How can blind tiger snakes (*Notechis scutatus*) forage successfully?

Fabien Aubret[A,B,E]*, Xavier Bonnet*[B,C]*, David Pearson*[D] *and Richard Shine*[C]

[A]School of Animal Biology, M092, University of Western Australia, Perth, WA 6009, Australia.
[B]Centre d'Etudes Biologiques de Chizé, CNRS, Villiers en Bois, France.
[C]Biological Sciences, University of Sydney, NSW 2006, Australia.
[D]Conservation and Land Management, Science Division, Woodvale Research Centre, Wanneroo, WA 6946, Australia.
[E]Corresponding author. Email: fab@congo.zzn.com

Abstract. On a small island off south-western Australia, tiger snakes (*Notechis scutatus*, Elapidae) continue to survive, feed, grow and reproduce successfully after being blinded by seagulls defending their chicks. We propose two alternative hypotheses to explain this surprising result: either vision is of trivial importance in tiger snake foraging, or the blinded snakes survive on a diet of abundant immobile prey that cannot escape their approach. Laboratory studies in which we blindfolded snakes falsified the first hypothesis: snakes that were unable to see had great difficulty in capturing mobile prey. Field data support the second hypothesis: blind snakes feed almost entirely on seagull chicks, whereas normal-sighted animals also took fast-moving prey (lizards and mice). Thus, the ability of tiger snakes on Carnac Island to survive without vision is attributable to the availability of abundant helpless prey (seagull chicks) in this insular ecosystem.

Introduction

Predators locate and capture their prey on the basis of a diverse array of sensory modalities, but vision is one of the most important for many taxa (Land and Nilsson 2002; Oakley 2003). This sense is used during day-to-day activities such as moving about, selecting habitats and shelters, acquiring resources, reproducing, and detecting predators (Salvini-Plawen and Mayr 1977; Land and Nilsson 2002). Although individuals from visually oriented species do not rely entirely on vision, this sense nonetheless is critical for their survival. For example, seals are 'blind' when they hunt in deep and dark waters (Dehnhardt *et al*. 1998), but rely upon vision to escape predators, to find mates, and to move on land. Hence, a sudden loss of vision (due to either disease or injury) will prove fatal almost immediately (Brown *et al*. 1984; Gauthier 1991). In natural situations, the deleterious effects of sudden blindness are so strong that very few populations are likely to contain accidentally blind individuals. Indeed, the phenomenon mostly has been observed only briefly (during epizootics) with blind animals dying quickly (Martin 1981; Brown *et al*. 1984; Gauthier 1991; Callait 1992; Langon 1996).

Two studies of snakes on islands provide dramatic counter-examples to these generalisations. First, Wharton (1969) reported the occurrence and good health of congenitally blind adult pit-vipers (*Agkistrodon piscivorus*) on Seahorse Key in Florida. Second, Bonnet *et al*. (1999, 2002) reported that on a small island off the coast of south-western Australia, ~5% of adult tiger snakes (*Notechis scutatus*) are blind, due to injuries inflicted by seagulls (*Larus novae-hollandiae*) that defend their chicks. Remarkably, these blinded snakes exhibit survival rates, growth rates and body condition comparable to that of vision-intact snakes, suggesting that blindness does not affect their frequency of feeding (Bonnet *et al*. 1999).

We tested two alternative hypotheses that might explain the continued foraging success of snakes after they have lost their sight. First, vision may be unimportant for foraging success. For example, the snakes might forage mostly at night, or on prey sequestered in burrows and located by chemical trails left on the substrate. Indeed, many scolecophidian snakes possess rudimentary eyes and manage to forage successfully in this way throughout their lives (Webb and Shine 1993). However, most 'advanced' (caenophidian) snakes, including elapids, use vision to identify and target prey (Naulleau 1965; Herzog and Burghardt 1974; Drummond 1985; Teather 1991; Mullin and Cooper 1998; Cooper *et al*. 2000; Shine and Sun 2003; Shine *et al*. 2004). Nonetheless, an animal may be able to develop enhanced acuity in other senses to compensate for sudden loss of vision (Parsons and Terman 1978; Rauschecker and Korte 1993; Cohen *et al*. 1997; Lessard *et al*. 1998). For instance, fish blinded by murky water exhibit sensory compensation under predatory threat (Hartman and Abrahams 2000).

The alternative hypothesis is that vision is indeed critical for capturing some types of prey, but not others. It is known that a predator's efficiency (including search distance, search speed, pursuit dynamics) may affect prey selection (Bakker 1983; Endler 1991; Emerson *et al*. 1994; Garland and Losos 1994). Thus, blinded snakes may be able to survive by

feeding on immobile prey unable to escape. Fast-moving prey, on the other hand, would quickly detect and avoid the predator. The tiger snakes of Carnac Island provide a unique opportunity to test predictions from these two hypotheses, and hence to clarify the impact of sudden loss of vision on foraging abilities in a natural ecological context.

Methods

Laboratory studies

We captured adult snakes from two nearby populations (25 km apart) in Western Australia: Carnac Island and Herdsman Lake (see Aubret 2004 for details on field sites). Carnac Island is a small limestone plateau surrounded by sand beaches (total area of 16 ha), ~12 km off the coast of Fremantle (32°07′S, 115°39′E). Carnac Island hosts a large population of tiger snakes (~400 adult snakes). In total, 8% of the adults are half-blind (one eye destroyed), and 4.5% are totally blind (Bonnet *et al.* 1999, 2002). On Carnac Island, the snakes feed on lizards (*Egernia kingii*, *Morethia obscura*), mice (*Mus musculus*) and bird chicks (*Larus novaehollandiae*, *Puffinus pacificus*) (Bonnet *et al.* 1999). Silver gull chicks are very abundant in spring and autumn (Nicholls 1974).

Herdsman Lake (31°55′44″S, 115°48′19″E) is a natural reserve in Perth. A dredged moat encircling the 300-ha lake ensures permanent open water. Frogs (*Litoria insignifera*, *L. adelaidensis*, *Crinia moorei*) and mice (*Mus musculus*) are abundant, and constitute the main diet of snakes in this population (respectively, 53% and 47% of all prey items recorded: Aubret *et al.* 2004).

Two adult snakes from Carnac Island (one male, one female) and five adults from Herdsman Lake (two males, three females) were captured between 13 December 2001 and 3 September 2002. Another three adult snakes from Carnac Island, born in captivity in March 2002, were used. All snakes were intact (notably sighted) and healthy at the time of capture. They were kept in a room maintained at 27°C by day and 20°C by night, and were housed individually in transparent plastic boxes (50 × 40 × 30 cm) with water dish, shelter, and paper towel as substrate. A heat source provided basking opportunities four times a day (4 × 15 min day^{-1}, 600-W Na lamp). Water was available at all times and food was offered once a week (previously euthanased laboratory mice supplied by the University of Western Australia animal care unit). All snakes were long-term captives (average 296 ± 188 days, range 90–603 days) and were feeding regularly before the experiments (which took place between 28 October 2002 and 27 February 2004).

Ethics note

All experiments complied with the current laws of Australia. The Animal Ethics Committee of UWA approved all procedures (permit # RA/3/100/245) and the Department of Conservation and Land Management (WA; permit SF004604) issued fauna-collection permits. Upon arrival in the laboratory colony, and every six months thereafter, snakes were individually treated against worms (Nematodes) with PANACUR® (100 mg kg^{-1}; injected into snake food before feeding). Snakes were also checked for external parasites such as ticks or mites upon arrival in the colony. However, no external parasites were found either in wild snakes or within the colony. All snakes were returned to the wild at the end of the study, after a final treatment against worms. Mouse food and water were always available in the snake cage.

Experimental procedure

To test the effect of sudden loss of vision on foraging efficiency, we ran tests before and after rendering snakes blind by covering their eyes. A rectangular piece of black tape was affixed across the snake's head, covering both eyes and left in place until all artificially blinded tests had been completed. Because snake eyes are covered by transparent scales, the application and removal of tape was painless. Tape was reapplied immediately after snakes shed their skin. The period that the snakes were deprived of vision before testing averaged 11 days (range 4–25 days). The animals adjusted quickly to blindness, easily finding their usual shelter, water dish, and basking spot. Importantly, they continued to feed on dead mice (see Results).

Admittedly, studies involving larger sample sizes are necessary to reveal whether Carnac Island and Herdsman Lake snakes exhibit similar predatory behaviour. However, preliminary data (see Results) did not indicate any obvious differences in behaviour and data for snakes from both populations were pooled for analysis.

Experiment 1: effect of blindness on acceptance of dead mice by snakes

Dead mice were offered to the snakes weekly throughout the experiment, so we can compare the rate of prey acceptance before and after snakes were rendered blind by tape application. Dead mice were placed in front of the snake's snout and left for 24 h. In nine adult snakes (four from Herdsman Lake and five from Carnac Island), we recorded whether the mouse was eaten.

Experiment 2: effect of blindness on hunting ability of adult snakes

A live mouse was introduced into the snake's shelter-box, limiting disturbance to the snake as much as possible, after which we recorded the chronology of events with a stopwatch. The snake and mouse were left together for 30 min, after which the trial stopped if the snake was not searching for prey. In total, 58 trials were conducted on 10 different snakes (see Table 1). We recorded the time elapsed before the first strike (and whether or not venom was injected), and time to paralysis of the prey, and to death of the prey (cessation of breathing). We counted the total number of missed versus successful bites over the trial; and noted whether the mouse was held or released after a successful bite. Data on some variables were unavailable for some trials because of difficulties in seeing encounters without disturbing either the snake or mouse.

Field study

The population of tiger snakes of Carnac Island was monitored regularly from 1997 to 2003 (Bonnet *et al.* 2002) with increased field work effort from September to May of each year. Snakes were captured by hand and each animal was individually marked (scale-clipped), and carefully examined to determine its visual ability. We scored the snake as 'normal' when both eyes were intact, 'half-blind' when one eye was destroyed, and 'blind' when both eyes were destroyed (Bonnet *et al.* 1999). We palpated the stomach of each snake for the presence of prey; faeces were also examined for the presence of feather, hairs or reptile scales (from seagull chicks, mice, and lizards respectively). Gull chicks are taken soon after they hatch, so are immobile prey (Bonnet *et al.* 2002; Aubret *et al.* 2004). In contrast, lizards and mice are mobile prey.

Results

Laboratory studies

Captive adult snakes from Carnac Island and Herdsman Lake did not differ significantly from each other in mean snout–vent length (respectively 74.00 ± 21.98 cm *v.* 80.80 ± 6.04 cm, Kruskal–Wallis ANOVA: $H_{1,10} = 0.27$, $P = 0.60$), body mass (392.28 ± 353.47 g *v.* 330.86 ± 63.35 g; $H_{1,10} = 0.27$, $P = 0.60$), or body condition (calculated using the residual values of the linear least-squares regression of log(BM) against log(SVL): 0.040 ± 0.075 *v.* –0.040 ± 0.057; $H_{1,10} = 1.84$, $P = 0.17$).

Table 1. The effects of blindness on hunting ability in ten captive adult tiger snakes tested over 58 trials with live mice

For each individual snake, mean values were calculated for each trait for an average of 3.5 ± 0.85 control tests and 2.3 ± 0.82 'blind' tests. Wilcoxon matched-paired tests were run using those means per individuals. Data are presented as a chronology of events: 'Strike time' = time elapsed from prey introduction to the first strike delivered by the snake (either missed or successful); 'Envenomation time' = time elapsed from prey introduction to the first successful strike; 'Paralysed prey' = time elapsed from prey introduction to the immobilisation of the prey on the substrate; and 'Dead prey' = time elapsed from prey introduction to the end of detectable respiratory movements. Other key results include 'Death time' = time elapsed between the first successful bite and the death of the prey; and 'Holding time' = duration for which the prey was held in the snake's mouth

Trait	Control	'Blind'	n	Z	P
Prey body mass (g)	27.86 ± 2.42	29.03 ± 3.21	10	1.07	0.290
Chronology of events					
Strike time (s)	12.65 ± 8.44	256.27 ± 527.33	10	2.60	0.009
Envenomation time (s)	16.54 ± 10.54	467.10 ± 705.55	10	2.00	0.009
Paralysed prey (s)	128.56 ± 28.57	360.40 ± 263.43	6	2.20	0.028
Dead prey (s)	145.10 ± 25.28	871.17 ± 1202.82	7	2.37	0.018
Key results					
No. missed strikes	1.10 ± 0.68	3.90 ± 3.65	10	2.19	0.028
No. successful strikes	2.58 ± 1.41	1.86 ± 0.80	10	1.58	0.110
Death time (s)	117.81 ± 27.82	176.27 ± 89.82	7	1.52	0.130
Holding time (s)	80.08 ± 37.12	37.19 ± 34.58	6	1.99	0.046
Prey held (%)	41.66 ± 30.68	48.33 ± 41.90	10	0.42	0.670

Experiment 1: effect of blindness on acceptance of dead mice by adult snakes

The proportion of trials in which mice were taken did not differ between the island and mainland snakes either during the control tests (Kruskal–Wallis ANOVA: $H_{1,9} = 1.26$, $P = 0.26$) or during the 'blind' tests ($H_{1,9} = 1.35$, $P = 0.24$). Hence we pooled data for Carnac Island and Herdsman Lake snakes and conducted the analysis on a total of 91 control tests and 61 'blind' tests in nine different snakes. Prey size was similar in control tests (22.49 ± 9.95 g) and 'blind' tests (23.77 ± 0.73 g) (*t*-test for dependant sample: $n = 9$, $t = -1.29$, $P = 0.55$). There was no difference in the rate of acceptance of dead mice between the control and the 'blind' tests (respectively $86.4 \pm 14.0\%$ *v.* $93.1 \pm 10.5\%$) (*t*-test for dependant samples: $n = 9$, $t = 1.26$, $P = 0.24$).

Experiment 2: effect of blindness on hunting ability of adult snakes

Kruskal–Wallis ANOVAs did not detect any significant differences between Carnac Island and Herdsman Lake snakes either in the control tests (all $P > 0.17$) or in the 'blind' tests (all $P > 0.13$) for any of the variables recorded. Therefore, we pooled data for snakes from both localities. Artificial blindness severely impaired the hunting ability of the snakes, especially their capacity to locate, strike and kill their prey (Table 1). In comparison with snakes in control trials, blind snakes delayed the initial strike, missed their target more often, and thus took longer to consume the prey item.

Field study

Blind snakes and half-blind snakes preyed almost exclusively on seagull chicks (immobile prey) whereas snakes with normal vision regularly consumed lizards and mice (mobile prey) ($\chi^2 = 12.78$, d.f. $= 2$, $n = 257$, $P < 0.002$) (Table 2). There is also an ontogenic shift in diet in this population (adult snakes consume mostly seagull chicks: Bonnet *et al*. 1999) so we repeated this analysis after restricting the data to adult snakes only; the results remained significant ($\chi^2 = 6.82$, d.f. $= 2$, $n = 236$, $P = 0.033$).

Discussion

Blindness and prey-targeting ability

Although sudden loss of vision did not reduce the snakes' willingness to feed, it strongly compromised the animals' ability to locate and effectively strike mobile prey.

Table 2. Prey items recorded from alimentary tracts of free-ranging tiger snakes on Carnac Island, Western Australia, with reference to whether the prey were immobile (seagull chicks eaten soon after hatching) or mobile (lizards and mice)

Data on visual status indicate whether both eyes of the snakes were intact ('normal'), one eye was destroyed ('half-blind'), or both eyes were destroyed ('fully blind')

Visual status	Immobile prey	Mobile prey	Total
Normal snakes	156 (72%)	60 (28%)	216
Adult snakes	156 (80%)	39 (20%)	195
Half-blind snakes	21 (95%)	1 (5%)	22
Fully blind snakes	18 (95%)	1 (5%)	19

The time necessary to kill mobile prey dramatically increased when snakes were artificially blinded. For example, the time taken to initiate a first strike increased 20-fold, and the time to successful envenomation increased 28-fold. These results support other studies showing a decreased prey-targeting ability by snakes after their eyes were covered (Naulleau 1965; Chiszar *et al*. 1981; Kardong 1992; Haverly and Kardong 1996). Observations of normal snakes, as well as congenitally totally or unilaterally blind snakes, have demonstrated that prey movements detected by visual as well as infrared senses are important to elicit hunting behaviour, and for snakes to localise and capture their prey (Drummond 1985; Kardong and Mackessy 1991; Haverly and Kardong 1996; Lindberg *et al*. 2000; Grace *et al*. 2001).

Moreover, wild mice or lizards would presumably pose an even more challenging target than the naive laboratory rodents used in our study (Amo *et al*. 2004). In the field, mobile prey would likely evade the strike of blind snakes.

Blindness and post-strike feeding behaviour

Despite their reduced striking abilities, artificially blinded snakes were able to inject a lethal dose of venom and swallow their prey. Although there was no significant difference in the percentage of prey held after a bite in control versus artificially blinded animals, blinded snakes that held their prey after the initial strike did so over a shorter time, perhaps because the initial strike was less precisely targeted and the mice managed to escape more often. Nonetheless, any prey item that was seized was eventually consumed. Similarly, a lack of visual and infrared senses decreases the capacity of rattlesnakes to find and kill prey, but does not alter their ability to relocate and swallow prey after a lethal strike has been delivered (Haverly and Kardong 1996). Indeed, immobile prey items are mostly found (or relocated after a strike) using chemosensory cues (Naulleau 1965; Chiszar *et al*. 1981, 1990; Furry *et al*. 1991; Haverly and Kardong 1996). On Carnac Island, gull chicks are very abundant (Dunlop and Storr 1981) and remain virtually immobile even if a snake tongue-flicks them (authors' observations). Hence, although the entire prestrike feeding sequence is prolonged in blind snakes (at least in the laboratory), the situation still allows snakes to feed effectively on this abundant and immobile food source. Further work is required to clarify the cues used by blind snakes to locate gull chicks.

Diet composition

The absence of any particular item from a predator's diet can be due to a lack of detection, to a shift in prey preferences, to unsuccessful pursuit tactics, or to difficulties in subduing a potential prey type (Eifler and Passek 2000). We recorded one lizard and one mouse in the diet of blind snakes on Carnac Island, suggesting that blind snakes were still prepared to consume such items if they could capture them (unless they were found dead by the snakes). In our laboratory experiments, however, blindfolded tiger snakes fed readily on mice. Thus, the scarcity of mice and lizards in the diet of blind snakes in the field suggests that mobile prey might escape capture, rather than there being any active selection against such items (for instance, a change in prey preferences in blind snakes).

Tiger snakes in captivity are renowned for their willingness to take dead (even decomposing) prey (Fearn 1993) and they also do so in the field. On Carnac Island, we collected two maggot-covered prey items from the stomachs of two different snakes. Similar scavenging behaviour has been recorded in other species of snake that usually hunt mobile prey, and olfaction seemed to be the overriding sensory modality used for carrion detection (see DeVault and Krochmal 2002 for a review).

These observations reinforce the notion that prey movement is not an obligatory trigger for prey recognition, even for snake species that usually hunt mobile prey. Moreover, it is possible that both sighted and blind snakes use the same non-visual modality to find immobile prey.

Our results clarify the mechanisms underlying the survival of blind tiger snakes. Blindness substantially impedes a snake's ability to locate and capture mobile prey. On Carnac Island, however, the availability of an abundant immobile food source (seagull chicks) enabled snakes to forgo hard-to-capture prey items (mice, lizards) and alter their diet towards more easily captured prey.

References

Amo, L., Lopez, P., and Marti, J. (2004). Wall lizards combine chemical and visual cues of ambush snake predators to avoid overestimating risk inside refuges. *Animal Behaviour* **67**, 647–653. doi:10.1016/j.anbehav.2003.08.005

Aubret, F. (2004). Aquatic locomotion and behaviour in two disjunct populations of Western Australian tiger snakes, *Notechis ater occidentalis*. *Australian Journal of Zoology* **52**, 357–368. doi:10.1071/ZO03067

Aubret, F., Bonnet, X., Maumelat, S., Bradshaw, S. D., and Schwaner, T. (2004). Diet divergence, jaw size and scale counts in two neighbouring populations of tiger snakes (*Notechis scutatus*). *Amphibia-Reptilia* **25**, 9–17. doi:10.1163/156853804322992797

Bakker, R. T. (1983). The deer flees, the wolf pursues: incongruencies in predator–prey coevolution. In 'Coevolution'. (Eds D. J. Futuyma and M. Slatkin.) pp. 350–382. (Sinauer Associates: Sunderland, MS.)

Bonnet, X., Bradshaw, S. D., Shine, R., and Pearson, D. (1999). Why do snakes have eyes? The (non-)effect of blindness in island tiger snakes (*Notechis scutatus*). *Behavioral Ecology and Sociobiology* **46**, 267–272. doi:10.1007/s002650050619

Bonnet, X., Pearson, D., Ladyman, M., Lourdais, L., and Bradshaw, S. D. (2002). 'Heaven' for serpents? A mark–recapture study of tiger snakes (*Notechis scutatus*) on Carnac Island, Western Australia. *Austral Ecology* **27**, 442–450. doi:10.1046/j.1442-9993.2002. 01198.x

Brown, A. S., Carrick, F. N., and Gordon, G. (1984). Infertility and other chlamydial diseases and their effects on koala populations. *Australian Mammal Society Bulletin* **8**, 97.

Callait, M. P. (1992). Le massif de Chaudron (Hautes Alpes), étude d'une endozootie de kérato-conjonctivite infectieuse contagieuse du mouton de Corse (*Ovis ammon musimon*). Ph.D. Thesis, ENVL, Lyon.

Chiszar, D., Taylor, S., Radcliffe, C., Smith, H., and O'Connell, B. (1981). Effects of chemical and visual stimuli upon chemosensory searching by garter snakes and rattlesnakes. *Journal of Herpetology* **15**, 415–424.

Chiszar, D., Melcer, T., Lee, R., Radcliffe, C., and Duvall, C. (1990). Chemical cues used by prairie rattlesnakes (*Crotalus viridis*) to follow trails of rodent prey. *Journal of Chemical Ecology* **16**, 79–86. doi:10.1007/BF01021269

Cohen, L. G., Celnik, P., Pascual-Leone, A., Corwell, B., Faiz, L. *et al.* (1997). Functional relevance of cross-modal plasticity in blind humans. *Nature* **389**, 180–183. doi:10.1038/38278

Cooper, W. E., Jr, Burghardt, G. M., and Brown, W. S. (2000). Behavioural responses by hatchling racers (*Coluber constrictor*) from two geographically distinct populations to chemical stimuli from potential prey and predators. *Amphibia-Reptilia* **21**, 103–116. doi:10.1163/156853800507318

Dehnhardt, G., Björn, M., and Bleckmann, H. (1998). Seal whiskers detect water movements. *Nature* **394**, 235–236. doi:10.1038/28303

DeVault, T. L., and Krochmal, A. R. (2002). Scavenging by snakes: an examination of the literature. *Herpetologica* **58**, 429–436.

Dunlop, J. N., and Storr, G. M. (1981). Seabird Islands: Carnac Island, Western Australia. *Corella* **5**, 71–74.

Drummond, H. (1985). The role of vision in the predatory behaviour of natricine snakes. *Animal Behaviour* **33**, 206–215.

Eifler, D. A., and Passek, K. M. (2000). Body size effects on pursuit success and interspecific diet differences in *Cnemidophorus* lizards. *Amphibia-Reptilia* **21**, 477–484. doi:10.1163/1568538003000 59359

Emerson, S. B., Greene, H. W., and Charnov, E. L. (1994). Allometric aspects of predator–prey interactions. In 'Ecological Morphology: Integrative Organismal Biology'. (Eds P. C. Wainwrightand and S. M. Reilly.) pp. 123–139. (University of Chicago Press: Chicago.)

Endler, J. A. (1991). Interactions between predators and prey. In 'Behavioural Ecology: an Evolutionary Approach'. (Eds J. R. Krebs and N. B. Davies.) pp. 169–196. (Blackwell Scientific Publications: Oxford.)

Fearn, S. (1993). The tiger snake *Notechis scutatus* (Serpentes: Elapidae) in Tasmania. *Herpetofauna* **23**, 17–29.

Furry, K., Swain, T., and Chiszar, D. (1991). Strike-induced chemosensory searching and trail followed by prairie rattlesnakes (*Crotalus viridis*) preying upon deer mice (*Peromyscus maniculatus*): chemical discrimination among individual mice. *Herpetologica* **47**, 69–70.

Garland, T., Jr, and Losos, J. B. (1994). Ecological morphology of locomotor performance in squamate reptiles. In 'Ecological Morphology: Integrative Organismal Biology'. (Eds P. C. Wainwright and S. M. Reilly.) pp. 240–302. (University of Chicago Press: Chicago.)

Gauthier, D. (1991). La kérato-conjonctivite infectieuse du chamois: étude épidémiologique dans le département de la Savoie 1983–1990. Thesis, ENVL, Lyon.

Grace, M. S., Woodward, O. M., Church, D. R., and Calisch, G. (2001). Prey targeting by the infrared-imaging snake *Python*: effects of experimental and congenital visual deprivation. *Behavioural Brain Research* **119**, 23–31. doi:10.1016/S0166-4328(00)00336-3

Hartman, E. J., and Abrahams, M. V. (2000). Sensory compensation and the detection of predators: the interaction between chemical and visual information. *Proceedings of the Royal Society of London. Series B. Biological Sciences* **267**, 571–575. doi:10.1098/rspb. 2000.1039

Haverly, J. E., and Kardong, K. V. (1996). Sensory deprivation effects on the predatory behavior of the rattlesnake, *Crotalus viridis oreganus. Copeia* **1996**, 419–428.

Herzog, H. A., and Burghardt, G. M. (1974). Prey movement and predatory behavior of juvenile western yellow-bellied racers, *Coluber constrictor mormon. Herpetologica* **30**, 285–289.

Kardong, K. V. (1992). Proximate factors affecting guidance of the rattlesnake strike. *Zoological Journal of Anatomy* **122**, 233–244.

Kardong, K. V., and Mackessy, S. P. (1991). The strike behavior of a congenitally blind rattlesnake. *Journal of Herpetology* **25**, 208–211.

Land, M. F., and Nilsson, D. E. (2002). 'Animal Eyes.' (Oxford University Press: New York.)

Langon, X. (1996). La kérato-conjonctivite infectieuse contagieuse des ongulés de montagne. Etude du rôle étiologique de *Staphylococcus aureus* chez le mouton (*Ovis ammon musimon*). Thesis, ENVL, Lyon.

Lessard, N., Pare, M., Lepore, F., and Lassonde, M. (1998). Early-blind human subjects localize sound sources better than sighted subjects. *Nature* **395**, 278–280. doi:10.1038/26228

Lindberg, A. C., Shivik, J. A., and Clark, L. (2000). Mechanical mouse lure for brown tree snakes. *Copeia* **2000**, 886–888.

Martin, R. W. (1981). Age-specific fertility in three populations of the koala, *Phascolarctos cinereus* Goldfuss, in Victoria. *Australian Wildlife Research* **8**, 275–283. doi:10.1071/WR9810275

Mullin, S. J., and Cooper, R. J. (1998). The foraging ecology of the gray rat snake (*Elaphe obsoleta spiloides*) – visual stimuli facilitate location of arboreal prey. *American Midland Naturalist* **140**, 397–401.

Naulleau, G. (1965). La biologie et le comportement prédateur de *Vipera aspis* au laboratoire et dans la nature. *Bulletin Biologique de la France et de la Belgique* **99**, 295–524.

Nicholls, C. A. (1974). Double-brooding in a Western Australian population of the silver gull, *Larus novaehollandiae. Australian Journal of Zoology* **22**, 63–70. doi:10.1071/ZO9740063

Oakley, T. H. (2003). The eye as a replicating and diverging, modular developmental unit. *Trends in Ecology & Evolution* **18**, 623–627. doi:10.1016/j.tree.2003.09.005

Parsons, L. M., and Terman, C. R. (1978). Influence of vision and olfaction on the homing ability of the white-footed mouse (*Peromyscus leucopus noveboraceasis*). *Journal of Mammalogy* **59**, 761–771.

Rauschecker, J. P., and Korte, M. (1993). Auditory compensation for early blindness in cat cerebral cortex. *The Journal of Neuroscience* **13**, 4538–4548.

Salvini-Plawen, L. V., and Mayr, E. (1977). 'On the Evolution of Photoreceptors and Eyes.' (Plenum Press: New York.)

Shine, R., and Sun, L. S. (2003). Attack strategy of an ambush predator: which attributes of the prey trigger a pit-viper's strike? *Functional Ecology* **17**, 340–348. doi:10.1046/j.1365-2435.2003. 00738.x

Shine, R., Brown, G. P., and Elphick, M. J. (2004). Field experiments on foraging in free-ranging water snakes *Enhydris polylepis* (Homalopsinae). *Animal Behaviour* **68**, 1313–1324. doi:10.1016/ j.anbehav.2004.03.004

Teather, K. L. (1991). The relative importance of visual and chemical cues for foraging in newborn blue-striped garter snakes (*Thamnophis sirtalis sirtalis*). *Behavior* **117**, 255–261.

Webb, J. K., and Shine, R. (1993). Dietary habits of Australian blind-snakes. *Copeia* **1993**, 762–770.

Wharton, C. H. (1969). The cottonmouth moccasin on Sea Horse Key, Florida. *Bulletin of Florida State Museum, Biological Science* **14**, 227–272.