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Original article

Reproduction in the Madagascar leaf-nosed snake, *Langaha madagascariensis* (Serpentes: Colubridae: Pseudoxyrhophiinae)

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Abstract.—Aspects of reproduction including courtship behaviour, ovipositioning, egg characteristics, and hatchling descriptions are documented for the Madagascar leaf-nosed snake (*Langaha madagascariensis*). Courtship behaviour is described from laboratory settings and takes place in vegetation above ground. Oviposition occurred at night time in August and September. Clutch sizes averaged 11 eggs. Fertile eggs measured a mean 22.6 mm long and 12.0 mm wide at oviposition, and 25.6 mm long and 15.4 mm wide one to three days before hatching. Incubation of eggs at 28 °C lasted a mean 65.3 days. Offspring consisted of eight live hatchlings and one dead full-term baby, yielding of a sex ratio of 7:2 (Male:Female). Sexual dimorphism in both nasal extensions and colour patterns were evident immediately after hatching. Hatchlings weighed a mean 1.40 g, and measured 134.3 mm SVL and 92.9 mm TL. The first ecdysis occurred eight to 12 days after hatching. Hatchlings consumed only arboreal prey items including *Anolis sagrei*, *Hemidactylus garnotii*, *H. mabouia*, and *H. turcicus*. Hatchlings performed an unusual behaviour of hanging vertically and motionless on vegetation, which appeared to be a state of sleep.

Key words.—*Langaha madagascariensis*, leaf-nosed snake, Colubridae, reproduction, behaviour, Madagascar.

The flora and fauna on the island of Madagascar have evolved in isolation into some of the most fascinating organisms. Madagascar leaf-nosed snakes, *Langaha madagascariensis* Bonaterre 1790, *L. alluaudi* Mocquard 1901, and *L. pseudoalluaudi* Domergue 1988, are opisthoglyphous serpents endemic to Madagascar. They are renowned for their unusual head appendages and their sexual dimorphism is unparalleled by any other snake species (Greene 1997). *Langaha madagascariensis* females have a laterally-compressed leaf-shaped nasal extension, and are grayish-brown with irregular markings; males have a spear-shaped nasal extension, and are brownish with a lower lateral white stripe and yellow venter (Glaw & Vences 1994; Greene 1997; Henkel & Schmidt 2000).

Little is known about the life histories for the three recognized species of *Langaha*. Information in the scientific literature has been mainly focused on their obvious morphological differences (Mocquard 1901; Guibe 1949, 1958; Brygoo 1982; Domergue 1988), and presently no other purposes are known for their nasal extensions other than camouflage. This study describes aspects of reproduction for *L. madagascariensis* including courtship behaviour, ovipositioning, egg characteristics, and hatchling descriptions.

MATERIALS AND METHODS

Until recently, relatively few *L. madagascariensis* have made it into U.S. collections for

captive propagation. In December 2000, one male (KLK 633, Table 1) was acquired and housed in a 110 l (760 x 305 x 455 mm) terrarium with live pothos (*Epipremnum aureum*), weeping figs (*Ficus benjamina*), and muscadine grape vines (*Vitis rotundifolia*). Mean daytime (28 °C) and night-time (20 °C) temperatures were achieved by using a timer and two hooded lights (610 mm, 20 W, GE full spectrum and 60 W, GE incandescent soft white bulbs). The enclosure was placed near windows to aid in obtaining a natural photoperiod.

On 18 Aug 2001, four gravid females were acquired. One female, dead on arrival, was measured to the nearest mm for snout-vent length (SVL) and tail length (TL), dissected, and deposited in the Florida Museum of Natural History (FLMNH), University of Florida (UF 125922, Table 1). The three remaining females (KLK 635-37) were housed individually as above, except a plastic box (330 x 190 x 90 mm) with moist sphagnum moss (*Sphagnum* sp.) was placed at the bottom of each enclosure as an oviposition site. Because *L. madagascariensis* drink mainly from moisture on leaves, enclosures were misted each day to ensure adequate hydration, in addition to providing a water bowl. Females were observed randomly throughout the daytime, and last viewed at ca. 22h00 each night to determine approximate time of oviposition. All females were measured to the nearest mm for SVL and TL, and weighed to the nearest 0.1 g immediately after oviposition using an HP-320 Ohaus scale (0.1 - 320 g). Clutch mass was added to each female's mass immediately after oviposition to obtain a pre-oviposition mass (Table 1).

Incubation techniques.—Eggs were covered with moist live *Sphagnum* sp., placed in covered plastic boxes (160 x 160 x 50 mm), and incubated at 28 °C in a Hova-Bator incubator (G.Q.F. Manufacturing Company, Inc., Savannah, Georgia, USA). At five-day intervals, each clutch (and egg if separated from clutch) was weighed to the nearest 0.1 g, and length and width (at maximum point) of each egg was measured to the nearest mm with a dial caliper (Manostat Corporation, New York, NY, USA). SVL, TL, mass, and gender of hatchlings were recorded.

Table 1. *Langaha madagascariensis* used in reproduction experiments. Measures are in mm and g.

ID #	Sex	SVL	Tail length	Mass
KLK 633	♂	563	418	40.3
UF 125922	♀	535	332	N/A
KLK 635	♀	532	344	49.5
KLK 636	♀	586	367	65.4
KLK 637	♀	570	340	84.7

Hatchlings from each clutch were housed together as above. After first ecdysis hatchlings were offered both terrestrial and arboreal lizards, including ground skinks (*Scincella lateralis*), brown anoles (*Anolis sagrei*), and Indo-Pacific (*Hemidactylus garnotii*), tropical house (*H. mabouia*), and Mediterranean (*H. turcicus*) geckos.

Courtship.—The single male was introduced into each female's enclosure after oviposition, and the snakes were closely observed for signs of breeding behaviour. The male was initially measured and weighed at first introduction (Table 1). Eggs and any deceased hatchlings and adults were deposited in the FLMNH. All statistics were preformed using SPSS for Windows (SPSS Inc., version 10) with $\alpha = 0.05$. Means ± S.E. are reported.

RESULTS AND DISCUSSION

Courtship.—Description of mating sequence and terminology for courtship behaviours follows Gillingham (1979) as they are in wide usage (e.g., Gillingham *et al*. 1983; Secor 1987; Schuett & Gillingham 1988; Walker & Ford 1996; Ball & Ford 1999; Greene & Mason

2000; Mehta & Ford 2001). Eight courtship acts were recorded between the single male and two females (KLK 635 and KLK 636; Table 1). All courtship behaviour occurred above ground in vegetation. Courtship ranged from 20 - 70 min. Only phases I and II were observed. The character terms below were observed for *L. madagascariensis* and are modified after Chiszar *et al*. (1976), Gillingham (1979), Schuett & Gillingham (1988), and Mehta & Ford (2001).

1. *Touch-mounting* (TM).—Male approaches female and makes contact with her using his snout, his head and neck are elevated and placed on the female's dorsum.

2. *Tongue-flicking* (TF).—Tongue-flicking the female's body.

3. *Swaying with head-raised* (SHR).—Male flattens anterior body by expanding ribs, and sways from side to side while raising his head.

4. *Dorsal-advance movement* (DM).—Anteriorly directed movement of mounted male with chin pressed to dorsum of female.

5. *Advancing* (AD).—Forward advancing of both snakes while male is mounted.

6. *Tail-search copulatory attempt* (TSCA).—Complex tail movements as male attempts cloacal juxtaposition and intromission or insertion of hemipenis in female's cloaca.

7. *No movement while mounted* (NM).—All body movements stop, yet mount is maintained.

8. *Discontinuation* (DS).—Male dismounts female without copulation.

Gillingham (1979) further categorized mating behaviours into three standard phases: I) tactile-chase, II) tactile-alignment, and III) intromission. Phase I begins when male initiates courtship (TM), and ends at the first copulatory attempt (TSCA). Phase II begins when male initiates TSCA, and ends when intromission is achieved. Phase III begins when intromission is achieved, and ends when hemipenis is retracted from female's cloaca.

On 5 Sept 2001 from 15h50-16h15, courtship behaviour was observed between the male and female KLK 635. The female had oviposited 14 days earlier. The male approached the female in vegetation and began SHR. The female followed the male's side to side movement, and the male preceded to TF and TM. As the female began to move forward through tree branches, the male illustrated TF, AD, and DM while his head followed every contour of her body until both snakes were head to head. With the male on top, it exhibited TSCA. Both snakes moved forward between branches before NM and again AD until eventually DS. On 9 Sept 2001 from 14h05-14h50, courtship was observed with female KLK 635. The male immediately exhibited TM, DM, and TSCA. On two occasions, the male extended a hemipenis, but missed the female's cloaca. Both snakes were observed exhibiting NM for 20 min before DS. From 16h30-16h50, the male was introduced into the female's (KLK 636) enclosure. The male immediately began TF and TM as above. At one point their heads and forebodies were hanging vertically ca. 300 mm from branches as the male extended a hemipenis once, but missed before DS. On 15 Sept 2001 from 12h05-13h15, courtship was observed with female KLK 636 as male began TF and TM. With the male on top, it exhibited TSCA and extended one hemipenis, but missed the female's cloaca before DS. The courtship acts observed in phases I and II for *L. madagascariensis* are similar to other colubrid snakes. However, the typical jerking movement seen in most colubrids was not observed.

Ovipositioning.—Only one previous record on the reproduction of *L. madagascariensis* exists

Table 2. Reproduction data for female *Langaha madagascariensis*. Note that KLK 635 and KLK 636 were last observed at ca. 22h00 without oviposition beginning, and by 07h00 h the following morning oviposition was nearly completed; KLK 637 began oviposition at 20h30, and by 07h00 h the following morning oviposition was completed. Hatchling sex ratio is male:female. Mean ± S.E. is given for clutch mass, # eggs, and incubation.

Female #	Oviposition date	Oviposition time	Clutch mass (g)	# Eggs	Date hatched	# Hatched	Incubation (days) at 28 °C	Hatchling sex ratio
UF 125922	N/A	N/A	N/A	12	N/A	N/A	N/A	N/A
KLK 635	22 Aug 2001	? - 12h00	15.1	8	28 Oct 2001	3	67	2:1
KLK 636	6 Sept 2001	? - 14h00	14.7	12	11 Nov 2001	2	66	2:0
KLK 637	18 Sept 2001	20h30 - < 07h00	19.6	12	21 Nov 2001	4	63	3:1
Total	Aug - Sept	20h30 - 14h00	16.4 ± 1.57	11.0 ± 1.15	Oct - Nov	9	65.3 ± 1.20	7:2

in the scientific literature: A wild-collected, gravid female was acquired by the Dallas Zoo on 10 Sept 1997. This snake laid five eggs on 2 Oct 1997 (Reams 1999). The four clutches in this study averaged 11.0 eggs (Table 2), more than twice the size of the single clutch reported by Reams (1999). Oviposition of all females began during night time in Aug and Sept, and sometimes lasted until 14h00 the next day (Table 2). On 22 Aug 2001 at 07h00, female KLK 635 was completing oviposition: seven eggs were laid and an additional egg was oviposited by 12h00 (Table 2). All eggs were attached to each other, apart from the last egg, which appeared infertile because of its atypical wet appearance and semi-transparent yellowish coloration (see Krysko *et al*. 2000). The female weighed 49.5 g before oviposition (Table 1), and the clutch weighed 15.1 g total (Table 2), or 14.2 g excluding the infertile egg. On 6 Sep t2001 at 07h00, female KLK 636 had oviposited 10 eggs and another two eggs by 14h00 (Table 2). Three of these eggs were fertile and attached together, while nine were infertile and were not connected to the clutch. The female weighed 65.4 g before oviposition (Table 1), and the clutch weighed 14.7 g total (Table 2), or 5.5 g excluding infertile eggs. On 30 Aug 2001, female KLK 637 completed the typical pre-oviposition ecdysis (see Krysko *et al*. 2000), oviposition began 19 days later at 20h30, and by 07h00 the next morning 11 eggs were oviposited (Table 2). Four of these eggs were fertile and attached together, while seven were infertile and not connected to the clutch. On 21 Sept 2001, an additional infertile egg was manipulated by hand from the oviduct through the female's cloaca. The female weighed 84.7 g before oviposition (Table 1), and the clutch weighed 19.6 g total (Table 2), or 9.2 g excluding infertile eggs.

Egg sizes and incubation.—The five eggs reported by Reams (1999) measured 24.4 mm long and 11.5 mm wide. In this study, fertile eggs were significantly longer and wider ($P < 0.01$) than infertile eggs immediately after oviposition. Fertile eggs ($N = 14$) measured a mean 22.58 mm long and 11.97 mm wide at oviposition, and ($N = 9$) 25.56 mm long and 15.44 mm wide one to three days before hatching (Table 3). Infertile eggs ($N = 18$) measured a mean 17.55 mm long and 10.28 mm wide after oviposition.

The single infertile egg from female KLK 635 weighed 0.9 g, and four fertile eggs failed during incubation (Table 3): three on day 35, and one on day 40. Infertile eggs from female KLK 636 weighed 1.0 - 1.1 g (mean = 1.06 ± 0.01), and one fertile egg failed during incubation on day 25. Infertile eggs from female KLK 637 weighed 1.1 - 1.4 g (mean = 1.30 ± 0.03). Only 43.7% of eggs ($N = 32$) oviposited were fertile, indicating a low fertility rate. Incubation lasted a mean 65.3 days at 28 °C (Table 2), shorter than the 81 days at 24-27 °C reported by Reams (1999), as embryos develop faster with a high-

Table 3. Egg measurements for *Langaha madagascariensis*. Range (mean ± S.E.) is given for length and width in mm.

Female #	# Eggs oviposited	Length and Width	# Eggs remaining 1-3 days before hatching	Length and Width of remaining eggs
KLK 635	Fertile 7	22.1-26.1 (23.92 ± 0.51)	3	25.3-32.9 (28.43 ± 2.29)
		10.7-11.9 (11.42 ± 0.15)		13.9-14.9 (14.43 ± 0.29)
	Infertile 1	19.7		
		7.8		
KLK 636	Fertile 3	18.0-21.1 (19.83 ± 0.93)	2	23.4-24.2 (23.80 ± 0.40)
		11.5-12.6 (12.06 ± 0.31)		14.3-16.5 (15.40 ± 1.10)
	Infertile 9	14.9-17.6 (16.30 ± 0.29)		
		8.9-10.6 (10.10 ± 0.19)		
KLK 637	Fertile 4	20.0-25.7 (22.30 ± 1.34)	4	21.8-27.6 (24.30 ± 1.41)
		12.0-13.4 (12.87 ± 0.31)		15.2-17.0 (16.22 ± 0.38)
	Infertile 8	16.5-20.8 (18.68 ± 0.48)		
		9.8-11.7 (10.80 ± 0.21)		
Total	Fertile 14	18.0-26.1 (22.58 ± 0.63)	9	21.8-32.9 (25.56 ± 1.13)
		10.7-13.4 (11.97 ± 0.21)		13.9-17.0 (15.44 ± 0.37)
	Infertile 18	14.9-20.8 (17.55 ± 0.39)		
		7.8-11.7 (10.28 ± 0.21)		

er incubation temperature (Zug 1993; Krysko *et al*. in press).

Hatchling descriptions and behaviour.—Prior to hatching, the usually dry eggs appeared moist, and small scrape marks from the hatchling's egg tooth (see Greene 1997) were noticed on the inside of the egg shell. All hatching began and neonates emerged from the egg during late afternoon and night time, and hatchlings immediately climbed to vegetation. Offspring consisted of eight live hatchlings and one dead full-term baby, yielding a sex ratio of 7:2 (Male:Female) (Table 2). There were no significant differences (all P values > 0.05) in mass, SVL, or TL between males and females. The three eggs from female KLK 635 began hatching on 28 Oct 2001 at 19h00, yielding a sex ratio of 2:1. The first hatchling emerged from the egg at 14h15 the following day, and by 22h00 the remaining two hatchlings had emerged. The two eggs from female KLK 636 began hatching on 11 Nov 2001 at 21h00, resulting in a sex ratio of 2:0. At 07h00 the following day the first hatchling emerged from the egg, which had a slight kink on its neck. Although scrape marks were also observed on the second egg, this egg did not hatch and was manually slit on 13 Nov 2001. It contained a dead full-term baby with a severely kinked spine. These developmental abnormalities may be due to non-optimal incubation temperatures for *L. madagascariensis*. The eggs from female KLK 637 began hatching on 21 Nov 2001 at 15h00., yielding a sex ratio of 3:1. All hatchlings had emerged by 07h00 the following day. The hatchlings reported by Reams (1999) weighed a mean 1.5 g and measured 125.6 mm SVL. In this study, hatchlings weighed a mean 1.4 g, and measured a mean 134.33 mm SVL and 92.88 mm TL (Table 4).

Hatchlings exhibited sexual dimorphism in nasal extensions and dorsal patterns immediately upon hatching. The scaly nasal extensions were folded backwards and adhered to the hatchling's head (Fig. 1A), allowing for the use of the egg tooth to breakout of the egg. Within 36 hours, nasal extensions were pointing forward (Fig. 1B), possibly to aid in camouflage as hatchlings hid in vegetation. Females were grayish with lighter bands and black speckling

Table 4. Hatchling data for *Langaha madagascariensis*. Mean ± S.E. is given for each clutch and total.

Female #	Sex	Mass (g)	Snout-vent length (mm)	Tail length (mm)
KLK 635	♂	1.1	127	89
	♂	1.3	135	87
	♀	1.3	141	83
		1.23 ± 0.06	134.33 ± 4.05	86.33 ± 1.76
KLK 636	♂	1.1	133	106
	♂	1.1	109	99
		1.1	121.00 ± 12.00	102.50 ± 3.50
KLK 637	♂	1.6	146	99
	♂	1.7	142	93
	♂	1.6	148	101
	♀	1.8	128	79
		1.67 ± 0.04	141.00 ± 4.50	93.00 ± 4.96
Total		1.40 ± 0.09	134.33 ± 4.02	92.88 ± 3.01

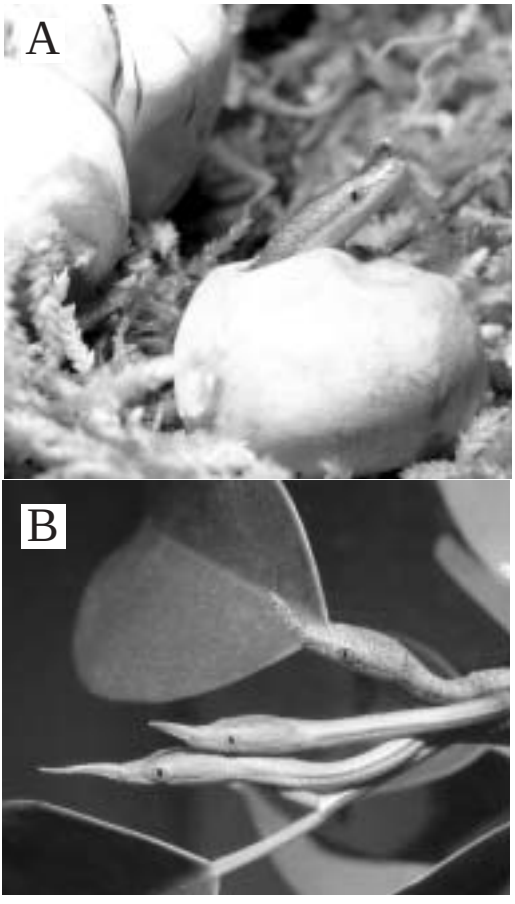

Figure 1. Hatchling *Langaha madagascariensis*: A) with nasal extension folded backwards and adhered to the top of head; B) with nasal extensions pointing forward exhibiting sexual dimorphism (top = ♀, bottom = ♂♂); C) ♀ (left) and ♂ (right) hanging vertically and motionless in vegetation.

over the dorsum, gular chin shields, and venter; males were light tan with one dark mid-dorsal and two dark lateral stripes.

First signs of the ecdysis cycle (e.g., darkened coloration and opaque eyes) were noticed three to four days after hatching. Ecdysis occurred eight to 12 days after hatching. Within three weeks after first ecdysis, hatchlings from each clutch consumed small *Anolis sagrei*, *Hemidactylus garnotii*, *H. mabouia*, or *H. turcicus*, which climbed on vegetation and terrarium walls. Terrestrial *Scincella lateralis* were not eaten, suggesting that *L. madagascariensis* may have a preference for small arboreal lizards such as *Phelsuma* that are common in their natural habitat. I also documented an unusual behaviour in hatchlings not recorded for any other snake species: Frequently each hatchling was observed hanging vertically and motionless from a branch by as little as only half of the tail, and sometimes for nearly the entire day (Fig. 1C). This did not appear to be a foraging behaviour, rather, the neonates appeared to be asleep. The neonates appeared to be completely unaware of terrestrial *S. lateralis* moving below them. Hatchlings are highly cryptic while hanging motionless as they show a striking resemblance to fruit of a trumpet-creeper, *Ophiocolea floribunda* (Bignoniaceae), a species that occurs in their natural environment.

Future studies in *L. madagascariensis* are needed to document phase III and further help recognize communication and behaviour in this species. A hatching success rate of 57.1% (N = 14; excluding single full-term dead baby) was recorded. Although failure of eggs during embryonic development could have been due to mishandling of gravid females during shipment, the incubation conditions used in this study that have yielded high hatching success rates for North American colubrids (Krysko *et al*. 2000) may not be optimal for *L. madagascariensis*. Additional reproduction data are needed to identify conditions yielding a more successful hatch rate.

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