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FIELD OBSERVATIONS ON THE BEHAVIORAL ECOLOGY OF THE MADAGASCAN LEAF-NOSED SNAKE, *LANGAHA MADAGASCARIENSIS*

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Abstract.—Langaha madagascariensis **is a vinesnake endemic to Madagascar. Although it was first described in 1790, few publications document the ecology or behavior of the species, and none does so for animals in the wild. This vinesnake is unique in displaying high levels of sexual dimorphism and its possession of an elongated nasal appendage, the function of which is not yet understood. The purpose of this study was to obtain information on the natural history of the snake via observations on free-living specimens. The study took place in the quickly disappearing littoral forest of southern Madagascar. I observed six adult males, but found no females. Observations from this study help to elucidate foraging and feeding behavior and activity patterns in *L. madagascariensis*. With respect to foraging behavior, the vinesnake proved largely to be a sit and wait predator, although it actively pursued prey on some occasions. Contrary to expectations, it consumed both arboreal and terrestrial lizards. One male I observed for several days and nights demonstrated an interesting behavior whereby each night he returned to the same branch and hung from it pointing straight downwards until the morning. These observations help shed light on a little-studied snake that faces high levels of habitat loss.**

*Key Words.—*feeding ecology; foraging behavior; Madagascar; natural history; sexual dimorphism; vinesnake

INTRODUCTION

Langaha madagascariensis, the Madagascan Leaf-nosed Snake, is an arboreal colubrid found in low-altitude dry and wet forest habitats in widespread localities ranging from the northern tip to the southern coast of Madagascar (Glaw and Vences 2007). Although first described by Bonaterre in 1790, very little has been published on the species, and no prior field studies have focused on its behavior and ecology. Guibé (1948, 1949) described dramatic sexual dimorphism in *Langaha* and revised the genus, and currently three species are recognized: *L. madagascariensis, L. alluaudi* Moqcquard 1901*, and L. pseudoalluaudi* Domergue 1988 (Glaw and Vences 2007). Almost nothing is known about the latter two species (Kuchling 2003; Glaw and Vences 2007). Two articles concerning reproduction in *Langaha madagascariensis* (Reams 1999; Krysko 2003) and one on feeding behavior (Krysko 2005) have involved captive rather than wild specimens. One researcher recorded the effects of a bite from this rear-fanged snake (D'Cruze 2008). A study in southeastern Madagascar found it restricted to the largest remaining fragments of closed-canopy littoral forest within the conservation zones of Mandena and Petriky (Ramanamanjato 2007). The destruction and fragmentation of littoral forest in the south increases the need to study the forest's inhabitants before it disappears.

Convergent ecomorphologies occur frequently in snakes, and unrelated vine snakes in Asia, Africa, and the New World superficially resemble each other in having unusually slender bodies, long pointed snouts, and a diet of mainly lizards and/or frogs (Henderson and Binder 1980; Greene 1997). Among vine snakes, species of *Langaha* are unique in possessing highly exaggerated, often sexually dimorphic, nasal appendages. In males, the appendage has a smooth, spear-like shape, whereas in females a leaf-like shape prevails. The sexes also differ in their coloration. Because ecology can shape evolution, aspects of the ecology and behavior of this snake should shed light on their morphological specializations. Here I provide multiple field observations of resting and foraging behavior in free living *L. madagascariensis* as a step towards filling in the knowledge gap of the behavioral ecology of this vine snake.

MATERIALS AND METHODS

My study sites were Mandena and Petriky, littoral forest conservation zones around the southeastern city of Tolagnaro, Madagascar. Mandena is just north of the city, while Petriky is to the south. There remain 3,128 ha of littoral forest around Tolagnaro divided into 250 fragments, including 890 ha at Petriky and 738 ha at Mandena. Both sites have heavy human impact, and the fragments are surrounded by bare sand and heavily degraded vegetation. Between 1972 and 2005, the littoral forest in the Tolagnaro region lost 26,563 ha, 40% of its surface area. As of 2005, only 36% of the forest was classified as in good condition (Vincelette et al. 2007a).

The average temperature of Tolagnaro in November, during which this study took place, is 24.7 °C. Because annual rainfall decreases from north to south along the coast, Petriky is the drier site and contains several plant species whose ranges extend into dry forest, serving as a transition zone between littoral and dry forest. Approximately 70% of annual precipitation falls during the wet season, generally from November to May. Between 2002 and 2004, Mandena's average yearly rainfall was ca. 2,000 mm, while Petriky's was only ca. 1,000 mm. The average rainfall in November was ca. 300 mm for Mandena and ca. 100 mm for Petriky (Vincelette et al. 2007b).

During four weeks in November 2010, guides and I walked through the forest between 0600 and 1630 looking for *Langaha*, alternating between trails and undisturbed forest. We spent 18.75 h total looking for *Langaha* in forest fragments M15 and M16 of Mandena without finding snakes, then moved to Petriky, where a villager had sighted and captured an individual. We spent the next two weeks at Petriky searching for *Langaha* in the same fashion as at Mandena. At Petriky, we spent 11.25 h actively searching for snakes and 50.5 hours observing snakes that we had found. Whenever we sighted *Langaha*, we stayed with the snake for as long as possible and I recorded its activities and characterized the microhabitat. I stayed 2–6 m away from the snakes during observation and minimized my movements so as not to disturb the animals. I judged that because the snakes foraged and even consumed prey in my presence, I did not disrupt their activities. I characterized microhabitat by estimating the height of the snake above the ground and the diameter of any branches that the snakes contacted as well as periodically recording the air temperature near the animal. I later calculated the duration of each activity to quantify time usage and quantified the amount of time spent at given perch heights and perch diameters to examine microhabitat preferences.

Activities comprised several categories. I noted three directions of movement: forward in the horizontal plane, up, and down. Other behaviors included holding the body completely still, swaying the head from side to side (which may or may not accompany locomotion), tongue flicking, hooding, opening and closing the mouth, and stalking, striking, and swallowing prey. Hooding involves dorsoventral compression and lateral expansion of the neck, making the snake look larger. Stalking involves movements towards potential prey items, which may be interspersed with periods of stillness.

RESULTS

I found six individuals, all males. In two cases I followed an individual for multiple days, observing Male 2 for two days and Male 3 for four. I did not include Male 1 in the final analysis because he had been captured and held captive for several hours prior to observation. Upon release he appeared frightened and fled immediately, evading us after 30 min of observation, so his behavior cannot be considered natural. I also did not include Male 4 because a guide discovered him while I was observing Male 3, and I could not observe both at the same time. The final data set included just over 50 h of observations on four snakes.

FIGURE 1. Typical habitat for Madagascan Leaf-Nosed Snake (*Langaha madagascariensis*) in Petriky, littoral forest conservation zones around the southeastern city of Tolagnaro, Madacascar. This is where I observed Males 1 and 2. (Photographed by Jessica L. Tingle).

All individuals were among branches and vines measuring < 1 cm in diameter. When moving, snakes usually crossed several branches rather than along a single branch. All of the snakes were at the edge of the forest near trails or the campsite (Fig. 1). They spent nearly all of their time in shade or mostly in shade, where nearby air temperature varied between 22 °C and 37 °C. The exception was Male 6, who was in full sunlight at 0617 and remained there until 0730. It was 26 °C in the sun at the beginning of the observation period and 34 °C when he moved into the shade.

The snakes occurred between ground level and ca. 5.3 m above the ground. All individuals except Male 3 spent most of their time 0–2 m above the ground. Male 3 spent most of his time over 4 m above the ground. Because Male 3 accounted for over half of the hours of observation, the combined time of all snakes spent in each height class is skewed towards this male (Table 1). Any time the snakes changed locations, they alternated between moving for periods generally lasting 5–20 s and holding still. Movements were often accompanied by lateral swaying of the head and neck, particularly when there was a breeze, and they typically coincided with gusts, whereas inactivity coincided with periods of still air between gusts. The vast majority of their time (90%) was spent not moving at all. All activities observed more than twice are included in Table 1, but some activities observed only once or twice (e.g., feeding

TABLE 1. Summary of time of day and total time observed, perch height, and activities of individual Madagascan Leaf-Nosed Snakes (*Langaha madagascariensis*) by day and for the total sample.

	Male 2, Day 1	Male 2, Day 2	Male 3, Day 1	Male 3, Day 2	Male 3, Day 3	Male 3, Day 4	Male 5	Male 6	Total Sample
Time Observed	1413–1846	0633–0910	0628–1850	0612–1915	0550–1630	0530–0805	0842–1020	0617–1117	0530–1915
Total Time	4h 31m	2h 35m	11h 20m	12h 53m	10h 18m	2h 25m	1h 34m	4h 51m	50h 27m
Perch Height (m)									
0–0.9	0%	44%	0%	0%	5.2%	0%	0%	89%	12%
1–1.9	72%	23%	0%	0%	11%	0%	62%	11%	13%
2–2.9	17%	29%	0%	0%	12%	0%	17%	0%	6%
3–3.9	5%	0.7%	0%	0%	0%	0%	18%	0%	11%
4+	7%	3%	100%	100%	71%	100%	3%	0%	68%
Behaviors									
still	82%	74%	93%	96%	87%	92%	67%	97%	90%
head sway	13%	5%	6%	3%	8%	0.5%	2%	0%	5%
move forward	10%	5%	1%	0.4%	3%	1%	13%	1%	3%
move upwards	2%	2%	0.4%	0.5%	1%	0.8%	4%	0.6%	1%
move downwards	0.9%	1%	0.5%	0.5%	0.9%	0.1%	2%	0.4%	0.7%

behavior and hooding) as well as those occurring instantaneously (e.g., tongue flicking) are not included.

I observed Male 3 for four days, and for three nights he returned to the same branch about 4 m high. The branch was less than 0.5 cm in diameter, and there were many vines and seed pods hanging straight down from other branches in the vicinity. The snake positioned himself with the posterior half of his body resting across vines and branches, and the anterior half pointed rigidly downward (Fig. 2). I initially found him in this position during early morning, and he returned to this "night perch," presumably to sleep, each of the three evenings that I observed him. He moved to the night perch in the evening between 1800 and 1900, when it got dark, and he began to stir and moved from the night perch within 20 min of 0700 every morning. Because I did not observe the snake throughout the night, there is a chance that he moved without my knowledge. However, if he did, then afterwards he returned to the same position on the same perch that I had last seen him at dusk. He spent much of his time each day on a specific branch (diameter < 0.5 cm) near a central tree, which I termed his "ambush perch" (Fig. 3). His position brought his head within 5–10 cm of the trunk.

I observed several individual day geckos (*Phelsuma* sp.*)* on the tree trunk, but many were too far away to attract the attention of Male 3, and none was captured successfully despite the efforts of the snake. Some of the geckos attracted the attention of the snake, and the snake oriented his head and body towards them, in some cases moving to different branches that were closer to the position of the gecko on the tree trunk. In at least one instance, a gecko looked at the snake and thereafter responded to the movements of the snake by crawling farther away from him. Other geckos may have observed the presence of the snake, but if they did, then it was not as clear to me that they avoided the snake on purpose rather than by chance.

Four snakes stalked prey during observations, and two successfully captured and consumed prey. The two prey items consumed were a terrestrial iguanid lizard (*Chalarodon madagascariensis*, eaten by Male 2) and an arboreal day gecko (*Phelsuma modesta*, eaten by Male 5). Other prey stalked but not captured included several individuals of *C. madagascariensis* (stalked by Male 6), three terrestrial skinks (*Trachylepis elegans*, stalked by Males 3 and 6), and another arboreal day gecko (*P. antanosy*, stalked by Male 3). Male 2 spent an hour in the bottom branches of a tree waiting to ambush terrestrial *Chalarodon madagascariensis*, several of which were moving around nearby. When one finally appeared under the tree, the snake followed the movement of the lizard with its head as the lizard approached, then apprehended it after 1 min 7 s. The lizard was approximately 15 cm away and the two reptiles were face to face when the snake struck. The snake grasped the lizard on the nose. This capture location is unlike captive snakes studied by Krysko (2005), which always grasped prey near the neck, but was similar to a captive female studied by Love (1993). The snake wrapped several body loops around the lizard until it was subdued (Fig. 4). It took 50 s for the lizard to stop struggling, an additional 1 min 25 s for the lizard to stop twitching, and then a further 1 min 20 s until the snake began to swallow. In total, 3 min 35 s elapsed between the strike and the start of swallowing.

FIGURE 2. Madagascan Leaf-nosed Snake (*Langaha madagascariensis*), Male 3 (arrow), in sleeping position. (Photographed by Jessica L. Tingle).

Swallowing the entire lizard took 12 min 24 s. Male 6 also stalked *C. madagascariensis*, but none of the lizards ever came within striking distance, even though they approached the snake four times.

In addition to *Chalaradon madagascariensis*, the terrestrial skink *Trachylepis elegans* is apparently an appropriate prey item for *Langaha*. Males 3 and 6 stalked a skink on one occasion each, though both were unsuccessful. Male 3 came briefly out of the branches onto the ground and actively chased first one skink and then a second as soon as the first one disappeared. Male 6 displayed hooding behavior for 1 min 9 s while unsuccessfully stalking a skink, the only instance of that behavior observed.

The second observed capture by a vine snake was of the arboreal gecko *Phelsuma modesta* by Male 5 at ca. 2 m above the ground. I did not see the gecko until the snake struck it, thus I cannot provide details leading up to the strike. The snake grasped the gecko just anterior to the hind limbs and placed two loops around the gecko's head and neck (Fig. 5). This capture was similar to those observed by a captive female, which

FIGURE 3. Madagascan Leaf-nosed Snake (*Langaha madagascariensis*), Male 3, in ambush position next to tree trunk. (Photographed by Jessica L. Tingle).

regularly grabbed its prey by the head or midbody (Love 1993). The gecko waved its tail in a struggle for 1 min 58 s before succumbing. The time elapsed between striking and commencing to swallow was 9 min 27 s. During that time, the snake made chewing motions every few seconds, presumably to deliver venom with its grooved posterior maxillary teeth. Swallowing took 4 min 13 s.

DISCUSSION

If one were equally likely to encounter male and female *Langaha madagascariensis*, then the probability of encountering six males and no females is 0.016. This extremely low probability leads me to believe that something other than random chance caused the sex bias in my data. There may simply be fewer females than males, females may be better camouflaged and therefore harder to see than males, they may be inactive during the time of year of the study, or they may have microhabitat preferences that make them less frequently encountered than males (such as higher up in the canopy than 5.3 m, the highest that I managed to continuously observe a male).

Several factors contribute to *Langaha*'s excellent camouflage. Coloration and the nasal appendage help the snake to appear physically very similar to a branch or vine. When Male 3 hung rigidly from a branch at night, the nasal appendage streamlined his shape and made his silhouette even more difficult to distinguish from a vine or a fruit. Similar behavior has been observed in captive hatchlings, although they performed it during the day rather than at night (Krysko 2003). Several Malagasy plants, including many in the families Papilionaceae, Mimosaceae, and Caesalpiniaceae, have long pointed seed pods that hang down from the plant, providing possible models that the snake may imitate with its posture and nasal appendage. The vinesnake's tendency

FIGURE 4. Madagascan Leaf-nosed Snake (*Langaha madagascariensis*), Male 2, feeding on *Chalarodon madagascariensis*. (Photographed by Jessica L. Tingle)

to move across small branches of similar diameter to its body possibly aids in camouflage. Additionally, by moving only for short spurts of time, swaying the head from side to side, and taking advantage of gusts of wind for movement, *Langaha* may capitalize on its resemblance to a branch swaying in the wind. Similar behavior has been observed in other reptiles, such as the Green Iguana (*Iguana iguana*), the Eastern Fence Lizard (*Sceloporus undulatus*), and the Florida Scrub Lizard (*S. woodi*; Jackson 1974; Greene et al. 1978).

Prior to this study, *Langaha* was assumed to specialize on a diet of arboreal lizards, much like vine snakes elsewhere (Henderson and Binder 1980). Moreover, captive hatchling *Langaha* ate arboreal anoles (*Anolis* sp.) and geckoes (*Hemidactylus* sp.) but refused terrestrial skinks (*Scincella* sp.; Krysko 2003). However, my observations demonstrate that *Langaha* will eat and even seek out certain terrestrial lizards as prey. It is not the only vine snake to prey on terrestrial lizards. The African Twig Snake *Thelotornis capensis*, eats arboreal and terrestrial species in roughly equal proportions, the Mexican Vinesnake, *Oxybelis aeneus*,

FIGURE 5. Madagascan Leaf-Nosed Snake (*Langaha madagascariensis*), Male 5, grasping *Phelsuma modesta*. (Photographed by Jessica L. Tingle)

eats whiptail lizards (*Aspidoscelis* spp.) and Southern Pygmy Skinks (*Plestiodon parvulus*) in addition to anoles and the Hispaniolan vinesnake, *Uromacer frenatus*, eats Curly-tailed Lizards (*Leiocephalus vinculum*) and whiptail lizards (*Ameiva* sp.) in addition to anoles (Henderson and Horn 1983; Shine et al. 1996; Madrid Sotelo and García Aguayo 2011). Perhaps the refusal of terrestrial lizards by captive hatchlings (Krysko 2003) demonstrates an ontogenetic shift in prey preference.

The study also provides evidence that *Langaha* is largely a sit and wait predator, but will sometimes actively pursue prey. The snakes spent 90% of their time holding completely still, in most cases waiting for arboreal prey to pass by on a tree trunk or terrestrial prey to pass by on the sand. For example, Male 3 spent much of his time on a perch that brought his head within 5–10 cm of the trunk, an advantageous position for ambushing any gecko that may pass on the tree. However, *L. madgascariensis* may not be entirely a sit and wait predator. Male 3 actively chased skinks after failing to ambush a gecko. Another vine snake, *Oxybelis aeneus,* also spends most of its time motionless and waiting for prey, but unlike *Langaha* it has not been observed in active pursuit (Madrid Sotelo and García Aguayo 2011).

Although this project has provided a first look at the behavior and ecology of *Langaha madagascariensis* in the wild, much remains to be done, and a special effort should be made to observe females. The latter could give insight into the purpose of *Langaha*'s unusual nasal appendage as well as the extreme sexual dimorphism found in the species, given that niche divergence may lead to sexual dimorphism in other snakes (Shine 1989). Perhaps the females have different behaviors and microhabitat preferences than the males such that the nasal appendage helps provide camouflage to each sex in its own niche. Further field studies are required to learn more about these and other aspects of the behavior and ecology of *Langaha madagascariensis*.

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