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NESTING MOVEMENTS, NESTING BEHAVIOR, AND NEST SITES OF GREEN SNAKES (*OPHEODRYS AESTIVUS*) REVEALED BY RADIOTELEMETRY

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ABSTRACT: Nesting ecology was studied in arboreal green snakes, *Opheodrys aestivus*, by monitoring the behavior of nine gravid females bearing implanted radiotransmitters. Prior to ovipositing, activities of females were restricted to small ranges within a narrow band of edge vegetation at the shoreline of a lake. As the time of oviposition neared, snakes descended from their arboreal habitats and moved terrestrially away from the shoreline. Snakes nested in small chambers within the hollowed interiors of living trees. Some nest chambers contained eggshells of *Opheodrys* from previous years. Moisture levels of nest substrates were within the range supporting normal development as determined in laboratory studies. The behavior of some individual snakes suggested that nesting individuals returned to a specific tree each year.

Key words: Colubridae; *Opheodrys aestivus*; Nesting ecology; Water relations; Radiotelemetry

NESTS of most squamates are inconspicuously located in or under rocks, logs, or other surface cover, or in preformed subterranean chambers (Packard and Packard, 1988). Discovering such nests is usually fortuitous. Systematic search for natural nests of snakes in known nesting areas has been successful in at least two cases, one resulting from search under uprooted clumps of grass (Sexton and Claypool, 1978), and one from search for distinctive nesting excavations (Burger and Zappalorti, 1986). Certain techniques may increase the probability of finding nests. For example, nests of *Masticophis* were found in rodent burrows by following gravid females that had been implanted with radiotransmitters (Parker and Brown, 1972).

Knowing where snakes oviposit would benefit at least two areas of research: (1) it could provide a source of hatchlings for mark-recapture studies, thereby providing valuable information on a poorly known stage of life history (Parker and Plummer, 1987; Plummer, 1985*b*), and (2) it would permit tests of hypotheses derived from laboratory studies on the physiological requirements of eggs (Packard and Packard, 1988). For example, recent laboratory

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studies of incubating snake eggs have underscored the need for available moisture for normal development (Gutzke and Packard, 1987; Packard and Packard, 1987; Plummer and Snell, 1988). Furthermore, when given a choice among laboratory substrates differing in moisture content, gravid *Opheodrys aestivus* chose moist substrates on which to oviposit (Plummer and Snell, 1988).

The purpose of this study is to describe the nesting ecology of an arboreal snake (*O. aestivus*) inhabiting a narrow band of thick, brushy vegetation at the shoreline of a lake (Goldsmith, 1984; Plummer, 1981) and to provide much needed descriptions of natural nest chambers (Packard and Packard, 1988). However, the initial impetus was to answer the question posed by Plummer and Snell (1988): "Do green snakes nest in wet environments in nature?"

MATERIALS AND METHODS

The study area was the forest surrounding a 21 ha lake (Ransom's Lake) 2 km west of Denmark, White County, Arkansas. The vegetation at the shoreline (primarily alder, *Alnus rugosa*) formed a distinct, brushy stratum approximately 1.5–4 m in height and 1–5 m in width. Behind the alder was an oak-hickory forest typical of the region. The forest had been logged in recent years, so that most remaining trees were small. In six 10 × 50 m transects containing 284 oak (*Quercus* spp.) and hickory (*Carya* spp.) trees, 36 ± 3.2% (range 25–44%) were in various stages of developing hollow interiors. The ground was rocky and sloped upwards around the lake at approximately 5–15°.

Miniature radiotransmitters (218 MHz, 2.4 g, Model SOPI-1038-LD, Wildlife Materials, Inc.) were implanted into nine large [>500 mm snout–vent length (SVL)] gravid *Opheodrys*. After implantation, the females were released on 19 June 1988 at the site of their captures made the previous week. I relocated telemetered snakes several times each day until oviposition and once each day thereafter. At each relocation after long movements, the site was marked with plastic flagging, and distance and compass heading from the last relocation site were recorded. On occasion, I visually monitored individual snakes through binoculars for up to 2 h. Nests were located by examining those hollow trees in which snakes entered. To expose potential nest chambers, trees were carefully opened with a chain saw by removing wedges of wood sufficiently large to extend into the tree hollow. Nests were classified as "new" if fresh eggs were found and "old" if eggshells from previous nesting seasons were found. I judged the identity of old eggshells by their size and shape in comparison to those of reptilian species known to inhabit the area, the eggs of which are known. Substrate samples were taken from nesting sites and from other randomly-determined locations within 20 m of those sites (e.g., substrates under logs and rocks, within rotted logs on ground, leaf litter). Water potential was measured in the laboratory with a Wescor C-52 sample chamber and a HR-33T dew point microvoltmeter. Temperatures in one nest were measured periodically with an indwelling thermocouple. Means are presented as $\bar{x}$ ± 1 SE.

RESULTS

Movements

Movement data were collected on only five snakes, because early in the study, four snakes either were eaten by predators or were lost to unknown causes. Prenesting movements of telemetered females were restricted primarily to the band of alder at the shoreline and averaged only 1.3 ± 0.17 m from the edge of the vegetation. Distances between relocations on successive days and length of activity ranges were small (Table 1).

Distinct nesting movements, involving snakes descending from alder habitat and traveling overland to a nesting site in a hollowed, but otherwise living and growing tree, began abruptly in the form of extensive directional movements (Table 1). Relocations averaged 30.0 ± 9.0 m from the shoreline during this time, and distances between relocations were large (Table 1). After ovipositing, snakes moved

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TABLE 1.—Patterns of movement in telemetered gravid *Opheodrys aestivus*. Data are mean distance between relocations on successive days (m/day), number of days monitored (days), length of activity range (len.), and distance from activity range to nest site (dist.).

Snake	Prenesting movements			Nesting leg of migration			Postnesting leg of migration		Postnesting movements		
no.	m/day	(days)	Len.	m/day	(days)	Dist.	m/day	(days)	m/day	(days)	Len.
5	5.4 ± 0.8	(21)	38	38.0 ± 11.0	(4)	80	19.2 ± 8.0	(8)	4.6 ± 2.1	(14)	10
104	3.0 ± 1.3	(6)	5	28.0	(1)	28	18.0	(1)	1.6 ± 0.7	(18)	15
110	1.9 ± 0.6	(16)	13	35.0 ± 6.0	(2)	70	21.0	(1)	—		
37	2.8 ± 0.9	(18)	14	24.5 ± 9.0	(2)	50	—		—		
604	1.2 ± 0.7	(5)	3	54.8	(1)	53	—		—		
$\bar{x}$	2.9 ± 0.4	(13)	15	32.7 ± 5.3	(2)	56	19.4 ± 6.4	(3)	3.1 ± 1.0	(16)	13

quickly back toward their original activity ranges (Table 1). In this postnesting migration, three snakes either died from unknown causes or were eaten by predators. After the postnesting migration, two snakes exhibited patterns of short movements within activity ranges at the vegetation edge similar to prenesting movements (Table 1). The location of the activity range of snake no. 104 was similar to its original range before nesting. The activity range of snake no. 5 was located approximately 45 m from its original range.

Each of the four snakes that oviposited passed hollow trees along their paths to nesting sites, but only snake no. 5 entered a tree without ovipositing in it. Snake no. 604 moved 55 m directly to a tree, climbed 3 m up the trunk to a small opening difficult to detect by two humans from the ground, and for 30 min attempted to enter a cavity containing old eggshells. Along her path she passed within 5 m of 52 trees, 22 of which were hollow.

TABLE 2.—Nest site characteristics of *Opheodrys*. Moisture measurements were taken immediately after oviposition. Measurements are in cm except distance from shoreline, which is in m. H = hickory, O = oak.

Snake no.	Distance from shore	Tree dia. at 1 m	Elevation of tree opening	Nest elev.	No. eggs	Moisture (kPa)*
New sites (1988)						
104	15	15 (O)	4	100	4	−1300
110	46	10 (O)	4	64	7**	−950
37	5	15 (H)	5	75	4	−650
5	75	18 (H)	5	25	3	−500
Old sites (pre-1988)						
	40	14 (H)	125	190	4	−400***
	15	15 (O)	7	100	4	—
604****	53	20 (H)	300	300	16	—

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* In order to measure water potential of the relatively solid substrates of nest chambers in the laboratory, samples were taken by scraping the walls of nest chambers with a knife. The effect of disrupting the integrity of substrates on water potential is unknown.

** One egg broken upon discovery.

*** Not measured at oviposition.

**** Did not oviposit; see text.

Nests

Nests were located in small ($\bar{x}$ diameter = 15 ± 1.2 cm) hollow oak and hickory trees averaging 36 ± 9.5 m from the shoreline (Table 2). Elevation of nest chambers averaged 122 ± 35.3 cm. Chambers were accessed by snakes through small openings averaging 64 ± 42.3 cm from ground level.

Nest chambers, narrow vertical slits in tree interiors resulting from rotting, were similar at both old and new nest sites (Table 2). In each chamber, the width approximated that of an egg (approximately 10 mm), restricting egg deposition to a single vertical layer, each egg contacting at least one, but in most cases, two walls of the cavity. Eggs occurred both separately and contacting other eggs. In no case were eggs embedded in loose duff.

Moisture levels of 19 substrate samples in proximity of nest sites were more variable and dry ($\bar{x}$ = −1025 ± 244 kPa) than moisture levels in five nests (−760 ± 164 kPa, Table 2). The lowest nest temperatures (25–28 C) occurred on cool overcast days, whereas the highest temperatures (29–34.5 C) occurred on warm clear days.

Three of the four new nests were lost to predators or to damage when the nest chamber was opened. After 42 days of in-

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cubation, I briefly opened and inspected the one remaining nest (snake no. 110, Table 2). The eggs appeared turgid and larger than at oviposition, being firmly wedged in the narrow nest chamber. On 25 August, each of six eggs hatched after 50 days of incubation at temperatures ranging 25.0–34.5 C ($\bar{x} = 30.7$). The hatchlings appeared vigorous and healthy and averaged 138 ± 2.1 mm SVL and 1.35 ± 0.017 g.

DISCUSSION

Although gravid *O. aestivus* in the laboratory most often chose substrate moisture levels of −100 to −200 kPa on which to nest, eggs developed normally in a wide variety of moisture levels, including substrates as dry as −1500 kPa. However, eggs incubated in very dry substrates (−2000 kPa) produced smaller hatchlings than eggs incubated in moister substrates. From these results, Plummer and Snell (1988) predicted that in the field, *Opheodrys* ought to select the wettest sites available within the favorable moisture range. Despite a major drought occurring during the course of this study, most substrates randomly sampled had water potentials greater than −1500 kPa. The limited data indicate that moisture content of sites selected by snakes in the field were drier and more variable than sites selected in the laboratory but were within the favorable range (Table 2). Moisture requirements of eggs may be satisfied in ways other than with the moisture present at the time of oviposition. For example, flexible-shelled eggs deposited on dry substrates may receive sufficient moisture provided such substrates are periodically recharged by rainfall (Packard and Packard, 1988). Moisture received at such times may have greater impact on increasing hatchling size than moisture conditions at oviposition (Clark, 1953; Gutzke and Packard, 1986). Thus, for *Opheodrys* eggs deposited in any reasonably sheltered site, the probability of having sufficient moisture for normal development may be quite high.

Eggs of *Opheodrys* in the field were not exposed to the same conditions as in Plummer and Snell's (1988) laboratory study. In the laboratory, eggs were embedded in substrates of constant moisture and temperature (28 C). In the field, eggs were not embedded nor were nest temperatures or moisture levels constant. Despite the differences, hatchling sizes in the field were similar to those in the laboratory. The higher nest temperatures in the field should have resulted in greater metabolic rates (Zarrow and Pomerat, 1937) and shorter incubation periods (Muth, 1980) compared to the laboratory (36–39 days). However, the diel patterns of temperature and moisture variation in tree cavities and their effects on rate of development are unknown. As for subterranean nests, the primary determinants of temperatures in tree cavity nests are probably the diurnal cycles of air temperature and radiation (Packard and Packard, 1988). The amount of temperature fluctuation in nests of *O. aestivus* (10 C) was similar to that found in shallow nests of other lepidosaurians (Packard and Packard, 1988).

Whether nesting migrations in *O. aestivus* confer a selective advantage, are evolutionary relicts, or simply reflect a lack of suitable nesting sites within activity ranges, is unknown. More radiotelemetric studies of gravid snakes are needed to document the nature of such migrations and to determine their evolutionary significance, if any. Especially useful would be comparative nesting studies in different populations of widely ranging species. Nesting migrations in snakes previously have been reported in *Natrix natrix*, *Masticophis taeniatus*, and *Laticauda colubrina* (Madsen, 1984; Parker and Brown, 1972, 1980; Saint Girons, 1964).

Why *O. aestivus* nests in hollow trees is unknown, but the behavior seems consistent with the ecology of an arboreal species. On Guam, arboreal *Boiga irregularis* may nest in rotting vegetation in the crown of palm trees (J. Savidge, personal communication). However, nesting in hollow trees is unknown for snakes other than *O. aestivus*, a void which may have more to do with the lack of examination of trees by field workers rather than an avoidance by snakes. Since routine field use of chain saws is neither desirable nor recommended, this

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problem is not likely to be overcome except in focused telemetric studies.

The directional nesting movements of all snakes and especially the behavior of snake no. 604 strongly suggests either a remarkable ability for remote detection of a suitable nest site or, more likely, a return to a site previously used. All telemetered *Opheodrys* exceeded 500 mm SVL, indicating an age of at least 6 yr and 3–4 previous nesting seasons (Plummer, 1985*a*). Perennial use of nesting sites in a communal sense has been reported for several snakes (Gregory et al., 1987), but it has yet to be demonstrated whether individual snakes use a site perennially. Perennial use of specific trees used as focal points in their home range is known for individual *Elaphe obsoleta* (Stickel et al., 1980).

If the nesting behavior of *O. aestivus* at Ransom Lake is typical for the species, it is conceivable that suitable primary nesting sites (small hollow trees) could be limited, thus increasing the chances of communal oviposition (Palmer and Braswell, 1976; Plummer, 1981), or of oviposition in secondary sites such as in or under surface material (Clark, 1949; Goldsmith, 1984; Mount, 1975; Sabath and Worthington, 1959; Smith, 1961). Such secondary sites are also much more likely to be discovered by field workers. It is noteworthy that the 74 eggs of *O. aestivus* found by Palmer and Braswell (1976) were contained by rock wool insulation inside a narrow metal refrigeration panel which was standing upright against an oak tree, a condition that apparently simulated a natural nest site in a hollow tree.

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A QUANTITATIVE ANALYSIS OF COURTSHIP BEHAVIOR IN CAPTIVE GREEN SEA TURTLES (*CHELONIA MYDAS*)

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ABSTRACT: Reproductive behavior of captive green sea turtles (*Chelonia mydas*) was observed at the Cayman Turtle Farm, British West Indies. Observed components of courtship behavior included gular rubbing, biting, cloacal checking, circling and biting, chasing, following, attempted mounting, mounting, and escorting. Data analysis indicated that in each of the observed components, reproductively attractive females were the target of the behavior significantly more often than reproductively nonattractive females. Cloacal checks may be used by both males and females to assess reproductive condition of females. Males may escort mounted pairs to disrupt copulation attempts by rivals and increase their own reproductive success; females may act as escorts to enhance later mate availability. In general, females appear to signal approaching reproductive receptivity to males, but females may exercise mate selectivity by avoiding mounting.

Key words: Sea turtle; *Chelonia mydas*; Courtship behavior

MATING and courtship behaviors of marine turtles are not well documented. Indeed, except for nesting and hatching, what is known about marine turtle behavior comes almost entirely from reports of incidental observations. However, in two publications (Booth and Peters, 1972; Bustard, 1973) marine turtle courtship has been described in general but not in detail.

Bustard (1973) reported a courtship sequence for *Chelonia mydas* consisting of the male facing and nuzzling the female, then biting her neck and rear flippers, and finally chasing her if she swam away. If a female was in water deeper than the height of her carapace, a male was able to mount by swimming onto her back and hooking his foreflipper claws over the anterior rim of her carapace. A female could avoid mounting by entering shallow pools where males were unable to mount her highly domed carapace. Booth and Peters (1972) reported similar behavior in *Chelonia mydas*, and added observations of circling and biting by females as well as a female "refusal" position. In the "refusal" position, an unreceptive female presented her plastron vertically to an approaching male. Although both reports provided valuable data

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