

ORIGINAL ARTICLE

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Why do snakes have eyes? The (non-)effect of blindness in island tiger snakes (*Notechis scutatus*)

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Abstract Large (to > 1 m), diurnally active tiger snakes (*Notechis scutatus*) are abundant on Carnac Island, near the coast of Western Australia. Our behavioural and mark-recapture studies provide the first ecological data on this population, and reveal a surprising phenomenon. Many adult tiger snakes have had their eyes destroyed, apparently during nest defence, by silver gulls (*Larus novaehollandiae*). This loss of vision did not reduce the snakes' body condition (mass relative to length), or their rates of growth or survival (measured over a 12-month period). Blind male snakes trail-followed females, and mated successfully. Thus, destruction of a major sensory modality had no detectable effect on these predators. This result is strongly counter-intuitive, but mirrors an earlier report of congenital blindness (without ill-effects) in American viperid snakes. Similarities between the two systems (island populations, highly venomous snakes, reliance on sessile prey) clarify the circumstances under which the loss of vision does not reduce an organism's viability. These natural experiments support Gans' hypothesis of "momentarily excessive construction" in that the snakes possess a complex organ system that they do

not actually require for successful feeding, survival or reproduction.

Key words Blindness · Foraging · Natural experiment · Snake · Venom · Vision

Introduction

Animals possess complex sensory organs. The notion that these systems are indispensable for day-to-day life is a widely accepted assumption of scientific studies. The evidence to support this assumption comes from examples where loss of a sensory modality has severe consequences for organismal fitness. For example, disease-induced blindness causes a rapid loss of body condition, and consequent mortality, in free-ranging mammals (Martin 1981; Brown et al. 1984; Gauthier 1991; Callait 1992; Langon 1996). Although such examples certainly indicate that blindness *may* have catastrophic effects on viability, this is not always the case – at least over evolutionary time-scales. Many lineages of ectothermic vertebrates and invertebrates have evolved blindness, often in response to fossoriality or troglodytism (e.g. Duellman and Trueb 1986). Blindness has clearly evolved gradually in these cases, such that adaptive modifications to other systems have compensated for the decrease in visual abilities. Another possibility is that a sudden loss of vision may have very little impact on viability for some types of organisms in certain circumstances. The hypothesis of "momentarily excessive construction" (Gans 1979) suggests that animals are "overdesigned": for example, they may sometimes possess more sensory systems than they actually need for survival and successful reproduction.

Snakes differ from most other kinds of animals in the degree to which they rely on different sensory modalities. Almost uniquely among vertebrates, they are apparently unable to hear airborne sounds (e.g. Greene 1997). They are highly dependent on chemoreception for activities

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Supplementary material Two digital pictures of blind tiger snakes (Figures S1 and S2) are available on Springer Verlag's server at <http://link.springer.de/journals/bes/index.htm>.

such as prey detection and mate location (e.g. Mason 1992). The importance of vision varies greatly among living snakes, with one major lineage (the blindsnakes, or Scolecophidia) being essentially sightless (e.g. Greene 1997). Among other living snakes, relative eye size shows substantial variation within single lineages, and may even differ between the sexes within single species (Shine et al. 1996). Unique structural and functional attributes of snake eyes suggest that the earliest snakes may have passed through a stage where the eyes were non-functional (McDowell 1987).

The extreme phylogenetic lability of visual systems within this group raises the question as to what ecological circumstances influence the importance of vision. In particular, what circumstances permit the loss of effective visual systems without a corresponding loss of fitness? Our observations on island tiger snakes provide a startling example of this situation. Although it is difficult to imagine how a predator which normally hunts visually could continue to hunt and survive were it to lose its sight, that is just what we have observed among these snakes. We first provide some basic information about the studied population as a foundation from which we can examine the impacts of blindness.

Methods

Study site

Carnac Island (32°07' S 115°39' E) is situated approximately 10 km off the southern coast of Western Australia. The island was formed < 6000 years ago by rising sea levels (Seddon 1972). It is a small limestone and sand island (total area of only 16 ha), with a maximum elevation of 17 m and a thick low shrubland of *Acacia rostellifera*, *Rhagodia baccata*, *Olearia axillaris* and *Frankenia pauciflora* over about 80% of the island surface. The remaining areas are outcropping rock and open sand. The vegetation of the island was described by Abbott (1980). There are no freshwater sources available to the snakes except rainfall or dew.

The tiger snakes that inhabit this island (*Notechis scutatus*; referred to as *N. ater* by some authorities, e.g. Schwaner 1985) are the descendants of 80 snakes that were released onto the island some 70 years ago by a travelling showman (after his wife was killed by one of them; Cann 1986). Tiger snakes are large, widely searching foragers, primarily active by day (e.g. Schwaner 1989, 1991). The habitat and prey resources available on the island differ considerably from those on the mainland where the snakes originated (Abbott 1978). Presumably because of the small size of the island and lack of standing water, there are no frogs (the major prey item for mainland tiger snakes; Shine 1987) on Carnac. Although several bird species (including pied cormorants *Phalacrocorax varius*, little penguins *Eudyptula minor*, and wedge-tailed shearwaters *Puffinus pacificus*) nest on Carnac, the silver gull (*Larus novaehollandiae*) is by far the most abundant bird species (Lane 1979; personal observation). Large lizards [*Egernia kingii*, to 24.0 cm snout-vent length (SVL)] are common, and smaller skinks (*Morethia obscura*, to 5.5 cm SVL) also occur on the island (Bush et al. 1995). The only mammals are house mice (*Mus domesticus*) and sea lions (*Neophoca cinerea*) (Abbott 1978; Young 1981).

Animals and procedures

During 21 trips (9 in September 1997, 7 in September 1998, 5 in October 1998) a total of 212 tiger snakes was hand-captured. We

caught 99 different individuals in 1997, and 153 (including 40 recaptures) in 1998. Each snake was sexed by eversion of the hemipenes, and individually marked by scale-clipping. To limit further disturbance, a silver number was painted on the back of all adult snakes. These markings enabled us to identify basking snakes without recapture. SVL and total body length were recorded to the nearest 0.5 cm, and body mass was recorded to the nearest 1 g. Prey items were identified either by palpation of the snake's abdomen (mice, lizards and chicks are easily differentiated by their shape) or from remains in faecal samples. Some snakes regurgitated their prey during handling, and in all cases, our prior palpations had correctly identified both the prey species and number of prey items. We also observed snakes feeding in the field. Body masses of snakes with prey in the stomach were not used for statistical analyses.

Many snakes had injuries (see Results). We carefully examined the eyes, the head and the body of every individual. We also examined 71 tiger snakes from other populations (10 live specimens from near Perth, 61 preserved animals in the Western Australian Museum and the Australian Museum) to compare the incidence of scarring. For analysis, we simply classified each snake into a discrete category: with or without head or body injuries. The snakes were released at the exact place of capture.

Statistical analyses

All statistical tests were performed using Statistica 5.1. software. Yates correction was applied for cases involving small sample sizes. Means are expressed \pm SD in all the results.

Results

Body size

The mean SVL of the Carnac Island snakes was 82.0 ± 17.9 cm ($n = 211$, range 25.0–109.0 cm; mean total length = 96.0 ± 20.4 cm, $n = 203$, range 30.0–127.0 cm). In this population, males (86.2 ± 16.1 cm, $n = 147$) averaged significantly larger than females [72.6 ± 17.9 cm, $n = 63$; one-factor ANOVA with $\ln(\text{SVL})$ as the dependent variable and sex as the factor, $F_{1,208} = 23.79$, $P < 0.0001$]. Body mass was highly correlated with body length ($r = 0.98$, $n = 143$, $P < 0.0001$). The overall relationship between these two variables did not differ between the sexes [ANCOVA with $\ln(\text{body mass})$ as the dependent variable, $\ln(\text{SVL})$ as the covariate and sex as the factor: slopes $F_{1,138} = 2.58$, $P = 0.11$, and intercepts $F_{1,139} = 1.65$, $P = 0.20$], but varied significantly between years (ANCOVA with year as the factor: $F_{1,140} = 4.14$, $P = 0.044$). Consequently, we need to take annual variation into account when considering whether blindness affects body condition.

Annual growth in body size

Annual growth rate in SVL (in cm, calculated from September 1997 to September–October 1998) was negatively correlated with the snake's mean SVL over that period: $r = -0.81$, $n = 40$, $P < 0.001$ (Fig. 1), i.e. larger snakes grew more slowly (at least in terms of SVL). Males grew faster than females [ANCOVA with size

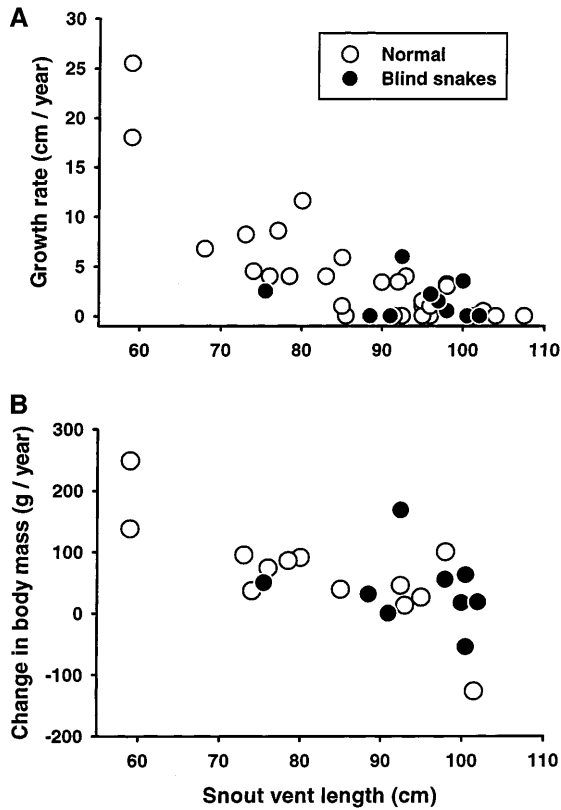


Fig. 1 **A** Growth rates of tiger snakes as a function of body size. The increment in body length (snout-vent length, SVL) over a period of 12 months (spring 1997 to spring 1998) was greatest for small snakes; growth in length ceased in larger (older) snakes. **B** Similarly, changes in body mass of tiger snakes as a function of body size over a period of 12 months were greatest for small snakes. Growth rate (adjusted to SVL) and changes in body mass (adjusted to SVL) were similar for blind snakes (closed circles) and “normal” snakes (open circles)

increment as the dependent variable, $\ln(\text{mean SVL})$ as the covariate and sex as the factor: slopes $F_{1,36} = 2.89$, $P = 0.10$, and intercepts $F_{1,37} = 9.34$, $P = 0.004$]. Thus, analyses of the effect of blindness on SVL growth rates need to take into account the sex as well as mean body size.

Changes in body mass were also negatively correlated with SVL ($r = -0.65$, $n = 22$, $P = 0.001$; Fig. 1), i.e. larger snakes added less mass between years. However, males and females did not differ in this respect [ANCOVA with mass increment as the dependent variable, $\ln(\text{SVL})$ as the covariate and sex as the factor: slopes $F_{1,18} = 0.034$, $P = 0.86$, and intercepts $F_{1,19} = 0.95$, $P = 0.34$].

Comparisons between blind and normal tiger snakes

From a total of 212 tiger snakes that we captured and marked in 1997 and 1998, 16 (7.54%) were totally blind (i.e. both eyes destroyed), and 14 (6.60%) were half-blind (one eye destroyed) (Table 1). The totally blind animals all showed heavy scarring to the head, and their eyes were completely destroyed. Most of the tiger snakes

Table 1 Comparisons of body size and body condition (mass relative to length) in island tiger snakes. The total number of tiger snakes captured and marked was 212 [*Blind* individuals in which both eyes were destroyed; *Half-blind* snakes with one eye destroyed; *Head + body* scars were found on both the head and the body, but both eyes were intact; *Head* individuals with scars on the head only; *Body* snakes with scars on the body only; *Intact* snakes without injuries; *Body condition index* body mass corrected for body length, using residual scores from the regression between these traits (Jayne and Bennett 1990; Naulleau and Bonnet 1996)]

	Number captured	Snout-vent length (cm)	Body condition index
Total	212	81.9 ± 17.8	0.00 ± 0.18
Blind	16	97.0 ± 6.9	-0.08 ± 0.19
Half-blind	14	93.5 ± 20.9	-0.05 ± 0.10
Head + body	86	91.4 ± 11.5	-0.01 ± 0.16
Head	19	84.9 ± 17.4	0.03 ± 0.13
Body	31	80.0 ± 9.7	-0.01 ± 0.16
Intact	46	64.3 ± 19.9	0.16 ± 0.24

on Carnac Island exhibited significant scarring (78%); only 46 snakes had no discernible injuries to the head or body (Table 1). The proportion of injuries found on Carnac snakes was much higher than on conspecifics from other areas. None of 71 mainland specimens showed any evidence of head scarring or eye loss ($\chi^2 = 16.9$, 1 *df*, $P < 0.001$), or any discernible scarring to the body. However, 9 of 10 tiger snakes from the vicinity of Perth exhibited tail injuries, probably due to freshwater turtles (personal observation).

The incidence of scarring to the head on the Carnac Island snakes was non-random with respect to sex and body size.

(1) Sex. Most of the snakes with eye damage were males (15 and 12 males with total and partial eye loss, respectively, versus 1 and 2 females, respectively). Thus, eye damage occurred disproportionately more often in males than in females (comparing the numbers of vision-impaired versus undamaged snakes among males versus females: Fisher's exact test, 1 *df*, $P < 0.02$).

(2) Body size. Blind snakes (95.4 ± 14.7 cm, $n = 29$) averaged larger than the rest of the population [79.8 ± 17.3 cm, $n = 182$; ANOVA with eye damage as the factor and $\ln(\text{SVL})$ as the dependent variable $F_{1,209} = 12.45$, $P = 0.0005$]. This difference was not an artefact of the bias towards eye damage being more common in males (the larger sex): the bias was apparent even when the analysis was restricted to males only ($F_{1,145} = 16.87$, $P < 0.0001$; the small sample size for females precluded a test on this sex). Totally blind snakes did not differ from half-blind snakes in mean SVL [ANOVA with $\ln(\text{SVL})$ as the dependent variable, $F_{1,27} = 0.71$, $P = 0.41$], or body mass ($F_{1,20} = 1.25$, $P = 0.28$). Visual detection efficiency in snakes with one eye destroyed was low (they often failed to detect us in the field during capture-recaptures, or at least ignored us), they always had large injuries on the head, and were quite similar in that respect to the fully blind individuals. Because “half” and “fully” blind snakes

were indistinguishable in size and mass, and both had a low visual dependence for the observed behaviors, we have pooled half-blind and totally blind snakes in a single category (hereafter called “blind snakes”) for subsequent analyses. Presumably, many half-blind snakes become fully blind at a later date, after additional injuries had been incurred. None of our results were altered when analyses were limited to fully blind snakes (see below).

Effects of blindness

Intuitively, blindness should greatly impede a snake’s food intake, survival and growth rate. Our data allow us to test these predictions.

(1) Survival. In 1998, we recaptured 10 of the 17 blind snakes that we had marked in 1997 (8 of 13 totally blind animals and 2 of 4 half-blind snakes). We also recaptured 30 of the 82 previously marked non-blind snakes. Thus, the recapture rate was actually higher among the blind animals (59%) than among the non-blind snakes (37%), although not significantly so (Fisher’s exact test, 1 *df*, $P=0.11$).

(2) Growth rate. The increments in SVL of the 10 recaptured blind snakes over the period 1997 to 1998 were similar to those exhibited by the 30 other snakes at the same mean SVL [two-factor ANCOVA with growth rate as the dependent variable, eye damage and sex as the factors and $\ln(\text{mean SVL})$ as the covariate: for eye-damage effect, slopes $F_{1,34}=1.44$, $P=0.24$, intercepts $F_{1,35}=0.39$, $P=0.53$, and $F_{1,35}=0.79$, $P=0.38$ for the interaction]. Using fully blind snakes in this analysis did not change the results (same-design ANOVA: $F_{1,33}=0.88$, $P=0.37$, intercepts $F_{1,34}=0.92$, $P=0.34$, and $F_{1,34}=1.27$, $P=0.27$ for the interaction).

(3) Annual changes in body mass. Similarly, blindness did not significantly affect changes in body mass (one-factor ANCOVA with body mass increments as the dependent variable, eye damage as the factor, and SVL as the covariate: slopes $F_{1,18}=0.95$, $P=0.34$, intercepts $F_{1,19}=0.54$, $P=0.47$). Although the low sample size weakens the power of this test, inspection of the mean values shows no trend for smaller mass gain in the blind snakes. Indeed, the mean mass change (adjusted for SVL) was greater in the blind animals than in the non-blind snakes (63.13 ± 60.09 g versus 41.93 ± 84.37 g). Using fully blind snakes only did not alter the results (same-design ANOVA: $F_{1,17}=0.98$, $P=0.34$, intercepts $F_{1,18}=0.91$, $P=0.35$).

(4) Body condition. A snake’s body condition (i.e. its mass relative to its SVL) may offer a useful index of its overall energy balance over the preceding several months (e.g. Forsman and Lindell 1996; Shine and Madsen 1997). Due to annual variation in body condition (see above), we analysed years separately. In both years, there was no consistent difference in body condition between undamaged snakes and those that had lost their eyes [ANCOVA with eye damage as the factor, $\ln(\text{body mass})$ as the dependent variable, and $\ln(\text{SVL})$ as the covariate:

for 1997, slopes $F_{1,58}=0.44$, $P=0.51$, and intercepts $F_{1,59}=2.64$, $P=0.11$; for 1998, slopes $F_{1,105}=0.35$, $P=0.5$, and intercepts $F_{1,106}=2.99$, $P=0.09$].

Food habits

Palpation and regurgitation of prey from live snakes showed that juvenile tiger snakes on Carnac Island feed on small mammals (*M. domesticus*) and lizards (*M. obscura* and juvenile *E. kingii*). Medium-sized snakes ate mice and seagull chicks, whereas large snakes fed mainly on seagull chicks (Table 2). A one-factor ANOVA [with prey type (mammal, bird, reptile) as the factor, and snake SVL as the dependent variable], confirmed that prey types changed with snake body size ($F_{2,102}=87.8$, $P < 0.0001$). Snakes that had consumed lizards were smaller (mean SVL = 43.7 ± 20.6 , $n=5$) than those containing mammals (mean SVL = 62.6 ± 15.2 cm, $n=14$), which in turn were smaller than snakes that ate birds (mean SVL = 91.5 ± 9.7 cm, $n=86$; $P < 0.0001$ for all post hoc comparisons).

Discussion

Rare and novel environments might act as spawning grounds for the evolution of new traits (e.g. Galis and Metz 1998 and references therein), and this is exactly the kind of ecological situation that tiger snakes confronted 70 years ago after their release on Carnac Island. Our data offer insight into the ecological circumstances that may favour the evolution of blindness. Carnac Island is quite unique in being a predator-free environment for the adult snakes, and its gull rookery provides them with an extremely rich food source. These conditions may explain why blindness can be tolerated by predators that normally rely on vision to hunt and/or escape from predators. However, plasticity is also a prerequisite for survival under any brutal shift in environmental conditions (Liem 1980; Vermeij 1974; Meyer 1990). Previous

Table 2 Prey recorded (via palpation, regurgitation, or in faeces) for Carnac Island tiger snakes in 1997 and 1998. Two to four mice or chicks were often found at the same time in one snake; *Number of observations* refers to numbers of prey items, with the number of individual snakes indicated in *parentheses*. In addition, three adult tiger snakes were found catching and eating seagull chicks

Prey type	Number of observations	Size of the snakes (snout-vent length, cm)
Suckling mice (<i>Mus domesticus</i>)	9 (4)	42.5–79
Adult mice (<i>M. domesticus</i>)	13 (10)	43–81.5
Lizard (unidentified)	3 (3)	42–74
Juvenile <i>Egernia kingii</i>	1 (1)	25
Adult <i>Morethia obscura</i>	1 (1)	25.5
Seagull chicks (<i>Larus novaehollandiae</i>)	118 (88)	63–109

studies of island populations of tiger snakes in south-eastern Australia have revealed an extraordinary lability in diets, body sizes and their scalation compared to their mainly anurophagous mainland conspecifics (e.g. Shine 1987; Schwaner and Sarre 1988, 1990; Schwaner 1990; Bush et al. 1995). The same flexibility is also evident within the lifetime of a single snake. The ontogenetic shift from lizards to mammals to birds presumably involves substantial shifts in foraging tactics. It also substantially changes the risks experienced during foraging. Our data suggest that the snakes' eyes are destroyed by seagulls: the incidence of head injuries increases with the growing snakes' shift to a diet of seagull chicks. Adult gulls protect their young vigorously, attacking the snakes with their sharp beaks and inflicting head wounds (personal observations). Silver gulls are adroit at evading bites from tiger snakes, which would almost certainly prove fatal, as this species has an extremely potent venom (Broad et al. 1979). Male snakes may be at greater risk than females (and hence, display a greater frequency of head injuries) because they feed more often (to support their larger body size), or because they move about more in the course of mate-searching activities. Alternatively, male snakes may be less easily driven away by nest-defending gulls, and hence more likely to sustain serious injury. Sex differences in behaviour are widespread in snakes (e.g. Shine 1986).

Remarkably, the blind animals were in no worse condition than normal snakes (intact or merely scarred). This similarity suggests that the snakes' hunting ability was not reduced to the extent that it had any measurable impact on body condition. Nuclear magnetic resonance imaging of a blind tiger snake revealed very substantial fat deposits, supporting the notion that the blind animals were in excellent condition (Bonnet et al. 1996). Recapture rates over a 12-month period indicated that blind snakes survived as well as undamaged animals, grew as much, and gained as much in body mass. Radio-tracking of four blind male snakes (two in 1997 and two in 1998) suggested that they were also not substantially impaired in other activities: two of the males located females (presumably by following pheromonal trails: Gartska and Crews 1981; Mason et al. 1989, 1990) and subsequently mated in our presence.

We know of only one other case analogous to that documented above, and there are striking similarities in the ecological circumstances involved. Wharton (1969) reported finding two congenitally blind cottonmouths (*Agkistrodon piscivorus*: Viperidae) on a small seabird-inhabited island in Florida, where the snakes feed on fish dropped by adult birds in the process of feeding their offspring. Both of the blind cottonmouths were in excellent body condition, and both were recaptured several times over a long period (Wharton 1969). The major similarities are that in both cases: (1) the snake populations live on small islands, essentially without predators; (2) the snakes are highly venomous, and hence relatively invulnerable to predation and capable of killing prey rapidly; (3) the major prey for the snakes is very

abundant and sessile and hence does not require active (visually oriented) pursuit, and (4) the snakes are relatively sedentary, heavy-bodied species that do not rely on active pursuit to capture prey.

These strong similarities clarify the kinds of factors that influence the relative importance of vision for diurnal terrestrial snakes. The ability of totally blind individuals to hunt their prey effectively and find mates (presumably relying entirely on chemoreception) highlights the role and effectiveness of tongue-flicking and the Jacobson organ system in such animals (Naulleau 1965; Kubie and Halpern 1978; Halpern and Kubie 1984; Schwenk 1995). The link between blindness and low predation pressure (i.e. large highly venomous snakes living in relatively predator free environments) suggests that for many snakes, vision may be important in predator detection. The use of sessile prey in both cases reinforces the importance of visual acuity for visually hunting predators that must capture fast-moving prey. Bizarre situations such as the occurrence of viable blind individuals may thus provide a unique opportunity to clarify the kinds of factors that may have been involved in the multiple phylogenetic shifts in dependency on visual systems within snakes. Such situations also confirm the suggestion that evolution may sometimes result in "momentarily excessive construction" (Gans 1979), whereby organisms possess complex features not necessary for their immediate survival or reproductive success.

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