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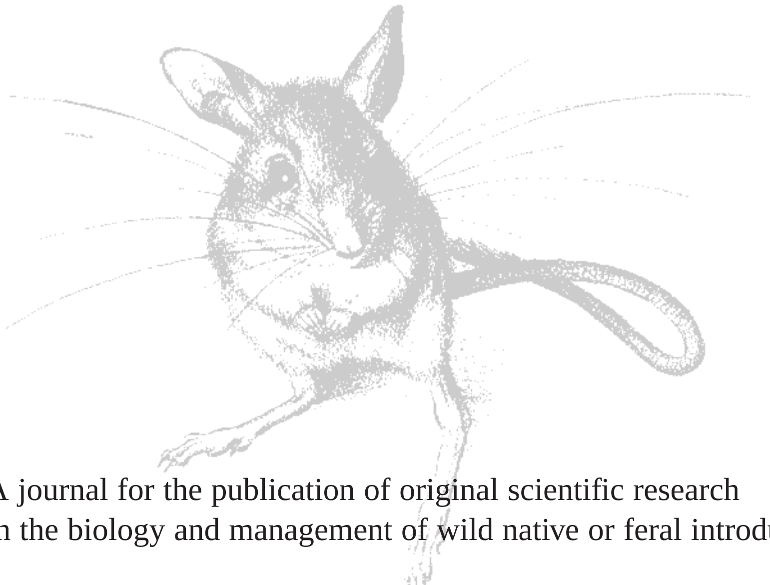

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When, where and why do people encounter Australian brownsnakes (*Pseudonaja textilis* : Elapidae)?

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Abstract

Encounters between humans and dangerously venomous snakes put both participants at serious risk, so the determinants of such encounters warrant attention. *Pseudonaja textilis* is a large fast-moving elapid snake responsible for most snakebite fatalities in Australia. As part of a broad ecological study of this species in agricultural land near Leeton, New South Wales, we set out to identify factors influencing the probability that a human walking in farmland would come into close proximity to a brownsnake. Over a three-year period, we walked regular transects to quantify the number and rate of snake encounters, and the proportion of snakes above ground that could be seen. The rate of encounters depended upon a series of factors, including season, time of day, habitat type, weather conditions (wind and air temperature) and shade (light *v.* dark) of the observers' clothing. Interactions between factors were also important: for example, the effect of air temperature on encounter probability differed with season and snake gender, and the effect of the observers' shade of clothing differed with cloud cover. Remarkably, even a highly-experienced observer actually saw <25% of the telemetrically monitored snakes that were known to be active (i.e. above ground) nearby. This result reflects the snakes' ability to evade people and to escape detection, even in the flat and sparsely vegetated study area. The proportion of snakes that were visible was influenced by the same kinds of factors as described above. Most of the factors biasing encounter rates are readily interpretable from information on other facets of the species' ecology, and knowledge of these factors may facilitate safer coexistence between snakes and people.

Introduction

Over much of the world, people live in close proximity to venomous snakes that have the potential to inflict serious or fatal injury. Although the interaction between dangerous snakes and humans attracts considerable public interest, there have been no substantial scientific attempts to quantify the determinants of such encounters with free-ranging snakes. Instead, influences on rates of encounter have been inferred indirectly from knowledge of a species' ecology and behaviour (e.g. Mirtschin and Davis 1982; Starin and Burghardt 1992). In this paper we describe a more direct method, with less reliance on inference. We walked a large number of standardised transects through an area inhabited by a venomous snake species, in order to quantify determinants of the probability of encountering these animals at close range. The resulting data set enables us to carry out the first rigorous analysis of the way in which factors such as environmental variables (e.g. habitat type, weather, season, time of day) and snake characteristics (e.g. gender, body size) influence the probability that a person will come into contact with a dangerous snake.

There are two main justifications for a study such as this. First and most obvious are the implications for public health. At present, the scarcity of reliable information impedes our ability to make sensible recommendations on how people can minimise potentially dangerous confrontations with snakes. Requests for information on this topic are frequent in rural areas. Unfortunately, although advice is easy to come by in the bar of any country hotel, it is generally based on very unreliable information. Secondly, a better understanding of the factors predisposing towards encounters between snakes and people would be of benefit from a conservation perspective, because several of the animal species dangerous to humans

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(especially, large predators) are becoming increasingly rare and are of significant conservation concern in their own right. By minimising risky encounters, both the snakes and humans can benefit.

Australia has no native mammal species that pose a significant danger to humans, and over most of the continent the only 'dangerous' native terrestrial vertebrates are elapid snakes. Australia is unique in having most of its endemic snake fauna composed of venomous species, and snakebite fatalities have been recorded since the earliest days of European settlement (e.g. Fairley 1929). Snakebite fatalities continue to occur, and recent surveys suggest that brownsnakes (genus *Pseudonaja*) are the most important taxon in this respect (Sutherland 1992). These agile, fast-moving snakes are abundant in disturbed agricultural landscapes over much of the continent (e.g. Longmore 1986) and have highly toxic venom. Indeed, on the basis of laboratory testing with rodents, the eastern brownsnake (*P. textilis*) has the second most highly toxic venom (at least for rodents) of any snake species yet tested worldwide (Broad *et al.* 1979). Because the eastern brownsnake is the single most important Australian snake species in terms of snakebite fatality (Sutherland 1992), it is the logical choice as a study organism to examine the determinants of dangerous encounters between snakes and humans.

This paper describes one component of a wide-ranging ecological study of *P. textilis*, based primarily on radio-tracking (Whitaker 1999; Whitaker and Shine, unpublished data). In related work, we have also examined the snakes' response to human intrusion, and the temperature dependency of offensive behaviour and strike speed (Whitaker 1999; Whitaker and Shine 1999).

Methods

Details of the techniques used for telemetry and the monitoring of body temperature, activity, movement and weather conditions are given elsewhere (Whitaker 1999).

Study area

We chose the intensely farmed Murrumbidgee Irrigation Area for study, near the town of Leeton in inland New South Wales (34º39′S, 146º28′E), because it is fairly typical of the topography, climate and land-use patterns experienced over much of the southern portion of the geographic range of *P. textilis*. Although this snake extends into much warmer regions as well (Cogger 1992), the incidence of snakebite is greatest in south-eastern Australia (White 1981; Sutherland 1996). The Murrumbidgee Irrigation Area experiences hot dry summers and cool moist winters. Average annual rainfall is less than 450 mm and, while rainfall occurs in all months, the highest falls occur in October and the lowest in February. Mean maximum and minimum air temperatures (T_a at 1.8 m height) are 31.6 and 16.8ºC in January (the hottest month) and 13.6 and 3.2ºC in July (the coolest month).

The study area was predominantly flat pasture and cropland at an approximate elevation of 150 m above sea-level; the only significant relief consists of irrigation embankments. The study focused on an ungrazed 3000 m × 25 m wide section of canal bank ('central refuge area'), approximately 40% of which was continuously occupied by brownsnakes, and on surrounding farmland. The central refuge area represents relatively uniform and undisturbed brownsnake habitat. This area comprised red-to-grey clay and sandy-loam soils, covered with weeds, tussock grasses and sparse tree cover (eucalypts). Domestic animals were excluded from the refuge area during our study, and had been for the preceding seven years. The site was bordered by non-irrigated farms to the north and irrigated farms to the south. Farm produce during the study included wheat and wool (non-irrigated bi-annual regime), and rice or sorghum and wool (irrigated tri-annual regime, including a fallow year).

Study species

Pseudonaja textilis is a slender, agile, fast-moving elapid snake which in morphology and behaviour closely resembles the American coachwhip, *Masticophis flagellum*. The snake may reach 2 m in total length (Cogger 1992), although Leeton specimens rarely exceed 1.7 m (adult mean of 1.45 m). Hatchlings in our study area exhibit a banded head and neck, but attain the adult colouration (monotonal brown dorsally and cream or brown, often flecked with orange or brown, ventrally) by their third year of life. These snakes are active generalised predators on small vertebrates, but in agricultural habitats (where they often attain high densities) adult snakes feed mostly on introduced house-mice, *Mus domesticus*, switching to other vertebrates when mouse numbers are low (Shine 1989).

Transects

In much of the area occupied by *P. textilis,* the dominant human activities that bring people close to snakes involve day-to-day agricultural tasks. We thus used a relatively simple system to record the number of snakes encountered, by walking predetermined transects and recording the number of snakes seen. Our intention was to simulate this component of a farmer's normal activities. The transects we walked were along relatively undisturbed routes that we judged to be optimal for encountering snakes. Thus, we walked along northern aspects during spring and southern aspects and fence-lines during summer on the central refuge area; and along vegetated irrigation channel banks, edges of dense vegetation, and fence lines (especially next to cereal crops) on surrounding farmland. All transects were walked slowly (at approximately 1 km h^{-1}) and, where possible, while facing into the wind and away from the position of the sun, in order to maximise sightings while scanning the ground to 5 m each side of the line walked.

These data have the benefit of controlling for other factors, but may fail to incorporate other situations, or inadvertently bring in biases. Therefore, in addition to transects on the central refuge area, we walked transects each month on surrounding farmland in order to estimate the rate of encounter in other rural situations. These additional transects were walked only after completing a transect on the central site, to control for temporal shifts in snake activity. The location and timing of 'farm transects' were not fixed due to frequent disturbance from farm practice. We also recorded all occasions, throughout the entire three-year study, when brownsnakes were encountered.

We used three different measures for determining the probability of encounter: the overall number of encounters (summed over the entire study period in the general study area), the hourly rate of encounter (on standardised transects), and the number of snakes sighted as a proportion of the total number that we knew (from telemetry data) to be 'active' (i.e. above-ground) at that time (central refuge area transects only). We incorporated this third measure because the first two variables include only a sub-set of encounters, i.e. those in which the human observer became aware of the snakes' presence (by sight or the noise of a snake moving through dry grass). Many other 'encounters' (with the potential for snakebite) may occur in situations where the observer is unaware of the snakes' proximity. Because the adult snakes in the central study area were telemetered it was often possible to determine from the telemetry signal (body temperature, movement, signal strength) when a given snake emerged from below-ground. This allowed us to determine the number of snakes that were active at the time a transect was walked. Thus, for a sub-set of transects, we could determine the proportion of active snakes in close proximity (<5 m) that were sighted by the observer, as well as the absolute number of snakes that were seen. We restricted these analyses to times when at least two snakes were known to be active in a given transect area.

Because snakes of different size and gender may differ in their patterns of activity (e.g. Gibbons and Semlitsch 1987; Shine 1993), as well as in their venom yield (Sutherland 1992) and response to human proximity (Whitaker and Shine 1999), we also examined the ways in which these attributes influenced the probability of encounter.

Results

Trends in overall frequency of encounter in the general study area

Overall, the frequency of encounter in the general study area (on and off transects) during daylight hours (0601 to 2000 hours) for the first two years of study (1 September 1993 to 31 August 1995) showed significant differences among seasons ($n = 350$, $\chi^2 = 14.24$, d.f. = 3, $P < 0.01$). Of these 350 encounters, 67.0% were recorded in spring, 13.8% in summer, 12.6% in autumn, and 6.6% in winter (Fig. 1). Most of the overall daylight encounters recorded during these two years occurred in the afternoon (67.1% between 1201 and 1700 hours). However, the tendency for afternoon encounter did not extend to summer, where overall encounter rates were similar in the morning and afternoon (Fig. 1).

Transects

During 32 months of study (October 1993 to March 1996) 305 transects were walked over a total of 510 hours. Transects on the central refuge site were walked on 213 occasions (69.8% of transects) over a total of 423.5 hours and an average length of 2.0 km. Those on surrounding farmland were walked on 92 occasions over a total of 86.5 hours and an average length of 0.94 km.

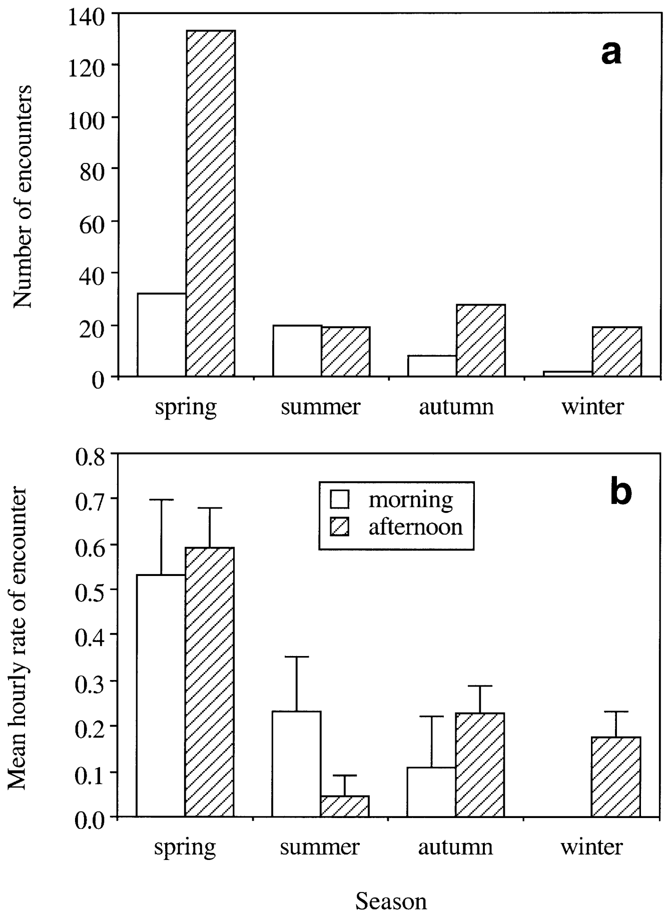

Fig. 1. (*a*) Overall frequency of encounters with eastern brownsnakes in the morning (0701–1200 hours) and afternoon (1201–1700 hours) during spring (September–November), summer (December–February), autumn (March–May), and winter (June–August), during two years (September 1993 to August 1995). (*b*) Mean rates of encounter with brownsnakes (± s.e.) on transects during the morning and afternoon in each season.

Overall encounter rates on transects

In total, 231 brownsnakes were encountered on transects (mean rate = 0.45 snakes h^{-1}); 210 of these were recorded on the central refuge area (mean rate = 0.50 h^{-1}). The resident population on this area consisted of 41–45 adult snakes (Whitaker 1998), so many of these encounters were undoubtedly with the same individuals. However, we did not attempt to control for this non-independence in our analyses. In many cases, we could not discern the identity of individual snakes seen on transects, and we saw no evidence of any behaviour modification (e.g. habituation) in the central refuge area snakes during our study, nor any overt differences in response between the (frequently disturbed) refuge area snakes *versus* snakes in other areas (Whitaker and Shine 1999). In practice, human activities in this intensively farmed region are sufficiently frequent that most snakes probably encounter humans on a regular basis.

In contrast to the high encounter rates on the central refuge area, only 21 brownsnakes were encountered in comparable habitats on surrounding farmland (mean rate = 0.24 snakes h^{-1}).

Thus, the mean hourly encounter rate was significantly higher on the central refuge area than on the 'farm' transects (one-factor ANOVA, $F_{1,303} = 6.52$, $P = 0.01$). However, our preliminary analyses showed that general patterns of encounter were similar in refuge and farmland areas, so we have pooled these data sets (where appropriate) in the following analyses.

Overall proportion of active snakes that were sighted

Of the transects in the central refuge area, 122 (40.0%) were walked at times when at least two brownsnakes were known to be active on the 10-m wide transects. On average, only 23.2% (s.d. = 30.2) of these snakes were sighted by the observer.

Differences in encounter rates and observability between years

The study included two full years, allowing annual comparison using data from a total of 264 transects. Mean hourly encounter rates did not differ significantly among years (one-factor ANOVA, $F_{1,262} = 0.95$, $P = 0.33$), with rates of 0.33 h^{-1} ($n = 120$, s.d. = 0.56) during the first year and 0.41 h^{-1} ($n = 144$, s.d. = 0.68) during the second. Similarly, the total mean percentage of active snakes sighted was virtually identical in the two years (one-factor ANOVA, $F_{1,92} = 1.67 \times 10^{-7}$, $P = 1.0$; mean = 24.6% in each year; for Year 1, $n = 46$, s.d. = 35.45; for Year 2, $n = 48$, s.d. = 28.91).

Differences in encounter rates and observability among seasons

Mean hourly rates of encounter varied among seasons (one-factor ANOVA, $F_{3,301} = 13.35$, $P < 0.0001$). Fig. 2*a* shows that the highest encounter rates were recorded in spring (September), and the lowest in summer (no encounters were recorded in February) and winter (July). Deletion of randomly selected transects to achieve equal sample sizes (20 per season) and control for time effects (all walked between 0801 and 1600 hours) did not change the overall seasonal pattern, nor alter significance of the differences (one-factor ANOVA, $F_{3,76} = 4.77$, $P < 0.01$). The mean percentage of active snakes that were seen by the observer also differed among seasons (one-factor ANOVA, $F_{3,118} = 3.80$, $P = 0.01$), being highest in spring and lowest in summer (Fig. 2*b*).

Differences in encounter rates and observability at different times of day

Brownsnakes were primarily diurnal, with few records of nocturnal activity (2.4% of 462 encounters); hence, analyses were restricted to daylight hours. Data for encounter rate versus time of the day were taken on standardised transects (1500 m long) walked wholly between 0700 and 1700 hours. These data showed no significant difference in mean hourly rate between morning versus afternoon (after 1200 hours) (one-factor ANOVA, $F_{1,211} = 1.45$, $P = 0.23$), or in the percentage of active snakes that could be seen (one-factor ANOVA, $F_{1,90} = 2.74$, $P = 0.10$). However, the rate of encounter during the morning in spring and summer was higher on sites that we judged to be optimal for brownsnakes than was the case in surrounding areas (Fig. 1*a* cf. 1*b*).

Effects of weather on encounter rates and observability

Air temperature

Transects for recording mean hourly rate of encounter were walked on 244 occasions when mean shaded air temperature (aspirated T_a at 4 cm height) was known. Overall, there was a significant difference in the hourly rate of encounter in relatively cool ($T_a \leq 24$ºC) versus warm ($T_a > 24$ºC) air (one-factor ANOVA, $F_{1,243} = 5.55$, $P < 0.05$). Fig. 3 shows a positive correlation between mean hourly rate of encounter and T_a (for 6.0°C categories, $r^2 = 0.88$, $P < 0.05$). However, Fig. 3 also presents a paradox: although we encountered more snakes in warmer conditions, each telemetered snake was actually less likely to be seen as T_a increased ($r^2 = 0.97$, $P < 0.01$). Hence, under cooler conditions we saw fewer snakes, but saw a higher proportion of the snakes that were above-ground at the time.

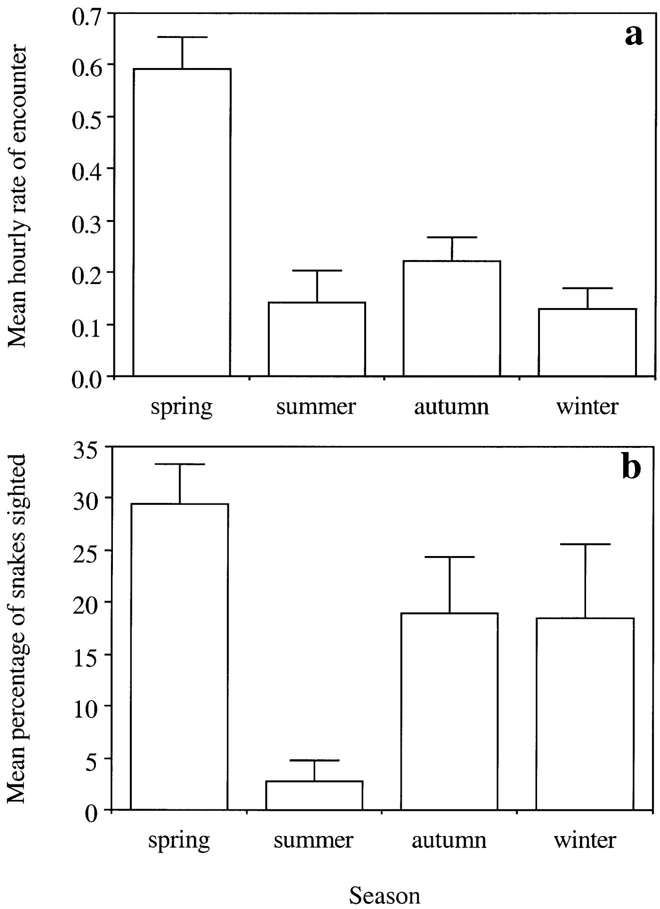

Fig. 2. Seasonal variation in the rate of encounter with brownsnakes, and in the percentage of brownsnakes known to be active (by radio-telemetric monitoring) that were actually seen by the observer. The upper graph (*a*) shows mean hourly rates of encounter with brownsnakes in each season (± s.e.). The lower graph (*b*) shows the mean percentage of active brownsnakes seen in each season (± s.e.).

Mean hourly encounter rates during spring showed a positive correlation with T_a (for 6.0°C categories, $r^2 = 0.93$, $P < 0.05$), with the highest mean rates occurring in the highest temperature ranges (Fig. 4). During summer, in contrast, mean rates showed no significant correlation with T_a and the highest probability of encounter occurred between T_a = 24° and 30°C (typical mid-morning and late-afternoon T_a range). During autumn, mean encounter rates were similar between T_a = 18° and 30°C (mean: 0.24 h^{-1}, $n = 55$, s.d. = 0.42) with encounters rare outside of this range. Hence, the relationship between encounter rate and ambient temperature varied among seasons.

Cloud cover and wind speed

Plausibly, the number of snakes encountered might be affected by cloud cover and wind speed, because these variables might affect snake activity levels, behaviour and observability. To test this possibility we used one- and two-factor ANOVA, with cloud cover and wind speed as the factors.

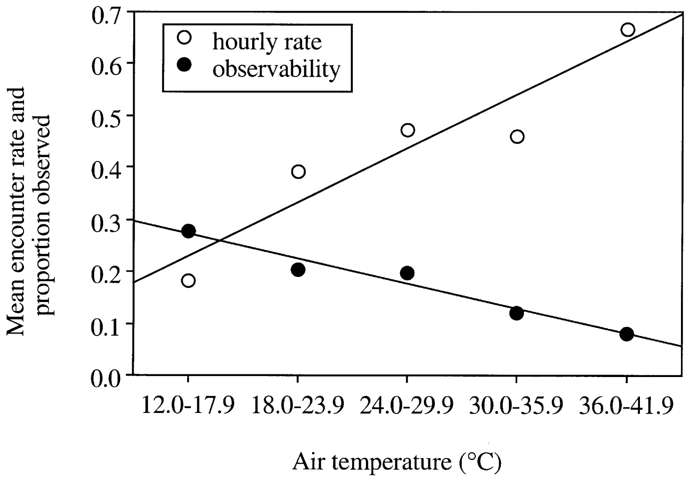

Fig. 3. The relationship between air temperature versus brownsnake activity and encounter rates. The graph shows the mean hourly rate of encounter with brownsnakes (○), and the percentage of active brownsnakes above-ground (●) that were seen by the observer, as a function of air temperature (ºC). These data are derived from the transect surveys.

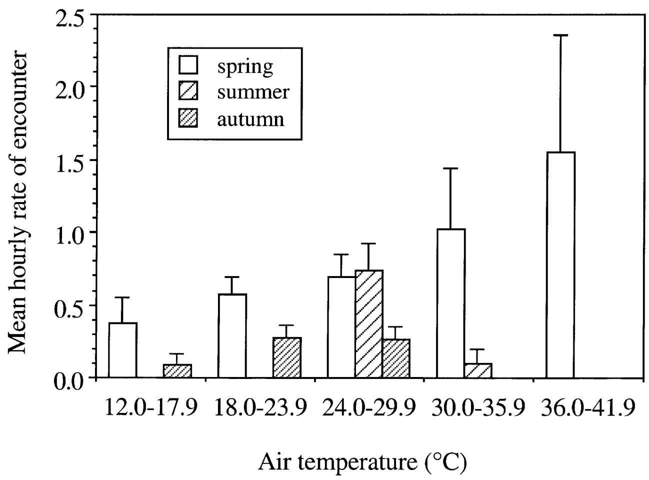

Fig. 4. Seasonal variation in the relationship between air temperature (ºC) and hourly rates of encounter with brownsnakes. Error bars show ±1 s.e.

We found no significant differences in the hourly rate of encounter with amount of cloud cover (for nearest 10% cloud, one-factor ANOVA, $F_{10,231} = 1.19$, $P = 0.30$) or wind speed (for nearest 1.0 m s^{-1}, one-factor ANOVA, $F_{10,231} = 1.43$, $P = 0.17$). However, while encounter rates were similar with differing amounts of cloud, the rate tended to increase in stronger wind in all seasons except winter (overall means: 0.23 h^{-1} in <2.0 m s^{-1} and 0.38 h^{-1} in ≥ 2.0 m s^{-1} wind). Similarly, there were no significant differences in observability with cloud cover (for <50 and ≥ 50% cloud, one-factor ANOVA, $F_{1,91} = 2.35$, $P = 0.13$) or wind speed (for <2.0 and ≥ 2.0 m s^{-1}, one-factor ANOVA, $F_{1,87} = 3.55$, $P = 0.06$); however, the snakes tended to be more visible in stronger wind (overall means: 10.8% in <2.0 m s^{-1} and 20.2% in ≥ 2.0 m s^{-1} wind).

Gender and size of the snakes encountered

Overall results

Snake gender was known for 362 encounters and, of these, the proportion that involved male snakes did not differ significantly from that expected under the null hypothesis of equal probability of encounter with respect to gender ($\chi^2 = 2.21$, d.f. = 1, $P > 0.10$). Overall, 55.5% of all encounters involved males. There was, however, a significant difference in the percentage of encounters with males on surrounding farmland versus the central refuge area ($\chi^2 = 4.46$, d.f. = 1, $P < 0.05$), with 63.7% of encounters on farms involving male snakes.

Seasonal variation

The bias for male versus female encounter did not differ significantly among seasons ($\chi^2 = 3.41$, d.f. = 3, $P = 0.33$), with males encountered more frequently than females in all seasons except autumn (Fig. 5).

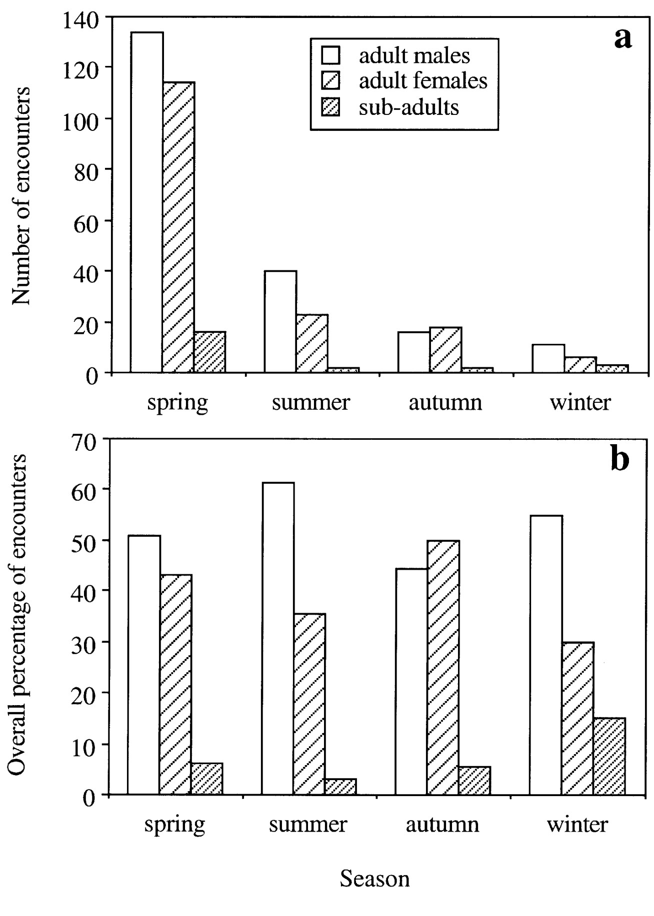

Fig. 5. Encounter as a function of snake age (adult *v.* juvenile) and gender. The upper graph (*a*) plots the overall number of encounters with adult males, adult females, and sub-adults for each season. The lower graph (*b*) plots the overall percentage of encounters with adult males, adult females, and sub-adults in each season.

Effects of weather

Given the behavioural differences between male and female brownsnakes, and between snakes of different body size (Whitaker 1998), we predicted that brownsnakes of different gender and size might respond differently to various weather conditions.

Air temperature. Thermal conditions affected the snake gender likely to be encountered; most of the snakes encountered in cool weather (<20ºC) were males, whereas the sexes were found in approximately equal numbers in warmer weather (χ^2 = 5.03, d.f. = 1, P < 0.05) (Fig. 6).

Wind speed. The relative number of male and female brownsnakes we encountered was related to wind speed (χ^2 = 5.45, d.f. = 1, P < 0.05). Most females (54.0% of encounters with females) were encountered in light wind (<2.0 m s^{-1}) whereas most males (59.0% of males) were encountered in stronger wind.

Wind direction. Analysis also revealed a significant bias in the number of male versus female encounters in northerly (315–45º of true north) versus southerly wind (135–225º of true north; χ^2 = 3.70, d.f. = 1, P = 0.05). Snakes of either gender were more likely to be encountered in the relatively warm northerlies; however, the proportion of females encountered was higher in northerly wind (especially in spring).

Cloud cover. The tendency to encounter male versus female brownsnakes was not affected by percentage cloud cover (for 50 *v.* ≥ 50% cloud cover; n = 335, χ^2 = 2.76, d.f. = 1, P = 0.10), nor the presence of cloud (for <10 *v.* ≥ 10% cloud cover, n = 347, χ^2 = 1.15, d.f. = 1, P = 0.23). Similarly, no significant difference was found in the tendency for male versus female brownsnakes to be encountered as a function of cloud height (for ≥ 10% low, high, and mixed level cloud cover, n = 239, χ^2 = 2.75, d.f. = 2, P = 0.25).

The rates at which we encountered snakes of different body sizes were relatively unaffected by weather conditions. The likelihood of encountering adults versus sub-adults was unaffected by T_a (for <24.0 *v.* 24.0ºC, χ^2 = 0.42, d.f. = 1 P = 0.52), wind speed (for <2.0 *v.* ≥ 2.0 m s^{-1}, χ^2 = 1.31, d.f. = 1, P = 0.25) or wind direction (for 45º of true north *v.* 45º of south, χ^2 = 0.48, d.f. = 1, P = 0.49). Sub-adults were more often found under cloudless sky conditions than were adults: 20.7% of the adult encounters occurred without cloud compared with 43.5% of the sub-adult encounters (χ^2 = 6.46, d.f. = 1, P = 0.01).

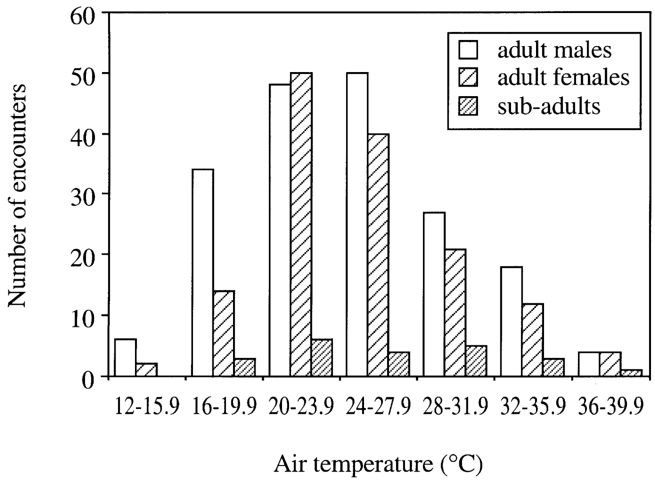

Fig. 6. The relationship between air temperature and the overall number of encounters with adult male, adult female, and sub-adult brownsnakes.

The observer's clothing as a determinant of encounter rate

Plausibly, the number of snakes seen by someone walking in farmland might depend on the observers' visibility to the snakes. Hence, clothing that offers camouflage against a background (i.e. the sky, since the vegetation in the study area is rarely tall enough to obscure a walking human) may enable an observer to approach closer to a snake than would otherwise be the case. To examine this possibility we recorded the shade of clothing worn while searching for snakes (long-sleeved shirts, excluding black or white garments). The shade of clothing worn significantly affected the number of encounters as a function of the presence of cloud (for <10 *v.* ≥ 10% cloud cover, $\chi^2 = 6.82$, d.f. = 1, $P < 0.01$) and cloud height ($\chi^2 = 8.82$, d.f. = 2, $P = 0.01$). That is, dark clothing enhanced the probability of encounter under cloudless skies and light clothing under cloudy skies (see Table 1).

Table 1. The frequency of encounters between the observer and brownsnakes as a function of cloud cover, and shade of the observers' clothing

See text for statistical analysis of these data. Alto-level cloud was rarely present as a major component during the study, and thus was not included in this compilation

	Light clothing		Dark clothing		
	%	*n*	%	*n*	Total
Presence of cloud					
Absent	38.6	27	61.4	43	70
Present	56.3	134	43.7	104	238
Percentage cloud cover					
10–20	57.4	35	42.6	26	61
30–40	56.8	21	43.2	16	37
50–60	53.7	22	46.3	19	41
70–80	55.8	29	44.2	23	52
90–100	57.4	27	42.6	20	47
Height of cloud					
Low	49.2	30	50.8	31	61
High (cirrus)	69.3	52	30.7	23	75
Multi-layered	47.3	35	52.7	39	74

Discussion

This study provides a quantitative evaluation of several factors that influence the probability that a person and a brownsnake will come into risky contact. Such encounters occur frequently in the Murrumbidgee Irrigation Area and result in the deaths of many snakes, and occasional human fatalities as well (Whitaker 1999). Our study is the first to demonstrate that a person's appearance influences their likelihood of encountering a dangerous snake, and to quantify the likelihood of people seeing the snake during an encounter. We hope that the results of this study will allow the development of recommendations to reduce the risk of dangerous confrontation.

Perhaps the most surprising result from our study was the relatively low rate of encounter overall, in an area chosen for its high brownsnake abundance. Also surprising was the relatively low overall percentage of above-ground snakes that could be seen: less than one in four closely encountered snakes were actually sighted by an observer with more than 20 years' experience in working with Australian snakes. These results reflect the snakes' ability to avoid human encounter and/or evade detection. Depending on season, a relatively high proportion of the snakes were in underground retreats during most days (even in apparently suitable weather: Whitaker 1999). Relatively few of the snakes above ground are likely to be seen because they either flee before people get close enough to see them, or rely on their cryptic coloration to escape detection (Whitaker and Shine 1999). This contrasts strongly with the commonly held belief in the Murrumbidgee Irrigation Area that brownsnakes will launch savage and unprovoked attacks if approached too closely. Furthermore, the complexity of the relationship between hourly rate, observability and air temperature (e.g. Fig. 3) illustrates the potential for error when relying on sight-only methods for estimating snake numbers. Increased rate of encounter was associated with higher temperatures, but this effect was due to increased above-ground activity levels. Under such conditions, most snakes were underneath relatively dense ground cover (Whitaker 1999), and hence were rarely seen (Fig. 3). Seasonal shifts in habitat use, plus the snakes' reliance on crypsis, might plausibly lead to the conclusion that brownsnakes are locally or seasonally rare.

The determinants of encounter rates between snakes and humans can broadly be divided into characteristics of the environment, the snake, and the person involved. Some of these are obvious. For example, it is not surprising to find a higher encounter rate on an undisturbed area (central refuge area) close to permanent water. Agricultural activities may facilitate encounter as well, on a local scale; for example, mechanical soil disturbance and the removal of vegetation may encourage the snakes to concentrate in undisturbed areas while causing their presence to become more obvious.

A primary determinant of encounter rates was season, with a several-fold increase in encounter rate and observability during spring (Figs 1, 2). These data mostly reflect the fact that brownsnakes are more easily seen in spring than in other seasons. In turn, this bias arises from seasonal changes in the available vegetation cover, the snakes' willingness to remain in the open, and mating activity. However, the snakes were particularly difficult to see in early spring if they remained under vegetation after emerging from their winter burrows (especially when coated in moist earth following wet winters). As spring progressed, however, the snakes were more frequently encountered in the open. Males usually began to search for receptive females by late September, with the females frequently being found in the open at this time. Most of the road-killed snakes in spring were male, confirming increased activity and movement (Whitaker 1999). Male brownsnakes are generally less likely to notice human intrusion during the breeding season, due to their concentration on reproduction at this time (Whitaker and Shine 1999). Hence, mating and basking behaviour both contributed to increased encounter rates during spring.

The time of day also appeared to influence the overall frequency of encounter, hourly encounter rate and observability. Strong differences between the morning and afternoon were evident depending on season and weather. In the morning, the snakes were more likely to be encountered on refuge area transects than on surrounding areas, reflecting a tendency for movement in the afternoon. However, both in the general area and on the relatively undisturbed transects, encounter rates were higher in the afternoon than in the morning (except during summer). Prior and Weatherhead (1994) found a non-significant increase in the capture rate of rattlesnakes (*Sistrurus catenatus catenatus*) as air temperature increased, while our study found significant correlations between encounter rate and temperature. The relatively high thermal preference of *P. textilis* (Witten 1969; Heatwole and Taylor 1986), and the positive correlation between encounter rate and air temperature in spring, may explain why these snakes are generally not found on the ground surface until air and in-ground temperatures increase around the middle of the day. In cool seasons these snakes are often in deep burrows. Soil temperature at this depth ($\geq$ 30 cm deep) typically rises after midday, at about the time when many brownsnakes emerge from their burrows (for detail on activity with temperature see Whitaker 1993, 1999).

Previous studies have shown seasonal shifts in the activity patterns and thermal biology of elapid snakes (e.g. Schwaner 1989; Shine and Lambeck 1990; Webb 1996). Brownsnakes frequently bask in late winter and early spring, and reproduction requires increased and overt activity in relatively cool air. However, in warmer months (mid-spring to mid-autumn) activity during the early morning and late afternoon allows the snakes to avoid excess radiation.

Typically, there are few midday encounters in midsummer; indeed, nocturnal encounters may occur in 'hot' conditions. However, all encounters at night involved inactive snakes that were covered by vegetation (Whitaker and Shine 1999). Above-ground activity during summer may be further discouraged during the day due to soil temperature being within the snakes' preferred range (Whitaker 1999). Conversely, temperatures on the ground surface during late-autumn, winter, and early-spring may reach the snakes' preferred range only during the afternoon.

Weather conditions affect the probability of encounter in several ways. Conventional wisdom in New South Wales is that 'you see more brownsnakes in hot weather', but the reality is far more complex. For example, during summer (the hottest season) fewer of the snakes were active above-ground (Whitaker 1999) and, while encounters were relatively frequent in hot weather (e.g. during summer mornings), fewer of the active snakes were actually seen. Air temperature influenced encounter probabilities, but the form of this relationship differed among seasons. During late autumn, winter, and early spring warmer weather led to increased encounter rates, yet during summer the encounter rate was increased only within the thermal conditions typical for mid-morning and late-afternoon. The snakes that were above ground during hot weather tended to remain under vegetation and were difficult to see even when their locations were positively known by telemetry.

Cloud cover had little effect on encounter rates or observability, despite its influence on incident radiation and temperature. We suspect that wind speed did affect encounter rate and observability overall, although the differences did not attain statistical significance in our data. Walking transects in strong wind generally resulted in higher encounter rates in all seasons except winter, perhaps because the human form was less obvious to the snakes in swaying vegetation (Jackson 1974; Greene 1978).

Attributes of the snake (such as sex, condition and body size) influence encounter probability as well. Ecological studies on several species of snakes have shown clear behavioural and ecological differences between juveniles and adults, and between adult males and females (e.g. Duvall *et al.* 1985; Houston and Shine 1993; Shine 1994; Webb 1996). For example, juvenile *P. textilis* feed primarily on lizards, switching to mice and other vertebrates as they grow larger (Shine 1989). This ontogenetic dietary shift may well be accompanied by a habitat shift, with adults attracted to places with higher densities of rodents. Such a shift is likely to increase encounter rates with farmers, because numbers of mice are higher in agricultural landscapes. Activity and thermoregulatory behaviour may also differ between conspecific adult male and female snakes, often in concert with seasonal shifts in reproductive activity (Shine 1977*a*, 1977*b*; Duvall *et al.* 1985). Consistent with these findings, and with the differences in gender activity patterns in *P. textilis* (Whitaker 1999), our study revealed significant differences in the factors that influence encounter. Males were the more frequently encountered sex in all seasons except autumn, and were significantly more likely to be encountered in disturbed farmland areas. Encounters with females were more dependent on weather conditions than was the case with males. Females were more likely to be encountered in mild temperatures and were more likely to be encountered in light wind (especially in warm northerly winds during spring).

Seasonal and spatial differences between male and female snakes may help explain the effect of weather conditions on the sex ratios of snakes encountered. Activity and movement in female brownsnakes is limited during early spring and early summer (Whitaker 1999). Males typically become active several weeks before females at the end of winter, and their activity levels and movement are elevated during mate-searching in early spring. These factors may result in males being encountered more frequently in inclement weather.

Because smaller individuals can more easily remain hidden, one cannot assume equal observability for all sizes of snakes. The same is true for snake gender: male brownsnakes are larger than females (Shine 1978). Relatively few sub-adults were seen, suggesting a relatively high degree of crypsis in this group. Most sub-adults were encountered during spring, when the only environmental variable found to significantly influence their rate of encounter was the lack of cloud cover. Hence, most encounters with sub-adult snakes occurred in clear, sunny conditions.

Determinants of encounter may also involve attributes of the people involved. While people vary in their ability to detect or encounter snakes, this study focussed on one trait that is easily modified and which could feasibly allow encounters with snakes to be managed. Our findings suggest that the shade of clothing worn will influence the probability that a person walking in grassland will encounter a brownsnake; the probability of encounter is higher if the shade worn offers camouflage against the background of sky (see Götmark 1987; Whitaker and Shine 1999). As cirrus cloud is associated with bright diffuse conditions, and as brownsnakes are terrestrial and usually view approaching humans against a background of sky (in the grassland habitat studied), darker shades of clothing will contrast against this cloud type more than will lighter shades. Hence, dark clothing may more readily alert the snakes to human approach under cirrus cloud, and result in fewer close encounters, but may encourage encounter in the absence of cloud. These findings suggest that selection of the appropriate (contrasting) shade of clothing may reduce the probability of potentially dangerous confrontations with brownsnakes.

Undoubtedly, the causal processes leading to encounters between snakes and farmers are complex, and involve many other factors that are not dealt with in this paper. For example, several factors influence human participation. In related work, we examine this aspect, and describe snake and human responses to encounter (Whitaker and Shine 1999). Eastern brownsnakes play an important role in the anthropogenically disturbed agricultural lands of eastern Australia. As large predators, they may be significant in rodent control, as well as in other ecological processes. Such advantages have attracted little public sympathy, because of the snakes' negative role in inflicting dangerous bites. We hope that information on the determinants of encounters may help to reduce the potential risk to both participants and facilitate a more harmonious coexistence between snakes and people.

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