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# The defensive strike of the Eastern Brownsnake, *Pseudonaja textilis* (Elapidae)

P. B. WHITAKER,* K. ELLIS† and R. SHINE*

**School of Biological Sciences, A08, and †Department of Veterinary Clinical Sciences, B10, University of Sydney, NSW 2006, Australia*

## Summary

**1.** The Eastern Brownsnake, *Pseudonaja textilis*, is a large (to 2 m), slender-bodied, highly venomous elapid that causes most snakebite human fatalities in Australia. The response of recently captured snakes to human harassment was quantified. Using high-speed film, the type of neck display, time taken to strike, strike accuracy, strike speed and effectiveness of bite were recorded.

**2.** The snakes were surprisingly tolerant of harassment, especially at body temperatures similar to those that they exhibit in the field during the activity season. Smaller snakes spent more time trying to escape than did larger snakes. Most snakes gave warning prior to the strike, 58% by full (high) display and 19% by partial (low) display. Some 25% of strikes were bluff.

**3.** Body temperature (over the range 18–36 °C) had little effect on most of the variables measured, including: the frequency of display and bluff, the duration of the strike (mean 0·28 s), the strike distance (mean 0·34 m), the mean overall strike speed (1·1 m $s^{-1}$, range 0·25–1·80), the mean fastest strike speed (during 1/25 s, = 1·7 m $s^{-1}$, range 0·3–3·4), or the accuracy of the strike.

**4.** Instead, the type of prestrike display was related to strike speed and accuracy: strikes preceded by a full neck display were slower but more accurate (and more likely to involve venom transfer) than those preceded by minimal display.

**5.** Contrary to popular opinion, Eastern Brownsnakes are reluctant to deliver firm bites in response to human harassment even when continuously provoked. It is estimated that only 15% of the strikes recorded had the potential to cause significant envenomation.

*Key-words*: Antipredator behaviour, envenomation, motor function, prestrike display, strike speed

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## Introduction

When attacked either by humans or other species, many kinds of animals attempt to defend themselves. Thus, antipredator behaviours often involve some type of retaliation (e.g. Greene 1988). Plausibly, an animal's ability to retaliate effectively may well influence its probability of surviving the attack, and hence the ways in which antipredator responses are fashioned by natural selection. In order to understand this process, we need information on the alternative forms of retaliatory behaviour, on the stimuli that elicit those alternative responses, and on the factors that render such responses more or less effective. For example, does an animal's ability to retaliate effectively, or its 'decision' to do so, depend upon factors relating to the individual organism (e.g. its body size) and/or the environmental conditions (e.g. ambient temperature) at the time of the attack? Are there significant trade-offs between different components of the defensive response, such that organisms must sacrifice accuracy for speed (or vice versa)? Such issues are of particular interest when the organism in question is capable of killing people in the course of such retaliation.

Venomous snakes induce considerable fear in humans, and an extensive mythology surrounds the topic of the actual speed and accuracy of their strike, as well as the amount of provocation required to elicit retaliation from the snake. Many non-scientists attribute remarkably high speeds to striking snakes; one popular story advises people trying to kill a snake to shoot anywhere in its general direction, because the snake will bring about its own death through striking at (and invariably 'hitting') the speeding bullet (Klauber 1956; Minton & Minton 1973). The limited data from controlled experiments provide a more prosaic picture, with strike speeds generally < 3 m $s^{-1}$, and with many strikes missing their target (Van Riper 1954; Greenwald 1974; Webb

& Shine 1998; but see Oliver 1958). Data are available for very few dangerously venomous taxa in these respects, however, and there is almost no information on the ways in which strike speed and accuracy (and tolerance for human provocation) change with snake body size or temperature. Both of these factors might be expected to modify the defensive strike, because an extensive literature suggests that antipredator tactics shift with body size (e.g. Greene 1988; Ford & Burghardt 1993), and that locomotor performance in ectotherms is affected by body temperature (e.g. Heckrotte 1967; Greenwald 1974; Bennett 1980; Bennett 1984; Stevenson, Peterson & Tsuji 1985; Lillywhite 1987).

Our interest in this topic arose as part of a more extensive study of the behavioural ecology of the Eastern Brownsnake, *Pseudonaja textilis*. These snakes are the most important cause of human snakebite fatalities in Australia (Sutherland 1992), and information on the determinants of encounter and snake response may help to reduce the risk of human envenomation and fatality (Duvall, King & Gutzwiller 1985). Using repeated intentional encounters with free-ranging radio-tagged brownsnakes, we have documented the ways in which snake body size and temperature influence both the probability of a human encountering a snake, and the way in which the snake responds to that encounter (Whitaker & Shine 1999a,b). Given that a snake and a human find themselves in close proximity, and the snake perceives the human to be a threat, we set out to investigate the factors that determine whether or not a strike is launched; and if so, the speed and accuracy of that strike. To accomplish this aim, we quantified the defensive responses of captive brownsnakes when subjected to continued human provocation.

## Materials and methods

*Pseudonaja textilis* is a large (to 2 m: Cogger 1992), slender, fast-moving elapid snake which superficially resembles the American Coachwhip *Masticophis flagellum* in appearance and behaviour. Based on trials with laboratory rodents, *P. textilis* has the second-most toxic venom of any snake species world-wide (Broad, Sutherland & Coulter 1979). When first captured, these snakes display great agility and nervousness accompanied by vigorous defence. Although free-ranging brownsnakes are reluctant to bite, and the majority flees from human encounter (Whitaker & Shine 1999b), most individuals will readily display and strike when cornered and harassed.

The adult brownsnakes used in this study (five males and seven females, mean snout–vent length (SVL) 1·18 m, range 0·98–1·33 m; mean mass 444 g, range 152–685 g) had previously been surgically implanted with temperature-sensitive transmitters (Whitaker 1999). The animals were then radio-tracked in the field for periods of 5–15 months prior to the work reported in the current paper. During the field study, the snakes were encountered on a mean of four (and not more than eight) occasions (including recapture events). All of the animals responded 'passively' to these encounters (Whitaker & Shine 1999b). Owing to the low frequency of field encounters (especially compared with the frequency with which these snakes are likely to encounter farmers in the field study area), our prior field study is unlikely to have significantly affected the snakes' defensive responses in the laboratory.

The tolerance and strike-speed trials were conducted in the middle part of the animal's activity season (January 1996), following mating and oviposition. Because feeding may affect a snake's response to predators (Garland & Arnold 1983; Herzog & Bailey 1987), the snakes were not offered food until after the trials were completed.

The snakes were transported to the University of Sydney 3–6 days after capture, and individually housed for 7–12 days before the trials began. During this period they were kept in wooden cages (with sliding glass fronts), measuring 0·77 m long by 0·30 m wide by 0·30 m high (the eight smallest snakes) or $0{\cdot}87 \times 0{\cdot}36 \times 0{\cdot}34\ m^3$ (the four largest snakes), in a room with 22·0 °C air temperature and a 14:10 h photoperiod (lit from 0600 to 2000 hours Eastern Standard Time). Underfloor heating in each cage provided a thermal gradient of 23–45 °C during daylight hours, simulating the thermal conditions typically available to the snakes during summer (Whitaker 1999). Cage temperatures fell to ambient room temperature at night. Because handling might influence antipredator response (reviewed by Greene 1988), the captive snakes were handled as infrequently as possible. The snakes were visually isolated from operator movement between trials, except immediately before each trial when the snakes were bagged and placed into a dark incubator for 6 h.

Strike trials were conducted at snake body temperatures (and simultaneous air temperatures) of 18, 24, 30 and 36 °C. These temperatures span the range over which brownsnakes were encountered above-ground in the field (Whitaker 1999). Body temperatures were measured from telemeter pulse rates (the telemetry method is detailed elsewhere, see Whitaker 1999). The snakes were randomly allocated to one of four groups, and each group was randomly allocated an order of treatment. Each snake was trialled on 4 of 8 filming days over a total period of 14–20 days, depending on trial allocation. In each trial, the time taken to elicit a strike, the tendency for bluff (number of aborted strikes) and the type of bite (firm or glancing) were recorded. The speed (duration and distance), accuracy (hits on the target) and effectiveness (bites on the target) of the strikes were also recorded. Because the snake might indicate the type of bite ('dry' or envenoming) prior to striking, the frequency and type of neck display (full or partial) were also recorded. These are discrete displays exhibited by brownsnakes in the field as well as the laboratory (P. B. Whitaker, personal observation).

The snakes adopt a full display when confronting an adversary, and a low display when slowly retreating (see Whitaker & Shine 1999b). Most encountered brownsnakes, however, remain still or attempt to escape without display.

Snake response was recorded on Super VHS video tape, at a rate of 25 frames per second with 1/8000 second shutter speed. The snakes were filmed through Perspex (to protect the photographer) and were illuminated by two halogen lamps placed behind a sheet of white cardboard to limit heating. The trial arena was an oblong box 0·60 m high to allow the snakes room to move (strike) vertically, 0·40 m wide (to prevent use of the walls for additional purchase), and 1·40 m long. The floor of the arena was covered with clean (animal scent-free) short-fibre nylon carpet to provide traction, and the ends of the arena provided the snakes with a view of the operator throughout each trial.

Strike distances were read off two 0·02 m-wide grids, one in front of the snake and one behind it. This method allowed parallax distortion to be calculated for any point in a frame. Error in strike distance was corrected for by recording the line each snake's head travelled, as it struck down the length of the arena toward the operator, with reference to eight longitudinal divisions (each 0·05 m wide) along the floor. The length of time taken for the snakes to retaliate was recorded from when the target was introduced through one end of the arena, opposite to the snake, to when a strike was initiated. Strike length and duration were determined from when each snake's head began to move in a strike to a point where it either made contact with the target, changed in direction, or came to a halt.

The 'target' was a size-7 latex glove loosely stuffed with cotton wool to simulate a human hand (many 'real' bites to people in Australia are on the hand: Sutherland 1983; Whitaker 1999) and attached to the end of a 1-m rod. At the beginning of each trial, the snakes were slowly and gently tipped from their holding bags without touching them, and allowed to settle for ≈ 30 s. The target was then slowly introduced, in order to allow the snake an opportunity to strike at distance, to a position ≈ 0·20 m directly above the snake's back. The target in this position was then slowly waved for 10 seconds. If no bite attempt occurred, the snake's back was then firmly touched ≈ 20 times per minute until the snake struck.

Our experimental design meant that the same snakes were used for trials at each temperature. Only the first recorded strike at each temperature was used in the analysis. Because successive trials on the same animals were not independent, continuous variables were analysed using repeated-measures . Fisher's exact test was used in cases where we wished to examine dependent categorical variables (display, bluff, accuracy and type of bite) against physical attributes of the snakes (sex, body size and body temperature).

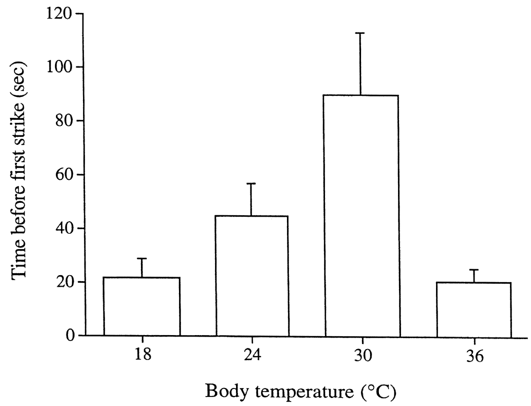


**Fig. 1.** Tolerance of Eastern Brownsnakes to continued human harassment at four body temperatures. The graph shows the mean time taken (in seconds) for the snakes to strike at a human 'hand' target (+ standard error).

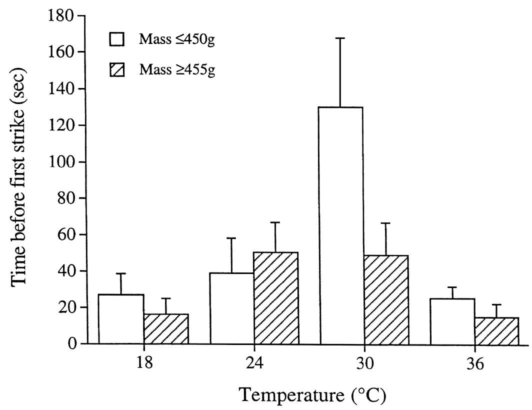


**Fig. 2.** Relative tolerance of Eastern Brownsnakes of different body sizes to continued human harassment at four body temperatures. The graph shows the mean time taken (in seconds) by the snakes to strike; tolerance was greatest in smaller individuals at 30 °C (+ standard error).

## Results

The overall mean time taken for the snakes to respond to harassment by striking at the simulated human target was 44 s ($n = 48$, SD = 54, range 0–265). The response time depended on snake body temperature (one-factor repeated-measures : $F_{3,33} = 6{\cdot}23$, $P < 0{\cdot}005$). The snakes were most tolerant of harassment at intermediate temperatures (Fig. 1); under these conditions, the snakes devoted most of their efforts to escape rather than retaliation. Relatively small adults (< 1·20 m SVL and < 450 g mass, $n = 6$) spent more of their time attempting to escape, and therefore delayed the strike, compared with larger snakes (two-factor repeated-measures , with body temperature and snake length or mass as categorical variables: $F_{3,30} = 6{\cdot}23$, $P < 0{\cdot}005$ and $F_{3,30} = 2{\cdot}85$, $P = 0{\cdot}05$, respectively). Tolerance was increased in both size classes at 24° and 30 °C, but escape effort was much greater in the smaller snakes at 30 °C (Fig. 2).

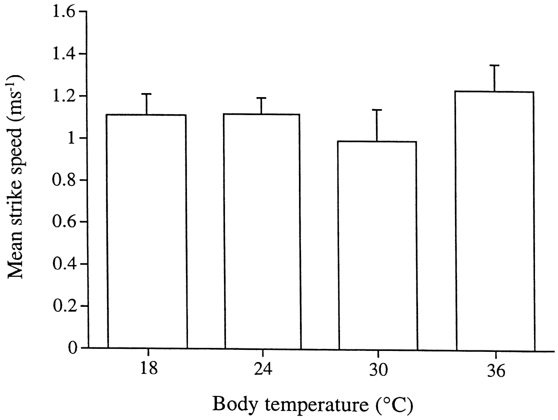


**Fig. 3.** The overall mean strike speeds of Eastern Brownsnakes at four body temperatures that encompass the snake's usual thermal range while active above-ground (Whitaker 1999). The figure shows mean values and associated standard errors.

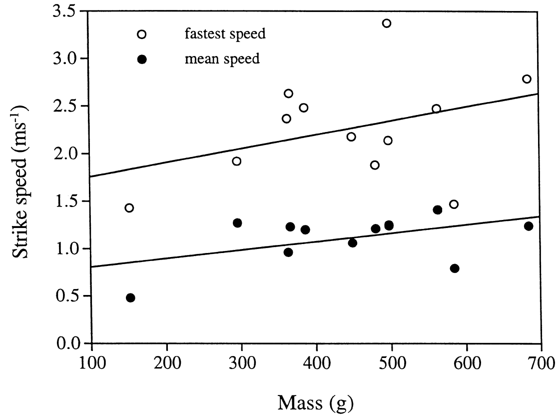


**Fig. 4.** Strike speeds of 12 Eastern Brownsnakes as a function of the snakes' body size. The figure shows the overall mean speed, and fastest speed recorded, for the first strike launched by each snake at each of the temperatures tested. These data show a non-significant trend for strike speed to increase with body mass.

The time taken to elicit a strike did not differ between males and females (with body temperature and gender as categorical variables: $F_{3,30} = 2{\cdot}22$, $P = 0{\cdot}11$).

The overall strike speed averaged $1{\cdot}11$ m s$^{-1}$ ($n = 48$, SD = $0{\cdot}40$, range $0{\cdot}25$–$1{\cdot}80$), and the fastest speed recorded in each strike (during 1/25 s) averaged $1{\cdot}72$ m s$^{-1}$ (SD = $0{\cdot}62$, range $0{\cdot}30$–$3{\cdot}37$). Unexpectedly, body temperature did not affect either the overall or fastest strike speeds (one-factor repeated-measures : $F_{3,33} = 0{\cdot}93$, $P = 0{\cdot}44$ and $F_{3,33} = 2{\cdot}12$, $P = 0{\cdot}12$, respectively; see Fig. 3).

Strike speed was not significantly affected by snake size at the four body temperatures tested (two-factor repeated-measures , with body length or mass as a second categorical variable: $F_{3,30} = 0{\cdot}25$, $P = 0{\cdot}86$ and $F_{3,30} = 0{\cdot}17$, $P = 0{\cdot}91$, respectively). Similarly, males and females did not differ in their mean or fastest strike speeds at these temperatures (with sex as the second categorical variable: $F_{3,30} = 0{\cdot}31$, $P = 0{\cdot}82$ and $F_{3,30} = 0{\cdot}29$, $P = 0{\cdot}83$, respectively). Regression of the mean and fastest speeds recorded during the first strike by each snake (i.e. independent of body temperature) against body mass, however, showed a non-significant tendency for larger snakes to strike more rapidly (Fig. 4).

The overall mean duration of strike was $0{\cdot}28$ s ($n = 48$, SD = $0{\cdot}12$, range $0{\cdot}12$–$0{\cdot}64$), and this duration did not vary with body temperature (one-factor repeated-measures , $F_{3,33} = 0{\cdot}07$, $P = 0{\cdot}98$), sex (two-factor repeated-measures , with sex as a categorical variable, $F_{3,30} = 1{\cdot}53$, $P = 0{\cdot}23$) or body mass ($F_{3,30} = 1{\cdot}02$, $P = 0{\cdot}40$). The overall mean distance covered by snake heads during strikes was $0{\cdot}34$ m ($n = 44$, SD = $0{\cdot}15$, range $0{\cdot}11$–$0{\cdot}67$), and this distance also did not vary significantly with body temperature ($F_{3,30} = 1{\cdot}49$, $P = 0{\cdot}24$), sex ($F_{3,27} = 2{\cdot}87$, $P = 0{\cdot}06$), or body mass ($F_{3,27} = 0{\cdot}23$, $P = 0{\cdot}87$).

Most strikes were preceded by neck displays. Overall, 58% (28) of the strikes were preceded by full display (a partly flattened triple-looped neck display, with the head held high above the substrate; Fig. 5a) and 19% (9) by a partial display (a flattened hook-shaped neck display, with the head held low; Fig. 5b). Hence, the snakes gave 'warning' before 77% of the strikes, although many of these displays were brief. Strikes preceded by full display were slower overall, with a mean speed of $0{\cdot}98$ m s$^{-1}$ ($n = 28$, SD = $0{\cdot}37$) compared with $1{\cdot}31$ m s$^{-1}$ ($n = 20$, SD = $0{\cdot}36$) without this type of display (for speeds of $< 1{\cdot}0$ *vs* $\geq 1{\cdot}0$ m s$^{-1}$ using Fisher's Exact Test, $P < 0{\cdot}05$). Strikes preceded by full display were also more accurate; 57% of the strikes preceded by full display hit the target, compared with 25% without this type of display (Fisher's Exact Test, $P < 0{\cdot}05$). One-quarter of all strikes were 'bluff', with the snake closing its mouth and aborting the strike before reaching the target (these strikes were classified as 'defensive advances' in Whitaker & Shine's 1999b field study). No relationship was found between the tendency for display or bluff and snake body temperature, sex or body size.

The snakes hit the target on 18 occasions (38% of strikes). The target was bitten on 15 of these occasions, but not in the other three cases. Hence, most strikes did not hit the target, but most hits on the target involved bites (83% of hits resulted in bites).

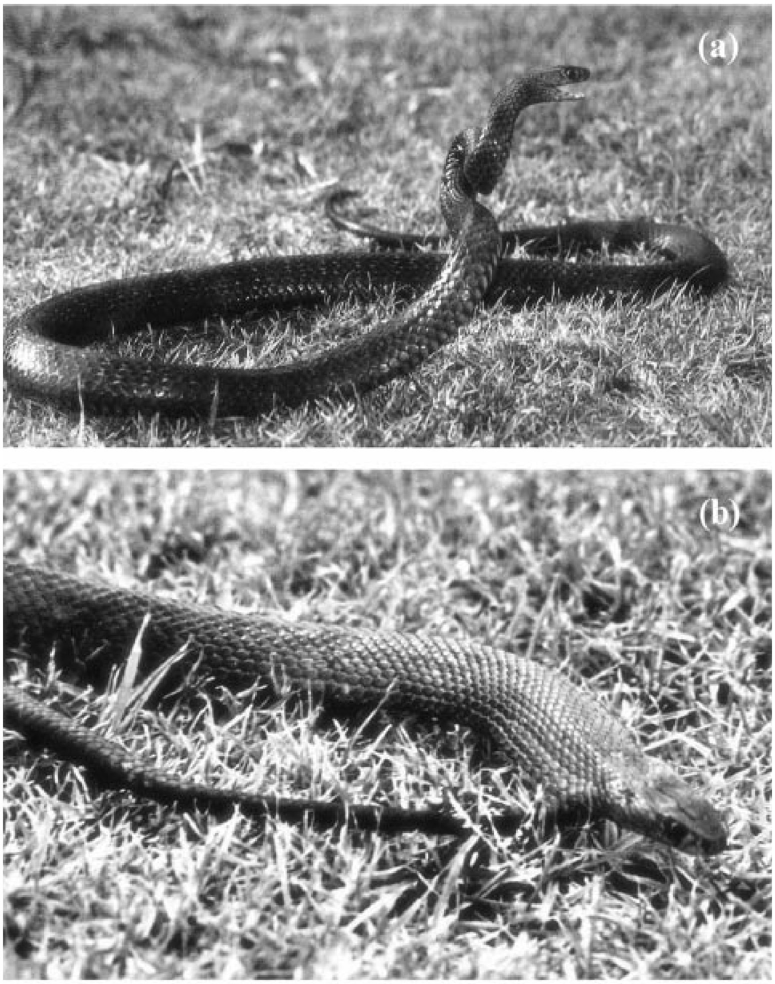


**Fig. 5.** Defensive displays of the Eastern Brownsnake. (a) A snake in full (elevated-neck) display with characteristic open-mouth stance. The ensuing strike will be directed forward and will be relatively slow, but it will be accurate and likely to result in envenomation. (b) A partial (low-neck) display, with the neck cocked to one side, allowing the snake to watch the antagonist while moving away. Strikes launched from this position are rapid, but are relatively inaccurate and unlikely to result in envenomation (see text for explanation).

Again, no relationship was found between hits or bites to the target and snake body temperature, sex or body size.

Two types of bites were distinguished: firm (where the snakes seized the 'hand') and glancing (where the snakes stabbed at the 'hand' while moving past). In both cases, the target was quickly released following the bite. Firm bites were associated with 15% ($n = 7$) of the strikes and left visible deposits of venom on the target. Glancing bites were associated with 17% ($n = 8$) of the strikes and left no visible venom deposits. Indeed, only firm bites left visible fang punctures. Hence, approximately half of all bites, resulting from 15% of all strikes, showed potential to cause significant envenomation. Some 67% of hits on the target (12 of 18) were associated with full display, as were 86% of firm bites (6 of 7). Hence, full display was associated with more accurate and determined strikes, which were slower in delivery.

## Discussion

Our data provide the first quantitative information on the Eastern Brownsnake's tolerance for harassment, its strike speed, and the accuracy and nature of its strike. This snake is generally considered irascible (e.g. White 1981) and aggressive (e.g. Kinghorn 1956), and farmers consider it more dangerous in hot weather (D. Hopkins, personal communication). Hence, many of our results are counter-intuitive, and run counter to prevailing opinions. For example (1) brownsnakes tolerated substantial harassment before launching a defensive strike, especially when close to their preferred body temperature; (2) small individuals were more tolerant of harassment; (3) the snake's strike was relatively slow ($< 2\ \mathrm{m\ s^{-1}}$); (4) strike speed was not significantly affected by body temperature, gender or size; (5) most brownsnakes gave warning of an imminent strike; (6) a quarter of all strikes were bluff or aborted; (7) most strikes missed the target; (8) strikes preceded by full display were slower, but more accurate and more often involved firm bites and venom expenditure; (9) thus, only 15% of all strikes had the potential to cause significant envenomation. The brownsnake's tolerance of harassment was linked to temperature, but the effectiveness of its strike was not.

Overall, these findings agree well with those of our field study on the same animals (Whitaker & Shine 1999a,b). Despite their fearsome reputation, brownsnakes are tolerant (as inferred from the relatively long periods of time required to elicit defensive strikes) of human harassment, during which most seek escape rather than retaliation. In the field, small *P. textilis* were more likely to flee from humans than were large individuals (Whitaker & Shine 1999b), and the same pattern was seen in our laboratory study. Even when brownsnakes did retaliate, they generally gave warning before striking and only a small proportion of strikes resulted in significant envenomation. One in three strikes resulted in bites to the target and approximately half of these did not result in visible venom deposits. These findings are consistent with frequent anecdotal reports of 'dry' bites to humans (e.g. Parrish 1959; Reid 1970; Russel 1980; White 1981). This phenomenon may reflect either motivational control over venom expenditure, or disruption of the envenoming mechanism when biting defensively (White 1981; Morrison, Charles & Pearn 1983a; Kardong 1986). The former is likely to be more important; many of the defensive strikes that were recorded did not appear to involve a serious attempt to bite the target.

Thermal effects on the snakes' tolerance for harassment introduce a time-dependency (i.e. threshold of stimulation) in antipredator response: snakes delay launching a defensive strike if they are close to their mean selected body temperature. Again, this pattern from our laboratory study fits well with results from our encounters with free-ranging snakes. Brownsnakes that were approached in summer (when their body temperatures were near 30 °C: Whitaker 1999) were most likely to rely on crypsis or flight, whereas snakes approached in spring (when their body temperatures were often much lower) were more likely to launch a defensive strike (Whitaker & Shine 1999b).

Performance capacities of ectotherms are typically temperature-dependent (e.g. Stevenson *et al.* 1985), and it is therefore surprising that the snakes' body temperatures had so little effect on the speed or accuracy of the strike (e.g. Fig. 3). The thermal independence of strike speed may reflect strong selective pressure for the ability to launch effective defence over a range of body temperatures (e.g. Greenwald 1974; Bennett 1980). Most of the strikes that were recorded covered a total distance of < 0·50 m and were concluded in less than half a second. Hence, the snake's reputation for great speed may in part be due to the short distances covered during a strike. The snakes are capable of covering the average strike distance (0·34 m) in just one-tenth of a second, even when they are relatively cool; the fastest strike speed recorded was 3·37 m $s^{-1}$ by a female with a body temperature of 18 °C. The absolute strike speed is close to those reported for other species (e.g. Greenwald 1974 (on a colubrid); Van Riper 1954 (on a viperid)). This similarity is surprising, given the anatomical differences among major snake lineages. Although the speed and accuracy of strikes at prey are temperature-dependent in some snake species (e.g. Webb & Shine 1998), the data are simply not available to judge whether or not the same is true for defensive strikes by venomous snakes.

The high toxicity of *P. textilis* venom suggests the amount required to produce serious systemic envenomation may be smaller than can readily be detected with the naked eye (Broad *et al.* 1979). Nonetheless, it is doubtful that the percentage of strikes from free-ranging brownsnakes that are potentially life-threatening has been underestimated, especially as captive individuals are far more likely to show vigorous retaliation than are free-ranging snakes (Whitaker & Shine 1999b). Published reports indicate low venom yields in 'milked' *P. textilis* (e.g. Fairley & Splatt 1929; Worrell 1963; Sutherland 1983) and in feeding bites (Morrison *et al.* 1983b). However, these low volumes may be misleading. Brownsnakes are reluctant to expel venom when 'milked' in the traditional manner (P. B. Whitaker, unpublished data), and some individuals deliver much larger quantities of venom than the average 'milked' yield (Broad *et al.* 1979; P. B. Whitaker, unpublished data).

Overall, unrestrained Eastern Brownsnakes are surprisingly tolerant of human harassment, and communicate their offensive intentions through elaborate display (often mistaken for aggression: Whitaker & Shine 1999c). Should a fully displaying brownsnake be pressed, however, it is likely to deliver an accurate and envenoming bite. Displays before launching a strike are common in many venomous taxa (reviewed in Australian elapids by Greer 1997), and our study demonstrates a link between the type of display and the type of ensuing bite. It would therefore be useful to examine this relationship in other species of dangerously venomous snakes.

More generally, further study of the defensive responses and capabilities of a wide variety of organisms are needed. As our own study demonstrates, intuition and 'conventional wisdom' may prove to be poor predictors of the form and effectiveness of anti-predator responses in animals. We began our study under the assumption that body size and body temperature would be the most important determinants of the snakes' capacity to deliver an effective retaliatory strike. These predictions were based on a voluminous literature on reptilian biology (e.g. Greenwald 1974; Bennett 1980; Duvall *et al.* 1985; Greene 1988; Webb & Shine 1998) but we were wrong on both counts. Body size and temperature affected the amount of stimulation (harassment) required to elicit a defensive strike from our brownsnakes, but neither of these variables exerted a significant influence on the animal's defensive ability (accuracy and speed of strike). Instead, these two components of strike effectiveness were subject to a strong trade-off (faster strikes were less accurate), and this trade-off was mediated by the animal's selection of a prestrike display posture. Hence, the potential effectiveness of the snakes' retaliatory strike was determined by its choice between alternative tactics, rather than by constraints associated with size or temperature. Such complexities may well prove to be common, and additional quantitative studies on a broad range of taxa are needed before simplistic assumptions can be replaced with reliable information.

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