Feeding behaviour of the Madagascar leaf-nosed snake, *Langaha madagascariensis* (Serpentes: Colubridae: Pseudoxyrhophiinae), with an alternative hypothesis for its bizarre head structure

KENNETH L. KRYSKO

*Florida Museum of Natural History, Division of Herpetology, P.O. Box 117800, University of Florida, Gainesville 32611, Florida, USA; kenneyk@flmnh.ufl.edu*

Abstract.—Feeding behaviour of the Madagascar leaf-nosed snake (*Langaha madagascariensis*) is described and an alternative use for its unusual nasal appendage is hypothesized. *Langaha madagascariensis* employs a sit-and-wait foraging strategy and stalking prey is initiated once a snake is conscious of potential prey. Stalking is preceded by hooding, swaying anterior portion of its body laterally, tongue flicking, and advancing toward prey. Strikes are typically made at an extremely close distance, sometimes while a snake places its nasal extension directly onto the back of the prey’s head. Prey was always grasped anterior to the pectoral girdle behind the head or neck region. Once prey is seized, it may be coiled around and is usually pulled off its perch and left to dangle in mid-air, while being worked into the back of the mouth toward the snake’s rear fangs. *Langaha madagascariensis* also exhibits hooding while stalking prey. These hooding and swaying behaviours along with its cryptic colour patterns, might allow *L. madagascariensis* to mimic a vine swaying in the wind. Because of the many behavioural and ecological similarities between *L. madagascariensis* and other arboreal snake species, I hypothesize that the nasal extensions in *L. madagascariensis* serve as an extension of its narrow head and is used as a point of reference during prey stalking.

Key words.—*Langaha madagascariensis*, Leaf-nosed Snake, Colubridae, reptile, feeding, behaviour, Madagascar.

The biology of the Madagascar leaf-nose snake, *Langaha madagascariensis* Bonaterre 1790, remains poorly understood despite some recent literature on its reproduction (Reams 1999; Krysko 2003). This opisthoglyphous serpent is endemic to Madagascar and is renowned for its sexual dimorphism, especially in its bizarre scaly head structures. Females have a laterally compressed leaf-shaped nasal extension, while nasal extensions in males are spear-shaped or pointed (Guibe 1949, 1958; Brygoo 1982; Preston-Mafham 1991; Glaw & Vences 1994; Bradt et al. 1996; Greene 1997; Henkel & Schmidt 2000; Krysko 2003; Kuchling 2003). It has been hypothesized that the thin body, unusual nasal extensions, and dull cryptic colour patterns have been to allow this arboreal and typically diurnal species to mimic vines or branches, thus camouflaging itself from potential predators and prey while amongst vegetation (Brygoo 1982; Preston-Mafham 1991; Glaw & Vences 1994; Bradt et al. 1996; Greene 1997; Henkel & Schmidt 2000). No other function has been proposed for its nasal extensions (Henkel & Schmidt 2000). While housing five wild-caught and nine captive-born *L. madagascariensis* since December 2000, I noticed interesting and consistent behaviour not yet documented for this species. Herein, I use three of these individuals to describe feeding behaviour in a captive setting and hypothesize an alternative use for its nasal extension.
Two wild caught adult *L. madagascariensis* (♀ = UF 140824, ♂ = UF 137512) were housed together in a 110 l (760 x 305 x 455 mm) terrarium with live pothos (*Epipremnum aureum*), weeping figs (*Ficus benjamina*), and dead muscadine vines (*Vitis rotundifolia*). Additionally, a single captive born female (KLK 1588), originating from a wild caught gravid female (UF 133819), was housed singly in the same manner as above. Enclosures were placed near windows to assist in an environmentally regulated photoperiod, and mean daytime temperature of 28 ºC and night-time temperature of 20 ºC was accomplished with a timer and two hooded lights (610 mm 20 W GE full spectrum and 60 W GE incandescent soft white bulbs).

**Feeding trials.**—At irregular intervals, readily available and live wild caught brown anoles, *Anolis sagrei*, Puerto Rican crested anoles, *A. cristatellus*, and tropical house geckos, *Hemidactylus mabouia* were introduced into the enclosures and snake and prey behaviours were observed. I recorded data on stalking behaviour (swaying and/or hooding of snake), time to strike (t-strike; time from when stalking is observed until snake grasps prey), time to subdue (t-subdue; time from grasping until all obvious physical movement of prey ceases), grasping location (on prey), presence or absence of snake coiling around prey, and prey snout-vent length (SVL).

Because not all variables were normally distributed, a Spearman Rank Order Correlation was preformed to determine relationships between prey SVL, t-strike, and t-subdue. A t-test was performed to determine differences in t-subdue between trials where snakes coiled around prey verses those where they did not. All statistical analyses were conducted using SigmaStat for Windows (1995).

Although only 22 feeding trials were performed for statistical analyses, these results were congruent with nearly four years of additional observations from 11 other *L. madagascariensis*. This species employs a sit-and-wait foraging strategy and is frequently motionless amongst vegetation until prey is introduced. Stalking took place once the snake was conscious of the potential prey. Stalking was preceded by hooding (Fig. 1A; raising head and expanding body or flattening ribs dorso-ventrally just posterior to the head), and advancing toward prey while swaying the anterior portion of the body back and forth laterally (Fig. 1B). *Langaha madagascariensis* exhibited hooding in 19 (86%) of the feeding trials. Vision appears to be acute and snakes are stimulated by prey movement - even the breathing movements of the prey was sufficient to illicit an approach by the snake. Sporadic tongue flicking occurs to pick up environmental chemical cues during advancement (see Burger 1990; Greene 1997), sometimes until its tongue touches the prey. Occasionally a snake would place its nasal extension directly onto the back of the prey’s head for up to 10 sec, while pressing downward bending its flexible appendage before grasping. Thus, strikes are typically made at an extremely close distance and the prey appears to be unaware of imminent danger. T-strike lasted between 14-425 sec (mean = 154.32 ± [SE] 28.30) and prey were always grasped anterior to the pectoral girdle, behind the head, or in the neck region (Fig. 1C, D). Once prey was seized, it was usually pulled off its perch and left to dangle in mid-air, while being worked back into the mouth toward the snake’s rear fangs (Fig. 1D).

Prey size ranged between 25.4-63.5 mm SVL, and all offered prey were consumed. I found a negative correlation between prey SVL and t-strike (Fig. 2; \( r = -0.683, P < 0.001 \)). As prey SVL increases t-strike decreases, suggesting that larger prey are more easily detected among vegetation. Snakes coiled around prey in 13 (59%) of the feeding trials (Fig. 1C). There was no difference (\( t = 0.292, P = 0.773 \)) in t-subdue when snakes coiled around prey (range = 47-
Figure 1. Feeding behaviour of Madagascar leaf-nosed snakes, *Langaha madagascariensis*: A & B) ♀ (UF 133819) and ♂ (UF 137512), respectively, exhibiting hooding and swaying behaviour while stalking prey; C) ♂ coiling around prey; D) ♂ striking precisely on the back of prey’s head. Note brown anole, *Anolis sagrei* in foreground in A.
221 sec, mean = 129.08 ± 12.85, N = 13) versus when snakes did not coil (range = 66-200 sec (mean = 134.67 ± 13.49, N = 9), suggesting that *L. madagascariensis* does not necessarily subdue prey by constriction, but rather by envenomation before swallowing. No relationships were found between prey SVL and t-subdue (r = -0.216, P = 0.329) nor between t-strike and t-subdue (r = 0.277, P = 0.208).

As a predator avoidance strategy, numerous snake species are known to expand or flatten their body just posterior to the head. These body expansions may occur laterally (i.e., throat expansion in *Boiga jaspidea*, *Dendrelaphis formosus* [see Lim & Lee 1989], *Pseustes* sp., *Thelotornis capensis* [see Greene 1997], and *Ptyas mucosus* [see Young et al. 1999b]) or dorso-ventrally (i.e., hooding in *Naja* spp. and *Ophiophagus hannah* [see Young & Kardong 1989; Greene 1997]). *Langaha madagascariensis* also exhibits hooding for defence, sometimes in combination with the discharge of cloacal contents, mouth gaping, and biting (see Henkel & Schmidt 2000:277). Interestingly, *L. madagascariensis* exhibits hooding while stalking prey, illustrating that this species performs hooding as both a defence mechanism as well as during feeding. This behaviour could have several functions: Make the snake appear 1) vine-like or non-snake-like and blend into its surroundings, 2) larger and cause prey to freeze, or 3) larger and more threatening to other *L. madagascariensis* in the near vicinity, allowing the individual to win disputes over prey. These hooding and swaying behaviours along with its cryptic colour patterns, might allow *L. madagascariensis* to mimic a vine swaying in the wind. Furthermore, it appears that lizards are completely unaware of the snakes while being stalked (see Fig. 1A). Neonates do not exhibit hooding, and the youngest snake observed exhibiting this behaviour was at 703 days of age and ca. 220 mm SVL. Many snakes that exhibit anterior body expansions are also known to produce audible sound via respiratory mechanisms, mainly as bluffing displays (as in *Bitis arietans* [see Young et al. 1999a], and *Heterodon platirhinos* and *Pituophis melanoleucus* [see Greene 1997]). No audible sound was detected in *L. madagascariensis*, nor was tail vibration. Tail vibration is commonly observed as a defence mechanism in many snakes (Greene 1997).

Henderson & Binder (1980) demonstrate that other arboreal snakes (i.e., *Ahaetulla*, *Oxybelis*, *Thelotornis*, and *Uromacer*) stalk prey using lateral head swaying similar to *L. madagascariensis*. These four genera have acute vision, the widest binocular fields of vision known for snake species, an eye-line or facial groove from eye to snout tip, and elongated heads (Henderson & Binder 1980). These morphological characters improve vision directly ahead of the snout and assist in the capture of active prey (Henderson & Binder 1980; Greene 1997). Swaying is believed to cause parallax (i.e., a noticeable change in direction of an object caused by a change in observational position presenting a new line of sight; Henderson & Binder 1980). Thus, a snake can acquire a different perception of a target when seen from more than one angle simultaneously (i.e., binocular vision) (Henderson & Binder 1980).

![Graph: Correlation between prey SVL and time until Madagascar leaf-nosed snakes, *Langaha madagascariensis*, grasps prey.](image)

**Figure 2.** Correlation between prey SVL and time until Madagascar leaf-nosed snakes, *Langaha madagascariensis*, grasps prey.
1980). However, this binocular field of vision is undocumented for *L. madagascariensis*. Henderson & Binder (1980:28) state that *Ahaetulla* also exhibits rigid tongue extension, which “acts as an extension of the eye-line and…[is used] for sighting prey or as a point of reference during prey stalking.” Because of the many behavioural and ecological similarities between *L. madagascariensis* and the four arboreal snake genera mentioned above, I hypothesize that the nasal extensions in *L. madagascariensis* serve as an extension of its narrow head and is used as a point of reference during prey stalking. This is evidenced by the precision of grasping location of prey behind the head or neck region (Fig. 1D; see Lim & Lee 1989:66), which reduces or eliminates retaliation and injury from prey (Henderson & Binder 1980). Although Henkel & Schmidt (2000:277) stated that *L. madagascariensis* “should be approached with caution because they have opisthoglyphic fangs and many small teeth...[and] will not hesitate to make full use of these formidable weapons,” the effect of its venom on humans is unknown. However, it is obvious that lizards used in this study succumbed to *L. madagascariensis* venom relatively quickly (t-subdue; range = 47-221 sec, mean = 131.36 ± 9.19, N = 22). Although it is not known why males and females have different shaped nasal extensions, differences could reflect microhabitat differences (Greene 1997), function in sexual selection in conjunction with pheromones, or aid in forward vision. Although the nasal appendages are different between genders along the vertical plane, they are similar along the horizontal plane, suggesting that the forward line of site might not be very different between males and females and may be used as a point of reference to assist in forward vision and prey stalking.

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