

The defensive behaviour of *Naja oxiana*, with comments on the visual displays of cobras

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ABSTRACT - The defensive behaviours of a group of freshly-caught central Asiatic cobras, *Naja oxiana*, were evoked by the proximity of an experimenter. The cobras responded by hooding and holding 13-22% of their total body length in an elevated or vertical posture. From this vertical posture the cobras would launch defensive sham (closed-mouth) strikes; these strikes were typically associated with a short “burst”-like hiss, and were more frequent in the smaller snakes studied. The presence of the experimenter provoked an increase in the cobra’s ventilatory rib movements as well as the tongue flick rates; the latter metric was strongly correlated with the height of vertical posturing, strike frequency, and hissing frequency. Most of the observed behaviours result from the cobras’ visual perception, are interpreted as a visual display intended as a deterrent. This interpretation raises interesting, and previously unexplored, questions about intra- and interspecific variation of these displays (within both *Naja* and the Hemibungarini), as well as the relationship between these defensive behaviours and (repeatedly evolved) ability to “spit” venom.

INTRODUCTION

Cobras are active-diurnal hunters that rely primarily on their visual system to locate both their prey and their potential predators (Kardong et al., 1997; Westhoff et al., 2010). As part of their predator deterrence strategy, cobras adopt what is perhaps the most iconic visual display of all snakes... the vertical elevation of the head coupled with the lateral spreading of the ribs to form the “hood” (Chiszar et al., 1983; Kardong, 1982; Kardong et al., 1997; Radcliffe et al., 1986; Young & Kardong, 2010). In many cobras vertical posturing and hooding are but two components of a defensive repertoire that may include striking, hissing, spitting venom, and death feigning (Radcliffe et al., 1986; Rasmussen et al., 1995; Young et al., 2004).

Despite the abundance of illustrations and descriptions of the defensive behaviours of cobras, there are some fundamental questions that have yet to be explored. The efficacy of vertical posturing and hooding as a visual deterrent presumably correlates with the prominence of the display. The naturally-occurring predators of snakes such as birds (Errington, 1932; Maklakov, 2002) and carnivorous mammals (Barchan et al., 1992; Vanderhaar & Hwang, 2003) usually target the head of snakes (Rasa, 1973; Francis et al., 1989; Langkilde et al., 2004). As such, any increase in the prominence of the defensive visual display likely comes at the cost of (direct) increase in vulnerability by moving the predator’s target (the cobra’s head) into a more elevated and prominent position.

The ability to “spit” venom has evolved multiple times in cobras (Wüster & Thorpe, 1992a). Spitting cobras

exhibit a range of defensive behaviours and differ in their spitting performance (Chiszar et al., 1987; Rasmussen et al., 1995; Young et al., 2004; Westhoff et al., 2010). But in all spitting cobras the spat venom travels beyond the range of the snake’s defensive strike, meaning that spitting cobras possess a form of “long distance” defense (when compared to non-spitting cobras). The efficacy of the spat venom in causing severe eye injury, loss of vision, and debilitating pain (Chu et al., 2010; Ang et al., 2014), suggests that hooding and vertical posturing may be more variable among spitting cobras than non-spitting cobras.

The Hemibungarini radiation of elapid snakes includes the true cobras (*Naja*) as well as several cobra-like taxa (including *Boulengerina*, *Ophiophagus*, *Pseudonaja*, and *Walterinesia*) (Castoe et al., 2007; Kelly et al., 2009). The genus *Naja* includes approximately 30 species, but previous behavioural and functional studies have disproportionately focused on five species: *Naja naja*, *N. haje*, *N. kaouthia*, as well as *N. nigricollis* and *N. pallida*, the latter two being spitting cobras. Herein we provide a description of the defensive repertoire of the central Asian cobra, *Naja oxiana* (Eichwald, 1831) which inhabits West Asia and Pakistan, with a limited distribution in India (Wüster & Thorpe, 1992b; Wallach et al., 2009). We chose to study *N. oxiana* in part because it has been rarely studied behaviourally, it is a non-spitting cobra, and is common in the Serpentarium of the Pasteur Institute of Iran. More fundamentally, *N. oxiana* is of a similar size (adult length of ~ 140 cm), general build, and colour pattern to the more commonly-studied black-neck spitting cobra, *N. nigricollis*. A more detailed comparison of these

two species may offer a unique opportunity to directly test the energetics, and behavioural effectiveness of venom spitting in cobras.

METHODS

This study used six *N. oxiana* which were wild-caught from the Khorasan province of Iran (Darvish & Rastegar-Pouyani, 2012; Nasoori et al., 2014) and had been kept for at least one month in the Serpentarium of the Pasteur Institute of Iran. The cobras were kept at 26°C under a 12:12 dark/light cycle, fed live and dead rodents, and given water ad libitum. All maintenance and experimental use of these animals conformed to both the internal regulations for keeping laboratory animals in our institute, and established international guidelines (ASIH, 2004). The animals were of roughly similar size (108.5 - 120.5 SVL) and all appeared to be healthy; at the time of the trials one of the cobras was approaching ecdysis and had opaque eyes.

Three days prior to the experiment, the cobras were immobilised with administration of an appropriate dose of diazepam (Chemidarou 10mg/2ml Amp, Iran). Each cobra was then weighed on a digital scale (A&D EK-1200 i NTEP 133 Jewelry Buyer Scale, USA), then both total length and snout-vent length were measured. Lastly, the snake's dorsal side was marked by small pieces of adhesive plaster placed in 5 cm intervals starting 5 cm from the snout.

For the behavioural trials, an individual cobra was placed on a wooden table (300 cm × 150 cm) within a room held at 26°C. The experimenter provoked the animal, by his physical presence, movement of his hands, and, in some instances, through direct contact with the end of a snake hook. The snakes' reactions were recorded with a digital camera (Handycam Video Camera, DCR-TRV265E, SONY, Japan) located 3 meters away from the table. Each behavioural trial lasted for a minimum of 2 minutes. Each snake was used for three trials, and the snake was always given a rest interval (during which it was removed from the table) between the trials.

The snake varied the height of the vertical posture regularly during the trials, so each trial [equal to 120 seconds] was divided into 3 parts of 40 seconds and the maximal height determined for each part. Vertical height was standardised by expressing it as a percentage of total body length. Other behavioural responses, including hissing, striking, tongue flicking and rib movement were assessed both by direct observation and via the video records. The data set was analysed using general linear model and the correlations between biometrics and vertical height were calculated and considered significant when $P \leq 0.05$.

RESULTS

Snake Biometrics - Four of the studied cobras had tail lengths that were longer, both absolutely (21-24 cm) and relative to total length (14.9-17.6%), than the other two (which had tail lengths of 10-14.5 cm which were 8.2-10.7% of their total length); The four snakes with longer

tails are believed to be males (Nasoori et al., 2014). Body masses ranged from 307-432.5 g and increased slightly against total body length, while decreasing slightly against snout-vent length (Fig. 1).

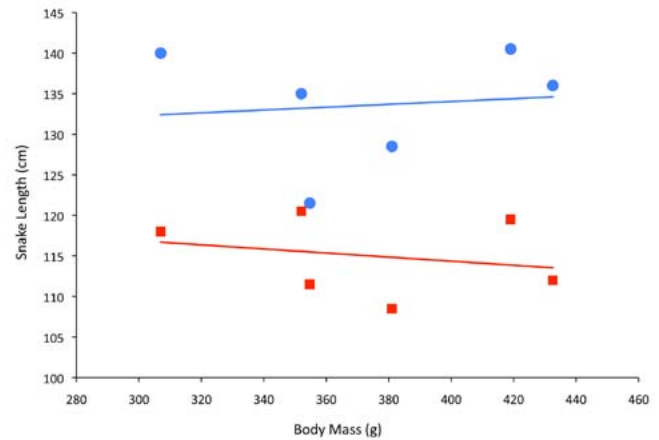


Figure 1. Biometric data for *N. oxiana* showing snake mass (X-axis) against snake length; blue circles are total length, red squares are snout-vent length.

Vertical Posturing - Every cobra held the forepart of its body vertically during every round of each behavioural trial; the average length of the body held vertically was 18.7% of the total length. The percent of body held vertically ranged from 13 - 22%; and did not vary significantly between rounds of the defensive trials (Fig. 2). No significant correlations were found between the height of vertical posturing and the biometric data collected. The snake nearing ecdysis consistently held less of its body vertically than most (or all) of the other snakes (Fig. 2) a difference that was significant (MANOVA, $F = 6.40$, $p=0.001$).

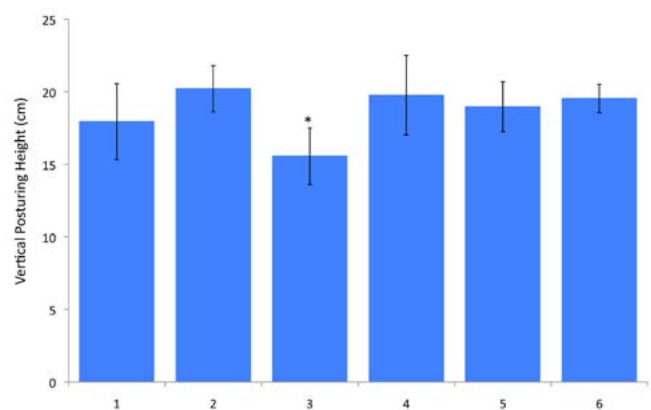


Figure 2. Mean and standard deviations for the vertical height achieved by the six specimens of *N. oxiana* during defensive posturing. Cobra 3 was in the early (eye opaque) stage of ecdysis and adopted a significantly lower vertical height while displaying.

Hooding - The hood of *N. oxiana* has an elongate, gradually tapering shape in contrast to the more ovoid hoods of some *Naja* species (Young and Kardong, 2010). Hooding was observed concurrent with all episodes of

vertical posturing. This species would also hood while the fore-body was horizontal, such as after a strike (see below), or immediately prior to adopting the vertical posture. We have worked with other (more relaxed) long-term captive specimens of *N. oxiana* in which the size of the hood was rapidly adjusted depending on the degree of stimulation provided; during the behavioural trials detailed herein the study snakes maintained a constant state of what appeared to be a maximally erect hood.

Striking - A total of 27 strikes were recorded during the behavioural trials. Of these, 26 (or 96%) were sham strikes during which the cobra's mouth remained closed. All of the strikes were launched while the forepart of the snake's body was being held vertically. During these strikes the cobra appeared to simply rotate the head and forepart of its body downward using the base of the vertically elevated segment as a pivot point. The cobras occasionally launched several strikes in quick succession, with each successive strike being launched from a less-elevated posture. The two smallest snakes accounted for 17 of the 27 strikes (or 63%), leading to a significant negative correlation between strike frequency and total length ($r = -0.859$, $p = 0.028$). Negative correlations were also found between strike frequency and both SVL and mass, but these were not significant.

Hissing - A total of 31 hisses were recorded during the 18 behavioural trials. Every strike was associated with a short, burst-like hiss. Additional, longer, hisses were produced while the animal was maintaining its vertical posture.

Tongue flicking - The tongue flick rate increased after the strike, while the cobra was in a more horizontal posture. Provocation of the cobra was consistently associated with an increased rate of tongue flicking. The tongue typically oscillated for about 1 second during each flick. However, this action was occasionally prolonged up to 5 seconds or even longer (maximum 10 seconds). The tongue flick rate showed a clear difference among the cobras, two of the snakes had tongue flick rates that were roughly 2-3x those of the other cobras.

Rib movements - Rib movement was divided into 4 groups including: no obvious movement, obvious movement, obvious and deep movement, and obvious and very deep movement. There was no indication that the body was being "inflated" as part of visual display. Rather, the costal movements seemed to be ventilatory, representing energetic demand and/or stress. The depth of breathing typically increased after the strike, and frequently increased following tongue flicking.

Behavioural integration - A cross-correlation analysis revealed significant ($p < 0.05$) correlations between four pairs of behaviours; the frequency of strikes and hisses ($r = 0.97$), the frequency of strikes and tongue flicks ($r = 0.63$), the frequency of hisses and tongue flicks ($r = 0.52$), and the tongue flick rate and the height of vertical

posturing ($r = 0.60$). When we incorporate hooding (which was observed during every period of vertical posturing, the basic defensive repertoire is clear - *N. oxiana* elevates roughly 19% of the forepart of its body, while hooding, and increasing the tongue flick rate.... from this posture the snake is most likely to emit a short hiss while performing a closed-mouth "sham" strike.

DISCUSSION

When provoked these recently captured specimens of *N. oxiana* showed little tendency to flee or attack. Instead, this cobra consistently responded with what is herein interpreted as a visual display the primary function of which was to make the snake appear threatening or dangerous. This visual display had three components: vertical posturing of the fore-body, hooding, and sham strikes. We interpret this suite of three characters as a mechanism to bring attention to the head of the snake (by vertically posturing), while making the head and fore-body appear both larger (by hooding) and more menacing (by sham strikes).

A consideration of these three display components illustrates the complexity of cobra behaviour. In the present study the cobras held 13-22% of the body elevated while displaying. The body shape of these cobras is such that the center of mass is likely slightly in front of the cranial-caudal mid-point of the body; this suggests that the 22% max value recorded in the present study is a behavioural, not a functional or morphological limit. Presumably this 13-22% postural range would differ interspecifically (between cobras) and intraspecifically when *N. oxiana* was presented with different threats.

The vertical postures observed in this study were such that the entire cranial-caudal range of the hood was visible. *N. oxiana* has black horizontal bars on the ventral surface of the hood, which we interpret as a combination of aposematic colouration and a visual pattern that serves to draw attention to the head. The cobras kept the ventral surface of the hood directed at the experimenter; in contrast species with "eyespot" or other markings on the dorsal surface of the hood will often turn away from a threat presumably to display these visual patterns (Young & Kardong, 2010). If these interpretations of *N. oxiana* are correct, it would suggest that a comparative study of defensive posturing in *Naja* (or, more broadly, within the Hemibungarini radiation) would reveal correlations between traits like relative vertical elevation, hood size, and hood/neck pigmentation patterns.

The 18 trials performed yielded 27 defensive strikes, 26 of which were sham strikes performed with the mouth closed. Sham strikes are frequently observed in cobras (e.g., Rasmussen et al., 1995). Herein these are interpreted as a visual display intended to make the snake appear more dangerous and to draw attention to the head. The defensive strike kinematics involve the (elevated) head and fore-body rotating forward and down toward the substrate. Interestingly, in the present study though all the cobras used vertical posturing and displayed their hood, the larger snakes were significantly less likely to perform defensive

strikes than were the smaller snakes. Presumably these defensive strikes have the least deterrent value when the strike ends and the snake is more horizontal; if true, there may be a strong correlation between the relative scarcity of ground cover and the species tendencies to perform sham defensive strikes.

This suite of visual displays may seem to describe all cobras, but that is not the case. Even among non-spitting true cobras there are distinctions. The forest cobra, *N. melanoleuca*, has a similar shape and ventral banding pattern on the hood (Broadley, 1983). When provoked *N. melanoleuca* holds a considerable portion of its body vertical (some photos suggest almost 50%), tends to move toward the threat (or “attack”), and launch multiple true (open mouth) strikes (Young, pers. obs.; Spawls & Branch, 1995).

Associated with these three visual displays was a fourth behaviour, the production of an audible hiss. The hiss of *N. oxiana* is of relatively short duration, as opposed to long duration hisses frequently encountered in pythons and larger viperids (Young, 2003); and becomes almost “burst-like” when performed during a defensive strike (all strikes of *N. oxiana* were accompanied by a hiss). Brief “explosive” hisses associated with the strike are common in the cobra radiation; they are particularly prominent in *Aspidelaps* (Young, pers. obs.; Spawls & Branch, 1995), and were (incorrectly) postulated to propel the venom during “spitting” in cobras (Rasmussen et al., 1995). There are at least two, non-mutually exclusive, functions for these defensive hisses: as broadband acoustic warning signals (Young et al., 1999) or as another means of drawing the other organism’s attention to the head of the cobra. In support of the latter, many cobras will “slap” the substrate with their erect hood at the end of a defensive strike.... a behaviour that blends acoustic and visual displays (Young, 2003). It would be interesting to explore the relationships between the elements of the visual display, the strike frequency, and the bioacoustic properties of the hiss within different cobras.

Two other behaviours were frequently observed during the trials of *N. oxiana*, an increase in tongue flick rate and an increase in costal movements. Herein these are both interpreted as signs of arousal or stress in the cobra (Young & Aguiar, 2002). Rib movements can be associated with defensive inflation of the snake’s body (Young et al., 2000) or with the production of defensive sounds (Young et al., 1999), or both (Kinney et al., 1998). In *N. oxiana* we did not observe body inflation, and the hisses that were produced were not associated with pronounced body expansion (again, as is seen in the large viperids).

The close proximity of an experimenter created arousal/stress in *N. oxiana*. Interestingly, tongue flick rate proved to be an excellent metric of arousal in this species; the tongue flick was strongly correlated with the height of vertical posturing, strike frequency, and hissing frequency. The primary stimulus provided by the experimenter was visual, and it is interesting to note that the one snake in early ecdysis (when the visual acuity is reduced) responded with significant lower levels of vertical posturing.

There is considerable inter-specific variation in the

effective distance of venom spitting (Rasmussen et al., 1995); however in all species the spat venom appears capable of traveling further than the length of the cobra’s defensive strike, making this a long-distance form of defense. Given the ability of spitting cobras to precisely target a typically moving target (Young et al., 2009; Westhoff et al., 2010), and both the short- and long-term consequences of spat venom contacting the eye (Ang et al., 2014), the deterrent value of venom spitting (though never documented) seems clear. The physical act of “spitting” venom is rather quick; mean durations of 66 and 40 ms were reported in Young et al., (2004) and Westhoff et al., (2010), respectively. This speed, coupled with the nearly translucent nature of the spat venom, suggest that spitting venom is purely a chemical defense and, unlike the other defensive behaviours described above, does not function to draw attention to the cobra’s head and/or make the cobra appear more dangerous.

The ability to spit venom appears to have evolved independently multiple times within the Hemibungarini radiation (e.g., Wuster & Thorpe, 1992; Keogh, 1998). Field and laboratory studies of the defensive behaviours of spitting and non-spitting cobras could explore the impact of the evolution of a long-distance chemical defense in species which rely primarily on visual display as a deterrent. Are there predator-specific defensive strategies in spitting cobras for the relative energy investment in visual display versus spitting? Could the visual display of a cobra actually lure a predator closer making the venom spitting more effective? This seemingly fruitful line of enquiry must begin with basic descriptions of spitting and non-spitting cobras which, if nothing else, will identify the shared features which can be quantified during comparative studies.

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