CSIRO PUBLISHING

Wildlife Research

Volume 26, 1999

A journal for the publication of original scientific research
in the biology and management of wild native or feral introduced vertebrates

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the Australian Academy of Science

 Wildlife Research, 1999, **26**, 689–704

Responses of free-ranging brownsnakes (*Pseudonaja textilis* : Elapidae) to encounters with humans

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Abstract

Eastern brownsnakes (*Pseudonaja textilis*) are large (to 2 m), slender, dangerously venomous elapid snakes that cause significant human mortality. We recorded the responses of free-ranging brownsnakes to 455 close encounters with a human observer, using 40 snakes implanted with miniature radio-transmitters, plus encounters with non-telemetered animals. Our study area (near Leeton in south-eastern Australia) is typical of many of the agricultural landscapes occupied by *P. textilis*. Contrary to public opinion, the snakes were rarely aggressive. About half of the encounters resulted in the snake retreating, and on most other occasions they relied on crypsis. Snakes advanced towards the observer on only 12 occasions (<3% of encounters) during initial approach, and only three of these advances were offensive. The snakes' responses to an approach depended on the observer's appearance (e.g. snakes were more likely to ignore an observer wearing light rather than dark shades of clothing) and behaviour (e.g. snakes were more likely to advance if approached rapidly, and touched immediately). Snakes were more likely to retreat if they were sub-adult rather than adult, if they were warm, or if they had been moving prior to an encounter. Weather conditions (air temperature, wind velocity and cloud cover) also influenced the snakes' responses, as did season and time of day. The snakes' response was relatively predictable from information on these factors, enabling us to suggest ways in which people can reduce the incidence of potentially fatal encounters with brownsnakes.

'Snakes are first cowards, next bluffers, and last of all warriors' (Pope 1958)

Introduction

Wild animals kill people in many parts of the world, and such interactions often cause major conflict between concern for human welfare and wildlife conservation (e.g. Conover and Dubow 1997). How are we to minimise human deaths, without total eradication of the dangerous animal? A crucial first step is to understand something of the dynamics of the interaction between wildlife and people. Information on the kinds of animals involved (ages, sexes, reproductive condition), and the circumstances under which attacks occur, can help to clarify the reasons why attacks take place (e.g. Pope 1961; Goode and Duvall 1989; Shine 1994; Conover and Dubow 1997). In some cases, animals kill people for food (e.g. Edwards 1997), whereas in other cases they behave defensively (e.g. Minton and Minton 1973). The vast majority of human fatalities due to snakebite fall into the latter category. Although large boid and pythonid species occasionally consume human prey (e.g. Minton and Minton 1973), the number of deaths from such activities is trivial compared with mortality from the bites of venomous snakes (Gopalakrishnakone and Chou 1990; Sawai 1992). Many authors have speculated on the reasons why venomous snakes sometimes bite people (e.g. Fritts *et al.* 1994) but there have been very few attempts to quantify the factors that determine how free-ranging venomous snakes respond to close encounters with humans (Duvall *et al.* 1985; Prior and Weatherhead 1994). Because such information may be useful both for reducing human fatalities and for facilitating conservation efforts, we carried out such a study in south-eastern Australia.

To understand the dynamics of the interaction between humans and snakes, we need answers to a series of questions. For example, what circumstances bring people and snakes into close and risky proximity? What factors influence the ways in which a person responds to this situation?

10.1071/WR98042 1035-3712/99/050689

What factors influence a free-ranging snake's response to humans? Our study focuses on encounters between people and snakes in inland Australia, and involves a snake species (*Pseudonaja textilis*) that is widely distributed, and causes most of the human fatalities from snakebite in Australia (Cogger 1992; Sutherland 1992). Elsewhere, we will report on the factors that influence the probability of people encountering snakes, the responses of people in such situations, and the snakes' ability to inflict a dangerous bite (Whitaker and Shine 1999; Whitaker *et al.*, unpublished data). In the present paper, we focus on a factor that is likely to play an important role in determining the outcome of an encounter with a brownsnake: the snakes' initial response. What factors determine why a snake will sometimes attack, but at other times will retreat or rely on crypsis?

Methods

Study area

The study was conducted in the Murrumbidgee Irrigation Area (MIA) of south-eastern New South Wales, in a 14-km^2 rural area (34º39′S, 146º28′E). Data collection focused on an ungrazed section of canal bank (3000 m × 25 m) and the surrounding farmland. The relatively undisturbed canal bank functions as a breeding and refuge area for brownsnakes (Whitaker 1999). The site is surrounded by farms under continuous alternate cropping and sheep-grazing regimes, with 'dry' farming to the north-east and a 35-m-wide canal and irrigated cereal-crop production to the south-west. The local climate is characterised by hot dry summers and cool moist winters (Whitaker 1999).

Study species

Eastern brownsnakes (*Pseudonaja textilis*) are large (to 2 m total length), slender, agile snakes that are widely distributed through the eastern third of Australia (Cogger 1992). Adults can be any shade of brown dorsally and pale brown or cream (often flecked with orange or brown) ventrally. Although the food habits and reproductive biology of this species have been described from dissection of field-collected specimens (e.g. Shine 1977*a*, 1977*b*, 1977*c*, 1989) and observations in captivity (Wells 1980; Banks 1983), no previous work has examined the ecology and behaviour of free-ranging brownsnakes. On the basis of laboratory studies of toxicity in mice, the venom of *P. textilis* is the second most potent yet studied (Broad *et al.* 1979). Snakebite fatalities in Australia are rare, and declining, but eastern brownsnakes remain a significant cause of serious envenomation. Indeed, recent work suggests that this species is probably the most important single taxon in terms of posing risk to humans (Sutherland 1992). This status may reflect the wide distribution of the species, its locally high abundance (especially in habitats disturbed by agricultural activities), its toxic venom, its speed, and its readiness to defend itself vigorously (Fleay 1943; Gow 1987; Shine 1991). Additionally, rural people attribute high levels of aggression to this species, and report frequent unprovoked attacks (Whitaker 1999).

Time-frame of the study

Encounters with snakes were recorded between May 1993 and April 1996. The first and third summers of the study experienced near-average rainfall, but during the second year drought considerably reduced vegetation cover. Although we did not deliberately seek out snakes for encounter purposes during the first active season (September 1993 to May 1994), many inadvertent encounters occurred and are included in the overall data set. During the two subsequent activity seasons each telemetered snake was approached at approximately two-weekly intervals, if active and in a situation where it could be approached, to obtain data on response. This level of interference was probably minor compared with the relatively frequent encounters between farm workers and these snakes (usually without the farmer being aware of the encounter).

Radio-telemetry and monitoring of snakes

Brownsnake–human encounters were recorded from two groups of brownsnakes: those that carried transmitters (the repeat-measure group) and those that did not (the single-measure group). The repeat-measure group included 40 telemetered snakes (18 adult females, 16 adult males, and 6 sub-adults) surgically fitted with miniature temperature-sensitive radio-transmitters. The transmitters represented ≤2.5% of the snakes' body mass in all cases. Repeat-measure animals carried transmitters for varying lengths of time (range 2–32 months), providing data for a total of 40 snake-years. Other papers from this study will provide detail on the techniques used to implant transmitters into the snakes, the effect of telemetry burden on snake condition, and the ways in which body temperature and weather conditions were monitored (Whitaker 1999). The single-measure group included initial encounters with individuals of the repeat-measure group (usually, at the time of their initial capture) and one-off encounters in the general area. All telemetered snakes were sought for encounter purposes, but some of them avoided direct human encounter for most of the period they were studied due to their relatively long periods of inactivity, alert nature and effective camouflage. Body temperatures of telemetered snakes were measured (via pulse interval of the telemetry signal) either immediately before or after an encounter.

Factors that might influence the snakes' responses

We divided the potential influences on snake response into four categories: (i) those associated with the humans' behaviour and appearance (i.e. speed of approach, approach distance, touching the snake, and shade of clothing); (ii) those associated with the snake itself (i.e. gender, size, prior activity, and body temperature); (iii) those describing the situation in which the encounter took place (i.e. weather conditions, vegetation cover, and drought); and (iv) those associated with the time the encounter took place (i.e. year, season, and time of day). The weather variables that we measured include shaded air temperature (aspirated air 4 cm above the ground), wind direction and velocity, and the presence, percentage, and height of cloud cover.

Method of approaching snakes

Our mode of approach was strongly influenced by the risk of potentially fatal envenomation. A slow approach was used most frequently because: (i) it reduced personal risk (see below), and (ii) it is more typical of 'natural' encounters between farm workers and brownsnakes, especially in the dense undergrowth often occupied by snakes in this area. However, if snake locations were known at distance (i.e. visually or via telemetry), and approach could be made safely to within approximately 0.5 m of the snakes' head without touching the animal, any one of three approach modes was randomly chosen. The three modes of approach comprised: a slow walk (1–2 km h^{-1}), a medium walk (5–6 km h^{-1}), and a sudden/rapid approach (>9 km h^{-1}). In each case, only a single person was involved. Any of these modes sometimes involved deliberately touching the animal (by means of nudging and gentle tapping with the foot). Touch was included as an additional factor only if a particular snake allowed prolonged close encounter for 10 s. Touching these snakes also depended on local topography allowing our unrestricted immediate withdrawal.

Types of brownsnake response recorded

Because free-ranging brownsnakes rarely adopt a prolonged 'defensive' posture, we scored snake response in terms of three variables: flight distance, initial response, and subsequent response. Flight distance was measured to the nearest 0.5 m and refers to the distance between the observers' foot and the snakes' head. Initial response was the snakes' immediate response to human approach, i.e. that which occurred between the initiation of the approach and when the snake was within 50 cm of the observers' foot (where snakes allowed close encounter). Subsequent response refers only to occasions where the snakes permitted close encounter, and (in the case of a stationary response) is that behaviour which occurred within 10 seconds of close encounter being achieved. We recognise four different response categories (initial and subsequent) by the snakes: 'advance', 'ignore', 'retreat', and 'stationary'. An 'advance' is any motion that results in a snake moving closer to the observer, and does not necessarily imply attack. Advances were further divided into four types (see below). Snakes were scored as 'ignore' if they continued their previous activity (e.g. kept moving at the same speed and in the same direction), and 'retreat' if they moved away from the observer. Snakes that did not move either toward or away from the observer were scored as 'stationary', whether or not they changed their posture (e.g. assumed a neck display).

Although 'advance' is the most important category in terms of the risk of snakebite, this behaviour occurred so rarely in the field (see below) that we could not further subdivide it without additional information (see Duvall *et al.* 1985). Such information was available from freshly captured snakes that were more than willing to exhibit offensive responses when harassed. On the basis of these observations, we divided advances into four types, as follows.

A 'type 1 offensive advance' is a prolonged motion directly towards the observer, often involving a full double- or triple-looped neck display, and is initiated by opening the mouth. The snake may give chase in order to deliver a bite and does not immediately retreat.

A 'type 2 offensive advance' begins with a low lateral movement that angles backward and upward before reaching the target. It is often initiated from a horizontally held hook-shaped neck posture and usually with the head not facing directly toward the antagonist. This bite attempt is delivered rapidly and unexpectedly, but is usually preceded briefly by a low, partially flattened neck display. This type of bite attempt is usually followed by a slow retreat.

A ‘defensive advance’ is defined as an intimidating short lunge often delivered indirectly at the target from a display posture. The advance usually occurs after a short pause and may be initiated from a full (triple-looped) display, but more often from a low display that involves a partially flattened neck, an open mouth, and an audible hiss. The advance is to approximately half (or less) of the snakes’ snout–vent length and always stops short of the antagonist. This type of advance is often immediately followed by a rapid retreat. This response is easily mistaken for an attack .

A ‘passive advance’ involves the snake moving slowly toward the observer in order to reach a burrow or cover. It usually does not involve a display, but it is sometimes accompanied by a faint hiss.

We treat each encounter as a separate data point for statistical analyses, and thus ignore the fact that many of the snakes were encountered more than once. This approach was adopted because: (i) treating the data in this way will not introduce statistical problems as long as the relative magnitude of response variation is similar among individuals as within individuals (Leger and Didrichson 1994). We saw no evidence that particular snakes were more or less likely to respond in individually consistent ways (Whitaker *et al.*, unpublished data), and (ii) in some cases we could not determine the identity of the snake. We knew the identity of snakes in 80% (362) of the encounters; from this sample, we estimate an approximate mean of 4 observations per snake (range 1–20).

Below, we first describe the overall patterns of snake response to human encounter, and then look in detail at some of the factors affecting those responses.

Results

Effects of site and telemetry on snake responses

Most encounters (323 of 455, 71%) were recorded on the central refuge area, with the remainder in surrounding farmland. Snakes encountered in the two areas did not differ in their flight distance (<1.0 *v.* >1.0 m: $n = 454$, $\chi^2 = 0.02$, d.f. = 1, $P = 0.88$) or their initial response ($n = 453$, $\chi^2 = 5.03$, d.f. = 3, $P = 0.17$). Subsequent responses differed between the two areas ($n = 205$, $\chi^2 = 6.04$, d.f. = 2, $P = 0.05$), because of a lower percentage of ‘ignore’ responses during prolonged (10 s) encounters on farmland than on the refuge area (7% *v.* 18%). More of the farmland snakes eventually retreated (40% compared with 26% on the refuge area). These differences were readily attributable to habitat effects. When courting or mating (which usually occurred in association with cover on the relatively undisturbed refuge area), male snakes showed an increased tendency to ignore human presence; also, vegetation cover (which strongly affects snake responses – see below) tended to be lower on farmland. Hence, because response patterns were similar, the data from farmland and refuge area encounters were pooled for further analyses.

Of the total daylight encounters, 179 (39%) were once-only or first-time encounters and the rest were repeat encounters. Implantation of transmitters apparently did not affect the snakes’ response: telemetered and non-telemetered snakes did not differ in their flight distance ($n = 454$, $\chi^2 = 1.90$, d.f. = 1, $P = 0.17$) or their initial response ($n = 453$, $\chi^2 = 6.34$, d.f. = 3, $P = 0.10$). We could not test subsequent response in this way, because many single-measures were capture events. Given this similarity in responses, we pooled the data from the single- and repeat-measure groups for further analyses.

Overall initial response

About half (48%) of the brownsnakes that we approached immediately retreated ($n = 220$). Most others (40%) remained stationary ($n = 182$) and a small proportion (9%) ignored us ($n = 41$). Only 12 snakes (<3%) advanced toward us when we encountered them. Of these 12 snakes that advanced, only 3 did so in a life-threatening manner. One of these snakes carried out a Type 1 offensive advance, and the other two carried out Type 2 advances (see above for definitions). Thus, even during close encounter with people, free-ranging brownsnakes tended to be inoffensive – if not touched.

Because advances were so rare, their inclusion in contingency-table analyses would invalidate many tests due to low expected values. Consequently, in the following we omitted the advance category in such cases, but included the response in tests for overall snake movement during encounter.

Characteristics of the human participant in the encounter

Speed of approach

The observers' speed of approach did not affect flight distance, or the snakes' initial or subsequent responses overall (Table 1). However, significantly fewer of the snakes moved during initial encounter when approached slowly (51%) than with more rapid approach (62%). The higher percentage of snakes moving with our increased approach speed included those that advanced on the antagonist; three of the four advances associated with rapid approach were offensive and accounted for all of the offensive advances recorded.

Approach distance

Overall, the snakes allowed us to approach very closely (<1 m) in about half of all encounters (Table 1). The observers' distance from the snakes strongly affected their responses, by definition: most retreats (85%) were recorded at >1.0 m distance, whereas the snakes that were approached more closely generally remained stationary or advanced toward us. Flight distance varied seasonally, in conjunction with the density of vegetation cover (see below); for example, snakes in thicker vegetation tended to allow closer approach.

Touching the snake

We touched snakes by inadvertently stepping on them (n = 6), by touching them immediately (n = 6), or by firmly nudging and tapping the snake after a 10-s delay (n = 55). Two of the three

Table 1. Responses of free-ranging brownsnakes (*Pseudonaja textilis*) to close encounter with a human
The snakes' response was scored in four categories (advance, ignore, retreat, stationary: see text for definitions). The table shows the frequency of these alternative responses as a function of the observer's approach speed, approach distance, the shade of clothing worn, and whether or not the snake was touched after a 10-s delay. The statistical results are based on contingency table tests. Because 'advance' responses were very rare we have excluded these data from some tests to maintain satisfactory expected frequencies. However, they are included in the test for movement

	Advance		Ignore		Retreat		Stationary		
	%	*n*	%	*n*	%	*n*	%	*n*	Total
Approach speed (km hr^{-1})									
≤3	1.7	5	10.4	31	46.1	137	41.8	124	297
5–7	3.2	3	5.4	5	54.8	51	36.6	34	93
≥9	7.4	4	7.4	4	51.9	28	33.3	18	54
Test for effect (3 *v*. >3) on movement	Total observations = 444, χ^2 = 4.57, d.f. = 1, $P < 0.05$								
Approach distance achieved (m)									
1.0	3.6	9	12.3	31	13.1	33	71.0	179	252
>1.0	1.5	3	4.9	10	92.1	187	1.5	3	203
Test for overall effect	Total observations = 455, χ^2 =289.84, d.f. = 3, $P < 0.0001$								
Touch after 10 s									
Not touched	0	0	20.1	29	21.5	31	58.3	84	144
Delay-touched	1.8	1	0	0	52.7	29	45.5	25	55
Test for effect excluding 'advance'	Total observations = 198, χ^2 = 25.33, d.f. = 2, $P < 0.0001$								
Shade of clothing worn									
Dark shade	0	0	12.2	9	32.4	24	55.4	41	74
Light shade	0	0	27.4	20	21.9	16	50.7	37	73
Test for effect excluding 'advance'	Total observations = 147, χ^2 = 5.97, d.f. = 2, $P = 0.05$								

offensive advances occurred in the small sample of 'inadvertently touched' snakes. The single immediately stepped-on advance resulted in a successful bite (the only one recorded) to a boot heel, delivered from behind while walking away after the snake's tail had been stepped on, and both advances were offensive ('Type 1' and 'Type 2'). Of the six stepped-on snakes, one advanced, two retreated, and three remained stationary. Of the six snakes that were immediately touched, two advanced, one retreated, and three became or remained stationary.

A total of 199 brownsnakes that initially ignored us or remained stationary, were approached to within 50 cm. Of these, 28% were then touched after a 10-s delay (Table 1). Omitting the single subsequent advance, the overall effect of delayed touch was highly significant (comparing touched with non-touched snakes). Most of the closely encountered non-touched snakes were stationary, and approximately equal percentages either retreated or appeared to ignore the stimulus. However, when delay-touched, one snake advanced (a defensive advance) and most of the others retreated.

All of the above data refer to encounters during daylight hours. Another 11 telemetered adult snakes were encountered during warm nights (between 2201 and 0600 hours), on the ground surface under dense ground cover. All of these snakes were touched as the vegetation that covered them was removed in order to determine snake position. None of the nocturnally encountered snakes moved, all were passive, and all relied on crypsis to avoid detection.

Shade of clothing

The shade of clothing (long-sleeved shirts) worn by the observer did not influence the snakes' flight distance or initial response. However, during prolonged encounter the snakes showed a significant tendency to ignore humans wearing light shades of clothing (Table 1).

Characteristics of the snake

Gender of the snake

There was no significant difference between the responses of male (n = 201) versus female (n = 161) snakes (Table 2).

Size of the snake

We obtained data for only 23 encounters with sub-adult (<95 cm snout–vent length) snakes. Sub-adults showed a stronger tendency to move during encounter than did adults, with 78% of sub-adults moving (mostly in retreat) compared with 52% of adults (Table 2). No sub-adult advanced during encounter and only one ignored human presence (while in ecdysis, and perhaps unable to see the observer clearly).

Prior activity of the snake

Brownsnake activity prior to encounter (moving *v.* stationary) was known on 427 occasions (Table 2). A snake's activity prior to approach significantly affected its response. Compared with stationary animals, snakes that had been moving prior to the approach were more likely to move during encounter. Overall, we recorded movement during encounter in 75% of snakes that had been moving beforehand, compared with 45% of snakes that had previously been still (see Fig. 1). The snakes were also more difficult to approach closely when moving (presumably because they are more aware of their surroundings at this time) and were more likely to retreat (Table 2).

Body temperature of the snake

The snake's body temperature was known for 36% (n = 163) of the encounters, and our analyses did not reveal any significant difference in the initial or subsequent responses of relatively cool versus warm snakes (Table 2). However, flight distance was affected, as a higher percentage of 'cool' snakes allowed closer approach ($T_b < 24°C$ *v.* $\geq 24°C$, $\chi^2 = 5.53$, d.f. = 1, $P < 0.05$). Overall, 82% of relatively cool snakes were encountered at <1.0 m compared with 59% of relatively warm snakes.

Table 2. The initial responses of free-ranging brownsnakes (*Pseudonaja textilis*) to close encounter with a human

See text for definitions of responses. The table shows the frequency of alternative responses as a function of the snakes' gender, body size, prior activity, and body temperature. The statistical results are based on contingency table tests. Because 'advance' responses were very rare we have excluded these data from some tests to maintain satisfactory expected frequencies. However, they are included in tests for movement

Advance	Ignore		Retreat		Stationary				
	%	*n*	%	*n*	%	*n*	%	*n*	Total
Snake gender encountered									
Male	4.5	9	12.9	26	45.8	92	36.8	74	201
Female	1.9	3	8.1	13	44.1	71	46.0	74	161
Test for overall effect	Total observations = 362, χ^2 = 5,69, d.f. = 3, P = 0.13								
Size of snake encountered									
Adult (≥95 cm)	3.3	12	10.8	39	45.0	163	40.9	148	362
Sub-adult (<95 cm)	0	0	4.3	1	73.9	17	21.7	5	23
Test for effect on overall movement	Total observations = 385, χ^2 = 6.03, d.f. = 1, P < 0.05								
Snake activity prior to encounter									
Was moving	1.6	2	12.0	15	61.6	77	24.8	31	125
Was still	3.0	9	8.3	25	42.4	128	46.4	140	302
Test for effect excluding 'advance'	Total observations = 416, χ^2 =18.2, d.f. = 2, P < 0.0001								
Relative body temperature									
'Cool' (<24ºC)	14.3	4	3.6	1	14.3	4	67.9	19	28
'Warm' (≥24ºC)	0.7	1	3.7	5	47.4	64	48.1	65	135
Test for effect on overall movement	Total observations = 163, χ^2 = 2.85, d.f. = 1, P = 0.09								

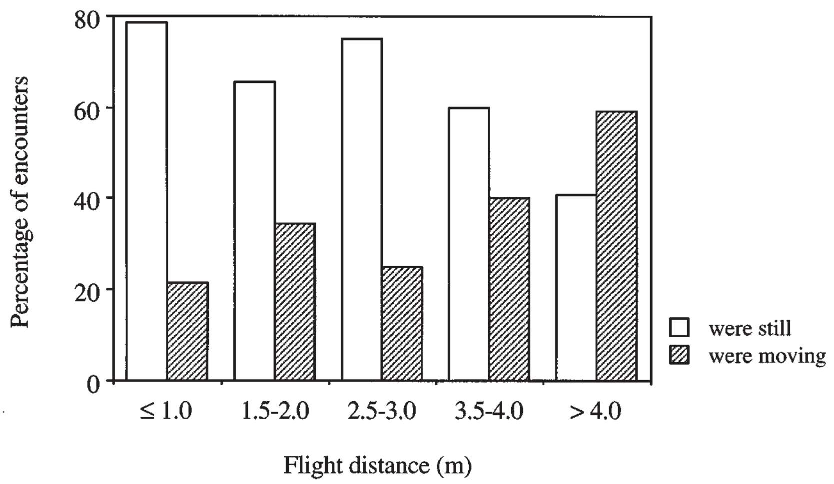

Fig. 1. The effect of prior snake activity on the flight distance of brownsnakes during human encounter.

Conditions prevailing during the encounter

Weather conditions

Wind velocity did not influence flight distance or the snakes' subsequent response, but did affect initial response (Table 3). Advances occurred in all wind speeds tested, but snakes were more likely to ignore human presence with increasing wind speed (perhaps because the animals were less likely to notice human presence in high wind, due to the swaying of vegetation). We found no evidence that wind direction affected snake response (Table 3).

At higher air temperatures more brownsnakes were moving when encountered, thus increasing flight distances (nearest metre – from ≤1 to >4 m in <24ºC *v.* ≥24°C air, $n = 412$, $\chi^2 = 16.66$, d.f. = 4, $P < 0.005$). Snakes tended to be stationary for longer periods during prolonged encounter in relatively cool air, were more likely to ignore intrusion, and were less likely to flee

Table 3. The initial responses of free-ranging brownsnakes (*Pseudonaja textilis*) to close encounter with a human

See text for definitions of responses. The table shows the frequency of alternative responses as a function of wind speed, wind direction, air temperature, vegetation cover, drought-affected vegetation cover, and season. The statistical results are based on contingency table tests. Because 'advance' responses were very rare we have excluded these data from some tests to maintain satisfactory expected frequencies. However, they are included in tests for movement

	Advance		Ignore		Retreat		Stationary		
	%	*n*	%	*n*	%	*n*	%	*n*	Total
Wind speed (nearest m s^{-1})									
≤1.0	0.8	1	8.1	10	43.5	54	47.6	59	124
2.0	3.6	3	8.3	7	52.4	44	35.7	30	84
3.0	1.2	1	9.3	8	60.5	52	29.1	25	86
4.0	4.8	3	19.4	12	45.2	28	30.6	19	62
Test for effect excluding 'advance'	Total observations = 348, $\chi^2 = 15.0$, d.f. = 6, $P < 0.05$								
Wind direction (±45° of true N & S)									
Northerly	3.6	6	10.1	17	46.4	78	39.9	67	168
Southerly	0	0	12.7	17	45.5	61	41.8	56	134
Test for effect excluding 'advance'	Total observations = 296, $\chi^2 = 0.42$, d.f. = 2, $P = 0.81$								
Relative air temperature									
'Cool' (<24°C)	3.9	8	12.3	25	46.1	94	37.7	77	204
'Warm' (≥24°C)	1.4	3	5.8	12	50.5	105	42.3	88	208
Test for overall effect	Total observations = 412, $\chi^2 = 8.14$, d.f. = 3, $P < 0.05$								
Relative vegetation cover									
Sparse (<50%)	4.5	8	11.2	20	59.6	106	24.7	44	178
Dense (≥50%)	1.7	4	6.1	14	41.6	96	50.6	117	231
Test for overall effect	Total observations = 409, $\chi^2 = 29.62$, d.f. = 3, $P < 0.0001$								
Test for effect on overall movement	Total observations = 409, $\chi^2 = 26.78$, d.f. = 1, $P < 0.0001$								
Drought-affected vegetation cover									
Average spring	2.0	4	13.0	26	48.0	96	37.0	74	200
Drought spring	2.6	3	6.8	8	56.4	66	34.2	40	117
Average summer	2.9	1	0	0	67.7	23	29.4	10	34
Drought summer	0	0	5.6	2	19.4	7	75.0	27	36
Average autumn	0	0	18.8	3	62.5	10	18.8	3	16
Drought autumn	6.9	2	0	0	31.0	9	62.1	18	29
Test for movement: between springs	Total observations = 317, $\chi^2 = 4.13$, d.f. = 1, $P < 0.05$								
between summers	Total observations = 70, $\chi^2 = 14.58$, d.f. = 1, $P < 0.005$								
between autumns	Total observations = 45, $\chi^2 = 7.77$, d.f. = 1, $P < 0.01$								
Overall seasonal response									
Spring	2.2	7	10.7	34	51.1	162	36.0	114	317
Summer	1.4	1	2.9	2	42.9	30	52.9	37	70
Autumn	4.4	2	6.7	3	42.2	19	46.7	21	45
Winter	8.7	2	8.7	2	39.1	9	43.5	10	23
Test for movement, excluding winter	Total observations = 432, $\chi^2 = 1.76$, d.f. = 2, $P = 0.41$								

under these conditions (Table 4). Most of the initial advances occurred in relatively low air temperatures (Table 3), but the three offensive advances occurred over a broad range of ambient temperature (19–35ºC).

Snake responses were apparently independent of cloud cover except that snakes tended to remain stationary, and not retreat, during prolonged close encounter in the presence of cloud (Table 4).

Table 4. The subsequent (10-s) responses of free-ranging brownsnakes (*Pseudonaja textilis*) to close encounter with a human

See text for definitions of responses. The table shows the frequency of alternative responses as a function of air temperature, presence of cloud, and vegetation cover. The statistical results are based on contingency table tests. Because the 'advance' response was very rare it has been excluded from tests to maintain satisfactory expected frequencies. However, it is included in the test for movement

	Advance		Ignore		Retreat		Stationary		
	%	*n*	%	*n*	%	*n*	%	*n*	Total
Relative air temperature									
'Cool' (<24ºC)	0	0	24.0	23	13.5	13	62.5	60	96
'Warm' (≥24ºC)	1.1	1	4.4	4	48.4	44	46.2	42	91
Test for effect, excluding 'advance'	Total observations = 186, $\chi^2 = 33.25$, d.f. = 2, $P < 0.0001$								
Presence of cloud (≥10% cover)									
Present	0	0	16.2	24	25.7	38	58.1	86	148
Absent	2.1	1	10.6	5	42.6	20	44.7	21	47
Test for effect on movement	Total observations = 195, $\chi^2 = 4.45$, d.f. = 1, $P < 0.05$								
Relative vegetation cover									
Sparse (<50%)	0	0	22.8	13	22.8	13	54.4	31	57
Dense (≥50%)	0.8	1	9.0	11	35.2	43	54.9	67	122
Test for effect, excluding 'advance'	Total observations = 178, $\chi^2 = 7.41$, d.f. = 2, $P < 0.05$								

Vegetation cover

The percentage vegetation cover over encountered brownsnakes was estimated on 409 occasions, and analyses suggest that this variable strongly affects brownsnake responses to encounters withhumans (Table 3). Overall, a significantly higher percentage of the snakes initially moved during approach when sparsely covered by vegetation (70%) than they did when densely covered (45%). Flight distance was also strongly affected, with snakes under thick cover tolerating much closer approach (overall, 64% of 231 snakes 50% covered were encountered at ≤1 m).

The snakes were also significantly more likely to remain stationary when densely covered, although the degree of vegetation cover did not influence the percentage of snakes recorded as subsequently stationary during prolonged encounter (Table 4). Most advances occurred with <10% vegetation cover, and two other snakes advanced with approximately 20% cover. Vegetation cover over encountered snakes was significantly related to prior activity (for <50 and >50% covered, $n = 394$, $\chi^2 = 13.71$, d.f. = 1, $P < 0.001$). Of the animals that were moving prior to encounter, 58% were sparsely covered compared with 38% that had been stationary; this result reflects the tendency for brownsnakes to restrict periods of immobility while above-ground to denser ground cover except during late winter and early spring.

Effects of drought

Seasonal differences in the snakes' response to encounter may be due to changes in vegetation cover – especially during the second (drought-affected) year, when vegetation was very sparse. Compared with the same (spring) season in the first and third years of our study, the percentage of snakes that initially moved when encountered was significantly higher during the drought-affected spring. Conversely, there was a significant decrease in initial movement during the drought summer and autumn (Table 3). Hence, drought affected the snakes' response differently in different seasons: it increased the snakes' tendency for initial movement during spring, but decreased it in summer and autumn (Fig. 2).

As would be expected from the snakes' greater tendency to remain stationary in thicker vegetation (see above), flight distances during spring were greater during the drought year than in the other years (for distances of ≤ 1 *v.* ≥ 1 m, $n = 317$, $\chi^2 = 3.82$, d.f. = 1, $P = 0.05$). The percentage of snakes fleeing at >4 m distance increased from 6 to 17% during the drought-affected spring. Reproductive males showed an increased tendency to retreat rather than to ignore the observer at this time (Table 3), which may reflect the lower intensity of reproductive activity during drought (Whitaker and Shine, unpublished data). Again, however, this pattern was reversed in summer and autumn, with most snakes allowing closer approach in the drought year (for summer: $n = 70$, $\chi^2 = 15.01$, d.f. = 1, $P < 0.001$; for autumn: $n = 45$, $\chi^2 = 5.94$, d.f. = 1, $P < 0.05$). This apparent paradox reflects an increased tendency for the snakes to remain in the limited patches of thick vegetation at these times.

Vegetation cover in the study area was markedly reduced during the summer and autumn of drought; brownsnakes during this period showed a reluctance to move when encountered and a stronger tendency to rely on crypsis than they did in near-average rainfall years (see Fig. 2). Most snakes fled when adequate cover was available, but not when cover was limited (Table 3). While response to encounter differed with low cover availability during drought, the proportion of snakes encountered under dense cover did not change (for <50 *v.* $\geq$50% cover, $n = 409$, $\chi^2 = 0.93$, d.f. = 1, $P = 0.34$). Hence, snake locations were generally more predictable during drought, due to the patchiness of dense vegetation.

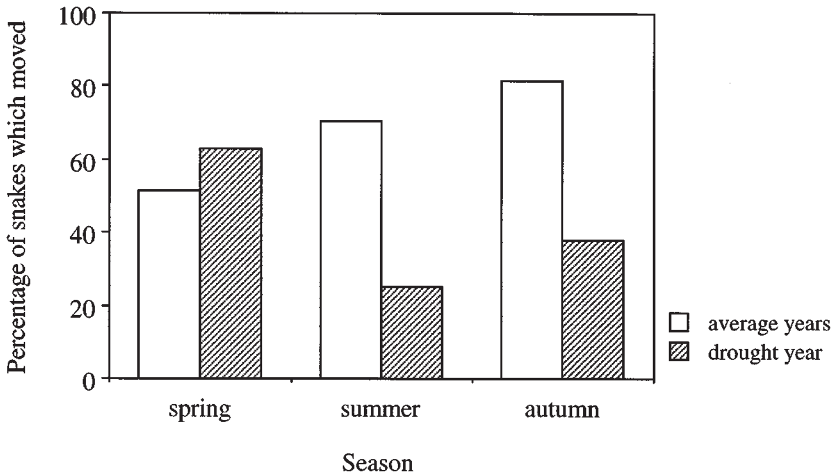

Fig. 2. The percentage of encounters where brownsnakes initially moved in response to human approach, under two circumstances: in seasons with average rainfall and in those affected by drought.

Temporal factors

Because a brownsnake's response to encounter depends on the amount of vegetation that covers it (above), we would expect temporal shifts in the responses of snakes if vegetation cover changed markedly through the seasons or between years (because of drought in one year). Our data show several such effects.

Effects of year

Half of the 12 initial advances, including all 'offensive' advances, occurred during the drought-affected year when cover availability was very low. All initial advances during the near-average rainfall years were either defensive or passive responses.

Effects of season

The percentage of vegetation cover over encountered snakes differed significantly among seasons ($n = 386$, $\chi^2 = 10.93$, d.f. = 2, $P < 0.005$). In all seasons when brownsnakes were active, they were typically encountered underneath vegetation. Nonetheless, the percentage of snakes encountered under dense cover increased significantly during summer (in all years): on average, 74% of the snakes encountered in summer were densely covered compared with 52% in spring and 56% in autumn. The snakes' selection of dense cover in summer resulted in increased rates of close encounter at this time (with 61% of snakes encountered at <1.0 m).

The snakes' initial response to our approach also varied among seasons. During spring, they were likely to retreat rather than remain stationary. In other seasons, they were likely to remain stationary. However, these results reflect the effect of drought on the snakes' response: in average-rainfall years the tendency for the snakes to retreat during summer and autumn was higher than in spring (Table 3). Overall, initial 'ignore' responses were also most likely during spring (in the mating season: late September to mid October), except during drought, and least likely during summer. Of all 'ignore' responses, 83% occurred in spring, largely while the snakes were hunting (males and females) or courting (males only).

The highest percentage of initial advances occurred in late autumn and winter, although most initial advances (in absolute terms) were recorded in spring (Table 3). All offensive responses were recorded in early spring, and initial advances during summer and autumn were either defensive or passive.

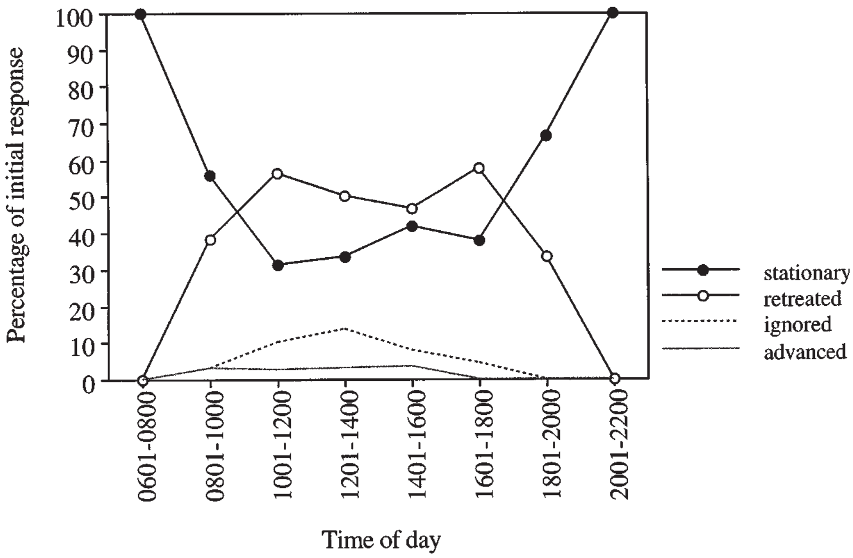

Fig. 3. The percentages of brownsnakes showing different kinds of initial responses (i.e. that advanced, ignored, retreated or remained stationary) in response to human encounter, as a function of the time of day when the encounter took place.

Effect of time of day

All snakes encountered before 0800 hours or after 2000 hours remained stationary, passive, and cryptic (see Fig. 3). More snakes retreated than remained stationary between 1001 and 1800 hours, and the snakes showed an increased tendency to ignore encounter during the middle of the day. All advances were recorded between 0801 and 1600 hours, and mostly between 1201 and 1600 hours. This latter period included all of the offensive responses.

Discussion

First, we summarise the results provided above, and speculate on the causal mechanisms underlying snake responses. Our major conclusions include the following:

(1) Contrary to public opinion, free-ranging brownsnakes are very reluctant to attack humans when encountered. Overall, fewer than 3% of encounters resulted in the snake advancing toward the antagonist, and only one in four of these advances were offensive. Instead, most snakes responded by retreating (about half of all encounters); the others either ignored us, or remained stationary. This result will not surprise herpetologists (e.g. Duvall *et al.* 1985; Prior and Weatherhead 1994), but runs counter to the prevailing (almost ubiquitous) opinion of the general populace. Numerous authors have mentioned that eastern brownsnakes defend themselves more vigorously than do other Australian snakes (e.g. Fleay 1943; Gow 1987; Shine 1991). We do not dispute this conclusion; when cornered, *P. textilis* will confront the aggressor and will sometimes pursue a fleeing adversary. If any Australian snake was likely to launch unprovoked attacks, the eastern brownsnake would be the most likely candidate. The fact that it does not do so suggests that unprovoked offence is likely to be very rare in other Australian snakes also.

(2) Whenever we approached a brownsnake slowly, it was likely to remain stationary, and very unlikely to attack. A similar effect of approach speed on flight distance is predicted by theoretical models (Ydenberg and Dill 1986) and has been documented in one lizard species (Cooper 1997). Most snakes tolerated surprisingly close encounter, depending on ground cover. Touching a snake immediately upon encountering it was likely to induce an attack, but a snake that was gently nudged and tapped after a 10-second delay tended to flee instead. Movement and tactile cues may be important in this regard; both may lead to increased offence in snakes (Scudder and Burghardt 1983; Herzog and Burghardt 1986; Herzog *et al.* 1989). These results suggest that brownsnakes opt for attack only in retaliation to a perceived danger to themselves (or as a last resort in a sequence of antipredator responses: Greene 1988). This inference might seem dubious, given the apparent invulnerability of a large and deadly snake. However, brownsnakes in our study area are frequently killed by humans, feral cats and raptorial birds (Whitaker and Shine, unpublished data), so predation pressure is strong. Light shades of clothing made it more likely that the snake would ignore us during prolonged close encounter, perhaps because we were not noticed, and this finding suggests a camouflaging effect against cloudy skies (see Götmark 1987; Whitaker and Shine 1999).

(3) A tendency to retreat rather than to rely on crypsis was most evident in sub-adult brownsnakes, in snakes with relatively high body temperatures, and in snakes (of all sizes) that were moving prior to the encounter. Plausibly, these patterns reflect variation in the snakes' ability to adopt different defences. Sub-adults flee because they are less able to repel attack (Ford and Burghardt 1993), warm snakes flee because locomotor ability is enhanced at higher temperatures (Heckrotte 1967; Bennett 1980), and moving snakes keep moving because crypsis is unlikely to be successful if the potential predator has already seen them (Davis 1953; Arnold and Bennett 1984; Greene 1988). Most advances occurred when snakes had not been moving prior to the approach, perhaps because the animals tolerated closer approach under these conditions. In contrast, rattlesnakes (*Sistrurus miliarius*) that were uncoiled when encountered, were more likely to strike at the observer (May *et al.* 1996).

(4) Some aspects of the weather (ambient temperature, wind speed, presence of cloud) affected snake responses, whereas other aspects (wind direction, percentage cloud cover, cloud height) apparently did not. The snakes moved more frequently under windy conditions, perhaps

because they are less obvious to predators in such weather (Jackson 1974; Greene *et al.* 1978). Low air temperatures and cloud cover increased the probability that snakes would remain stationary during prolonged close encounter. The effects of cloud and air temperature near the ground surface in this respect are likely to be independent, because these two variables were not significantly correlated over the course of our study (Whitaker 1999). Cool cloudy days in spring constrain the snakes' ability to attain high body temperatures, which may also constrain locomotor speed, and favour reliance on crypsis. However, the tendency for crypsis was also marked in summer when the snakes were reluctant to move away from available cover, possibly as a consequence of excessive thermal conditions. Hence, the effect of temperature on antipredator response varied with time of year and was tempered by availability of cover (see below).

(5) The thickness of vegetation cover over a brownsnake strongly influenced its response: snakes under dense cover were less likely to move away and more likely to tolerate close approach. These biases may reflect the snakes' difficulty in detecting the intruder, but shifts in the position of telemetered snakes as we approached them suggest that the majority of closely encountered snakes were aware of our presence. Hence, these snakes tend to rely on crypsis when well hidden. The ways in which rattlesnakes (*Crotalus viridis*) respond to human intrusion also depend on their proximity to cover (Duvall *et al.* 1985). All offensive advances in brownsnakes were recorded with <20% vegetation cover, suggesting that the snakes use offensive behaviour when crypsis is ineffective.

(6) Snake response differed between a drought year and two years of near-average rainfall. However, the effects were complex and differed among seasons. Some of the effects of drought were probably indirect consequences of changes in vegetation density, whereas others may reflect decreased reproductive activity in drought (Whitaker and Shine, unpublished data). All offensive advances occurred during the drought.

(7) The highest percentages of initial 'retreat' and 'ignore' responses occurred during spring, whereas the snakes were most likely to be stationary during summer – when availability of cover is typically low. However, the effect of drought on snake response biased this finding, because the snakes typically fled in average-rainfall years. All snakes encountered before 0800 and after 2000 hours were stationary, whereas most that were encountered between 1000 and 1800 hours retreated. This pattern is unlikely to result from increased locomotory abilities of warm snakes later in the day, because the pattern was evident during summer as well as in cooler seasons.

In summary, a snake's response to encountering a human was influenced by factors related to the observer, the snake, the habitat, and the time that the encounter occurred (see Fig. 4). Inevitably, many of the relevant variables are inter-correlated; for example, time of day versus ambient temperature. This makes it difficult to infer causal connections from the correlational patterns linking external variables to snake response. In practice, however, the end result is that snake behaviour is relatively predictable under given sets of circumstances, and our data thus enable us to suggest ways to manipulate snake responses so as to reduce the incidence of snakebite. Even if we do not understand the actual causation, we can use empirical patterns to generate useful recommendations.

The degree of danger to a human who encounters a brownsnake depends upon: (a) the probability of the snake remaining stationary (i.e. relying on crypsis) rather than moving; and (b) if it moves, the snakes' preparedness to attack rather than retreat. Our study provides extensive data on the first of these questions, but more limited information on the second (because offensive behaviour was exhibited so rarely).

Our data suggest that the risk of envenomation from brownsnakes can be reduced in the following ways:

(1) Walk slowly, wear dark shades of clothing, and do not move hands quickly at ground level. The slow walking speed will increase the probability of encountering a snake in close proximity, but will substantially reduce the probability that the snake will react offensively. The snakes are more likely to notice dark clothing and hence move away.

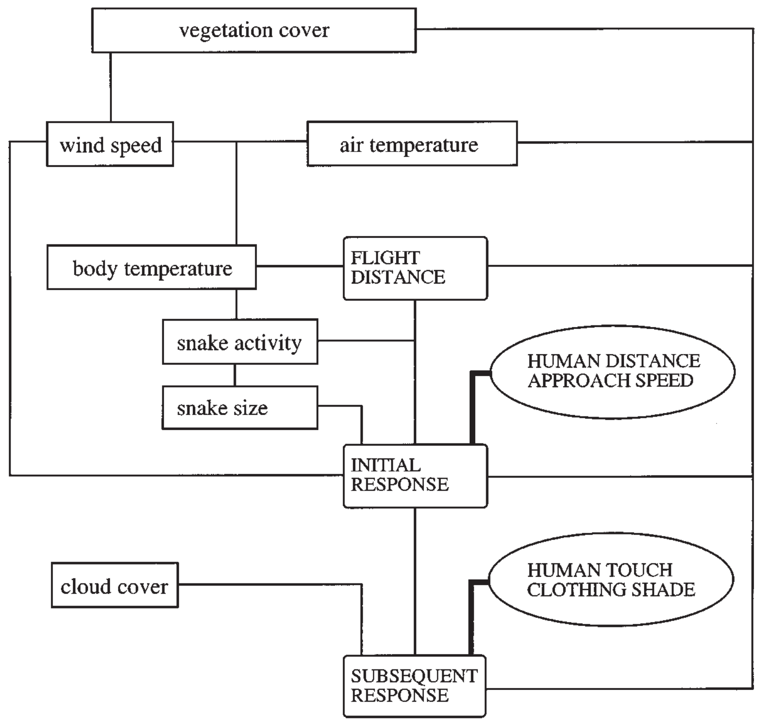

Fig. 4. Flow diagram showing the attributes of the environment, the snake, and the observer that significantly affected the ways in which brownsnakes responded to an encounter with a person.

(2) Avoid undisturbed areas (which are potential mating areas) on cool days during spring (especially in September and October). Avoiding these areas will reduce the chance of encounter with a courting or mating male snake (animals which are more easily startled, because they are often unaware of a persons' approach until he/she is very close). Similarly, very cool snakes (as is likely to be the case soon after emergence from winter inactivity) are less likely to flee, and thus constitute more of a danger.

(3) Be cautious on days with high wind (>4.0 m s^{-1}), especially if it is cool and cloudy, because the snakes are less likely to notice people in close proximity and may be more easily startled. Also, closely encountered snakes are more likely to remain stationary when cloud is present.

(4) Walking on thick ground cover is relatively safe during most of the year, especially during summer and during drought. The snakes will often not retreat, but are very unlikely to attack either. However, avoid tall tussock grasses with small open areas during spring (because these are often used as mating areas) and wear protective clothing (thick trousers and footwear) in ungrazed areas while walking between dense ground cover; this is especially important during drought. Roaming males in spring are less likely to notice people than they are at other times of the year, and are more likely to be startled and offensive. Brownsnakes are less likely to be closely encountered (although generally more visible) when cover is unseasonally low in spring (because flight distance increases), but there is an increased risk of offence if the snakes are startled. The snakes are more likely to be closely encountered, and their positions more predictable, if cover is extremely low and patchy in summer and autumn. However, there is a minimal risk of offence even when snakes are touched under these circumstances.

(5) Avoid walking in brownsnake refuge areas between late morning and mid-afternoon, especially during spring. More snakes are likely to advance during spring, and the risk of offence seems to be highest during the early afternoon.

(6) Although moving brownsnakes are more likely to be noticed by people than those that are stationary (as stationary brownsnakes are highly cryptic), our study shows that most encounters are with stationary snakes. Moving *P. textilis* are alert to human encounter, except during the breeding season. Hence, the snakes most often seen by people are less likely to advance and are more likely to continue on their way than are the snakes they don't see. Nonetheless, there is a distinct difference in antipredator response between stationary animals that are at least partly hidden and cryptic, and those that are stationary and away from cover. It is the *P. textilis* that do not retreat (as occurs in about half of all encounters) that pose the potential threat, especially if suddenly approached and touched while uncovered in spring. Most risk is associated with initial approach, and closely encountered animals that rely on crypsis pose little threat, even when gently stepped-on or prodded – providing the animals are covered and left unmolested. Brownsnakes may ignore encounter either because they are incapable of seeing the stimulus or because they are preoccupied (e.g. with their heads inside burrows or tussocks while hunting or courting). While apparently ignoring people in this situation, the animals are easily startled and may react vigorously with immediate offence.

Overall, our findings belie this animal's reputation for 'aggression'. Instead, eastern brownsnakes are very wary of people and avoid them whenever they can. We cannot speak with confidence about brownsnakes from other parts of the species' range, but our extensive experience with this taxon over many years does not suggest any marked geographic differences in snake response. We believe that virtually all 'attacks' by brownsnakes are launched as a response to real or perceived attacks upon the snakes by people, or by the dogs accompanying those people. Clearly, geographic differences in vegetation cover and weather conditions, as well as in the nature of human activities, will cause substantial variation in the contexts in which encounters occur. Nonetheless, our study area was chosen to be representative of the habitats and farming activities typical over much of the eastern brownsnakes' range. Thus, we anticipate that patterns of brownsnake response to human encounter in many other areas are likely to be similar to those that we have documented.

Acknowledgments

We thank G. Cann for his useful on-site comments, and S. Downes and M. Olsson for comments on the manuscript. This project was funded by the Australian Research Council.

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Manuscript received 3 June 1998; accepted 26 November 1998