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CAUSAL FACTORS LIMITING THE DISTRIBUTIONS OF  
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PREVIEW

CAUSAL FACTORS LIMITING THE DISTRIBUTIONS OF  
LEOPARD FROGS IN EASTERN NEBRASKA

by

Kipp C. Kruse

A DISSERTATION

Presented to the Faculty of  
The Graduate College in the University of Nebraska  
In Partial Fulfillment of Requirements  
For the Degree of Doctor of Philosophy  
School of Life Sciences

Under the Supervision of Professor John D. Lynch

Lincoln, Nebraska

July, 1978

**TITLE**

**CAUSAL FACTORS LIMITING THE DISTRIBUTIONS OF**

**LEOPARD FROGS IN EASTERN NEBRASKA**

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## TABLE OF CONTENTS

	Page
INTRODUCTION . . . . .	1
DESICCATION TOLERANCE . . . . .	10
Materials and Methods . . . . .	12
Results . . . . .	16
Discussion . . . . .	29
REHYDRATION RATES . . . . .	31
Materials and Methods . . . . .	33
Statistical Procedures . . . . .	38
Results . . . . .	40
Conclusions . . . . .	60
EMBRYONIC TEMPERATURE ADAPTATIONS . . . . .	62
Materials and Methods . . . . .	63
Results . . . . .	67
EMBRYONIC TURBIDITY TOLERANCE . . . . .	74
Materials and Methods . . . . .	74
Results . . . . .	76
SUMMARY AND CONCLUSION . . . . .	81
LITERATURE CITED . . . . .	87

## LIST OF FIGURES

Figure		Page
1	Sympatric zone (hatched area) between <u>Rana pipiens</u> and <u>Rana blairi</u> in Nebraska . . . . .	4
2	The distribution of <u>Rana pipiens</u> in Nebraska correlated with soil parent materials and climatic data . . . . .	6
3	The distribution of <u>Rana blairi</u> in Nebraska correlated with soil parent materials and climatic data . . . . .	7
4	Asymptotic relationship between standard weight (g) and total surface area (mm <sup>2</sup> ) in <u>Rana pipiens sensu lato</u> . . . . .	17
5	Linear regression relationship between standard weight (g) and time (min) to the critical activity point (CAP) . . . . .	21
6	Linear regression relationship between standard weight (g) and mg H <sub>2</sub> O lost at CAP/standard weight (g)/time (min). . . . .	22
7	Linear regression relationship between standard weight (g) and mg H <sub>2</sub> O lost at CAP/total surface area (mm <sup>2</sup> )/time (min) to CAP . . . . .	25
8	Least squares fit exponential relationship ( $Y = ae^{bx}$ ) between snout vent length (mm) and standard weight (g) . . . . .	27
9	Linear regression relationship between snout vent length, SVL, (mm) and ventral surface area (mm <sup>2</sup> ) . . . . .	39
10	Histogram indicating the adjusted mean milligrams of water uptake/mm <sup>2</sup> (ventral surface area)/hour (over all time intervals) for both species of Nebraska leopard frogs on the five soil-moisture treatments . . . . .	52

Figure

Page

- 11 Histogram indicating the adjusted mean percent of standard weight recaptured/hour (over all time intervals) for both species of Nebraska leopard frogs on the five soil-moisture treatments

53

PREVIEW



## LIST OF TABLES

Table		Page
1	Controlled desiccation responses of <u>Rana pipiens</u> and <u>Rana blairi</u> . . . . .	19
2	Standard weights and snout vent lengths with associated length/weight ratios and statistical tests in <u>Rana pipiens</u> and <u>Rana blairi</u> . . . . .	28
3	Soil # 2--Sand 16% moisture--Analysis of variance tables with probabilities of F values, sample sizes, adjusted means and slopes of covariate regression lines for dependent variable headings 1 and 2 . . . . .	41
4	Soil # 2--Sand 16% moisture--Analysis of variance tables with probabilities of F values, sample sizes, adjusted means and slopes of covariate regression lines for dependent variable heading 3 . . . . .	42
5	Soil # 3--Sand 10% moisture--Analysis of variance tables with probabilities of F values, sample sizes, adjusted means and slopes of covariate regression lines for dependent variable headings 1 and 2 . . . . .	43
6	Soil # 3--Sand 10% moisture--Analysis of variance tables with probabilities of F values, sample sizes, adjusted means and slopes of covariate regression lines for dependent variable heading 3 . . . . .	44
7	Soil # 5--Loess 50% moisture--Analysis of variance tables with probabilities of F values, sample sizes, adjusted means and slopes and covariate regression lines for dependent variable headings 1 and 2 . . . . .	45
8	Soil # 5--Loess 50% moisture--Analysis of variance tables with probabilities of F values, sample sizes, adjusted means and slopes of covariate regression lines for dependent variable heading 3 . . . . .	46
9	Soil # 6--Loess 25% moisture--Analysis of variance tables with probabilities of F values, sample sizes, adjusted means and slopes of covariate regression lines for dependent variable headings 1 and 2 . . . . .	47

Table		Page
10	Soil # 6--Loess 25% moisture--Analysis of variance tables with probabilities of F values, sample sizes, adjusted means and slopes of covariate regression lines for dependent variable heading 3 . . . . .	48
11	Soil # 7--Loess 20% moisture--Analysis of variance tables with probabilities of F values, sample sizes, adjusted means and slopes of covariate regression lines for dependent variable headings 1 and 2 . . . . .	49
12	Soil # 7--Loess 20% moisture--Analysis of variance tables with probabilities of F values, sample sizes, adjusted means and slopes of covariate regression lines for dependent variable heading 3 . . . . .	50
13	Developmental rate and corrected survival percentages of Nebraska leopard frog egg-embryos in five temperature treatments (8-12-18-24-28-32° C. (18° = control) with comparative Student's T values and probability levels. Survival data were transformed by dividing treatment percentages by control percentages . . . . .	68
14	Developmental rate and corrected survival percentages of Nebraska leopard frog egg-embryos in 3 environmental chamber temperature treatments 10-20-30° C (20° = control). Survival data were transformed by dividing treatment percentages by control percentages. . . . .	71
15	Corrected survival percentages (with means and standard errors) of Nebraska Leopard frog egg-embryos in five turbidity (suspended soil particles) treatments. Data were transformed by dividing actual treatment survival percentages by control survival percentages . . . . .	77
16	(SAS-Statistical Analysis System) Cross-classified, nested analysis of variance table with appropriate statistical tests for Nebraska Leopard frog egg-embryo turbidity tolerance . . . . .	78

## INTRODUCTION

Until the late 1960's, leopard frogs (Rana pipiens sensu lato) were thought to consist of one broad ranging species with gene flow between adjacent populations. This distribution was thought to be the largest of any anuran encompassing an area from northern Canada south to Panama, and from the eastern to nearly the western coasts of United States (Conant, 1958). This single species concept arose primarily out of diploid hybridization and embryonic temperature adaptation experiments (Moore, 1939; 1942a; 1942b; 1944; 1946; 1947; 1949; 1950; 1957; Volpe, 1954; and Ruibal, 1955). Moore suggested that adjacent (north-south) populations of leopard frogs were capable of genetic exchange, and that as the latitudinal distance between populations increased, genetic compatability decreased. Mayr (1963) cited leopard frogs as a classic example of geographic variation as well as illustrating physiological clines.

This single species paradigm was held in vogue from 1939 to 1966 but fell to more critical external and internal morphological analyses and the advent and quantitative use of modern probes such as tape recorders, sonographs, and electrophoresis (Littlejohn and Oldham, 1968; Brown and Brown, 1972; Post, 1972; Post and Pettus, 1966; Platz, 1972 and 1976; Platz and Platz, 1973; Dunlap and Kruse, 1976; Kruse and Dunlap, 1976; and Frost and Bagnara, 1976).

Brown (1973) suggested that the Rana pipiens complex consists of five distinct sibling species. Pace (1974) systematically revised the

leopard frogs of the continental United States and recognized five named species and three unnamed taxa. Moore (1975) speculated that the complex would eventually be fragmented further. The prediction is being fulfilled; Frost and Bagnara (1976) recently described a new species from western Mexico.

The Rana pipiens complex has been broken down into a number of distinct species and there is good indication that it will be even further subdivided in the desert southwestern part of the United States and Mexico.

Two species of leopard frogs live in Nebraska, i.e., the northern leopard frog, Rana pipiens Schreber and the plains leopard frog, Rana blairi Mecham, Littlejohn, Oldham, Brown and Brown. Korky (1976) differentiated the larvae of these two species and provided a mathematical account of geographic variability within each species in Nebraska. Hupf (1977) reported on the natural history of R. pipiens and R. blairi from a sympatric zone in northeast Nebraska.

The distribution of adults of these two species has been reported on by Pace (1974), and Dunlap and Kruse (1976), suggesting both R. pipiens and R. blairi have range limits within Nebraska, i.e., south-central and north-central range limits respectively. Extensive systematic collections done in Nebraska show that R. pipiens is generally distributed over the northern half of Nebraska above the Platte River while R. blairi is distributed primarily through the southeastern 40% of Nebraska generally south of the Platte River (Lynch, 1978).

Pace (1974) described the leopard frog complex as consisting of species with essentially contiguous geographic ranges with some overlap along contact zones. These sympatric areas are reported to be very narrow and sporadic and hence leopard frog species are described as parapatrically distributed. Key (1968) suggested that parapatry is a special case of sympatry, not allopatry, as thought by Smith (1965). Rana pipiens and R. blairi (Fig. 1) have an extensive area of distributional overlap (approximately 400 km N-S and at least 200 km E-W, the largest between any two members of the complex). Regardless of the semantic problems associated with distributional terminology; it is misleading to term their distributional relationship parapatric in Nebraska at present. "Contact sympatry" as used by Littlejohn (1969) might be more appropriate terminology because Pace (1974) submitted that failure to discriminate the extent of distributional overlap could obscure the history of speciation of this group.

Parapatry implies in part, biotic interactions, i.e., direct competition maintaining the distributional boundaries (Key, 1968). The competitive exclusion principle states that complete competitors cannot coexist, and yet R. pipiens and R. blairi occur together over a broad zone of sympatry. This extensive sympatric area would logically suggest a pair of potential alternatives: some type of ecological displacement leading to niche partitioning within the overlap zone and/or abiotic factors are limiting range distributions.

Relatively early in collecting micro-distributional data from areas of sympatry in northeast Nebraska, it was noticed that R. blairi

Fig. 1. Sympatric zone (hatched area) between Rana pipiens and Rana blairi in Nebraska.



was usually associated with silty, highly turbid (muddy) streams while R. pipiens was normally found on clear, sand bottom streams. When a soil parent materials map of Nebraska (Elder, 1969) is super-imposed on the Nebraska leopard frog distributions, there appears to be a strong correlation between the distribution of R. pipiens with large-particle soils (sands--characterized by a relatively weak attraction for water molecules and thus rapid percolation and evaporation rates) (Fig. 2). Likewise, the distribution of R. blairi is strongly correlated with small-particle soils (loess--characterized by a relatively high attraction for water molecules and therefore low evaporation and percolation rates (Fig. 3). Furthermore, the sympatric zone in eastern Nebraska is associated with a mosaic of soil types.

These distributional correlates and the anecdotal field observations that R. pipiens is very often collected far removed from open (free) water, i.e., pastures, meadows etc., whereas R. blairi is rarely or never collected away from a free water source, suggest that R. pipiens is more tolerant to desiccation and/or has a faster rehydration rate than R. blairi.

The distributional data also suggest a fairly strong correlation with mean annual temperature, R. blairi predominating below the 10° C. isotherm and R. pipiens predominating above. Dunlap and Kruse (1976) and Hupf (1977) concluded that the more northerly distributed R. pipiens has an earlier, more predictable breeding season (April to mid May), whereas the more southerly distributed R. blairi has a much longer, less predictable breeding season (April--throughout the summer).



Fig. 2. The distribution of Rana pipiens in Nebraska correlated with soil parent materials and climatic data (abiotic data after Elder, 1969). Mean annual precipitation in millimeters, isotherm = centigrade.

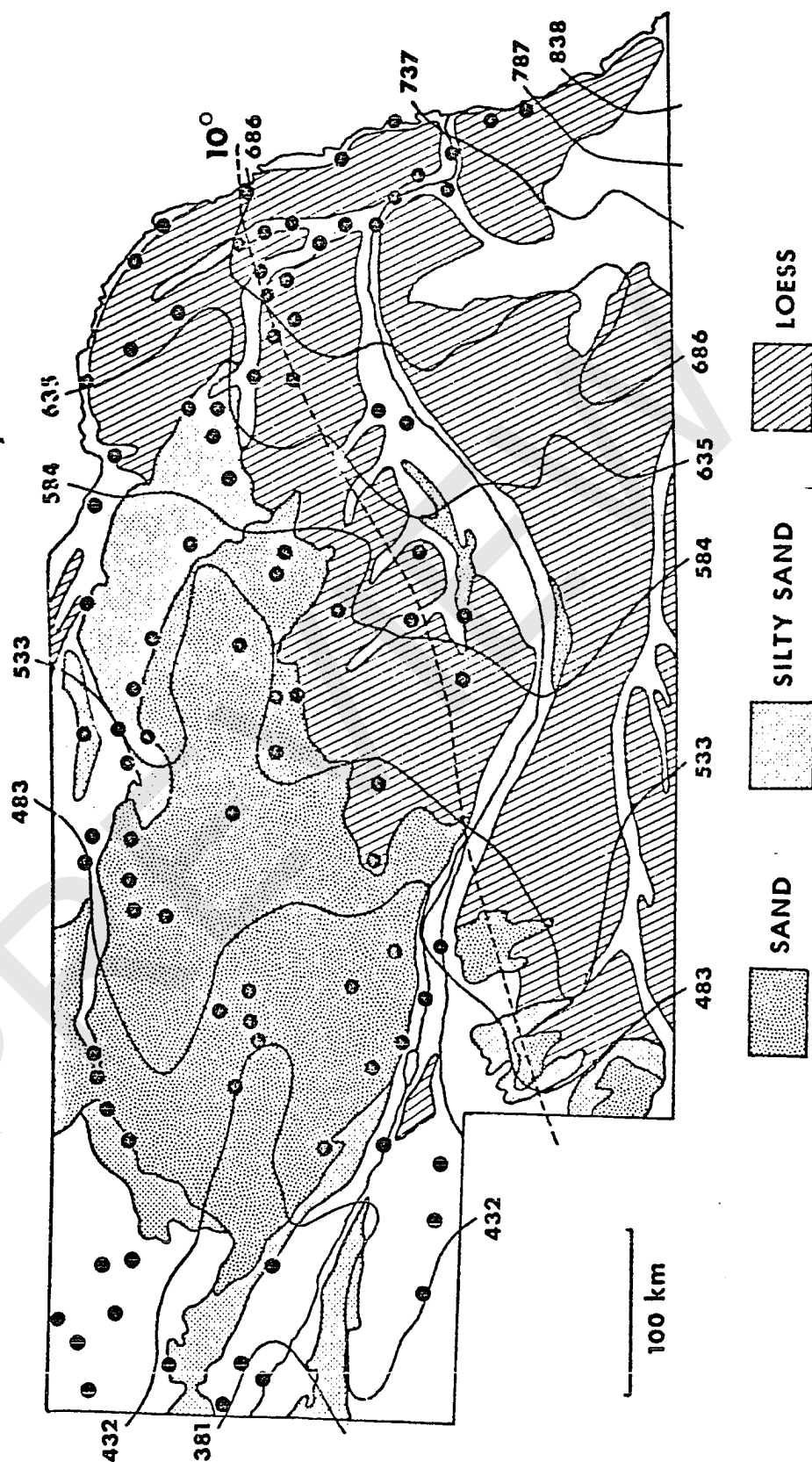
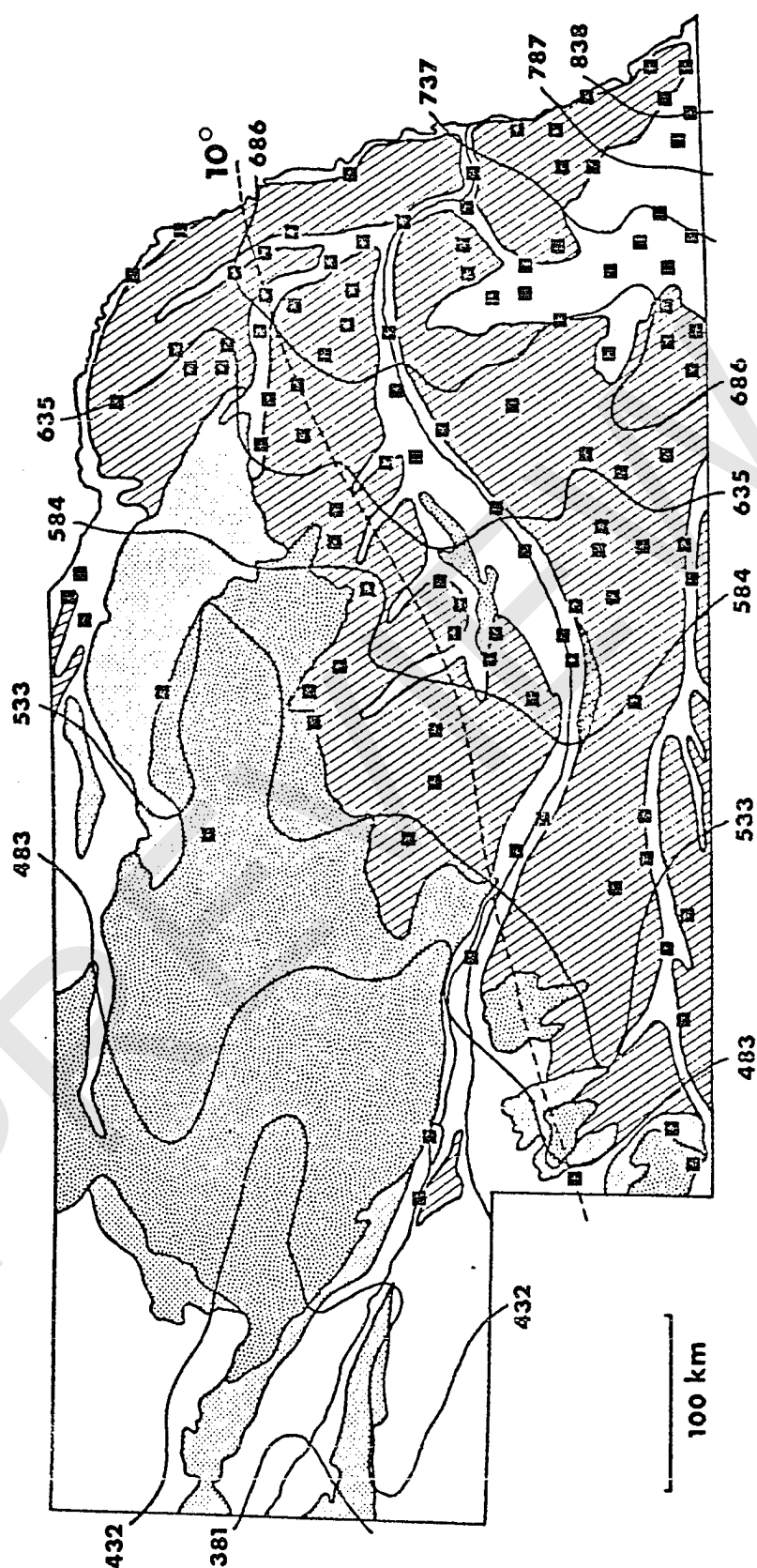


Fig. 3. The distribution of Rana blairi in Nebraska correlated with soil parent materials and climatic data (abiotic data after Elder, 1969). Mean annual precipitation in millimeters, isotherm = centigrade: See Fig. 2 for soil key.



These observations suggest that the egg-embryo stages of R. pipiens are adapted developmentally to relatively "cool" waters (15-20° C.) whereas egg-embryo stages of R. blairi are adapted developmentally to a broader spectrum of temperatures (15-30°C.).

Because R. pipiens is characteristic of sand bottom streams with clear water, a reduced turbidity tolerance of early developmental stages would help explain their apparent absence from turbid waters in sympatric zones and might account for their complete absence from areas having small particle substrata which are widespread in southeastern Nebraska.

Leopard frog biology has recently received a renewed interest, but most of this work has been of a descriptive nature (taxonomic and distributional). Little has been done in the way of assessing the ecological requirements of individual species. Compared to other terrestrial vertebrate groups, north temperate anurans can be viewed as eco-physiologically handicapped because they are: (1) poikilothermic and are therefore active only during favorable temperature regimes, and (2) because they possess a permeable integument forcing them to remain in close proximity to a water source. The extent of correlations between distributions and abiotic factors suggest that these factors might generally be more important than biotic factors in limiting frog distributions in the seasonal environment characteristic of the central plains states. It is the contention of this dissertation that the limits of distributions of R. pipiens and R. blairi in eastern Nebraska are functions of interactions of (1) differential tolerances to desiccation, (2) differential rehydrating capacities on

different soil types, (3) different embryo temperature tolerances, and (4) different embryo tolerances to soil turbidity. Two general parameters were examined: substrate and its role in various aspects of desiccation, rehydration and development; and temperature and its effect on embryo growth and development.

PREVIEW

## DESICCATION TOLERANCE

Anurans have a vascular, permeable integument and are therefore forced to exist in time and space in close proximity to a water source. This general inability to control body water is an obvious handicap in a terrestrial situation but this is not to say that members of this group do not show various degrees of terrestriality because anurans include a continuum of representatives ranging from totally aquatic to totally terrestrial species.

A review of past research indicates considerable disagreement concerning amphibian capabilities of physiologically controlling the rate of evaporative water loss (EWL). Hall (1922) demonstrated salamanders lose water only 3% as fast as does free water, but Rey (1937) suggested that EWL in Rana esculenta equaled that of free water of a comparable surface area. Gray (1928) and Adolph (1932) suggested that living specimens of salamanders and frogs lose water as rapidly as sacrificed counterparts, but Thorson (1956) found living specimens to have a lower EWL than dead or skinned specimens. MacMahon (1964a and 1964b) showed agar models and living salamanders to have equal EWLs. Rey (1937), Littleford et al. (1947), and Heatwole et al. (1969) suggested that EWL is a continuous function during progressive desiccation of salamanders and frogs, indicating no physiological adjustments. Thorson (1956), Warburg (1965), and Cloudsley-Thompson (1967) demonstrated that the

EWL decreased with increased desiccation, but suggested that this is expected with increased osmoconcentration and does not necessarily imply physiological control.

The most convincing evidence that under comparable conditions amphibian EWL is a function of surface area to volume ratio comes from comparative desiccation experiments on strongly terrestrial and strongly aquatic species. Kirk and Hogben (1946) indicate no rate differences in EWL between highly terrestrial members of the genus Bufo and aquatic members of the genus Rana. Thorson (1955), Rey (1937), Schmid (1965), Spight (1968), Heatwole et al. (1969), and Farrell and MacMahon (1969), among others, have found congruent results using a wide variety of amphibian species. There is, however, some limited evidence (Cohen, 1952; and Warburg, 1965) that terrestrial species have a lower EWL than do aquatic species.

It appears that amphibian terrestriality has not come about by selection operating to reduce EWL except in some tropical and fossorial forms which construct types of impervious cocoons and excrete uric acid (McClanahan, 1967; Lee and Mercer, 1967; Loveridge, 1970; Shoemaker et al., 1972; Shoemaker and McClanahan, 1975; Blaylock et al., 1976; and Drewes et al., 1977). Rather anuran terrestriality has been achieved by increasing tolerance to water loss (Thorson and Svihla, 1943). This direct relationship between osmoconcentration tolerance and terrestriality has been shown in a wide variety of amphibian species (Littleford et al. 1947; Gordon, 1952; Thorson, 1955; Hutchison, 1958; Ray, 1958; Main and Bentley, 1964; Schmid, 1965; Larson, 1971; Ralin and Rogers, 1972; and Pough et al., 1977).