UC Davis

UC Davis Previously Published Works

Title

Dehydration Reduces the Endurance Running Capacity of the Lizard *Uta stansburiana*

Permalink

<https://escholarship.org/uc/item/3pk6s4hp>

Journal

Copeia, 1989(4)

ISSN

0045-8511

Authors

Wilson, Bryon S

Wilson, Byron S

Havel, Peter J

Publication Date

1989-12-27

DOI

10.2307/1445998

Peer reviewed

these species is presented in Walls and Jaeger (1987). An alternative mechanism of growth inhibition may be that of differential exploitative abilities between larval *A. maculatum* and *A. talpoideum*. We hypothesize that *A. maculatum* reduces growth in coexisting larvae through more efficient assimilation of prey and/or foraging behavior.

Acknowledgments.—We thank G. Gassen for assistance in maintaining the larvae and constructing the experimental chambers. We also thank D. Holland for assistance with many aspects of this research.

LITERATURE CITED

- LICHT, L. E. 1967. Growth inhibition in crowded tadpoles: intraspecific and interspecific effects. *Ecology* 48:736–745.
- MORIN, P. J., AND E. A. JOHNSON. 1988. Experimental studies of asymmetric competition among anurans. *Oikos* 53:398–407.
- RICHARDS, C. M. 1958. The inhibition of growth in crowded *Rana pipiens* tadpoles. *Physiol. Zool.* 31:138–151.
- ROSE, S. M., AND F. C. ROSE. 1961. Growth controlling exudates of tadpoles. *Symp. Soc. Exp. Biol.* 15:207–218.
- RUGH, R. 1962. *Experimental embryology*. Burgess Publ. Co., Minneapolis, Minnesota.
- SEIGEL, S. 1956. *Nonparametric statistics for the behavioral sciences*. McGraw-Hill Book Co., Inc., New York, New York.
- STEINWASCHER, K. 1978. Interference and exploitation competition among tadpoles of *Rana utricularia*. *Ecology* 59:1039–1046.
- STENHOUSE, S. L. 1985. Interdemic variation in predation on salamander larvae. *Ecology* 66:1706–1717.
- , N. G. HAIRSTON AND A. E. COBEY. 1983. Predation and competition in *Ambystoma* larvae: field and laboratory experiments. *J. Herpetol.* 17:210–220.
- WALLS, S. C., AND R. G. JAEGER. 1987. Aggression and exploitation as mechanisms of competition in larval salamanders. *Can. J. Zool.* 65:2938–2944.
- WILBUR, H. M. 1972. Competition, predation, and the structure of the *Ambystoma-Rana sylvatica* community. *Ecology* 53:3–21.
- . 1987. Regulation of structure in complex systems: experimental temporary pond communities. *Ibid.* 68:1437–1452.
- ZAR, J. H. 1984. *Biostatistical analysis*. Prentice-Hall, Inc., Englewood Cliffs, New Jersey.
- SUSAN C. WALLS AND ROBERT G. JAEGER, *Department of Biology, University of Southwestern Louisiana, Lafayette, Louisiana 70504*. Accepted 3 Feb. 1989.
- Copeia*, 1989(4), pp. 1052–1056
© 1989 by the American Society of
Ichthyologists and Herpetologists
- DEHYDRATION REDUCES THE ENDURANCE RUNNING CAPACITY OF THE LIZARD *UTA STANSBURIANA*.—Because reptiles were the first truly terrestrial vertebrates and are now common in arid regions, their water relations have been the subject of intensive research (Mautz, 1982; Minnich, 1982; Nagy and Peterson, 1988). In laboratory studies for example, specific osmoregulatory adaptations have been described, rates and avenues of evaporative water loss have been measured, and physiological tolerances to dehydration have been determined (Roberts, 1968; Heatwole and Vernon, 1977; Thorpe and Kontogiannis, 1977; Mautz, 1982). Additionally, many field studies have constructed itemized water budgets and have assessed seasonal variation in hydric status (Bradshaw, 1970, 1986; Minnich, 1976; Nagy, 1973). Few studies, however, have explored the influences of dehydration on behavioral and physiological performance of reptiles (Mautz, 1982; Crowley, 1985, 1987). Because dehydration is known to have profound fitness consequences for desert lizards (Bradshaw, 1971), it is of interest to know how this reduction in fitness might be mediated. Here we examine the effect of dehydration on locomotor stamina (=treadmill endurance) in a desert lizard (*Uta stansburiana*). We chose *U. stansburiana* for study because it is well known ecologically and physiologically and because it inhabits extremely arid areas, where hydric stress could be an important selective force (Turner et al., 1976; Nagy, 1983; Waldschmidt and Tracy, 1983).
- Interestingly, dehydration reduces endurance capacity in two species of anuran amphibians, but has no effect on their burst locomotor ability (Gatten, 1987). Moreover, Crowley (1985) has shown that dehydration has no effect on the sprint running performance of the lizard *Sceloporus undulatus*, but no previous study has examined the effect of dehydration on the endurance capacity of a reptile. Are burst and endurance locomotor functions of reptiles differentially sensitive to the effects of dehydration, as is the case for anuran amphibians? We address this question indirectly by comparing our results for *U. stansburiana* to those of Crowley for *S. undulatus* (these species are closely related sceloporine lizards, see below).
- Methods.*—Adult *U. stansburiana* (six females, 11 males) were collected on 15 Nov. 1986, near

Desert Center, Riverside Co., Calif. (California Department of Fish & Game, permit #2048) and were maintained in a walk-in environmental chamber at the University of Washington, Seattle. Lizards were housed in plastic terraria with a sand substrate and with bark for hiding and perching. No more than five lizards were housed in the same terrarium. Chamber temperature was kept at 15 C for 24 h/d, and a 12L/12D photoperiod included both UV and incandescent light (the latter as a heat source). Water and food (*Tenebrio* larvae and crickets) were provided ad libitum. All animals used in the experiment either gained ($n = 16$) or maintained ($n = 1$) mass during the 2 mo acclimation period and appeared to be in excellent condition at the start of the experiment. Subjects for the dehydration group were chosen at random with respect to sex.

We used a paired experimental design, whereby both experimental (dehydration) and control lizards were raced before and after the dehydration of experimental subjects. Aside from the presence of water vs a desiccating medium during the dehydration procedure, control and experimental lizards were subjected to identical conditions throughout the study. Therefore, we could test specifically for the effect of dehydration on endurance capacity by comparing the relative changes, from baseline to final endurance time, of the control vs dehydrated lizards.

Experimental lizards (six males, four females) were placed individually in cloth sacks and were then put into plastic boxes (5–6 lizards/box) containing a 2 cm layer of a commercial desiccant (CaSO_4). This method is similar to the protocol used by Crowley to desiccate *S. undulatus* (Crowley, 1985, 1987, pers. comm.). Control animals (five males, two females) were housed similarly but without CaSO_4 and with a small cup of water to provide humidity. Additionally, the sacks containing control lizards were sprinkled with water at least once per day. Boxes containing experimental and control lizards were kept in the same environmental chamber (36 C d, 23 C night; 12L/12D cycle). Lizards were maintained under this regime for 75 h.

Endurance was measured by running the lizards on the moving belt (0.5 km/h) of a treadmill until exhaustion (Huey et al., 1984). Exhaustion was scored when a lizard failed to move after we prodded its tail base and hind limb region gently for 20 consecutive times. Endurance was measured for each lizard three times. The first measurements (18 Jan. 1987) served

to familiarize the lizards with the treadmill apparatus and allowed us to generate a consistent index of exhaustion. The second measurements (24 Jan. 1987) served as the baseline measures against which we compared the final endurance times (1 Feb. 1987) of all lizards (dehydrated and control). Before the initial and baseline endurance trials lizards were fasted for 48 h. Before the final endurance trial all lizards were fasted for 75 h, because an additional 27 h were required to effect the desired level of dehydration (~15% mass loss—based on previously reported values [Crowley, 1985] and on the magnitude of mass losses known to be incurred by *U. stansburiana* in the field) among experimental subjects. Two hours before trials, lizards were weighed to 0.01 g on a Mettler top-loading balance and were then housed individually in cloth sacks in a chamber at 36 C. Thus all subjects were run at the same T_b . All trials were conducted between 1000–1700 h inside an environmental chamber at 36 C. This temperature approximates both the mean T_b of *Uta* in the field and the optimal T_b for sprint speed (Parker and Pianka, 1975; Waldschmidt and Tracy, 1983).

Our statistical comparisons are based on the percent change observed between the baseline (24 Jan.) and final (1 Feb.) endurance time for each individual. We used percent change rather than absolute change because endurance times vary among individuals, but are highly repeatable within individuals (see below). Thus, we tested for a difference between the percent change observed in experimental (dehydrated) vs control lizards. Because the data did not differ significantly from a normal distribution (g_1 and g_2 tests for skewness and kurtosis respectively [Sokal and Rohlf, 1981]; F test for unequal variance; rankits plots [Weisberg, 1980]), we used t-tests in our statistical comparisons. Statistical comparisons of means within a treatment group (i.e., 24 Jan. vs 1 Feb.) were made with a paired t-test ($\alpha = 0.05$); statistical comparisons of means of different treatment groups (i.e., control vs experimental) were made with a two-sample t-test ($\alpha = 0.05$).

Results.—During the dehydration procedure, animals in the hydrated group ($n = 7$) lost $7 \pm 1.0\%$ of their original body mass (probably due to defecation and food deprivation). Dehydrated lizards ($n = 10$) lost $15 \pm 1.3\%$ of original body mass. The percent mass loss among dehydrated lizards was significantly greater than among hydrated controls ($t = -4.83$, $df = 15$,

TABLE 1. ENDURANCE RUNNING TIME FOR CONTROL AND EXPERIMENTAL (DEHYDRATED) LIZARDS. Mean time (in seconds) is followed by $\pm$ SE.

	Control (n = 7)	Experimental (n = 10)
Baseline time (24 Jan.)	686 $\pm$ 149	787 $\pm$ 186
Final time (1 Feb.)	460 $\pm$ 81	355 $\pm$ 69
P for paired t-test	>0.20*	<0.01**
Percent change	-21 $\pm$ 16	-49 $\pm$ 7

* Indicates a two-tailed test.

** Indicates a one-tailed test.

$P < 0.0005$ for a one-tailed test), and suggests that the experimental subjects lost more body water than did the control lizards.

Individual endurance times on 18 Jan. (initial trial) and 24 Jan. (baseline trial) were highly correlated ($r = 0.81$, $n = 17$, $P < 0.001$), suggesting that individual differences are stable, at least over short time periods (Bennett, 1987). Moreover, mean times on 18 and 24 Jan. did not differ significantly ($t = 1.76$, $n = 17$, $P = 0.10$). Endurance running time for the control group did not change significantly from baseline to final endurance trial (percent change = $-21 \pm 16\%$, $t = 1.38$, $df = 6$, $P > 0.20$ for a two-tailed test), whereas endurance time for the dehydrated group decreased significantly (percent change = $-49 \pm 7\%$, $t = 3.13$, $df = 9$, $P < 0.01$ for a one-tailed test) (Table 1). Moreover, the percent decrease among dehydrated lizards was significantly greater than among hydrated controls ($t = 2.54$, $df = 15$, $P < 0.025$ for a one-tailed test).

We also performed a correlation analysis to determine whether the percent change in the endurance times of dehydrated lizards was correlated with the degree of dehydration (percent mass loss). The relationship was positive but not significant ($r_s = 0.182$, $n = 10$, $P > 0.25$ for a one-tailed test).

Discussion.—Although many aspects of reptilian osmoregulation have been well characterized (Mautz, 1982; Minnich, 1982; Bradshaw, 1986), the consequences of hydric stress for physiological and behavioral functions of ecological importance are not well known (Mautz, 1982; Crowley, 1985, 1987). In this study we have demonstrated that the endurance running ca-

capacity of the desert lizard *U. stansburiana* is impaired by desiccation. In the field these lizards often endure dry season mass losses of up to 20% (Wilson, unpubl.), so the levels reported here should be ecologically relevant.

Whether reduced stamina affects fitness is presently unknown. Because *Uta* are ambush predators (Tinkle, 1967; pers. obs.), reduced stamina would probably not affect foraging success. Likewise, reduced stamina may not affect predator evasion tactics (but see below), because *Uta* typically escape predators by making short sprints to known retreats (Tinkle, 1967; pers. obs.). Furthermore, *Uta* move short distances and for short periods of time (Tinkle et al., 1962; Irwin, 1965; Tinkle, 1967), so reduced stamina may not interfere with their daily movement patterns.

Nevertheless, a reduction in endurance capacity could have profound effects on social interactions, which could then lead to lowered fitness. *Uta stansburiana* (especially males) engage in territorial and hierarchical contests (Tinkle, 1967; Ferguson, 1970; Nussbaum and Diller, 1976), so dehydration could result in low social status or relegation to unfavorable habitat (Fox, 1978; Fox et al., 1981). Either consequence could lead to direct (i.e., reproductive) or indirect (e.g., reduced quality of foraging opportunities, lack of suitable predator refugia) reductions in fitness (Fox, 1983).

Our result complements Crowley's (1985) finding that the sprint running ability of *S. undulatus* was unaffected by desiccation—even when lizards were subjected to higher levels of dehydration (average mass loss of 18.8%) than in the present study. Dehydration thus appears to have different effects on burst vs endurance locomotion in sceloporine lizards. Such differential sensitivity to desiccation already has been documented for anurans (Gatten, 1987) and may be a general rule for reptiles and amphibians. Because the present comparison (between *S. undulatus* and *U. stansburiana*) is potentially confounded by phylogenetic complications (Huey and Bennett, 1987), it would be instructive to measure the effect of dehydration on both sprint speed and stamina in the same species. Nevertheless, *U. stansburiana* and *S. undulatus* are very closely related (Etheridge and de Queiroz, 1988) and have probably experienced similar environmental conditions for a considerable period of time (Axelrod, 1950; Pianka, 1986), so our comparison may be valid.

Acknowledgments.—We thank C. Himmelwright for help collecting lizards and T. Garland, S. Crowley, and R. Huey for valuable discussion. We are especially grateful to R. Huey for critically reviewing earlier drafts of this manuscript and for providing equipment and facilities. B. Wilson thanks N. Al-Alawi and P. Havel thanks B. Uecker for added inspiration. We are indebted to F. Ward, for without his timely assistance with the treadmill this study would not have been completed. This research was funded by National Science Foundation grant BSR-8415855 to R. B. Huey.

LITERATURE CITED

- AXELROD, D. I. 1950. Evolution of desert vegetation in western North America. Carnegie Inst. of Washington, pub. no. 590:216–306.
- BRADSHAW, S. D. 1970. Seasonal changes in the water and electrolyte metabolism of *Amphibolurus* lizards in the field. *Comp. Biochem. Physiol.* 36:689–718.
- . 1971. Growth and mortality in a field population of *Amphibolurus* lizards exposed to seasonal cold and aridity. *J. Zool. Lond.* 165:1–25.
- . 1986. *Ecophysiology of desert reptiles*. Academic Press Inc., Orlando, Florida.
- BENNETT, A. F. 1987. Inter-individual variability: an underutilized resource, p. 147–169. *In*: New directions in ecological physiology. M. E. Feder, A. F. Bennett, W. Burggren and R. B. Huey (eds.). Cambridge University Press, Cambridge, United Kingdom.
- CROWLEY, S. R. 1985. Insensitivity to desiccation of sprint running performance in the lizard *Sceloporus undulatus*. *J. Herpetol.* 19:171–174.
- . 1987. The effect of desiccation upon the preferred body temperature and activity level of the lizard *Sceloporus undulatus*. *Copeia* 1987:25–32.
- ETHERIDGE, R., AND K. DE QUEIROZ. 1988. A phylogeny of Iguanidae, p. 283–367. *In*: Phylogenetic relationships of the lizard families. R. Estes and G. K. Pregill (eds.). Stanford University Press, Palo Alto, California.
- FERGUSON, G. W. 1970. Mating behaviour of the side-blotched lizards of the genus *Uta* (Sauria: Iguanidae). *Animal Behav.* 18:65–72.
- FOX, S. F. 1978. Natural selection on behavioral phenotypes of the lizard *Uta stansburiana*. *Ecology* 59:834–847.
- . 1983. Fitness, home-range quality and aggression in *Uta stansburiana*, p. 149–186. *In*: Lizard ecology: studies of a model organism. R. B. Huey, E. R. Pianka and T. W. Schoener (eds.). Harvard University Press, Cambridge, Massachusetts.
- , E. ROSE AND R. MYERS. 1981. Dominance and the acquisition of superior home ranges in the lizard *Uta stansburiana*. *Ecology* 62:888–893.
- GATTEN, R. E., JR. 1987. Activity metabolism of anuran amphibians: tolerance to dehydration. *Physiol. Zool.* 60:576–585.
- HEATWOLE, H., AND J. E. N. VERNON. 1977. Vital limit and evaporative water loss in lizards (Reptilia, Lacertilia): a critique and new data. *J. Herpetol.* 11:341–348.
- HUEY, R. B., AND A. F. BENNETT. 1987. Phylogenetic studies of coadaptation: preferred temperatures versus optimal performance temperatures of lizards. *Evolution* 41:1098–1115.
- , H. JOHN-ALDER AND K. A. NAGY. 1984. Locomotor capacity and foraging behaviour of Kalahari lacertid lizards. *Animal Behav.* 32:41–50.
- IRWIN, L. N. 1965. Diel activity and social interaction of the lizard *Uta stansburiana stejnegeri*. *Copeia* 1965:99–101.
- MAUTZ, W. J. 1982. Patterns of evaporative water loss, p. 443–481. *In*: Biology of the reptilia. Vol. 12. Physiology (C). C. Gans and F. H. Pough (eds.). Academic Press, New York, New York.
- MINNICH, J. E. 1976. Water procurement and conservation by desert reptiles in their natural environment. *Israel J. Med. Sci.* 12:740–758.
- . 1982. The use of water, p. 325–395. *In*: Biology of the reptilia. Vol. 12. Physiology (C). C. Gans and F. H. Pough (eds.). Academic Press, New York, New York.
- NAGY, K. A. 1973. Behavior, diet and reproduction in a desert lizard, *Sauromalus obesus*. *Copeia* 1973:93–102.
- . 1983. Ecological energetics, p. 24–54. *In*: Lizard ecology: studies of a model organism. R. B. Huey, E. R. Pianka and T. W. Schoener (eds.). Harvard University Press, Cambridge, Massachusetts.
- , AND C. C. PETERSON. 1988. Scaling of water flux rate in animals. *Univ. Calif. Publ. Zool.* 120:1–172.
- NUSSBAUM, R. A., AND L. V. DILLER. 1976. The life history of the side-blotched lizard, *Uta stansburiana* Baird and Girard, in north-central Oregon. *Northwest Sci.* 50:243–260.
- PARKER, W. S., AND E. R. PIANKA. 1975. Comparative ecology of populations of the side-blotched lizard, *Uta stansburiana*. *Copeia* 1975:615–632.
- PIANKA, E. R. 1986. *Ecology and natural history of desert lizards*. Princeton University Press, Princeton, New Jersey.
- ROBERTS, L. A. 1968. Water loss in the desert lizard *Uta stansburiana*. *Comp. Biochem. Physiol.* 27:583–589.
- SOKAL, R. R., AND F. J. ROHLF. 1981. *Biometry*. 2nd ed. W. H. Freeman & Co., San Francisco, California.
- THORPE, G. S., AND J. E. KONTOGIANNIS. 1977. Evaporative water loss in isolated populations of the coastal side-blotched lizard, *Uta stansburiana hesperis*. *Comp. Biochem. Physiol.* 57A:133–137.
- TINKLE, D. W. 1967. The life and demography of

- the side-blotched lizard, *Uta stansburiana*. Misc. Publ. Mus. Zool., Univ. Mich. 132:1-182.
- , D. MCGREGOR AND S. DANA. 1962. Home range ecology of *Uta stansburiana stejnegeri*. Ecology 43:223-229.
- TURNER, F. B., P. A. MEDICA AND B. W. KOWALEWSKY. 1976. Energy utilization by a desert lizard (*Uta stansburiana*). US/IBP Desert Biome Monograph No. 1. Utah State University Press, Logan, Utah.
- WALDSCHMIDT, S., AND C. R. TRACY. 1983. Interactions between a lizard and its thermal environment: implications for sprint performance in the lizard *Uta stansburiana*. Ecology 64:476-484.
- WEISBERG, S. 1980. Applied linear regression. John Wiley & Sons, Inc., New York, New York.

BRYON S. WILSON, *Department of Zoology, NJ-15, and PETER J. HAVEL, Department of Medicine, Division of Endocrinology, Metabolism, and Nutrition, University of Washington, Seattle, Washington 98195. Present address (PJH), Department of Physiological Sciences, School of Veterinary Medicine, University of California, Davis, California 95616. Accepted 27 Feb. 1989.*

Copeia, 1989(4), pp. 1056-1059
© 1989 by the American Society of
Ichthyologists and Herpetologists

INHERITANCE OF A NATURALLY OCCURRING COLOR POLYMORPHISM IN THE ORNATE CHORUS FROG, *PSEUDACRIS ORNATA*.—Many species of anurans exhibit discrete back pattern or color polymorphisms (Savage and Emerson, 1970; Milstead et al., 1974; Stewart, 1974). Although much has been written on the evolutionary maintenance of these polymorphisms (Milstead et al., 1974) we still do not know to what extent the variation is genetically based. Many frogs change color temporarily (Nielson and Dyck, 1978; Kats and Van Dragt, 1986), but a permanent environmental influence on dorsal pattern has been demonstrated in only two species. The proportion of gray to brown metamorphs of *Pseudacris ornata* depends on larval population density (Travis and Trexler, 1984) and temperature (Harkey and Semlitsch, 1988), and temperature affects dorsal spotting in *Rana pipiens* (Browder and Davison, 1964; Davison, 1964; Merrell, 1972). Some evidence exists for simple Mendelian inheritance of naturally occurring polymorphisms in a number of anuran species (see Table 1 in Blouin, 1989), but in many studies

TABLE 1. FREQUENCY OF GREEN *Pseudacris ornata* IN SAMPLES COLLECTED AT TWO PONDS NEAR TALLAHASSEE, FLORIDA. Morph frequencies do not differ significantly from year to year ($\chi^2_3 = 0.363$). Airport pond data from Travis and Trexler (1984).

Site	Year	Number non-green	Number green	% Green
Airport Pond	1982	24	4	14.3
	1983	20	2	9.1
Christmas Pond	1986	16	2	11.1
	1987	33	5	13.2
Totals		93	13	12.3

the results are inconclusive owing to small numbers of crosses (or none at all) and failure to test independently the proposed genetic mechanisms with a second set of crosses. This study examines the inheritance of a color polymorphism in the ornate chorus frog, *P. ornata*.

Pseudacris ornata exhibits a conspicuous polymorphism in which most individuals are reddish-brown or gray but a few are bright green. In populations near Tallahassee, Florida, approx. 12% of breeding individuals are bright green (Table 1). I address the inheritance of the green state and the effect of larval density on its expression. I tested for density effects on the green state because Travis and Trexler (1984) found density controls the relative proportions of brown to gray metamorphs.

Methods.—During Feb. 1986 and 1987 I performed crosses between individuals of the three color morphs collected from a pond 15 km southwest of Tallahassee. Although the 1986 data fit a simple Mendelian model, I did not perform tests of significance because using the same data to both generate and test a hypothesis is a basic violation of statistical inference. Such a posteriori tests are biased toward failure to reject the hypothesized model of inheritance (type II error). I therefore designed the 1987 crosses to test independently the genetic mechanism suggested by the 1986 results and to look for possible environmental effects on the expression of the green state.

I created half-sib families by stripping eggs from females into sperm suspensions created by macerating the testes of each male in 5 ml of spring water. Unless otherwise indicated, all tadpoles were raised in groups of 10 siblings/6