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Nest Site Selection and Water Relations of Eggs in the Snake, *Opheodrys aestivus*

MICHAEL V. PLUMMER AND HOWARD L. SNELL

When given a choice among nest boxes differing in water potential of the substrate, female green snakes (*Opheodrys aestivus*) preferred to nest in moister substrates of -200 and -300 kPa rather than in substrates ranging -600 to -2000 kPa. Green snake eggs incubated in six substrates with moisture levels from -200 to -2000 kPa increased in size and mass, the amount being positively correlated with water potential of the substrate. There was no difference in frequency of developmental abnormalities or hatching success among substrate treatments. The effect of substrate moisture on incubation time was inconsistent. Hatchlings from eggs incubated on the -2000 kPa substrate were smaller in length and mass than those from all other substrates.

Green snakes may nest on substrates within a wide range of moisture levels without adverse effects on the eggs or hatchlings. Because substrates in natural nests are subject to drying during incubation, it may be advantageous to nest in the wettest available site within the favorable range to minimize drying at the end of incubation. Greater survivorship of larger hatchlings may be a selective force contributing to the selection of moist nest sites by gravid females.

THE availability of water to flexible-shelled reptile eggs incubating in their nests affects the metabolism of developing embryos (Packard et al., 1983; Gettinger et al., 1984; Packard and Packard, 1984), the hatching success of eggs and the size of subsequent hatchlings (Packard et al., 1981; Packard et al., 1982; Tracy, 1982; Snell, 1984; Tracy and Snell, 1985; Packard and Packard, in press), and the amount of energy stored by emerging neonates (Gutzke, 1984). In turn, these characteristics of hatchlings may influence future survival (Swingland and Coe, 1979; Snell, 1984) and, consequently, the fitness of nesting females (Snell, 1984).

Lacking in previous studies on the water relationships of reptilian eggs is the role of female choice among available nest sites in providing an optimal environment for incubation. In this paper we examine the selection of nest sites according to water availability, and the subsequent water relations of incubating eggs of an arboreal snake (*Opheodrys aestivus*) in the laboratory. We predict that females will select nest sites with water availability (water potential) levels that yield high hatching success and/or large hatchlings.

Other than accounts of the fortuitous discovery of egg clutches, the only systematic study of nest site selection in a snake is a descriptive account of 22 natural nests of *Pituophis melanoleucus* (Burger and Zappalorti, 1986). Natural

nests of *O. aestivus* have been found under rocks (Smith, 1961; Mount, 1975), under rotting cardboard (Sabath and Worthington, 1959), and in the insulation of a discarded metal refrigeration panel (Palmer and Braswell, 1976).

METHODS

Two cages (floor dimensions 1.1×2.4 m) similar in design to those used by Plummer (1981) served as arenas in which snakes nested. Eighteen potential nesting sites were in each arena. Each site consisted of a styrofoam box ($18W \times 22L \times 3H$ cm) with a wood top painted black inside. A 1.5 cm hole in the side of each box permitted access to a nesting substrate of vermiculite (Terra Lite, grade 3) with a specific water potential. In each arena, each of six different water potentials (-200 , -300 , -600 , -1000 , -1500 , -2000 kPa) was represented by three boxes positioned randomly in one of three rows. The relationship between water potential and moisture content of the vermiculite was determined with a Wescor HP-115 water-potential-data-system and a C-52 sample chamber. The water potential of the various nest boxes was maintained by weighing each box daily, and replacing water lost by evaporation.

Gravid females were collected from various localities in White County, Arkansas. Snakes were measured (snout-vent length, SVL),

weighed, marked by clipping the ventral scales, and divided between the two arenas. Water and crickets were provided. Nest boxes were checked three times daily for the presence of eggs or ovipositing females. When eggs were found, the mother was identified and eggs were counted, measured (maximum width, length and mass), marked with a permanent felt-tipped pen, and systematically assigned to one of six different incubation treatments. Spent females were removed from the cages and the nest box was replaced with a new one to avoid possible social influences on nest site selection (Plummer, 1981). Because the average clutch size is six eggs (Plummer, 1984), most clutches were represented in each treatment.

Treatments consisted of incubating eggs half-buried in vermiculite at the six water-potentials above in plastic shoe boxes ($15 \times 30 \times 8$ cm) covered with clear plastic held tightly in place with a rubber band. Each of six different water-potential treatments (the same water-potentials as used in the nesting arenas) was represented by a different box. Each egg was weighed at ages 7, 14, 21, 28, and 35 d. Eggs appearing dead (shriveled, dark-colored, moldy) were removed as encountered and examined. Eggs in each treatment were transferred to fresh vermiculite weekly. We used time at pipping rather than hatching as a measure of the duration of incubation because the former is less variable and less likely to be influenced by extraneous factors (Gutzke et al., 1984). As eggs pipped (usually at age 37–39 d), each was measured (width, length) and placed on vermiculite in a separate small covered jar assuring correspondence between egg and hatchling (hatching invariably occurred within a day of pipping). Hatchlings were sexed, measured (SVL), and weighed. Spent females and hatchlings were released in the field or maintained in a laboratory colony. All experiments were conducted in a room maintained on a 14L:10D photoperiod at 28 ± 2 C. We used Sokal and Rohlf (1969) and SPSS Inc. (1986) for statistical analyses.

RESULTS

Nest site selection.—In a previous study (Plummer, 1981), females occasionally layed their clutches in places other than nesting boxes, a behavior attributed to laboratory stress. An unusually high number of snakes exhibited similar aberrant behavior in the initial stages of the present study. The first six snakes and the next

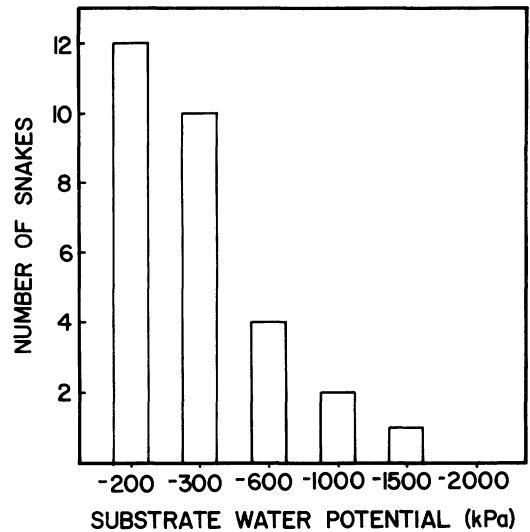


Fig. 1. Frequency of snakes nesting among nest sites differing in available substrate moisture.

8 of 12 snakes either dropped their clutches from elevated portions of the cage or layed them on the open floor. However, of the last 26 snakes, only one did not lay in a nest box. Thus, aberrant nesting behavior decreased with time and was related to a reduction of snake density in the cages. The frequency should have increased with time if the behavior resulted from the accumulation of olfactory cues outside the nest boxes (Plummer, 1981). Some eggs obtained immediately after oviposition from the 15 aberrantly laid clutches were used in the water relations portion of this study.

Snakes appeared to enter all boxes freely and indiscriminately. During routine checking, the vermiculite usually was found disturbed in all boxes. Inactive and active snakes frequently were found in or partially in boxes, and occasionally snakes spent the night in boxes.

Because of low expected frequencies, treatments were pooled into three groups (-200 and -300 kPa, -600 and -1000 kPa, -1500 and -2000 kPa) for chi-square analysis. Snakes discriminated among all boxes when laying, preferring the wettest substrates ($\chi^2 = 28.3$, $df = 2$, $P < 0.001$; Fig. 1). Apparently snakes did not discriminate among boxes containing the most preferred substrates (-200 , -300 kPa) suggesting that there was no position effect among boxes of like water potential ($\chi^2 = 0.35$, $df = 2$, $P > 0.50$). Communal nesting is common in the close confines of the laboratory (Plummer,

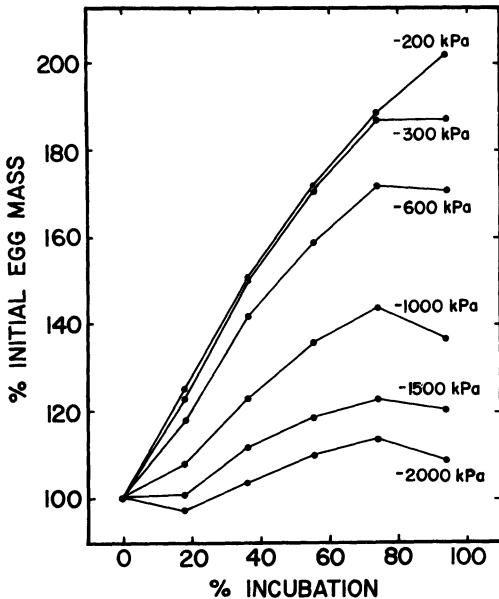


Fig. 2. Time course of the change in percent of initial mass of eggs incubated at various substrate moisture levels.

1981), but frequent checking and replacement of nest boxes usually reduced such social influences on nest-site selection. However, on two occasions two females were found nesting simultaneously in the same box (both occasions in -200 kPa). Assuming that one female chose the box and that the other followed, two snakes can be eliminated from the analysis. Despite this, the hypothesis of random nesting still could be rejected with high confidence ($\chi^2 = 24.9$, $df = 2$, $P < 0.001$).

Change in size of eggs.—As previously found (Plummer, 1984), mean initial mass of the eggs varied substantially, and was weakly related to the SVL of the mother ($r = 0.40$; $N = 36$; $P < 0.01$). After distributing the eggs from each clutch among the different treatments, mean initial mass of eggs among the six treatments did not significantly differ (ANOVA, $F_{5,143} = 0.51$, $P > 0.75$). However, by the end of week 1, differential uptake and/or loss of water among treatments resulted in significant differences in egg masses (ANOVA, $F_{5,142} = 16.91$, $P < 0.001$). Differential water uptake continued throughout incubation (Fig. 2), resulting primarily in an increase in egg width rather than in length (Table 1). The -200 and -300 kPa subgroups, statistically homogeneous throughout most

(80%, Fig. 2) of incubation (Student-Newman-Keuls Procedure), had the highest variances in egg mass each week. Variation in egg mass in these two groups was statistically different from the lowest variance group (-2000 kPa) in weeks 3–5 (F_{\max} , $P < 0.01$ in each case).

Incubation.—The number of days to pipping (incubation) among treatments was examined by analysis of covariance (ANCOVA) using initial egg mass as a potential covariate. Initial egg mass had no effects on incubation ($F_{1,142} = 0.088$, $P = 0.77$). However, the effects of treatment were significant (ANOVA, $F_{5,143} = 27.91$, $P < 0.0001$), but in no clear pattern (Table 1). A Student-Newman-Keuls procedure showed that the -300 kPa treatment, with the lowest mean, was significantly different from all other treatments. The -1500 kPa treatment, with the highest mean, was significantly different from other treatments except -2000 kPa.

Hatching success.—Eighteen of 24 eggs from three clutches died having various degrees of developmental abnormalities in gross morphology (primarily scoliosis). Abnormalities were found in all treatments, the frequency being independent of treatment ($\chi^2 = 0.53$, $df = 2$, $P > 0.40$, pooled treatments). Because of this and the fact that embryonic development of snakes in general and *Ophedrys* in particular is well advanced at oviposition (Shine, 1983; Plummer, 1984), non-treatment causes (e.g., genetic) are suggested. Thus, the three abnormal clutches were eliminated from all treatment effect analyses. Other than in these three clutches, only one other hatchling or dead embryo exhibited obvious developmental abnormalities. Restriction of developmental abnormalities to certain clutches has been observed in eggs of *Elaphe obsoleta* (Lillywhite and Ackerman, 1984). Availability of substrate moisture had no effect on the frequency of developmental abnormalities in *Pituophis melanoleucus* (Gutzke and Packard, 1987).

Sixteen of 166 fertile eggs among the six treatments died during incubation. The frequency of egg deaths was independent of treatment (Table 1; $\chi^2 = 1.3$, $df = 2$, $P > 0.90$, pooled treatments). Overall survival (90.4%) was similar to that obtained in an earlier study (90.0%) using incubation substrates which probably would have measured approx. -200 kPa at the beginning of incubation (1:1 water : vermiculite by weight, Plummer, 1984).

TABLE 1. STATISTICS OF EGGS AND HATCHLINGS IN THE SIX DIFFERENT TREATMENTS. Percent increase in egg width and length was calculated from data taken at pipping, whereas that of egg mass was calculated from data taken at week 5 of incubation. Adjusted mean hatchling lengths (SVL) and masses are adjusted for the covariate, initial egg mass. All dimensions and masses are in millimeters and grams, respectively.

Treatment (kPa)	No. eggs	Mean incubation (days)	Hatching success (%)	% change in mean egg size			Adjusted mean hatchling size		Hatchling mass/initial egg mass
				Width	Length	Mass	Length	Mass	
-200	27	37.8	88.9	28.3	3.1	102.0	130.7	1.30	0.82
-300	28	35.9	92.9	37.2	2.3	86.6	133.2	1.30	0.82
-600	27	38.0	96.3	27.6	2.6	71.0	132.8	1.31	0.83
-1000	26	37.1	92.3	14.2	-0.7	37.2	131.4	1.30	0.82
-1500	28	39.3	85.7	6.0	-3.5	21.3	127.2	1.28	0.80
-2000	30	38.7	86.7	5.7	0.1	8.9	123.0	1.18	0.75

Size of hatchlings.—The effect of treatments on the size of hatchlings was examined by ANCOVA using initial egg mass as a potential covariate. As found in an earlier study (Plummer, 1984), hatchling mass and length (SVL) were affected by the initial mass of eggs ($F_{1,142} = 335.18$, $P < 0.001$ and $F_{1,142} = 105.97$, $P < 0.001$). Treatments also affected size ($F_{5,142} = 5.36$, $P < 0.001$ for mass, and $F_{5,142} = 8.03$, $P < 0.001$ for length), with the driest substrate resulting in shorter and lighter hatchlings (Table 1). Hatchling mass, adjusted for initial egg mass, was not related to change in egg mass (water uptake) ($r = -0.15$, $P > 0.10$) in the treatments with the greatest variances in water uptake (-200, -300 kPa).

DISCUSSION

Our results indicate that the flexible shelled eggs of *O. aestivus* exchange water in response to different moisture availabilities in their environments in a manner typical of most lizards and, presumably, all snakes (Fitch and Fitch, 1967; Packard et al., 1982; Tracy and Snell, 1985; Gutzke and Packard, 1987; Packard and Packard, 1987). Eggs absorbed more water on more moist substrates, and gained water even from the driest substrate, suggesting that water uptake may be required for normal development. Such patterns characterize eggs whose water content at oviposition is insufficient to complete embryogenesis ("ectohydric," Tracy and Snell, 1985).

Because oviparous squamates usually retain eggs in utero for a substantial and variable portion of the total developmental period without suppression of embryogenesis (Shine, 1983), determining precise incubation times among

treatments assumes that all eggs are laid at the same stage of development. Eggs of *O. vernalis* have highly variable and often remarkably short incubation periods (Blanchard, 1933; Stille, 1954), but in *O. aestivus*, viable embryos at oviposition are developmentally similar and eggs have similar incubation periods on constant substrates (Plummer, 1984). In snakes, the duration of incubation has been reported to have no relation to substrate moisture (Packard and Packard, 1987) or to increase on more moist substrates (Gutzke and Packard, 1987), but we did not observe either pattern. In green snakes, as with *Dipsosaurus* (Muth, 1980), moisture level did not have a consistent effect on incubation, yielding data difficult to interpret. Considering our procedures, the possibility of different substrate temperatures confounding the results is highly unlikely. We cannot think of an experimental or biological reason why incubation should decrease only on moderately wet substrates and increase only on moderately dry substrates.

Eggs of different squamates do not necessarily respond to differences in substrate moisture in the same manner. For example, hatchling success is related to substrate moisture in some lizards (Packard et al., 1980; Tracy, 1980; Snell and Tracy, 1985), but not in snakes or in the tiny eggs of *Uta* (Gutzke and Packard, 1987; Packard and Packard, 1987; Ferguson and Snell, in press). Effects on hatchling size have been found in most species (Packard et al., 1980; Snell and Tracy, 1985; Gutzke and Packard, 1987; Ferguson and Snell, in press), but not in all (Tracy, 1980; Packard and Packard, 1987). Some of the differences among studies probably result from differences in experimental procedures, but others probably reflect real differences

among species (Andrews and Sexton, 1981). For example, eggs of *O. aestivus*, *P. melanoleucus*, *Coluber constrictor*, and *Uta stansburiana* apparently tolerate a wide range in substrate moisture with no effect on hatching success (present study, Gutzke and Packard, 1987; Packard and Packard, 1987; Ferguson and Snell, in press), whereas hatching success in *Sceloporus undulatus* and *Callisaurus draconoides* respond to variations of moisture within a range narrower than used in the above studies (Packard et al., 1980; Tracy, 1980).

The squamate egg represents a vulnerable life history stage with limitations that may affect the distribution and abundance of a species (Fitch and Fitch, 1967; Muth, 1980; Porter and Tracy, 1983). Some limitations may be compensated by the selection of appropriate microhabitats for the development of eggs (Muth, 1980; Porter and Tracy, 1983). Snakes do in fact select nest sites from available habitat in nature (Burger and Zappalorti, 1986). Selection of sites with regard to optimal moisture level may affect the survival of eggs and size of hatchlings, and consequently, the fitness of nesting females (Packard et al., 1982; Snell, 1984). Since green snakes preferred to nest on wet substrates, a reasonable inference is that they are under selection for their ability to locate nest sites with moisture levels that do not decrease hatchling size or hatching success. We did not provide saturated substrates which possibly could have negative effects such as infection by fungi (Tracy, 1980) or reduction in oxygen conductance (Tracy, 1980; Black et al., 1984), nor did we provide substrates so dry as to desiccate the eggs lethally. Studies of lizards and turtles have demonstrated higher survivorship by larger animals in the first year (Ferguson and Bohlen, 1978; Swingland and Coe, 1979; Snell, 1984) and field studies of snakes indicate that mortality is greatest during the first year of life (Parker and Plummer, 1987). However, correlates of survivorship in this critical period have not been identified clearly and the potential exists that size could be such a correlate in snakes (Saint Girons and Naulleau, 1981).

In our experiments, hatching success and hatchling size were largely unaffected over a wide range of substrate moisture levels. Only the driest substrate resulted in significantly reduced hatchling sizes. Why then, did snakes not oviposit independently among the remaining substrates? One answer may be that moisture levels are rarely as constant in nature as in our

laboratory. In north-central Arkansas, precipitation decreases and air temperature increases from spring through summer (Plummer, 1983: Table 1). Thus, on the average, water availability should decrease throughout incubation, and soils dry at oviposition could fall to levels affecting hatchling size or hatching success.

Do green snakes nest in wet environments in nature? All natural nests of *Ophedrys* spp. known have been in unexcavated subsurface conditions, such as under or within logs, rocks, vegetation, or manmade materials (Sabath and Worthington, 1959; Cook, 1964; Mount, 1975; Palmer and Braswell, 1976; Sexton and Claypool, 1978). Little can be said regarding the availability of water from these reports. Because all were subsurface, probably the nest atmosphere was saturated or nearly saturated thereby reducing transpirational water loss (Fitch and Fitch, 1967; Lillywhite and Ackerman, 1984). Green snake nests located under "clumps of uprooted weeds and grass" (Sexton and Claypool, 1978) suggest a favorable moisture level. Assuming such vegetation was living, the water potential of the soil probably was greater than -1500 kPa, a level below which soil water is unavailable to plants ("permanent wilting percentage," Bidwell, 1979) and wetter than our driest treatment. On the other hand, "under a board at the edge of the dry dirt road" (Stille, 1954) suggests an unfavorable moisture level. Clearly, further research is needed to determine the natural nesting ecology of reptiles in order to resolve these questions.

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The Rockhead Poacher, *Bothragonus swani* (Teleostei: Agonidae): Selected Osteology, with Comments on Phylogeny

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Selected osteological aspects of the rarely collected, eastern North Pacific agonid *Bothragonus swani* are described, illustrated, and compared to *Xeneretmus triacanthus*, as well as representatives of all agonid subfamilies. The phyletic implications of these characters are discussed and a cladistic hypothesis is advanced. The unusual feature of the cranial pit, a deep cavity bordered by the epiotics, exoccipitals, supraoccipital, and the anteriormost elements of the dorsolateral plate series, is compared to the cranial depression of *Agonopsis vulsa*, *B. occidentalis* and *Odontopyxis trispinosa*. It is proposed that the cranial pit is a mimic of the oscula and siphons of sponges and ascidians that cover the tide pools *B. swani* inhabits, thus affording a reduced level of predation and an enhanced ability to remain hidden from prospective prey.

THE genus *Bothragonus* Gill (Jordan and Gilbert, 1883) is recognized by its greatly compressed body posterior to the insertion of the first dorsal fin; expanded head in the occip-

ital region; small, spineless, terminal rostral plate; small eyes; lack of spines on dermal body plates (many of which bear raised knob-like centers); robust body; and unusual depression in

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