probe prohibited us from taking measurements from individuals with snout–vent lengths below 400 mm. From the 1995/96 field season onwards, we also measured the ambient air temperature of the capture site in the sun 1 cm above ground. No data on thermal characteristics were collected from specimens if they had been retrieved from burrows or from under corrugated iron sheets.

Statistical analysis

Data were examined for normality (Shapiro–Wilk *W*-tests) and, if necessary, transformed to natural logarithms prior to statistical analysis. For comparative purposes, we grouped data according to locality rather than by species. This enabled us to view the results for *A. ramsayi* in the context of local variation in environmental conditions. Depending on the homogeneity of variances (determined using Bartlett's *F*-tests), we used either analyses of variance (ANOVA) or Kruskal–Wallis non-parametric ANOVAs to compare means and variances among localities. Differences between localities were then evaluated with *post hoc* Tukey–Kramer HSD tests in order to avoid excessive Type II error rates (Zar 1996). In all comparisons we tested for the effects of sex and, where possible, reproductive status (i.e. gravid *v.* non-gravid females) but failed to identify significant effects.

Results

Thermal relationships

Between November 1994 and February 1997, we spent approximately 2432 hours in the field and captured 250 snakes, most of which (90.4%) were adults. Most snakes for which we recorded activity (91%; 150 of 164 individuals) were basking at the time of capture. The ambient environmental temperature at which these snakes were caught (Western Port: mean = 29.5°C ± 0.94 s.e., n = 57; Mt Disappointment: 27.6°C ± 2.26, n = 16; Mt Baw Baw: 24.6°C ± 1.66, n = 34) differed significantly among localities (Kruskal–Wallis ANOVA: χ^2 = 6.54, P = 0.04). *Post hoc* Tukey–Kramer HSD tests showed that *A. ramsayi* basked at significantly lower ambient temperatures than did *A. superbus* from Western Port.

In contrast, mean body temperature at the time of capture did not differ significantly among localities (Kruskal–Wallis ANOVA: χ^2 = 4.64, n = 95, P = 0.10; power test: least significant number, LSN = 113.5), even though that of *A. ramsayi* from Mt Baw Baw was somewhat lower than at the other two localities (Fig. 2). After excluding the six *A. ramsayi* with the lowest body temperatures (which we will argue are associated with a specific basking behaviour in autumn; see below), their mean body temperature was indistinguishable from that of *A. superbus* (Fig. 2). Maximum body temperatures differed little among localities (approximately 33°C), and there were no obvious differences between gravid females, and non-gravid females and males (see Fig. 2).

Within localities, statistical analyses showed no significant differences in body temperature of snakes between climatic seasons (all $P > 0.05$). However, when grouped by month of the active season (Fig. 2) we found that in *A. superbus*, body temperatures in the lower range (18.5–24°C) were prevalent in spring. These snakes were found foraging in ponds for frogs or were basking next to the ponds. They included a gravid female (Fig. 2). There was only one case (at Mt Disappointment) in which body temperature fell close to 15°C (Fig. 2). In contrast, for *A. ramsayi* we recorded the lowest body temperatures in autumn (12.5–17°C) (Fig. 2; this included both males and females). These individuals were basking in front of burrows that they utilised as winter retreats.

Annual and daily activity times

The emergence of copperheads in spring coincided with seasonal changes in temperature. The first to emerge were *A. superbus* from Western Port, followed by *A. superbus* from Mt

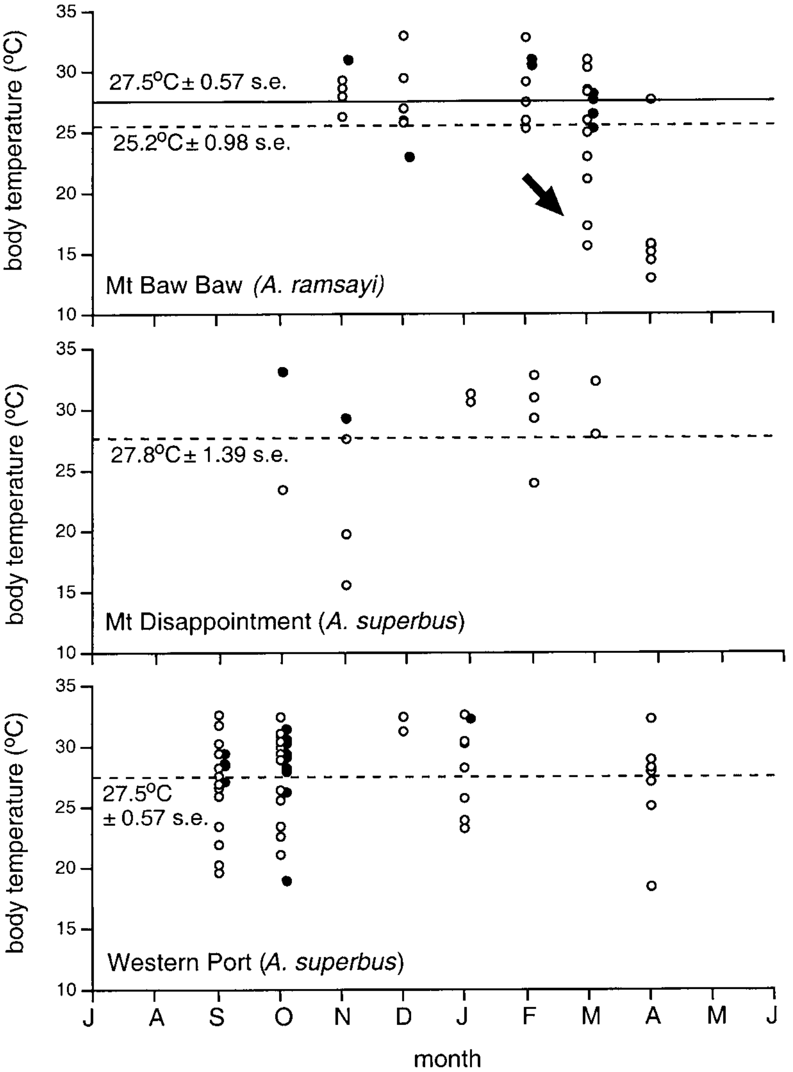

Fig. 2. Field body temperatures of *A. superbus* and *A. ramsayi* at capture, grouped by month and locality. Open circles represent adult males and non-gravid females, and solid circles gravid females. The data points for gravid females from Western Port and Mt Baw Baw are slightly offset to the right to assist in representation. Striated lines represent mean body temperatures of snakes for each locality. The solid line represents the mean for *A. ramsayi* after exclusion of individuals that were basking in unusually cold conditions (see arrow).

Disappointment and then *A. ramsayi* from Mt Baw Baw (Fig. 3). The length of the hibernation period also corresponded to the annual weather patterns, as *A. superbus* from Western Port emerged in August in 1995, which was warmer than the spring of 1996 (unpublished data), when they emerged in September (Fig. 3). A similar pattern was observed for Mt Disappointment, where *A. superbus* emerged in September in 1995, and in October in 1996. At Mt Baw Baw, *A. ramsayi* were first caught in November in both years.

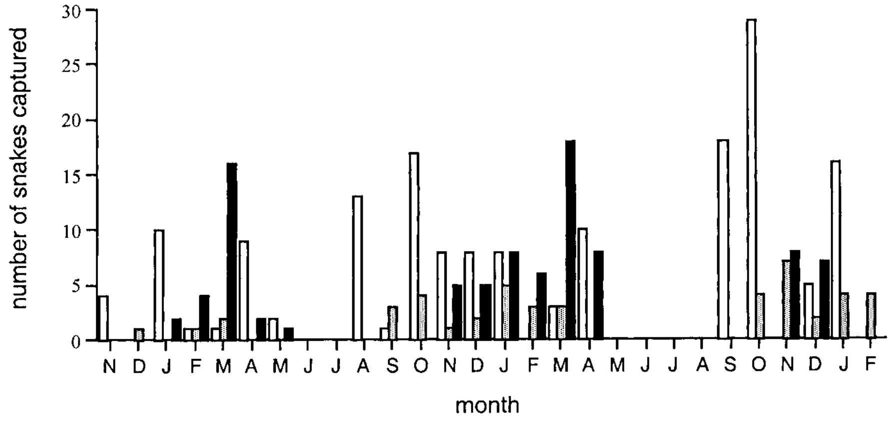

Fig. 3. Monthly capture success for *A. superbus* at Western Port and Mt Disappointment, and *A. ramsayi* at Mt Baw Baw. See Fig. 1 for explanation of symbols. Data commence in November 1994. June and July represent the austral winter, when snakes were inactive at all three localities. Times of retreat in autumn and emergence in spring for each locality can be recognised prior to and after the inactive winter periods.

In autumn, we found a different pattern (Fig. 3). *A. superbus* from Western Port were active until late April or early May, but their conspecifics from Mt Disappointment only until March. At the latter locality, *A. superbus* retreated earlier than tiger snakes (*Notechis scutatus*), which were active until April. Unexpectedly, however, *A. ramsayi* from Mt Baw Baw were still active in late April or early May even though ambient temperatures during this month were colder than at Mt Disappointment (Fig. 3).

Mean capture time during the day differed significantly among localities ($F_{2,164} = 11.75$, $P < 0.001$; Fig. 4). *Post hoc* Tukey–Kramer HSD tests showed that *A. ramsayi* from Mt Baw Baw were captured significantly later in the day than were *A. superbus* from both Western Port and Mt Disappointment. *A. superbus* from Western Port emerged earlier in the day and retreated later than did *A. superbus* from Mt Disappointment, and *A. ramsayi* emerged later and retreated earlier than did *A. superbus* (Fig. 4). We found the same differences when we restricted the analysis to individuals caught in summer (November–February) (ANOVA: $F_{2,70} = 5.19$, $P = 0.008$). Otherwise, climatic season (spring, summer and autumn) influenced only the capture time of *A. ramsayi* at Mt Baw Baw, which were captured significantly earlier in the day in autumn than in spring and summer (Fig. 4).

Discussion

Thermal relationships

For the most part, our data support the 'constant temperature scenario' that involves snakes displaying a similar body temperature, regardless of locality or species, and a corresponding reduction in daily and seasonal activity times as the general climate becomes colder and wetter. We found that mean body temperatures differed little among localities (approximately 27°C), and that the similarities were there irrespective of whether we investigated differences between *A. superbus* from Western Port and Mt Disappointment, or between *A. superbus* and *A. ramsayi*. This agrees with other measurements of body temperature taken from *A. superbus* and *A. ramsayi* (Rawlinson 1974; Shine 1975; Heatwole 1976; Lillywhite 1980) as well as with data for several other species of snakes describing field and preferred laboratory body temperatures of approximately 27–35°C

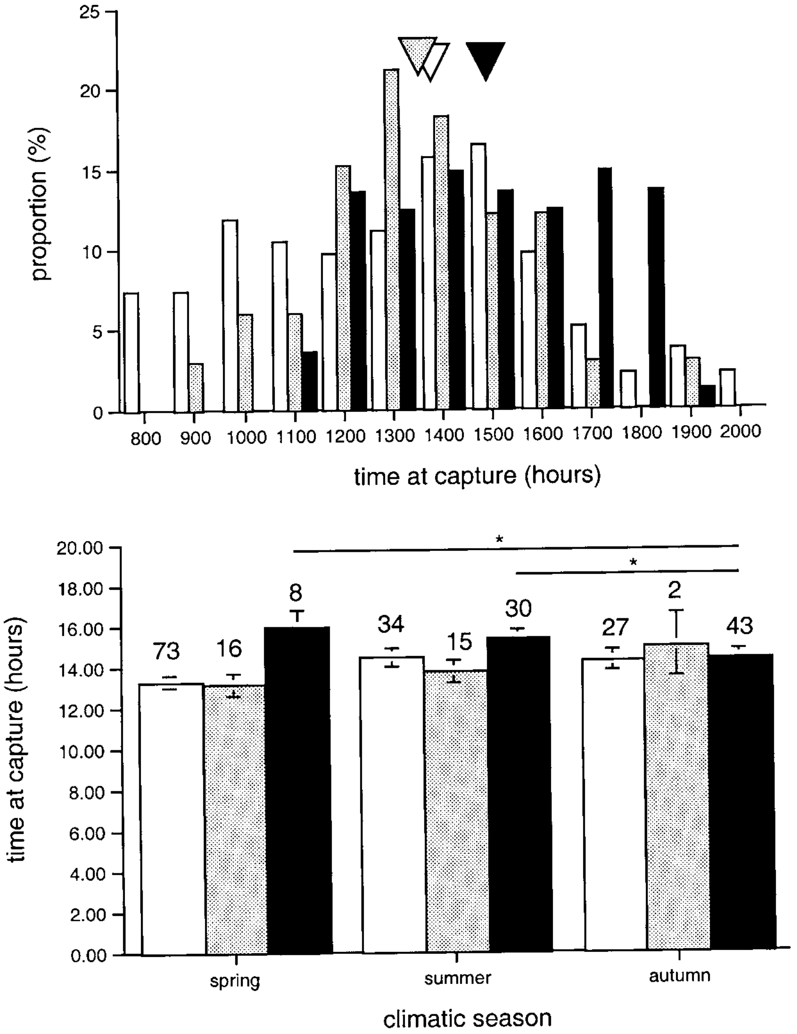

Fig. 4. Frequency distributions of copperheads according to the time of day at which they were captured. The results were grouped by locality (top) and by climatic season (bottom). See Fig. 1 for explanation of symbols. Mean daily activity times for each locality are shown by the arrows. On average, *A. superbus* from Western Port were captured at 1340 hours (s.e. = 0.23), their conspecifics from Mt Disappointment at 1330 (s.e. = 0.37), and *A. ramsayi* from Mt Baw Baw at 1455 (s.e. = 0.24) (see arrows). *A. ramsayi* from Mt Baw Baw were captured significantly earlier in the day in autumn than in spring and summer (all $P < 0.05$; symbolised by solid lines and asterisks).

(Duguy 1972; Lillywhite 1980, 1987; Rosen 1991; Beck 1995; Brown and Weatherhead 2000). Our data therefore build the frame work for functional explanations of local variation in activity times because snakes in cold environments that select similar body temperatures for activity as snakes in warm environments simply do not have the opportunity to reach them as often.

We emphasise 'frame work' because snake body temperatures taken at capture do not necessarily represent the full range of body temperatures experienced in a given environment (Lillywhite 1987; Reinert 1993). We presented a large data set on basking snakes but know little about body temperatures of snakes in their retreats or during foraging. Our method may also lack precision compared with approaches that use temperature-sensitive radio-telemetry (Beaupre 1995*a*; Reinert 1993). For example, when the latter method was used to compare mean body temperatures between two geographically separated populations of a rattlesnake, Beaupre (1995*a*) found significant differences in this trait. However, the magnitude of the differences between the two populations was very small (only slightly more than 1°C). Even if we missed differences at that scale, it is doubtful whether they would greatly impact on snake behaviour (i.e. activity times), given the severe climatic differences we found among our localities. Thus, experimental studies using temperature-sensitive radio-telemetry (a labour-intensive method that was out of the scope of our mainly life-history study; see also Reinert 1993) are clearly justified, but our data are powerful enough to identify an apparent inflexibility in snake body temperature to local environmental conditions.

Our method, together with behavioural observations, was also powerful enough to identify that there were some differences within localities during the active season. In *A. superbus*, we recorded the lowest body temperatures in spring. At that time, snakes were concentrated around ponds to feed on frogs. A similar interaction (or habitat correlation: Klopfer 1969) between the habitat of the prey and the body temperature of the snake has been recorded for *Thamnophis* species (Gregory and Nelson 1991). Indeed, the capacity or willingness to invade cool habitats and to accept relatively low body temperatures may be essential for successful resource exploitation in at least partially anurophagous snakes (which includes *Austrelaps*: Shine 1987). Interestingly, in *Pseudechis porphyriacus*, which feeds mainly on frogs, body temperatures are lower in summer than in spring, presumably because its prey become rare in summer (Shine and Lambeck 1990). In contrast to *A. superbus*, we recorded the lowest body temperatures for *A. ramsayi* in autumn when snakes were basking in front of their shelters, and we will argue below that this is linked to the need to extend their active season.

Annual and daily activity times

Most of our findings about annual and daily activity times fitted the 'constant temperature scenario'. We had predicted that daily and annual activity times would differ among localities if the body temperatures of basking snakes were similar. At Mt Disappointment, where the environment was cooler, *A. superbus* emerged later in spring and retreated earlier in autumn than did *A. superbus* from Western Port. Annual variation in emergence in spring coincided with annual variation in temperature, suggesting that spring emergence is linked to environmental temperature (Klauber 1972; Gregory 1984; Brown 1992; Sexton *et al.* 1992; Martin 1993; May *et al.* 1996). Mean activity times during the day were similar between the two populations, but *A. superbus* from Mt Disappointment started to bask later in the morning and finished earlier in the evening than did *A. superbus* from Western Port.

A. ramsayi emerged much later in spring than did *A. superbus*, commenced basking significantly later in the day and finished earlier. Therefore, their daily activity times were shorter than the ones we observed in *A. superbus*. Most importantly, their daily and seasonal activity times vary geographically, as they do in *A. superbus*. In the New England area of New South Wales, where climatic conditions are considerably warmer than at Mt Baw Baw, Shine (1977*b*) found that *A. ramsayi* were active for eight months of the year (September to April), compared with six months in our study, and that they emerged earlier in the morning (at 0900 hours) than did their conspecifics from Mt Baw Baw (at 1100 hours). With the exception of retreat time in autumn (see below), this difference among localities is the same as the one we found in *A. superbus*.

The link between body temperature and activity times

Two of our observations disagree with the 'constant temperature scenario' and point to the alternative, that is, that ectotherms may tolerate lower body temperatures in cold environments and extend their active season (the 'variable temperature scenario'). We found that *A. ramsayi* retreated up to two months later than high-altitude *A. superbus* (and at the same time as their conspecifics in the warmer New England area), even though it was much colder at Mt Baw Baw than at Mt Disappointment. At that time, several *A. ramsayi* also displayed body temperatures well below those we recorded for *A. superbus*. The intriguing questions are why and how these snakes were still active at a time when ambient temperatures were low and days with snowfall became more frequent.

Answering the 'why' may be easier than the 'how'. Because of the risks of feeding late in the active season (Scott *et al.* 1995; Prior and Shilton 1996), it is likely that the observed autumn basking (and perhaps also winter basking: Shine 1975) was used to facilitate exposure to mating partners (Gibbons and Semlitsch 1987), and to increase gonadal and follicular development (Aldridge 1975). During our study, we observed *A. ramsayi* mating in autumn and found that gravid females emerge in spring with nearly or fully developed follicles (see also Rohr 2001). Therefore, the extension of the active season in autumn may serve to reduce the negative effects of an already short active season on reproduction.

Exactly how this is done needs to be answered with experimental studies. We can suggest that it may be based on the temperature tolerance in the lower range because several *A. ramsayi* had body temperatures in autumn well below those we observed in *A. superbus*. Unlike preferred body temperature, the temperature tolerance limit in the lower range (critical minimum body temperature) has been shown to vary at both intra- and interspecific levels in snakes and may play an important part in their response to variability in thermal environments (Stewart 1965; Spellerberg 1972; Lillywhite 1980; Doughty 1994; Burghardt and Schwartz 1999). Thus, our data suggest that experimental studies are justified to test whether the differences in geographic distribution of *A. superbus* and *A. ramsayi* are linked to the degree of tolerance to low temperature. The fact that, at Mt Disappointment, tiger snakes (*Notechis scutatus*) were active longer in autumn than *A. superbus* suggests that the widely mentioned cold-hardiness of copperheads (see Greer 1997) may not apply to the lowland species, *A. superbus*.

Acknowledgments

We thank G. N. L. Peterson, B. Goodman, R. Dabal, S. C. Hudson, D. Hunter and C. Cold for their help during the extensive fieldwork. J. E. Girling and S. D. Sarre gave valuable comments on earlier versions of this manuscript. Melbourne Water allowed access to the restricted area at Mt Disappointment. Financial support was provided by *Australian Geographic*, the Royal Society of New South Wales (Ethel Mary Read Research Grant), the Department of Zoology, La Trobe University, and the Commonwealth of Australia. This research was conducted with permission of the Animal Ethics Committee, La Trobe University, and the Department of Natural Resources and Environment, Victoria.

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Manuscript received 14 March 2001; accepted 8 May 2001