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**Soil Moisture Preference and Water Relations of the Marbled Salamander,
Ambystoma opacum (Amphibia, Urodela, Ambystomatidae)**

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ABSTRACT—Marbled salamanders (*Ambystoma opacum*) in different reproductive and hydration states were tested in a round soil moisture gradient to determine the role of soil moisture in habitat selection. Breeding animals in the gradient chose soil moisture randomly suggesting that substrate moisture is not a significant cue for the placement of the terrestrial nests. Non-breeding animals displayed a mean preference of 74% available moisture. Dehydrated salamanders chose significantly higher moistures (mean of 89%).

Rate of water loss, rate of rehydration and tolerance to dehydration were estimated. The marbled salamander shows no special physiological adaptations to dehydration.

* * *

INTRODUCTION

Water availability is one of the most important factors influencing the behavior and frequently the existence of terrestrial salamanders. Migratory activity of some salamanders is limited to times of rainfall and high humidity (Anderson, 1967a; Baldauf, 1952; Blanchard, 1930; Murphy, 1962; Packer, 1960). Soil moisture may then be considered as a factor in limiting the movements and activities of these organisms. Salamanders have previously been shown to exhibit preferences for soils of certain moistures (Anderson, 1972; Batson, 1965; Jaeger, 1971; Rosenthal, 1957; Taub, 1961; Vernberg, 1955), with physiological state affecting the level of moisture choice (Anderson, 1972; Rosenthal, 1957).

Varying degrees of independence from moisture conditions may occur in amphibians through 1) behavioral adaptations (e.g. soil moisture preference, burrowing, coiling, aggregation), 2) reduced rate of cutaneous water loss, 3) high rate of rehydration when water is available, 4) high tolerance to water losses, and 5) utilization of urinary bladder water. The possession of any of the physiological adaptations (2-5) most certainly influences the organism's behavior.

The marbled salamander, *Ambystoma opacum*, is a terrestrial, lunged salamander, distributed from New England to Florida, west as far as eastern Texas (Anderson, 1967b). Migration to dry or reduced ponds occurs in the autumn, as opposed to the winter or spring migrations of most members of the genus *Ambystoma*. It contrasts again with most other ambystomatids in its avoidance of standing water (Noble and Brady, 1933). Instead of aquatic egg masses, the marbled salamander lays its eggs on land in moist depressions under objects or in tunnels where they are brooded by the female. In early winter the larvae hatch upon flooding of the pond basin.

These facts suggested that *A. opacum* might differ in responses to substrate moisture and/or water economy adaptations from truly terrestrial salamanders such as *Plethodon* and from aquatic breeding *Ambystoma*. This study compares responses in a soil moisture gradient of *Ambystoma opacum* in different physiological states, and additionally relates to this behavior some physiological adaptations for water economy.

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METHODS AND RESULTS

All experiments were performed in a walk-in, constant temperature room set at $13 \pm 1^\circ\text{C}$, with light conditions of 12 hr light and 12 hr dark. Animals were held before testing in 8 oz jars containing wet paper towels, and were not fed. They were collected from sites in Sussex County, New Jersey, and Jasper County, South Carolina.

Soil moisture gradient

Method.—The gradients consisted of 6 cylindrical clear plastic containers, 32.5 cm in diameter and 16.5 cm deep, with fitted covers. Waterproofed wooden separators 3.5 cm high, divided the box into 4 equal-sized compartments. Soil taken from a collecting site for *A. opacum* in Sussex County, N.J., was then added to form a continuous surface. The level of moisture was regulated by the addition of water or dry soil. The soil was mixed and allowed to equilibrate 1-2 days.

The circular nature of the apparatus avoided an "end effect" reported in studies utilizing linear gradients (e.g. Jaeger, 1971; Lucas and Reynolds, 1967). Most animals walked around the perimeter of the chamber, sampling similar areas of the 4 substrates.

Soil moisture was measured by means of electrical resistance readings of Bouyoucos gypsum blocks (Beckman (CEL-WFD) buried in the soil of each compartment of the gradient. A Beckman model BN-2B Bouyoucos moisture meter was used, with soil conditions measured as "per cent available soil moisture." Another measure of water availability is soil moisture tension, which is the force with which water is held by the soil (measured in atmospheres). Both "per cent available soil moisture" and "soil moisture tension" allow direct comparison of different types of soil; the percentage of moisture based on unit weight of soil tells nothing about the availability of that moisture. After excess water is drained from thoroughly soaked soil by gravity, it is considered to be at a soil moisture tension of 0.33 atm, and at 100 per cent available soil moisture. At the low end of the scale of per cent available soil moisture is

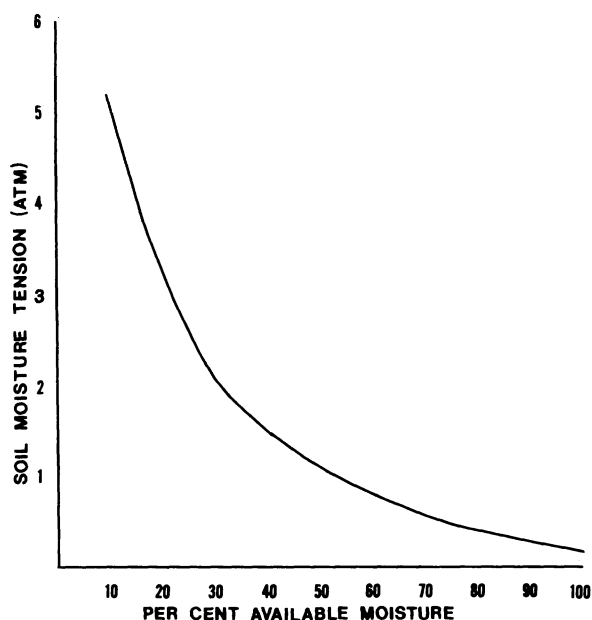


FIGURE 1. Relationship between per cent available moisture and soil moisture tension (from "Operating Manual for Bouyoucos Moisture Meter," Industrial Instruments, Inc., part no. 8455-D, 1962).

the "permanent wilting point" which represents the moisture content of the soil at which plants wilt and die. This point corresponds with a soil moisture tension of approximately 15 atm (Spight, 1967b). Figure 1 displays the relationship between soil moisture tension and per cent available soil moisture.

moistures maintained at approximately 25, 50, 75, and 100%. Animals were tested singly, in the dark, with observations recorded 24 hr after placing the animal in the center of the apparatus (facing random directions). The sex and breeding condition of each salamander was recorded, as was its choice of soil moisture. Animals dehydrated to 69-89% of their original weight were also tested.

Results.—During the breeding season, *Ambystoma opacum* chose soil substrates randomly (Table 1). "Gravid females" were those obvi-

ously egg-laden; "non-gravid females" were those captured during the breeding season but were not evidently carrying eggs. They may have consisted of non-breeding and post-breeding animals. "Nesting females" were those found with eggs, and "breeding males" were those found at egg-laying sites of females.

Both non-breeding dehydrated and control animals chose soil substrates non-randomly (Table 1). Controls chose soil of mean available soil moisture of 74% (SE = 18.9). Dehydrated animals chose mean available soil moisture of 89% (SE = 8.6). The difference between means is significant (1-tailed t-test, $P < .05$).

TABLE 1. Soil moisture preference of *Ambystoma opacum* (from Jasper County, South Carolina, except where noted).

Condition	Sex	N	Kolmogorov-Smirnov 1-sample test
Gravid	f	5	ns
Nesting	f	3	ns
Non-gravid	f	10	ns
Breeding (New Jersey)	m	13	ns
Breeding	m	8	ns
Non-breeding			
Controls	mf	22	$P < .05$
Dehydrated	mf	19	$P < .01$

Rates of dehydration

Methods.—Animals from Jasper County, South Carolina, were rinsed, dried, and their bladders emptied by gentle abdominal pressure. They were then placed singly in flattened fibreglas screen cages approximately 8 X 10 cm and of known weight. These cages were placed on gridded shelves in a walk-in temperature controlled room. Air was circulated by means of fans which are part of the cooling system. Relative humidity ranged between 55 and 84%; data were grouped for animals dehydrating under similar humidities. Salamander and cage were weighed at 2 hr intervals for 2-6 hr. Calculations were made for rate of water loss in mg of water lost per square centimeter of skin surface per hour ($\text{mg cm}^{-2} \text{hr}^{-1}$). Surface area of each salamander was calculated using the formula: surface area (cm^2) = $8.42 W^{0.694}$, where W = weight of the salamander in grams (Whitford and Hutchison, 1967).

Dehydration rate of 35 eggs of *A. opacum* was also recorded. After briefly washing and drying the eggs (at Harrison stages 40-41 from Rugh, 1948), they were placed in one layer in contact with each other on a paper towel in a petri dish and weighed. After 24 hr, at 11-12°C and 65-70% relative humidity, the eggs were weighed again and per cent weight loss calculated.

Results.—Mean rates of water loss for salamanders were calculated for the 6 hr dehydration period (Table 2), since no differences were found between observations at 2, 4, and 6 hrs. Two-tailed t-tests for comparison of mean rate of water loss at the 3 humidities showed all means significantly different from each other. Least squares regression equations were calculated for the relationship between weight of salamanders and rate of water loss (Table 2). There was a high correlation between increasing weight of salamanders and increasing rate of water loss.

The layer of 35 eggs initially weighed 2.30 gm. After 24 hr they had lost 1.22 gm of water, which is 53 per cent of the original weight. All but a few eggs survived this treatment.

TABLE 2. The relationship between body weight and rate of water loss for *Ambystoma opacum* at three humidities.

Humidity (Range)	N	Mean Rate of Water Loss (mg/hr) (St. Error)	Least Squares Regression Equation*	r	P	s ²	S _b	Mean Wgt (Range)
86 (85-87)	9	105.94 (10.4)	$y = 1.41 + .94x$.8391	$P < .01$.0063	.2283	4.49 (2.59-6.46)
66 (62-78)	9	217.62 (16.7)	$y = 1.93 + .61x$.7524	$P < .01$.0056	.2015	4.73 (2.36-6.46)
57 (55-61)	12	246.0 (32.3)	$y = 1.93 + .74x$.5837	$P < .05$.0129	.3629	4.74 (3.40-6.46)

*y = log rate of loss (in milligrams per hour); x = log body weight (in grams); r = correlation coefficient; s² = the estimated variance of the points about the line; S_b = the standard error of the estimate of the slope.

Rates of rehydration

Methods.—Animals exposed to circulating air as described for dehydration experiments were placed in closed jars overnight, weighed again, then placed singly in jars with 1-2 cm of water—enough to contact the entire ventral surface and sides but not enough to totally submerge the animal. They were weighed after 2 hr and rates of rehydration calculated.

Rate of rehydration was also computed for salamanders released into the soil moisture gradient after dehydration.

Results.—Rate of rehydration was found to correlate with the dehydration deficit of the salamander. The least squares regression for this relationship is $Y = -7.6 + .97x$, where Y is the rate of water uptake in $\text{mg cm}^{-2} \text{hr}^{-1}$, and x is the dehydration deficit ($r = .8628$, $P < .01$). The mean rate of water uptake for the 2 hr observation period was $5.4 \text{ mg cm}^{-2} \text{hr}^{-1}$ for 8 animals with a mean weight of 4.68 gm, and a mean dehydration deficit of 13.4%. The mean rate of water uptake for 5 salamanders that died from dehydration effects was $7.0 \text{ mg cm}^{-2} \text{hr}^{-1}$, which was not significantly different from the water uptake of live animals (2-tailed t-test).

After 24 hr in the soil moisture gradient, salamanders found on soil of 100 per cent available moisture, and showing a net increase in weight had a rehydration rate of $8.5 \text{ mg cm}^{-2} \text{24 hr}^{-1}$ (mean weight = 4.6 gm, mean dehydration deficit = 22.5%, $N = 11$).

Tolerance to water loss

Method.—Salamanders were dehydrated by exposure to circulating air after removal of bladder water. They were observed until cessation of buccal movements. This approximates the critical activity point (CAP) established as an ecological lethal point by Littleford, Keller and Phillips (1947). The per cent weight lost at this point was then calculated.

Results.—Mean weight loss due to dehydration at CAP was 29.0% of initial weight ($SE = .92$, $N = 10$). As the CAP was approached, animals became more active, then became quiescent. The normally white or silvery pigment darkened to a pale gray color, the toes became stiff and the skin appeared dry. Often the animals coiled their tails around the body. All animals survived the treatment.

DISCUSSION

Salamander orientation.—The cues used in migratory orientation are not well understood for salamanders. Homing to specific portions of a stream has been shown in *Taricha rivularis* (Twitty, 1959, 1961) with olfaction playing an important part in this ability (Grant, Anderson and Twitty, 1968). Sun compass orientation in conjunction with the sense of smell was suggested as the mechanism involved in homing orientation of *Taricha granulosa* (Landreth and Ferguson, 1967). Shoop (1968) found that *Ambystoma maculatum* return and leave the breeding pond by the same path. He believed this was accomplished through an "imprinted cue system obtained as they left the pond as juveniles." Shoop and Doty (1972) suggest that since *A. opacum* migrates to often-times dry basins, while *A. maculatum* enters water filled pond basins, if both species are using the same cues to orient to the breeding site, these cues are likely not concerning the pond water.

That precipitation and high humidity are important factors influencing migration of salamanders has been demonstrated (Baldauf, 1952; Bishop, 1941; Blanchard, 1930; Murphy, 1962; Packer, 1960; Wright and Allen, 1909). Additionally, moisture conditions have been shown to greatly influence the local distribution of salamanders (Cunningham, 1960; Hairston, 1951; Heatwole, 1962; Jaeger, 1971; Rosenthal, 1957; Stebbins, 1954; Taub, 1961). However, the importance of the presence of a gradient of moisture to ponds or streams is not known. Rose (1966) proposed that it was unlikely that female *Desmognathus auriculatus* displaced at right angles to a stream were responding to a moisture gradient when homing toward their nests because of the number of puddles found throughout the study area. However, Anderson (1972)

found breeding adults of *Ambystoma macrodactylum croceum* to select higher soil moisture than non-breeding adults. He suggested that this orientation may assist these animals in locating the breeding area.

There are probably two factors involved in the response toward water in salamanders. One, termed "water drive" by Chadwick (1940) is a taxis—"a directed orientation reaction" (Fraenkel and Gunn, 1961) toward water. The second orientation is in the form of a kinesis, which is "variation in intensity of activity which is dependent on the intensity of stimulation and not on the direction of stimulation" (Fraenkel and Gunn, 1961). Heatwole (1962) described this kinetic response in a humidity gradient where he found activity of *Plethodon cinereus* to increase at low humidities, "resulting in the eventual discovery of the moister environment." High activity was evident in this study for *A. opacum* at all humidities as they approached their CAP.

A number of species of salamanders have been shown to exhibit a soil moisture preference (Anderson, 1972; Batson, 1965; Jaeger, 1971; Rosenthal, 1957; Taub, 1961; Vernberg, 1955). Non-breeding *opacum* also chose soils of particular moisture content. All species studied in the above experiments except for *A. macrodactylum* (Anderson, 1972) are terrestrial salamanders (including *A. opacum* adults). Thus, these experiments describe a kinesis for optimal moisture substrates. This kinesis, which is heightened in dehydrated animals (Rosenthal, 1957, and this study) is a behavioral adaptation for maintaining body water equilibrium. The response for soils of high moisture content of *A. m. croceum* during the breeding season may be a combination of the kinesis and the taxis (water drive) which is affected by hormonal state (Chadwick, 1940, 1941).

Graham (1971) suggested that soil moisture among other factors may be an indicator of the optimal placement of nests. Since only non-breeding *Ambystoma opacum* chose soil moistures non-randomly, other factors are indicated as being more important in orientation to breeding habitats.

An alternate hypothesis is that after initial orientation to the pond or dry pond basin, egg laying takes place in any available site (in tunnels, under objects, under vegetation mats). Physiological and behavioral adaptations may then act toward the survival of eggs until permanent inundation.

Water relations.—Experiments on the water economy of *A. opacum* were done to investigate whether there are any adaptations allowing greater independence from moisture conditions.

The rates of water loss found for *A. opacum* (Table 2) are difficult to compare with rates found by other investigators. Conditions vary with respect to temperature, humidity, and rate of air flow. At about 66% relative humidity, water loss was $8.8 \text{ mg cm}^{-2} \text{ hr}^{-1}$ ($N = 9$, mean wgt. = 4.73 gm). At a similar humidity, but at 20°C, Spight (1968) found the rate of water loss to be $4.79 \text{ mg cm}^{-2} \text{ hr}^{-1}$ ($N = 7$, mean wgt. = 9.33 gm). Thus differences in temperature, mean weight, and air circulation all probably account for the large difference observed. Although one *A. opacum* lost water more slowly than any other salamander in Spight's (1968) study the average rate of 214 mg hr^{-1} (similar to our results of 217.6 mg hr^{-1}) does not differ much from other species of the same size. The range of published water loss rates (considering surface area) begins at $3 \text{ mg cm}^{-2} \text{ hr}^{-1}$ for *Desmognathus fuscus* and *Plethodon glutinosus* (Spotila, 1972). The highest rate is for *Plethodon cinereus serratus* at $10 \text{ mg cm}^{-2} \text{ hr}^{-1}$ (Spotila, 1972). MacMahon (1964) has shown that rate of water loss of several species of plethodontid salamanders is correlated with the body proportions of the animals.

The eggs of *A. opacum* were found to dehydrate quite rapidly upon exposure to air. However, the tolerance of these eggs to desiccation has been shown to be extensive. Noble and Brady (1933) placed eggs on dry packed sand in closed containers. After one month approximately 40 per cent had survived; about 3% survived an additional two months.

Rates of rehydration for *Ambystoma opacum* were not extremely high; the mean rate of $5.4 \text{ mg cm}^{-2} \text{ hr}^{-1}$ is similar to Spight's (1967a) estimate of $4.66 \text{ mg cm}^{-2} \text{ hr}^{-1}$. Animals with high dehydration deficits were found to gain water at a faster rate. This is due to the increased

osmotic gradient across the skin resulting from the increased concentration of body fluids. An *A. opacum* dehydrated 20% was calculated by Spight (1967a) to have increased its internal fluid osmotic concentration to 133 per cent of its original value. Rates of rehydration for salamanders are quite low compared to those for anurans. The highest rate for salamanders are $9.58 \text{ mg cm}^{-2} \text{ hr}^{-1}$ for a *Plethodon jordani* with a dehydration deficit of 13.9% (Spight, 1967a) and $8.5 \text{ mg cm}^{-2} \text{ hr}^{-1}$ for an *Aneides lugubris* with a deficit of 20% (Cohen, 1952, calculated by Spight, 1967a). Rates of anuran rehydration range from a low of $3.86 \text{ mg cm}^{-2} \text{ hr}^{-1}$ for *Xenopus laevis* with a deficit of 11.6%, to the rate of $140 \text{ mg cm}^{-2} \text{ hr}^{-1}$ for *Hyla moorei* with a deficit of 25% (Main and Bentley, 1964, calculated by Spight, 1967a). The difference between rehydration rates for frogs and salamanders is due to the fact that salamanders do not show an increase in skin permeability as a response to neurohypophyseal hormones as frogs do (Alvarado and Johnson, 1965; Bentley, 1963).

Rehydration rates for dehydrated *A. opacum* placed in a soil moisture gradient proved to be quite low ($8.5 \text{ mg cm}^{-2} \text{ 24 hr}^{-1}$). This is probably due to the time spent in locating the higher soil moistures. Thus soil moisture probably was not optimal over the 24 hour period. However, this rate may be more meaningful than rehydration rates in water, since this animal seldom enters standing water. Burrowing would probably increase the rate of rehydration by increasing the surface area in contact with the soil. Animals in the gradient did not burrow, but displayed a posture similar to that reported by Gehlbach, Kimmell and Weems (1969) for dehydrated *Ambystoma tigrinum*. The legs of the salamanders were spread at right angles to the body, with the ventral surface of the trunk flattened against the soil for maximal contact. This posture was also described as the "water absorption response" of dehydrated frogs (Johnson, 1969; Stille, 1958).

Tolerance to loss of body water in amphibians has been correlated with habitat preference and the degree of terrestriality (Littleford, Keller and Phillips, 1947; Ray, 1958; Schmid 1965; Thorson, 1955; Thorson and Svihla, 1943). In anurans, the largest mean losses tolerable have been reported as 47.9% for *Scaphiopus holbrooki* (Thorson and Svihla, 1943) and 45% for *Hyla coerulea* (Main and Bentley, 1964). The tolerance limits for salamanders range from 7.4% for *Rhyacotriton olympicus* (Ray, 1958) to 43.8% for *Plethodon richmondi shenandoah* (Jaeger, 1971) and to over 45% for *Ambystoma tigrinum* (Alvarado, 1972). *Ambystoma opacum*, with a tolerance limit of 29.0% loss of body weight in water (Spight (1968) found 30.1%) thus has only a moderate ability to survive dehydration.

Studies on the ability of salamanders to survive desiccation are usually performed on animals with bladders emptied, since water reabsorption occurs at this site, and bladder size varies. Perhaps survival time of dehydrating salamanders with full bladders would be an ecologically more meaningful measure of adaptiveness to dry surroundings. Urinary bladder capacity ranges widely in salamanders. *Salamandra maculosa* has the greatest reported capacity at 34% of total body weight (Bentley and Heller, 1965). *Ambystoma tigrinum* can retain 20% of its body weight in bladder storage (Bentley and Heller, 1964), whereas *Ambystoma opacum* may retain 12% (Spight, 1967a). Lower limits are found in *Triturus cristatus* at 2% (Bentley and Heller, 1964) and *Desmognathus fuscus* at 1.7% (Spight, 1967a). *Ambystoma opacum* is again moderately adapted for the storage of bladder water.

Although *Ambystoma opacum* is considered one of the more terrestrial members of the genus because of its terrestrial mode of reproduction, the species shows no special physiological adaptation to dehydration. It is average among salamanders with respect to water loss, rehydration rate, and bladder capacity. Non-breeding adults selected substrates of high moisture content, avoiding both low and saturated substrates. This behavioral trait in conjunction with a negative phototaxis (Marangio, 1975) is probably the major adaptation in its water economy.

SUMMARY AND CONCLUSIONS

Breeding *A. opacum* randomly choose soils of different moisture content in a soil moisture gradient suggesting that substrate moisture is not a significant cue for the placement

of the terrestrial nests. Cues used for finding sites for courtship and egg laying are not known. Salamanders may choose sites randomly after homing to the pond basin and then rely upon other behavioral and physiological adaptations to ensure survival of progeny. Nesting behavior of female *A. opacum* allows for a supply of moisture to the eggs and also probably allows some protection from predators. These nesting females may survive prolonged periods with their eggs through combination of moderate tolerance to water loss and an intermediate capacity for water storage in the bladder.

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