HERPETOLOGICAL JOURNAL, Vol. 15, pp. 213-219 (2005)

CLOSE ENCOUNTERS OF THE WORST KIND: PATTERNS OF INJURY IN A POPULATION OF GRASS SNAKES (*NATRIX NATRIX*)

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Injuries of various types are widespread in animals and presumably have implications at the population level (e.g. reduced future survivorship). We studied patterns of injury acquisition in a population of grass snakes (*Natrix natrix*) in south-eastern England. Injuries suffered by grass snakes were of various types, including broken bones, assorted scars and wounds, and tail loss. What causes such injuries is unknown, but predators seem most likely. We predicted that the probability of having an injury would be higher for larger snakes, for several reasons (e.g. larger snakes are older and thus have had more opportunity to be injured). We also predicted that injury rates would be higher in females because, when gravid, they are expected to bask in the open more than other snakes. Our data strongly supported the first of these predictions, but not the second. Males had significantly higher injury rates than females of the same body size. However, because males grow more slowly and mature at a smaller body size than females, higher injury rates of males might simply reflect their smaller size at a given age. Even if age plays a role in influencing acquisition of injuries, other, more directly size-related factors also might be important. Two possibilities are that small snakes might be less likely to survive an injury or that small snakes spend more time hidden and so are less likely to encounter large predators. We lack data on the first of these, but data on sizes of snakes found under cover versus those found in the open are consistent with the second. Studies of injury rates in snakes need to move beyond the descriptive stage and begin to test the broader consequences of injuries.

Key words: Colubridae, injuries, natricine, snake, predation, southern England

INTRODUCTION

Close encounters with predators, intraspecific aggressors, or other misadventure are common in the lives of animals. Although such encounters can result in death, they sometimes result in nonlethal injury. Injuries of various kinds, including loss of body parts, have been reported for diverse taxa (Vermeij, 1982; Harris, 1989), among them centipedes (Fründ *et al*., 1997), crustaceans (Rigaud & Juchault, 1995; Dyrynda, 1998; Plaistow *et al*., 2003), spiders (Taylor & Jackson, 2003), echinoderms (Aronson, 1987; Baumiller & Gahn, 2004), snails (Warren, 1985), fish (Reimchen, 1988), amphibians (Maiorana, 1977; Pfingsten, 1990; Gray *et al*., 2002), reptiles (Schoener & Schoener, 1980; Willis *et al*., 1993; Meek, 1989), birds (Randall *et al*., 1988), and mammals (Lidicker, 1979; Rose, 1979; Shargal *et al*., 1999; Macdonald *et al*., 2004).

What are the broader, population-level, consequences of injury? Whether injury rates can be used to infer predation rates is debatable (Jaksic & Greene, 1984; Greene, 1988; but see Baumiller & Gahn, 2004), especially in the absence of survival and other data (Schoener, 1979). Rather, incidence of injury might be more indicative of predator inefficiency (Reimchen, 1988; Mushinsky & Miller, 1993). However, injuries have possible costs in terms of future survival and reproduction, and, in some cases, might act to regulate population size (Harris, 1989). Injured animals may fare more poorly in intrasexual conflicts (Taylor & Jackson, 2003). Failed predation, as evidenced by injury, is a necessary condition for the evolution of antipredator characteristics (Vermeij, 1982). Conversely, injured and non-injured animals, which differ morphologically in some species, might reflect adaptations for surviving injury vs. avoiding injury, respectively (Seligmann *et al*., 2003). Wounds are also points of entry for infectious micro-organisms (e.g. Dyrynda, 1998) and might influence selection for investment in immune defences (Plaistow *et al*., 2003). In arthropods, wounds represent a possible means of horizontal transfer of the feminizing bacterium, *Wolbachia*, which in turn leads to sex-ratio distortion (Rigaud & Juchault, 1995). Thus, data on injury rates have potential value for revealing population-level phenomena.

In squamate reptiles, most studies of patterns of injury have been done on lizards, largely because many species of lizards autotomize the tail in response to attempted predation on them (review in Arnold, 1988). Although shedding the tail and escaping from a predator have immediate survival value, tail loss also has costs in many cases and most autotomizing lizards regenerate the tail (Arnold, 1988; see also plethodontid salamanders – Maiorana, 1977).

Studies of injuries in snakes are at a less analytical, more descriptive stage (but see Willis *et al*., 1993; Slowinski and Savage, 1995). However, numerous authors have reported injuries, including tail loss, in snakes (review in Greene, 1988). Taxa for which injury data are available include uropeltids (Greene, 1973), erycine boas (Greene, 1973; Hoyer & Stewart,

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2000*a,b*), colubrids (Fitch, 1963; Leavesley, 1987; Mendelson, 1992; Slowinski & Savage, 1995; Capula *et al.*, 2000), and viperids (Macartney, 1985). Among colubrids, much work has focused on the natricine genera *Nerodia* (Mushinsky & Miller, 1993; Fitch, 1999) and *Thamnophis* (Willis *et al.*, 1993; Fitch, 1999, 2003), and several other studies of these genera have incidentally noted injuries (e.g. Diener, 1957; Preston, 1970; King, 1987). Although snakes do not regenerate their tails once lost (Greene, 1988), some species may practise a form of caudal autotomy (Broadley, 1987; Greene, 1988; Cooper & Alfieri, 1993; Fitch, 1963, 1999; Akani *et al.*, 2002), which Slowinski & Savage (1995) argue is more correctly called 'pseudoautotomy'. Frequency of tail loss is higher in species with relatively long tails (Kaufman & Gibbons, 1975) and species with specialized pseudoautotomy may experience multiple tail breaks through life (Slowinski & Savage, 1995). Loss of part of the tail can lead to reduced mating success in males (Shine *et al.*, 1999), but apparently has little effect on locomotory speed (Jayne & Bennett, 1989). Potential consequences of other kinds of injuries have not been investigated.

In this study, we documented patterns of injury in a population of the natricine grass snake (*Natrix natrix*) in southern England. In addition to recording the incidence of injury, we tested two predictions. First, we predicted that the relative frequency of injury should be higher in older (and therefore larger) snakes because, all else being equal, older animals should have a higher probability of having acquired an injury sometime in their life (Willis *et al.*, 1993). An alternative, but not mutually exclusive, explanation for the higher occurrence of injuries in larger snakes is that larger snakes simply are more likely to withstand and survive a predation attempt than are small snakes (Willis *et al.*, 1993; Mushinsky & Miller, 1993). A third possible explanation, also not mutually exclusive with the others, is that because they are more vulnerable, smaller snakes spend more time hiding under cover, rather than exposing themselves to larger predators that forage in the open. One important distinction between these three hypotheses, however, is that in the first one, body size is merely a surrogate for age, whereas, in the other two, it is the variable of primary interest. Second, we predicted that female grass snakes would have higher injury rates than males because (1) when gravid, females spend more time basking in the open than other adults (Madsen, 1987), exposing themselves to increased risk of potential injury; and (2) females reach larger body sizes than males (Madsen, 1983; Gregory, 2004), so factors outlined above should apply.

MATERIALS AND METHODS

We collected the data for this study at Fordwich, near Canterbury, Kent in south-eastern England. The study site is centred around a series of water-filled gravel quarry pits on either side of the River Stour. We captured snakes by hand, mainly in the open but occasionally under cover objects, during 3-week to 4-month visits to the site in each year from 1999-2003, inclusive. We measured several variables on each snake at its capture site and released it within 10-20 min of capture. These included snout-vent length (SVL), tail length (TL), sex, and presence of injury. We did not begin to record TL until part-way through the 2000 sample. We did not tag animals, but identified them individually by patterns of anterior ventral markings, recorded either by drawings or photographs. In addition to field-caught snakes, we collected similar data from a few hatchlings obtained from eggs incubated in the laboratory; these eggs were laid by females from the Fordwich field site.

We analyzed the data using SAS 8.0 and a nominal rejection level of α=0.05. To maintain independence of data, we excluded all recaptures from analyses and used only original captures. We used logistic regression to test the influence of SVL and sex on occurrence of injury (binomial variable: presence/absence) and contingency tables to compare frequencies of categorical variables.

RESULTS

We obtained data from 87 female and 93 male grass snakes. Of these, 21 were captive-hatched (12 females, 9 males). The two sexes differed significantly in SVL (Kruskal-Wallis χ^2_1=32.55, P<0.0001), females reaching much greater maximum and median SVLs than males (960 mm vs 740, 715 vs. 562, respectively; hatchlings included).

No hatchlings showed any evidence of physical injury. Thus, we assumed that snakes do not commonly hatch with deformities that resemble injuries and that injuries therefore are acquired later in life.

Of 159 field-caught snakes for which we recorded the presence or absence of injuries, 71 had injuries of various types. Some (24) had lost part of their tail, ranging from just the tip to a larger amount that left a pronounced stump. Most snakes that had lost a large part of their tails (expressed as deviation from TL-SVL relationship for snakes with intact tails) were large (Fig. 1). Fifty-seven snakes, including 11 of those with stumped tails, had other kinds of injuries, some minor and others more serious, sometimes multiple, on various parts of the body from head to tail, inclusive. These other injuries included assorted scars, some old and others fresh, but some snakes showed evidence of having had broken bones (now healed), either spine or ribs.

We divided injuries into two main categories, tail loss and others, and found no association between their occurrence in field-caught snakes (χ^2_1=1.17, P=0.28); that is, snakes with stumped tails and those with intact tails were equally likely to also have other injuries. There also was no overall association between sex and the frequency of stumped tails, other injuries, or all injuries combined (latter: χ^2_1=0.005, P=0.94). These conclusions were not changed by including hatchlings in the analyses. However, distinct patterns emerged when

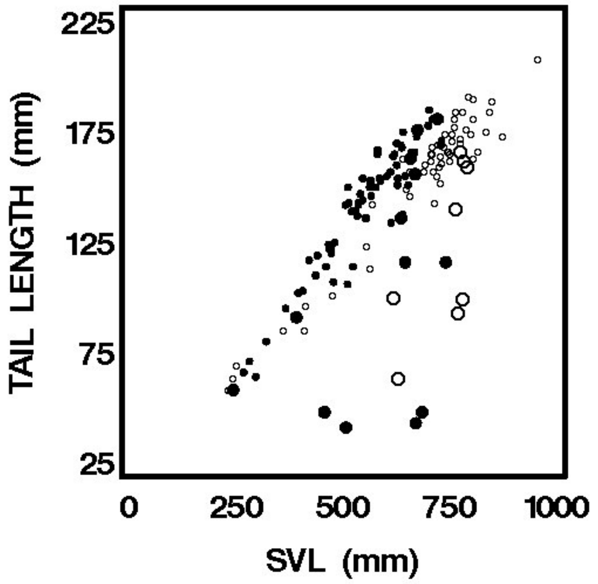

FIG. 1. Tail length vs SVL for grass snakes with intact (small symbols) tails and stumped (large symbols) tails. Open circles, females; closed circles, males. Deviation of large points from small points at same SVL indicates approximate amount of tail lost. Sample (N=141) includes field-caught snakes (original captures only), but not captive-born hatchlings.

we considered the effect of body size using logistic regression.

Because we had no reason to expect that captive-born hatchlings would differ from wild-born ones in injury status, we included the former in logistic regressions. Furthermore, although our conclusions were not affected by leaving hatchlings out, the fit to the model was substantially improved by including them (Hosmer & Lemeshow goodness-of-fit nonsignificant), which also slightly increased the range of SVLs in the analysis.

The regression of P(injury) on SVL was highly significant (Wald's χ^2_1=21.86, P<0.0001), with probability of having an injury increasing with SVL (Fig. 2A). Adding sex as a factor improved the model (AIC = 208.40 vs 214.18 for SVL alone) and showed that males had a significantly higher injury rate than females at a given SVL (Fig. 2B; Wald's χ^2_1=6.99, P=0.008), with the effect of SVL also remaining highly significant (Wald's χ^2_1=20.79, P<0.0001).

As a preliminary test of whether smaller snakes spend more time under cover and are therefore less likely to be exposed to predators that forage in the open, we compared the sizes of snakes caught under cover objects to those captured in the open. Although only nine of 159 field-caught snakes were found under cover objects, they were significantly smaller than those caught in the open (medians 410 mm SVL vs 656.5; Kruskal-Wallis χ^2_1=18.21, P<0.0001).

DISCUSSION

The results of this study provide strong support for our prediction that the occurrence of injury increases with body size, consistent with most other studies of snakes, including grass snakes (Borczyk, 2004). As we did not distinguish between old and recent injuries, it is possible that we may have underestimated the actual incidence of injury because we missed old injuries that had healed sufficiently to be no longer obvious. However, it is unlikely that this would have changed our overall conclusions. Mushinsky & Miller (1993) fo-

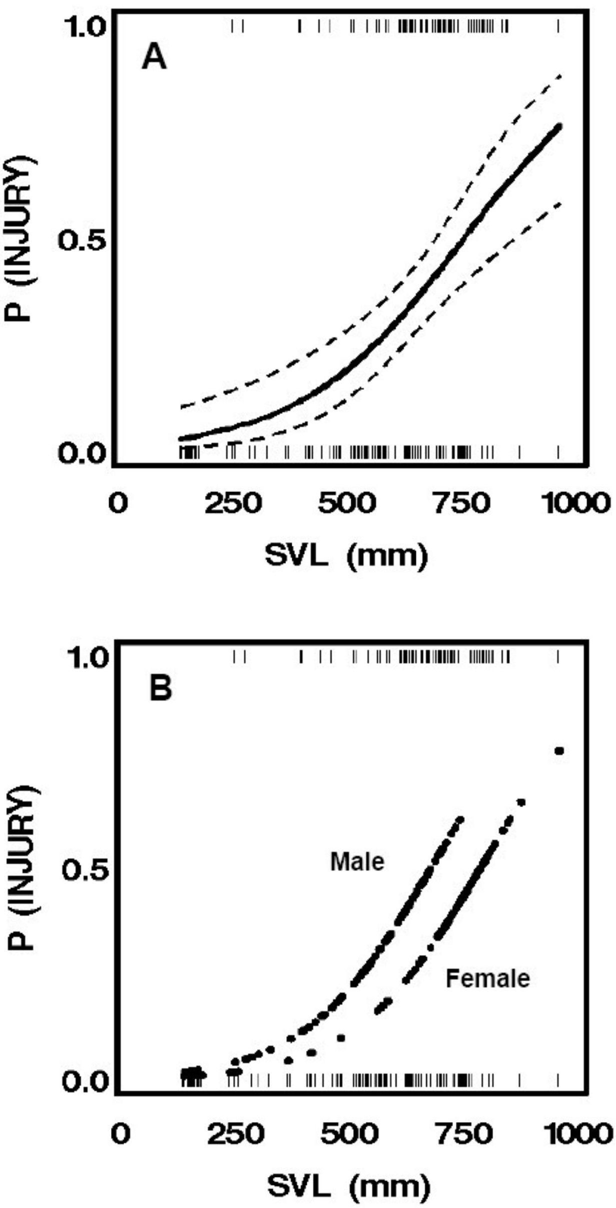

FIG. 2. Logistic regressions of probability of having acquired an injury vs SVL for grass snakes. A, both sexes pooled (vertical lines at top = injured snakes, vertical lines at bottom = uninjured snakes, N=180, including both field-caught snakes and captive-born hatchlings; solid line represents predicted values from logistic regression of injury/no injury against SVL; dotted lines represent 95% confidence limits on predicted values). B, sex treated as an independent variable with two levels (predicted values only shown; top curve – males, lower curve – females; regression lines for each sex analyzed separately are slightly different, but still show the same relative positions).

cused only on recent wounds and still found the same trend for increasing occurrence of injury with increasing body size. Most studies of tail breaks in snakes also have shown that the incidence of this kind of injury, which is permanent, is higher in larger snakes (e.g. Mendelson, 1992; Fitch, 1963, 1999, 2003). However, Willis *et al.* (1993) found no evidence of size-based variation in tail breakage in one of the three species that they studied.

In contrast, our prediction of higher injury rates in female grass snakes, compared to males, was not upheld. Data on other natricine species with female-biased sexual size dimorphism (SSD) apparently support this prediction, in general. For example, Fitch (2003) found that, among adult *Thamnophis sirtalis*, females had broken tails significantly more often than males. Fitch (1999) also compared tail injuries between the sexes in water snakes, *Nerodia sipedon*, by probable-age groups, and again showed a higher incidence of injury in females. Willis *et al.* (1993) also concluded that, overall, female *Thamnophis* had higher rates of tail breakage than males, but inspection of their Fig. 1 shows that the incidence of this injury was higher in adult males than females in *T. sirtalis*, similar to our findings. Mushinsky & Miller (1993) found no difference in the occurrence of fresh injuries on males and females of six species of natricines (five *Nerodia*, one *Regina*), but did not make any corrections for size or age variation. Such correction seems crucial for making comparisons between the sexes in species with pronounced SSD. Capula *et al.* (2000) found no difference in frequency of tail breakage in the colubrine *Coluber viridiflavus*, a species with male-biased SSD, but they also did not adjust for age or size differences. In the dipsadine *Coniophanes fissidens*, which lacks SSD, there were no consistent inter-sexual differences in tail-breakage rate among populations and no difference between the sexes overall (Mendelson, 1992).

We hypothesized that females would experience higher rates of injury partly because, when gravid, they are reported to bask more than other snakes (Madsen, 1987), presumably for thermoregulatory purposes. For example, Akani *et al.* (2002) found that gravid females of the African snake, *Psammophis philipsii*, had a significantly higher frequency of tail loss than nongravid snakes (which included both males and females). However, Isaac & Gregory (2004) found no evidence that gravid female grass snakes in an outdoor enclosure thermoregulated more precisely or maintained higher body temperatures than nongravid females. Although we have not tested male snakes, this might help explain why female grass snakes at our study site did not have a higher injury rate than males.

In fact, after adjusting for body size, we found that male snakes had a higher frequency of injury than females. Although we lack sufficient data to construct growth curves for grass snakes at Fordwich, this apparent difference could be an artefact of intersexual differences in growth rates. Growth rate in this species is phenotypically plastic and varies geographically, but females typically attain larger maximum sizes than males (Madsen & Shine, 1993*a*; Luiselli *et al.*, 1997). Furthermore, females also may grow faster than males (Madsen, 1983; but see Luiselli *et al.*, 1997). If so, the higher injury rate of males of a given SVL might only reflect the fact that they are older than similar-sized females. This can be tested directly with data on age (e.g. Waye & Gregory, 1998; Waye, 1999) and, if confirmed, would suggest that age *per se* is an important factor influencing the likelihood of having sustained an injury.

Age may be important, but what about other, size-related factors that might affect incidence of injury? For example, do smaller snakes have fewer injuries simply because they are less likely to survive an attack from a predator, either immediately or over the short term? Willis *et al.* (1993) detected a lower frequency of injury in garter snakes (*Thamnophis sirtalis* and *T. sauritus*) between 250-290 mm SVL relative to smaller neonates and larger adults. They suggested that injured juveniles do not survive their first year, possibly because of the stresses associated with hibernation. However, our data show no trend of especially low injury in small field-caught snakes and fitting a quadratic regression to the data in Fig. 2A did not reveal one either.

Diurnal activity, including basking behaviour, may make snakes particularly prone to being injured (Mushinsky & Miller, 1993). Thus, larger snakes might also be more likely to acquire injuries because they spend more time in the open than smaller snakes, for which such exposure is presumably more risky. Our finding that snakes found under cover are more likely to be small is consistent with this hypothesis and with Gregory's (1984) similar observations for three species of *Thamnophis*. Olson & Warner (2003) made similar findings for the colubrines, *Lampropeltis calligaster* and *Coluber constrictor*, but not for *Thamnophis sirtalis*. However, caution should be exercised in interpreting such data in terms of activity patterns. First, the frequency of snakes found under cover is only a correlate of relative activity in the open, which should be measured directly. This will be a challenge for small snakes, for which radiotelemetry is not possible. Second, if larger snakes require larger (or otherwise different) cover objects, then sampling only relatively small cover objects will necessarily bias a sample towards smaller snakes. Our study site lacks easily sampled natural cover objects, so we relied exclusively on artificial cover objects for finding hidden snakes. Although most of these cover objects appeared to be large enough for adult snakes, without testing specific requirements we cannot be sure. Presumably, natural cover, including the dense vegetation at the site, is important for snakes of all sizes, but cover objects, particularly those made of materials that retain heat, remove the risks inherent in basking, particularly for small snakes. For example, Mertens (1995) found that black plastic sheets were especially useful for catching smaller grass snakes. Alternatively, even if small and large snakes were to bask in the open equally often, larger snakes might be more obvious to visual predators and hence more likely to attract the attention of those predators and be injured (Leavesley, 1987).

What causes injuries in grass snakes? An assumption in most studies, including this one, is that injuries are the result of encounters with predators, but this is generally not supported by direct observation, thus limiting the inferences that we can draw. At our study site, we have not witnessed any encounters between grass snakes and potential predators, which we assume are mainly birds and mammals. Injury due to intraspecific aggression is improbable; even male grass snakes competing for mates do not exhibit overt agonistic behaviour, such as biting, towards one another (Madsen & Shine, 1993*b*; Luiselli, 1996). However, we cannot rule out other possible causes of injury.

One possibility is wounding by dangerous prey, but grass snakes at Fordwich feed mainly on anurans (Gregory & Isaac, 2004), which lack defensive mechanisms that are likely to inflict injury on a predator. Grass snakes at Fordwich also eat mammals, which could cause injury, but the mammals eaten are mainly very small, including nestlings. Although snakes that eat nestling rodents might be subject to injury from mothers defending their young (Hoyer & Stewart, 2000*b*), mammal-eating in grass snakes at our study site is not restricted to the largest snakes (Gregory & Isaac, 2004) and thus seems an unlikely explanation of the higher frequency of injury in larger snakes.

Some minor scars could be attributable simply to wear-and-tear, such as abrasions from scraping against vegetation or hard substrates. Others might be due to infection or disease; for example, loss of the tail tip in *Elaphe subocularis* can result from parasitization by ticks (Degenhardt & Degenhardt, 1965). Finally, although we assumed in our analyses that hatchlings lack deformities that resemble injuries, we cannot entirely dismiss this possibility. Our sample of hatchlings was small and all eggs were incubated over a narrow range of temperatures (27-29°C). Townson (1990), again from a small sample, found that eggs incubated at higher temperatures yielded some snakes with deformed tails (although none of the deformed babies hatched), so that further experimentation is needed to obviate this possibility in surviving hatchlings. Live hatchlings with missing tails apparently do occur, but rarely (one observation; P. de Wijer, pers. comm.).

Presumably, injuries also are related in some way to defensive behaviour, either because animals exhibiting particular kinds of defensive behaviours are more likely to be injured (Seligmann *et al.*, 2003) or because animals that have been injured respond by changing their defensive behaviour (Willis *et al.*, 1993). One kind of injury that seems clearly linked to defensive behaviour is tail loss in the natricines, *Nerodia sipedon* (Fitch, 1999) and *Thamnophis sirtalis* (Cooper & Alfieri, 1993), as well as the colubrine, *Coluber constrictor* (Fitch, 1963).

In all three of these species, snakes that are grasped by the tail often will twist the body vigorously, apparently attempting to break the tail (sometimes succeeding in doing so; Gregory, pers. obs.) and then escaping. This autotomizing behaviour is more common, and presumably more effective, in larger individuals because they have sufficient body mass to apply the necessary force to break the tail (Fitch, 1999). If so, this is an additional reason why larger individuals in these species should have a higher incidence of injury than smaller snakes. Surprisingly, however, *Natrix natrix*, despite its relatively large size, its general ecological similarity to *Nerodia* and *Thamnophis*, and its close phylogenetic relatedness to them, only occasionally rotates the body when held by the tail (C. Reading, pers. comm.) and we have not seen such behaviour at our study site. Thus, perhaps not all instances of tail loss in *Nerodia* and *Thamnophis* are attributable to this particular defensive behaviour.

Like other studies of injury patterns in snakes, our work raises more questions than answers. It will be a challenge to extend work in this area because we lack the most fundamental natural history observations that are relevant to its study (e.g. direct observations of close encounters between snakes and their predators). Nonetheless, mark-recapture and other methods should at least allow us to begin comparing survivorship and reproductive success of injured and uninjured animals in species that are particularly amenable for field study. In short, research on injury rates in snakes needs to move beyond the descriptive stage and begin to test the consequences of injuries at the population level.

ACKNOWLEDGEMENTS

We thank R. Griffiths of DICE at the University of Kent at Canterbury for logistical support and helpful advice, and L. Luiselli and C. Reading for valuable comments on the manuscript. Permission to study snakes on their land was given by N. Beamish of Brett and Sons and by C. Wacher of the Canterbury and District Angling Association. L. Gregory, R. Moore, and D. Schneider helped us catch snakes. This work was done under approval of the University of Victoria Animal Care Committee. Financial support for this work was provided by a Faculty Research Grant from the University of Victoria and a Research Grant from the Natural Sciences and Engineering Research Council of Canada.

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Accepted: 8.10.04