AN ABSTRACT FOR THE THESIS OF

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Title: Temperature-Mediated Characteristics of the Dusky Salamander (*Desmognathus fuscus*) of Southern Appalachia

Abstract approved: Lynnette Sievert

Desmognathus fuscus is a nocturnal plethodontid salamander of moist forest floor and stream banks of Appalachia and the Eastern United States. This study addresses the question of temperature selection and its accompanying variables in a terrestrial species. Using a thermal gradient in the laboratory, I found no preferred temperature for fasting or postprandial *D. fuscus*. I compared the rate at which *D. fuscus* cooled and heated with that of a similarly sized tube of physiological saline and found no significant difference, which indicates that *D. fuscus* exhibits no physiological control of its heating and cooling rates. I determined the desiccation rate at 16 °C and 26 °C and found a significantly higher rate of desiccation at 26 °C, which indicates that the only likely control over desiccation is behavioral. All of these findings fit very well with what is known of the life history of *D. fuscus* and with how this species fits into the range of life history traits found throughout this genus.

TEMPERATURE-MEDIATED CHARACTERISTICS OF THE DUSKY SALAMANDER (*Desmognathus fuscus*) OF SOUTHERN APPALACHIA

A Thesis

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by

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PREFACE

The data and results from my thesis project will be submitted to the Journal of Thermal Biology for publication. My thesis is, therefore, written in the style of that journal.

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INTRODUCTION

Temperature and moisture are controlling factors in the environment of amphibians. Water balance is critical in maintaining a moist skin for respiration and temperature determines the rate of chemical reactions that govern physiological processes. Over a broad range of tolerable body temperatures (T_b), reaction rates of processes like digestion and metabolism increase with increasing T_b (Hutchison and Dupré, 1992 and references therein). Thermoregulation in nocturnal salamanders may allow increased growth and digestive rates as well as increased speed and foraging efficiency (Brattstrom, 1963; Rome et al., 1992).

There is a potential conflict between the moisture requirements and temperature requirements of amphibians. An amphibian that moves out of its moist hiding place to seek warmer temperatures may not be able to return to moisture before it desiccates. This, in part, may be why little behavioral thermoregulation is observed in amphibians (Hutchison and Dupré, 1992).

Presumably, salamanders in the field often accept available body temperatures instead of showing temperature preferences (Brattstrom, 1963; Feder and Pough, 1975; Hutchison and Dupré, 1992), although some behavioral observations in the field may be due, in part, to temperature preference (Sievert and Andreadis, in review). When presented with laboratory conditions where thermoregulation is possible, both aquatic and terrestrial salamanders show temperature preferences (Dupré and Petranka, 1985; Hutchison and Hill, 1976; Hutchison and Spriestersbach, 1986; Sievert and Andreadis, in review). Furthermore, many ectotherms exhibit an endogenous circadian rhythm of preferred temperature (Reynolds, et al., 1978; Sievert and Hutchison, 1988; Hutchison and Spriesterbach, 1986; Sievert, 1991). However, in some species of amphibians no circadian cycles of thermoregulation have been observed (Lillywhite, 1971; Sievert, 1991).

Few, if any, studies have shown nocturnal salalmanders behaviorally thermoregulating in their natural conditions even though opportunities for thermoregulation do exist (Sievert and Andreadis, in review). Large rocks that have been in direct sunlight during the day will remain above ambient temperature long into the night. Rotting vegetation also can provide a source of heat. Though similar problems exist for nocturnal reptiles, there are examples in the literature of nocturnal reptiles selecting preferred temperatures. For example, some nocturnal reptiles thermoregulate in the field by basking on warm surfaces or by sitting near light bulbs on buildings (Bustard, 1967; Dial, 1978; Werner, 1990). Further, nocturnal geckos (*Gekko gecko*) show a distinct diel cycle of thermoregulatory behavior, selecting higher body temperatures at night than during the day (Sievert and Hutchison, 1988).

Factors that may influence the decision to thermoregulate include transcutaneous evaporation, desiccation, heating and cooling rates, and the degree of metabolic advantage that may be achieved at an elevated temperature. While lunglessness in the plethodontid salamanders does not restrict the uptake of oxygen from the air, thin skin, across which oxygen can diffuse into the blood, is necessary (Feder, 1976). Terrestrial amphibians, especially the lungless salamanders, must have a very thin, well vascularized skin in order to facilitate effective gas exchange. Skin that presents no barrier to gas exchange is, most likely, at the same time ineffective in restricting water loss (Feder and Burggren, 1985; Lillywhite et al., 1998). An absence of resistance to water loss by evaporation has been shown in several amphibians (Shoemaker et al, 1992 and references therein). While mechanisms such as vasoconstriction or the use of water-proofing substances could reduce the amount of water lost to evaporation (Shoemaker et al., 1992), in a lungless salamander this would also mean a fatal reduction in respiration (Spotila and Berman, 1976; Shoemaker and Nagy, 1977; Feder and Burggren, 1985). In fact, none of the amphibians that use waterproofing to reduce water loss are plethodontids.

Permeable skin allows for rapid water uptake as well as water loss. This is essential in a terrestrial amphibian that does not drink water even when dehydrated (Shoemaker and Nagy, 1977; Shoemaker et al., 1992). A desiccated plethodontid salamander must return to either water or a moist area to re-hydrate.

Assuming that an increase in temperature gives the animal some advantage metabolically and in locomotor ability, what is the cost in water loss at that increased temperature? Does the benefit ever outweigh the cost? Amphibians seek shelter and use other behavioral controls to slow water loss (Shoemaker et al., 1992). Tree frogs that do not have specialized skin for preventing water loss seek cooler temperatures during periods of heat and drought in an effort to limit water loss (Lillywhite et al., 1998). Many amphibians can tolerate some osmotic imbalances and can recover homeostasis quickly when water becomes available (Shoemaker and Nagy, 1977; Shoemaker et al., 1992), but the amount of water that a 3.5 g animal, the average mass of *D. fuscus*, can stand to lose is still minuscule.

Feeding has been shown to have an effect on temperature selection in some amphibians (Lillywhite et al., 1973) but not in others (Mullens and Hutchison, 1992). Fitzpatrick et al. (1972) found that both *D. fuscus* and *D. ochrophaeus* maintained a temperature-independent metabolism over the range of temperatures normally experienced during activity (10-15°C, normal ground temperatures at night). Given that oxygen consumption , and therefore, metabolism, of temperate zone plethodontid salamanders are not affected as severely by low temperature as for other amphibians (Feder, 1976), it makes the quest for higher temperatures less important in these salamanders.

Salamanders of the genus *Desmognathus* are spatially distributed across a habitat continuum from stream dwellers to terrestrial occupants of the forest floor and trees (Hairston, 1949; Organ, 1961; Hairston, 1980). Hairston (1980) and Tilley (1968) have presented evidence that one of the most important interspecific interactions in streamside salamander communities is predation, which drives the smaller species toward a terrestrial habitat. Later, Hairston (1986) presented more evidence that predation is probably the predominant interspecific interaction in the guild and presented evidence against interspecific competition as the driving force for the adaptive radiation observed in the *Desmognathus* complex. The presence of predatory larval *D. quadramaculatus*, a stream dwelling member of the *Desmognathus* complex, has been shown to have significant effects on the smaller species of the stream community (Beachy, 1997; L. Sievert, pers. comm.). Competition between *D. fuscus* and *D. monticola* has been noted and *D. fucus* stays farther from the stream bed and less active when the larger and more aquatic *D. monticola* is present (Keen, 1982; Sievert and Andreadis, in review). Similar relationships among the plethodontid species inhabiting the forest-stream ecotone in southwestern Virginia have been shown by Jaeger et al. (1998). The decrease in size of *Desmognathus* species as they inhabit areas that are increasingly terrestrial has been explained in terms of heavy predation on the smaller species in and near the streamside habitats by the larger species, which provides selective pressure for becoming more and more terrestrial as species size decreases (Hairston, 1986). The relationship between body size and habitat may also be due to adaptation to the size and availability of cover objects and the nature of the substratum along the stream to forest gradient (Bruce, 1996; Grover, 2000).

While behavioral thermoregulation may be found in the more aquatic species of the *Desmognathus* genus, is this likely to be a strategy that would have developed in the more terrestrial *D. fuscus*? The first objective of my study was to test my hypothesis that there should not be selection for a preferred temperature in this species, whether fasted or post-prandial. Is it possible that the more terrestrial species can maintain some control over the rate at which it heats and cools or the rate at which water is lost cutaneously? The second objective of my study was to test the hypothesis that there is no physiological control over heating and cooling rates in *D. fuscus* nor is there control over the rate of desiccation.

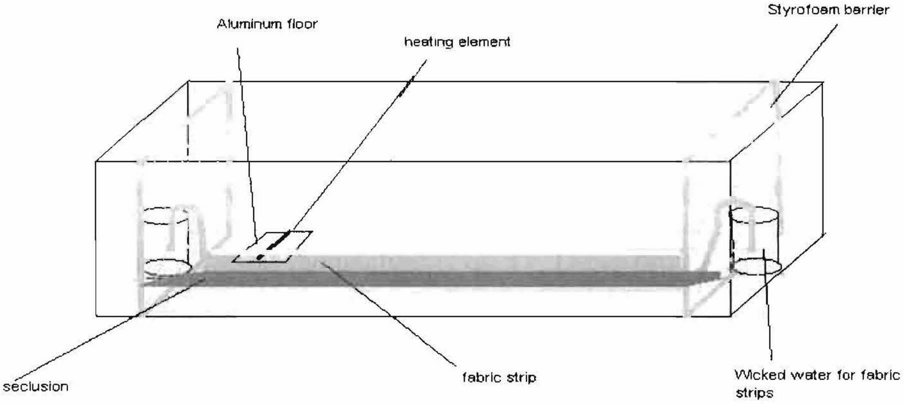
MATERIALS AND METHODS

I collected ten *Desmognathus fuscus* in Blount Co., TN. The salamanders were maintained in the laboratory for eight weeks prior to experimentation to allow them to habituate to their surroundings, to ensure that they were eating and healthy, and to allow them to become familiar with human handling. Spotila (1972) determined that the mean preferred temperature of *Desmognathus* over a 24 h period ranged from 17.4°C to 25.6°C. Therefore, I maintained the salamanders at an approximate temperature of 20 ± 1 C with a 12:12 LD photoperiod with scotophase centered at 2400 hr. The relative humidity in the room fluctuated between approximately 33% and 71%, depending on the outside weather. The salamanders were housed individually in clear round (18.5 cm diameter) plastic containers with damp paper towels providing both seclusion and moisture. The salamanders were fed nymphal crickets or fruit flies three times per week.

Preferred Temperature

Three thermal gradients were constructed for the experiment. Each gradient consisted of a wooden box with an aluminum floor (Fig. 1). The gradients were housed in a walk-in environmental chamber with the temperature at 8 ± 1°C and the light cycle on a 12:12 LD photoperiod, the same as used in habituation. A heating element under the warm end of the aluminum floor of the gradient kept the warm end of the gradient at 30 ± 1°C. The gradient used in this experiment ranged from 10 ± 1°C to about 30 ± 1°C along its 156 cm length, which gave the salamanders access to a 20°C range in substrate temperatures. To provide adequate moisture at all temperatures in the gradient, a strip of moist cloth was placed along the middle of the thermal gradient. The strip was kept

Figure 1. Apparatus for establishing a thermal gradient. The floor temperature ranged from 10 ± 1 to 30 ± 1°C with both shelter and moisture provided along the entire length.


Aluminum floor
heating element
Styrofoam barrier
seclusion
fabric strip
Wicked water for fabric strips

moist by wicking it into containers filled with aged water at each end of the gradient chamber. The water containers were separated from the rest of the chamber by a styrofoam wall. This kept the salamander from getting into the water containers. Concealment from predators may be a confounding factor in the choice of available habitat (Keen, 1982). To control for this factor, a strip of thin Styrofoam was placed along the length of the gradient at a 45° angle to the floor, to create a crevice that allowed the salamanders to conceal themselves (Fig. 1). These provisions allowed the salamanders to choose either a dry or moist substrate and concealment at any temperature along the gradient.

Each of ten salamanders had its substrate temperature preference tested two times: The first time after fasting for one week and the second time right after feeding. Each salamander was introduced to the gradient the afternoon before the experimental period, which allowed the salamander to explore and become habituated to its new environment. From 1200 h until 2400 h on the day of the experiment, substrate temperature under the salamander's abdomen was measured at 2 h intervals. This yielded seven substrate temperatures per salamander. My objective was to measure the substrate temperature preference rather than salamander body temperature.

I used a 2-way repeated measures Analysis of Variance (ANOVA) to determine if substrate temperature preference differed between fed and fasted salamanders and if preference varied over the seven time periods. The interaction term showed whether or not the pattern of temperature selection over time differed between the two groups. Sample size was the number of individuals (ten), not the number of observations on all individuals (Hutchison and Dupré, 1992, Hutchison and Maness, 1979) I used a Student-Neuman-Keuls pairwise comparison to determine which hours of the day *D. fuscus* selected significantly different substrate temperatures.

Heating and Cooling Rates

I determined heating and cooling rates of eight of the salamanders in the laboratory by placing eight individual animals in a temperature-controlled chamber and monitoring the temperature of the salamander via a thermocouple placed 1 cm into its cloaca and attached to a Kane May (KM 1242) data logger. I weighed each salamander and then rank-ordered their masses from smallest to largest. I did not use two of the salamanders that were available because of their extremely large size. I calculated the mean mass of every two salamanders that I used in the rank-ordered list (Table 1). Four pieces of dialysis tubing filled with physiological saline matched to the masses calculated above and thermocouples inserted in the middle of the tube were placed in the temperature-controlled chamber with the salamanders. Temperatures for the controls were recorded at the same intervals and at the same time as those of the salamanders. One dialysis tube served as the control for two similarly sized salamanders.

The test animals were fed 24 h before the experiment. Just before the experiment began, each salamander was secured in a small tube made of netting to hold the salamander securely in one position, and prevent movement. A thermocouple was inserted into the cloaca of the animal and secured with a small piece of tape. The salamanders were placed on a piece of plastic canvas over a wet paper towel in a sealed container. This allowed the animal to be almost completely in contact with the surrounding air in the container and controlled for changes in humidity throughout the experiment. The wires of the thermocouples were secured with tape to the side of the container. The temperatures of the salamanders were affected slightly by handling but soon returned to ambient. The temperatures were allowed to stabilize at the laboratory temperature (25 ±1 °C) and then the animals and the control tubes were placed in the cold temperature (1 °C) chamber. Temperatures were recorded at 1 min intervals within the range of 20 to 10°C . The entire group was then removed from the cold chamber and temperatures were recorded at 1 min intervals from 10 to 20°C.

Heating and cooling data were treated separately. Mean times for cooling and heating from the four control tubes were compared to overall mean times of the eight salamanders by using an un-paired t-test. Mean times for cooling vs heating were compared by using a paired two-sample t-test.

Desiccation Rate

Desiccation rate was determined at 16 ±1 °C and 26 ±°C and 33% relative humidity. Temperature and relative humidity were measured with a digital thermometer/hygrometer. Salamanders were fed 24 h before the beginning of the experiment. Prior to the experiment, the salamanders were weighed and moved into individual tubes made of plastic canvas. Masses of the salamanders were recorded at 15 minute intervals until the animals had lost 10% of their original body masses, 2% below the amount at which *D. ochrophaeus* has been shown to suffer reduction in normal body function and 2% above the amount of loss at which they have been shown to give up foraging (Feder and Londos, 1984). As each salamander passed the 10% point, the 15 min interval during which it reached that point was recorded and the animal was released from its tube back into its cage where it could immediately re-hydrate and rest. The salamanders were allowed to rest and were fed on their regular schedule for one week prior to measuring desiccation rate at 26°C. A paired t-test was used to compare dehydration times at 16°C and 26°C.

RESULTS

Preferred Temperature

The mean selected temperature for ten *D. fuscus* was 16.8 ± 4.5°C for fed salamanders and 17.9 ± 4.6°C for fasted salamanders. Substrate temperature selection (Fig. 2) did not differ significantly between fed and fasted salamanders(df = 17, F = 0.759, $P = 0.3966$) but temperature selection over time did vary (df = 6, F = 2.549, $P = 0.0247$). The interaction term showed that the curves (Temp. vs Time) between the two groups (fed and fasted) were not significantly different (df = 6, F = 1.044, $P = 0.4018$). Body temperatures at 2200 h (Fig. 2) were significantly lower than at 1200 h ($P = 0.043$).

Heating and Cooling Rate

Comparison of the heating and cooling rates between the salamanders and the control tubes of water showed that the heating and cooling rates of *D. fuscus* do not vary significantly with those of the control tubes of water. Data for mass and heating and cooling times are shown in Table 1. Means from the salamander data in each treatment did not differ significantly from the controls of each treatment (cooling, d.f. = 7, t = 2.365, $P = 0.814$; heating, d.f. = 7, t = 3.182, $P = 0.353$, d.f. = 7). At no point in the experiment did the salamanders exhibit any physiological control over their heating or cooling rates.

Desiccation Rate

Desiccation at 33% relative humidity at 26°C occurred significantly faster than at 16°C (Fig. 3; d.f. = 9, t = 5.284, $P = 0.0005$,). At 26°C the mean time for a water loss equal to 10% of body weight was 69 ± 13 min. At 16°C the mean time for a water loss equal to 10% of body weight was 102 ± 14 min.

Figure 2. Temperature selection over time for fed and fasted *D. fuscus*. Filled squares represent fed animals. Open circles represent fasted animals. Vertical bars show one SE of the mean.

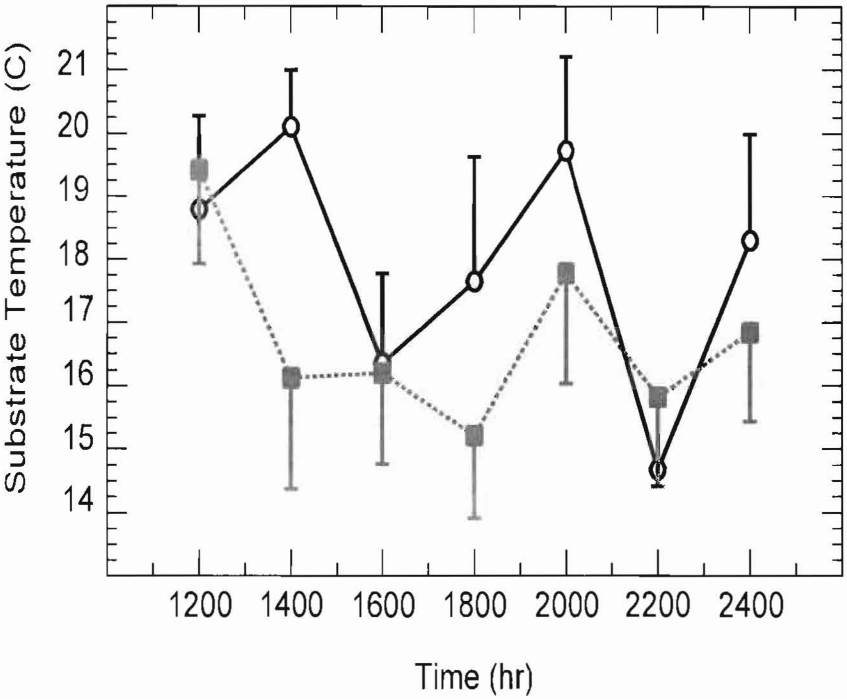
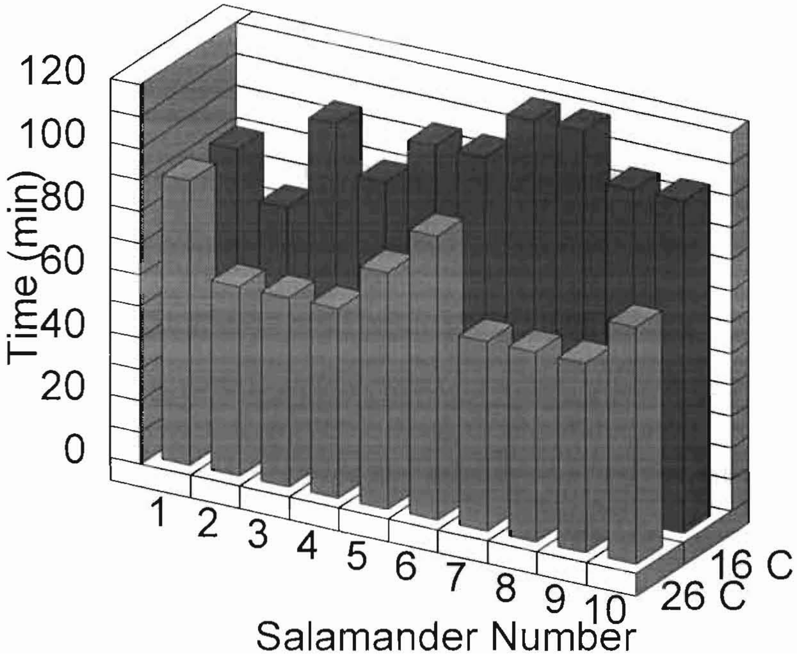

Substrate Temperature (C)
21
20
19
18
17
16
15
14
1200
1400
1600
1800
2000
2200
2400
Time (hr)

Table 1. Cooling (from 20 to 10°C) and heating (from 10 to 20°C) rates for *Desmognathus fuscus* and experimental controls.

Salamander No.	Mass	Cooling time	Heating time
7	2.7	12	12
2	2.85	13	12
4	3.06	14	13
8	3.32	12	13
3	3.79	16	14
1	3.8	16	13
9	3.88	15	13
10	3.9	16	14
Tube No.			
7-2	2.78	12	13
4-8	3.19	14	12
3-1	3.8	16	15
9-10	3.89	14	17

Figure 3. Desscation rates at 16 and 26 C in *D. fuscus*. Light grey bars represent individual times at 26 ° C. Dark grey bars represent individual times at 16 ° C.


120
100
80
60
40
20
0
Time (min)
1
2
3
4
5
6
7
8
9
10
Salamander Number
16 C
26 C

DISCUSSION

Physiological thermoregulation in amphibians is most likely limited to vasoconstriction and vasodilation, which may affect the rates at which they heat and cool. However, comparisons of heating and cooling rates in many anurans have revealed no significant physiological control. Some control over cutaneous gas exchange has been demonstrated, however (Hutchison and Dupré, 1992 and references therein).

My data indicate that *D. fuscus* exhibits no physiological control over its rates of heating and cooling. Salamander heating and cooling rates did not differ from the rates of heating and cooling in the similar-sized tubes of physiological saline. Higher body temperatures may be advantageous as digestive rate and muscle performance are increased at higher temperatures (Brattstrom, 1963; Rome et al., 1992; Shealy, 1975). Assuming an advantage to increased body temperature, the only way in which these salamanders might raise their body temperature is by behavioral thermoregulation. Opportunities to thermoregulate in the field do exist for these animals even though such opportunities may be slightly reduced in the nocturnal environment. Nocturnal salamanders could potentially encounter surfaces where they might seek to elevate their body temperatures (Feder, 1982; Hutchison and Dupré, 1992; Sievert and Andreadis, in review).

My data did not show a pattern of temperature selection in either fed or fasted *D. fuscus*. Even though precise selection did not occur predictably over time, the overall mean temperatures for the groups fell within the range of expected temperature preference for this species (Spotila, 1972). The general trend of the individual salamanders in the gradient was to pick a spot and stay there through most of the experiment. The temperatures of the chosen places in the gradient varied widely between individual salamanders.

The significant temperature difference found at 2200 h most likely reflects a change in activity and not a real change in temperature selection. This was the time of night when I observed salamanders moving about the most. Since these are nocturnally active animals, this is not surprising. In many cases at this time of night the salamanders were found up on the wall of the gradient and even up by the top where they were trying to escape. The temperature in this case was predictably colder but probably not a factor in what the salamander was doing. The walls of the gradient did not vary in temperature. The walls were consistently at the lowest temperature in the box, approaching that of the temperature in the cold chamber where the apparatus was housed.

The major environmental factor critical to terrestrial salamanders is the availability of water (Heatwole, 1983). The hydric constraints encountered by foraging terrestrial salamanders are severe. Littleford et al. (1947) determined that a water loss of 18-26% of the salamander's body mass is lethal to the animal. Foraging ability and locomotor performance is affected at about 12% dehydration. However, Feder and Londos (1984) found that *D. ochrophaeus* voluntarily abandoned foraging when it encountered a dehydration deficit of 3 to 8% of their body mass. This may indicate an unwillingness to risk encountering problems that would delay their return to their moist "safe" area. Such problems might include, but are not limited to, predator avoidance, competition, and prey item movement.

Evaporation accounts for the majority of water loss in terrestrial amphibians (Heatwole, 1983; Shoemaker et al., 1992). Therefore, any time spent out in the open is time in which the animal would be losing a major amount of water. Many amphibians are known to use behavioral and physiological mechanisms to regulate their water content (Brattstrom, 1979; Heatwole, 1983; Hutchison and Dupré, 1992 and references therein; Pough et al., 1983). My data indicate that *D. fuscus* did not display physiological control over desiccation. The differences between individuals in my experiment may be explained by behavior. While some of the salamanders either moved about or remained in the middle of the tube, others curled themselves up at the very end of the tube. Even though these possible behavioral attempts at control were observed, the differences between the rate of water loss between individuals were minimal.

As temperature increases, so does the rate of desiccation. There exists, therefore, a conflict between thermoregulation and osmoregulation in terrestrial salamanders. In light of what is known of the high priority osmoregulation plays in the life of the terrestrial salamander (Heatwole, 1983; Hutchison and Dupre, 1992), an urge to move in order to find a specific substrate temperature is less likely in those salamanders living farthest from the stream. Any movement by the salamander outside of its wet retreat brings about a loss of water via evaporation (Heatwole, 1983). If a terrestrial species moves to find a "better" temperature, it increases its chances of dehydration. While some movement in the pursuit of prey items is inevitable, temperature seeking is not.

Desmognathus quadramaculatus and *D. monticola*, both much more closely associated with the stream environment than *D. fuscus*, have shown temperature preferences in the laboratory and *D. monticola* selected significantly higher temperatures at night, when it may be found foraging away from the water (Sievert and Andreadis, in review). These more aquatic species do not have the same hydric constraints placed on them by their environment as does *D. fuscus*. For *D. fuscus*, the number of wet retreats are fewer, the predation pressure is higher, and its body size is smaller. In light of these considerations, it follows that, even though its more aquatic congenerics may be selecting for preferred temperatures available in their environment, such behavior may not have evolved in the more terrestrial *D. fuscus*.

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Temperature-Mediated Characteristics of the of the Dusky Salamander (*Desmognathus fuscus*) of Southern Appalachia

Title of Thesis

Roy Cooper

Signature of Graduate Office Staff

July 11, 2000

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