

SEDENTARY BEHAVIOR BY GREEN MAMBAS *DENDROASPIS ANGSTICEPS*

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Snakes may employ two divergent foraging strategies, sit-and-wait (= ambush) and widely-foraging (= active foraging): two extremes of a continuum of foraging modes displayed by animals (Pianka 1978). Typically, viperids are thought to be sedentary ambush hunters, while elapids are wide-ranging active foragers (Mushinsky 1987; Shine 1980). This apparent dichotomy has been supported by field studies involving feeding behavior of viperids (e.g., Greene & Santana 1983; Reinert et al. 1984) and elapids (e.g., Shine 1979; Zinner 1971). An exception to these stereotypes is the Australian elapid, *Acanthophis antarcticus*, which shows convergence with viperids (Shine 1980). I present evidence that another elapid, the green mamba (*Dendroaspis angusticeps*), may also employ a sit-and-wait strategy of foraging.

Branch (1988) described the green mamba as an active, arboreal snake feeding exclusively on birds and small mammals. Mambas are considered shy and elusive snakes which are rarely seen (Branch 1988; Ionides and Pitman 1965). The scarcity of observations is usually attributed to *Dendroaspis angusticeps*' cryptic coloration and arboreal lifestyle. However, low activity levels associated with a sedentary foraging pattern might be an alternative explanation for its inconspicuousness. Here, I report the activity of two adult *D. angusticeps* for a 27 day (d) period in the coastal forest of Gede/Jimba, Kenya.

MATERIALS AND METHODS

The Gede/Jimba area (3° 18' S, 40° 1' E) is approximately 5 km from the shore of the Indian Ocean and 15 m above sea level. The climate is influenced by monsoonal air currents of the Indian Ocean resulting in two rainy seasons, the "short rains" (i.e., rain showers of short duration) from October-December and the "long rains" (i.e., rain showers of long duration) from April-June, provid-

ing an annual rainfall of 1040 mm (Gerhardt & Steiner 1986). The relative humidity and temperature are high year round (RH 85-100%, 25-30 C; Gerhardt & Steiner 1986). The vegetation consists of secondary, semi-deciduous, lowland forest, interspersed with cultivated fields of mango (*Mangifera indica*), palm (*Cocos nucifera*), and cashew (*Anacardium occidentale*) trees. The site used in this study was a 3.8 ha patch of forest (Fig. 1) bordered by dirt roads to the south and east, and cultivated fields (Fig. 1) on the north and west. The 10-15 m canopy consisted mainly of *Azadirachta indica*, *Lecaniodiscus fraxinifolius*, and *Lonchocarpus bussei*, and was rich with climbers of the genus *Cissis*. For a more detailed description of the general area, see Gerhardt & Steiner (1986).

Two *Dendroaspis angusticeps* (1 male, SVL 96 cm, 284 g; 1 female, SVL 103 cm, 369 g) were collected on 15 November 1991 and brought to the laboratory of Bio-Ken Reptile Farm (Watamu, Kenya) where radiotransmitters (LF1, L.L. Electronics, Mahomet, IL) weighing 2.2 g and 2.6% of body mass were intraperitoneally implanted following Reinert & Cundall (1982). The snakes were released at the site of capture within 48 hours (h) of collection. Both snakes were relocated daily for a period of 27 days in November-December. At each relocation, 1-6 h of behavioral observations were recorded. Movement was measured and plotted to scale on a map of the study area. Activity range areas were calculated by harmonic mean transformation (Dixon & Chapman 1980), minimum convex polygon (Jennrich & Turner 1969; Southwood 1966), and 95% ellipse (Jennrich & Turner 1969) methods using *Micro-computer Programs for the Analysis of Animal Locations* (M. Stuwe & C. E. Blohowiak, National Zoological Park of the Smithsonian Institution).

RESULTS AND DISCUSSION

Each snake used three sites (defined as a single tree or entanglement of two trees; Fig. 2) during the study. Each site was used for 6-10 d, during which

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only minor shifts in position (< 5 m) were noted. Longer movements between sites (> 10 m), averaging 20.84 m ($SE = 2.84$ m), occurred after molting and/or defecation. Long movements occurred between 1600-1900 h, while shifts within sites occurred throughout the day. Ionides and Pitman (1965) observed that *Dendroaspis angusticeps* shifts its position within a tree, such that it basks in the lower branches in the morning and retreats to the thicker heights at mid-day. They attributed those movements to thermoregulation but it is difficult to say whether those or the small shifts observed in this study are thermoregulatory in nature without the appropriate biophysical data (see Hertz et al. 1993). All observed movement was within the canopy but there is some reason to believe that the female may have crossed open ground at one point. At 1606 h on 12 December the female was observed coiled at the base of a tree, in route from her third site back to her second. When located at 1042 h the next morning she had returned to her second site, a total trip of 21.2 m (straight-line distance).

Overall, movement of 3 m or more occurred only 29.2% and 46.8% of the days for the male and female, respectively. Figure 3 shows the activity ranges resulting from harmonic mean transformation, and minimum convex polygon methods. Activity centers (50% isopleths; Fig. 3A) for both snakes were relatively small, being 33 m² for the female and 5, 11, and 22 m² for the male. Activity range areas (Table 1) for harmonic mean transformation, minimum convex polygon, and 95% ellipse methods are provided for comparison with published values for other species.

The mean daily movement of *Dendroaspis*

angusticeps was 5.4 m ($SE = 0.32$ m, $n = 2$, range = 0-31.0 m). Data for similar-sized, active foraging elapids (Shine 1979) suggest extensive daily movements up to 400 m. Similarly, a mean daily movement of 186.2 m ($SE = 37.0$, $n = 8$) was reported for the widely-foraging colubrid, *Masticophis flagellum* (Secor 1992). Compared to these active foragers, *D. angusticeps* was much less mobile. However, the mean distance traveled per day for the two snakes is comparable to that of sit-and-wait predators. Reinert and Kodrich (1982) reported a mean daily movement of 9.1 m ($SE = 1.61$ m, $n = 18$) for the massasauga, *Sistrurus catenatus catenatus*. Further, the mean daily movement of *Crotalus horridus*, a known ambush hunter, was 34.2 m ($SE = 4.97$ m, $n = 2$) for males and 16.5 m ($SE = 4.68$ m, $n = 3$) for females (Reinert & Zappalorti 1988). Likewise, Secor (1992) reported a mean daily movement of 41.6 m ($SE = 7.86$, $n = 22$) for the sit-and-wait forager *Crotalus cerastes*. Interestingly, the widely foraging *Coluber constrictor* moved less than 40 m per day when studied with ingested radiotransmitters (Brown & Parker 1976; Fitch & Shirer 1971). However, ingestion of radiotransmitters may alter movement and other activities of snakes (Lutterschmidt & Reinert 1990).

The most compelling evidence for ambush behavior in *Dendroaspis angusticeps* comes from relocations just after feeding (feeding was assessed by noting distinct bulges at mid-body, revealing interscalar skin). The female ate a meal between observations on d 14 and d 15, without a change in location. The male fed between d 16 and d 17 with a displacement of only 2.6 m. The apparent lack of movement suggests that these feedings resulted from



Figure 1. (Left) The study site was a 3.8 ha patch of forest dominated by *Azadirachta indica*, *Lecaniodiscus fraxinifolius*, and *Lonchocarpus bussei*. (Right) The forest was bordered by cultivated fields of cashew (*Anacardium occidentale*) and palm trees (*Cocos nucifera*).



Figure 2. The male *Dendroaspis angusticeps* coiled at 5.5 m height in *Lecaniodiscus fraxinifolius*. The male remained in this tree for seven days before moving 13.7 m to a new site.

ambush behavior rather than active searching.

To establish that the activity of *Dendroaspis angusticeps* was indicative of a sit-and-wait foraging strategy, it is necessary to rule out other possible reasons for the observed movement patterns. The transmitters did not seem to alter behavior, as both snakes fed, defecated and molted during the study. Mean daily movement during the last 7 d of the study was not different from that of the first 20 d (Kruskal-Wallis tests, for both snakes $p > 0.05$), suggesting that movement was not impaired by recovery from surgery. *Dendroaspis angusticeps* does not hibernate, and aestivates only during the "long rains" April-June (J. Ashe, pers. comm. 1991), so these causes can be discounted for the sedentary behavior.

Predator avoidance is another possible cause of sedentary behavior, however, it is difficult to separate from sedentary foraging behavior. Predator avoidance and sit-and-wait foraging are not always mutually exclusive, because predator avoidance is thought to be inherent in a sit-and-wait foraging

strategy (Dunham 1983; Greene & Santana 1983; Huey & Pianka 1981; Shine 1980). No sign of predator encounters were noted at any time during the study, though natural predators include snake eagles (subfamily Circaetinae; J. Ashe, pers. comm. 1991; Broadley 1961), genets (*Genetta* spp.; J. Ashe, pers. comm. 1991), and mongooses (*Herpestes* spp.; Broadley 1961). Juveniles are also preyed on by hornbills (Bucerotidae; J. Ashe, pers. comm. 1991) and other snakes (Broadley 1961).

Reproduction can be ruled out as being responsible for the movement patterns. Shine (1979) found that gravid female Australian elapids are sedentary. However, mate-searching and courtship in *Dendroaspis angusticeps* occur during the "long rains," April-June (J. Ashe, pers. comm. 1991; Branch 1988; Haagner & Morgan 1989; Ionides & Pitman 1965), while the individuals were observed in November-December. The female was neither gravid nor reproductively active. Mate-searching by males would be associated with increased movements (Gre-

TABLE 1. Activity range areas for male and female *Dendroaspis angusticeps* calculated by harmonic mean transformation, minimum convex polygon, and 95% ellipse methods.

Method	Area (m ²)	
	Male	Female
Harmonic Mean Transformation		
Activity Area (95%)	494	1086
Activity Centers (50%)	5	33
	11	
	22	
Convex Polygon	341	928
95% Ellipse	900	2322

gory et al. 1987), so his sedentary behavior is in contrast with movements associated with reproduction.

Feeding is the most plausible cause of the observed movement patterns. The sedentary behavior displayed by *Dendroaspis angusticeps* in this study is characteristic of that of an ambush predator. Reinert et al. (1984) described the sit-and-wait tactics of *Crotalus horridus*, which remained poised in an ambush position near mammalian runways. Greene and Santana (1983) noted the sedentary behavior of *Lachesis muta*, which used three sites in 35 days, spending its nights in an alert posture. They concluded that the feeding strategy of *L. muta* consists of infrequent movements to locate suitable sites for ambushing prey. Similarly, Slip and Shine (1988) noted that the sit-and-wait tactics of the diamond python, *Morelia spilota spilota*, is characterized by very little movement, except when moving from one hunting site to another. These infrequent movements resemble the behavior displayed by *D. angusticeps*. The sites used by *D. angusticeps* were associated with the neem tree, *Azadirachta indica*, which bears a small, orange fruit favored by numerous bird species (J. Ashe, pers. comm. 1991; Faden 1972).

The preliminary evidence presented here suggests that *Dendroaspis angusticeps* displays a sit-and-wait strategy of foraging. This evidence does not preclude active foraging by this species. William York observed a *D. angusticeps* systematically hunt sleeping bats (J. Ashe, pers. comm. 1991). They have also been known to raid nests of young

birds (Phelps 1989). This species also feeds on eggs (Fitzsimons 1962), rodents (Broadley 1975; Ionides 1953; Lloyd 1974), and adult birds (Ionides 1953). It is possible that non-foraging movements may result in chance encounters with stationary prey, such as nest eggs, young birds, and sleeping bats, but it is likely that active foraging is necessary to feed on these prey regularly.

Sit-and-wait tactics might be successful with highly mobile prey, such as rodents and adult birds. Documented prey includes the greenbul, *Andropadus importunus* (Pycnonotidae; Pitman 1962), which inhabits dense portions of natural and cultivated vegetation on the coast of Kenya (Keith et al. 1992). *Andropadus importunus* forages in the heights of trees moving frequently among branches (Keith et al. 1992). The cryptic coloration of *D. angusticeps* might make it difficult to be detected by foraging birds, such as *A. importunus*. Ionides and Pitman (1965) reported a large naked-soled gerbil (*Tatera leucogaster*) in the stomach of a green mamba from Tanzania. While this species does not extend into Kenya, it is assumed that *D. angusticeps* will potentially feed on any of the seven species of *Tatera* that inhabit various portions of its range (see Musser & Carleton 1993). *Tatera* are gregarious, nocturnal rodents which feed on bulbs, roots, seeds, leaves, and insects (Walker et al. 1964). They inhabit plains, savannahs, and woodlands, making complex burrows in the soil or sand (Walker et al. 1964). The arboreal *D. angusticeps* would be likely to encounter *Tatera* which are actively foraging in trees or bushes. Since there is no evidence that *D. angust-*

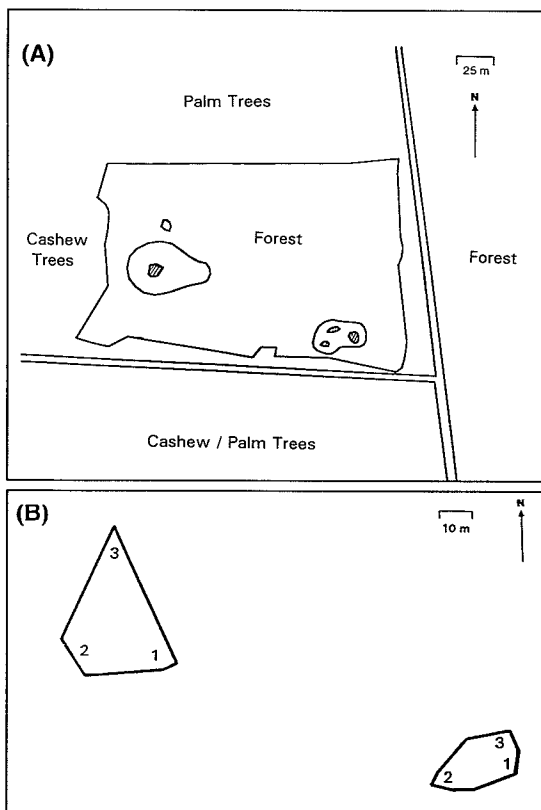


Figure 3. (A) A map of the study area containing activity ranges of the female (left) and male (right) *Dendroaspis angusticeps*, calculated by harmonic mean transformation. Activity centers (50% isopleths) are diagonally hatched. (B) Minimum convex polygons for the female (left) and male (right) *Dendroaspis angusticeps*. The sites used are labelled numerically in the order of use.

iceps is active nocturnally (Ionides & Pitman 1965; present study), it is probable that encounters with nocturnal rodents, like *Tatera*, are mediated by ambush behavior.

There are at least three possible, though not mutually exclusive, implications of my observations: 1) populations of *Dendroaspis angusticeps* may differ in foraging behavior, 2) previous descriptions of activity in this species may be based on limited observations, biasing our perception of its behavior (see Reinert 1993), and 3) there is plasticity in the foraging behavior of individuals. Individuals may shift foraging rate (speed and frequency) in response to environmental conditions (see Werner & Anholt 1993). A shift from active to sit-and-wait foraging may be an adjustment to changes in avail-

able resources, predator densities, or climatic conditions. It seems that simply assigning this species, or any other, to one side of this dichotomy may not be the best approach to understanding its foraging ecology. Behavioral plasticity could have interesting consequences for the ecology and physiology of this snake, which are missed when generalizations about behavior are drawn.

The sedentary behavior displayed by the two *Dendroaspis angusticeps* is surprising, in light of previous descriptions of this species as a highly active snake. Further investigation will be necessary to confirm plasticity of foraging behavior in this species.

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