

An experimental manipulation of food and water: growth and time-space utilization of hatchling lizards (*Sceloporus undulatus*)

S.M. Jones^{1,*}, S.R. Waldschmidt^{1,**}, and M.A. Potvin^{2,***}

¹ Department of Zoology, and ² Department of Botany, University of Wisconsin, Madison, WI 53706, USA

Summary. At a site in western Nebraska, we studied the effects of supplemental food and water on growth, survival, and habitat utilization of hatchling iguanid lizards, *Sceloporus undulatus*. Hatchlings were randomly assigned to one of four experimental groups and received either (1) supplemental food only, (2) supplemental water only, (3) supplemental food and water, or (4) neither supplemental food nor water (control). Neither supplemental food nor supplemental water affected growth rate in length, growth rate in mass, or size-specific body mass (i.e. robustness) at the end of the treatment period. Over the 45 day treatment period, there were no significant differences among treatment groups in survival, home-range size, or habitat utilization. There were, however, significant differences in the index of activity. Hatchlings in the treatment groups receiving supplemental water were sighted more often than hatchlings in the control group. We conclude that, during our study, neither food nor water limited growth but that water limited activity.

Key words: Supplemental food and water – Activity, growth rate – Home-range – Survival

Variation in growth rates of many organisms is commonly associated with variation in food abundance (amphibians, Claussen and Layne 1983; fish, Crowder and Magnuson 1983; insects, Scriber and Feeney 1979; mammals, Porter et al. 1984; mollusks, Garton 1984). This is particularly true of lizards as several studies have demonstrated a positive correlation between growth and food abundance (Stamps 1977; Dunham 1978; Schoener and Schoener 1978; Ballinger and Congdon 1980; Ferguson et al. 1983). Because food abundance is often correlated with precipitation (Janzen and Schoener 1968; Ballinger 1977; Dunham 1978), water availability can indirectly affect the growth of lizards through its effect on food abundance. Direct effects of water availability on the growth of lizards have also been demonstrated in the laboratory (Stamps and Tanaka

1981a) and in field populations (Stamps and Tanaka 1981a; Jenssen and Andrews 1984).

Variation in growth can also result from variation in foraging time. Periods of low water availability are typically accompanied by high ambient temperatures (Jones 1983), a combination which may induce water stress and reduce the time a lizard can forage (Nagy 1972). Reduced foraging time, in turn, restricts food intake and limits growth (Ballinger et al. 1970; Stamps 1976; Porter and Tracy 1983). Growth, therefore, may depend on the interaction among food availability, net water budget, and time available for activity.

Individuals that vary in their net food and water budgets should exhibit differential growth. Differential growth and the resulting size differences can have significant ecological consequences, especially if it occurs in the juvenile stage. For example, compared with small hatchling lizards, large hatchlings have a higher probability of survival (Ferguson and Bohlen 1978; Ferguson and Fox 1984) because they typically occupy higher quality home-ranges characterized by refugia from predators and higher prey densities (Fox 1978; Fox et al. 1981). Hatchlings occupying areas with higher prey densities may require smaller home-ranges, forage for shorter periods of time, or both (Simon 1975; Fox 1978; Ferguson et al. 1983).

The objective of our study was to determine the effects of both food and water on growth, patterns of behavior, and home-range quality of free-ranging hatchling iguanid lizards, *Sceloporus undulatus*, in western Nebraska. We determined these effects by supplementally feeding and watering experimental groups of hatchlings. We selected hatchlings because their high rate of growth provides the best opportunity to detect any effects of supplemental food and water. Several long-term studies of *S. undulatus* in western Nebraska provide abundant background data (Jones and Droge 1980; Ballinger et al. 1981; Jones 1983; Ballinger and Jones 1985; Jones et al. 1987) that can be used for comparison with our results.

Methods

Study site

Our study site was Arapaho Prairie (Arthur Co.) in the Sandhills of western Nebraska. Arapaho Prairie is a mixed grass prairie characterized by both tall and short grass species and an abundance of *Yucca glauca* Nutt. A detailed

* Present address: BCM Eastern Inc., One Plymouth Meeting, Plymouth Meeting, PA 19462, USA

** Present address: Department of Biology, Leidy Lab G-7, University of Pennsylvania, Philadelphia, PA 19104, USA

*** Present address: Department of Biology, West Chester University, West Chester, PA 19383, USA

description of the plant associations of Arapaho Prairie is provided by Keeler et al. (1980). Our study area was a 150 m × 150 m (2.25 ha) grid located on a west-facing dune slope.

Experimental design

Field manipulations. Each day between 29 August and 13 October 1984, weather permitting, we searched the entire grid for hatchling *S. undulatus*. We intensively searched for lizards during all hours favorable for lizard activity; a total of 313 person-hours. On many occasions, we were able to search the entire grid two or more times. We searched for lizards in a broadly overlapping pattern such that each hatchling could have been encountered at least twice during each pass of the grid.

Hatchlings captured for the first time between 29 August and 8 September were randomly assigned to one of four experimental groups. One group ($N=16$) was offered supplemental food, one item at a time, until they refused to eat. Supplemental food was offered either *in situ* by placing the prey items on the end of a small hook or by hand to captured hatchlings. Food items (grasshoppers, crickets, and moths) were collected ~1 km from the field site. We estimated the mass of supplemental food consumed by recording the number, type (grasshopper, cricket, moth), and size (small, ~20 mg; medium, ~70 mg; large, ~100 mg) of prey items eaten by each hatchling.

A second group ($N=19$) was offered supplemental water through the tip of a syringe, one drop at a time, until they refused to drink. The mass of water consumed by each hatchling was estimated by multiplying the number of drops consumed by the mass of representative drops.

A third group ($N=17$) was offered both supplemental food and water. Methods used for this treatment were the same as for the food only and water only groups. In this group, food was always offered first.

A fourth group ($N=20$) served as a control and received neither supplemental food nor supplemental water. Although these hatchlings received no treatment, they were captured and handled with the same frequency as hatchlings in the three treatment groups.

Hatchlings in the three treatment groups were individually offered supplemental food, supplemental water, or both, at each sighting. With this procedure we avoided the habitat modification that would have occurred with feeding or watering stations, or by simply broadcasting food and water over a large area. Furthermore, hatchlings in all four groups lived among each other and therefore had equal access to the same natural food and habitat resources. This arrangement provided a more powerful test of treatment effects because the confounding effects of differences among study areas were avoided.

Each hatchling was marked by clipping toes and with an individual color code using Testor_R model paint applied to the dorsal surface. Paint-marking in this manner does not increase the mortality of lizards (Jones and Ferguson 1980). For each hatchling, we recorded sex, snout-vent length (SVL), and body mass (prior to treatment). Lengths were measured to the nearest 0.5 mm and body mass to the nearest 0.1 g using a Pesola_R spring balance. Whenever possible, measurements were taken every fourth day.

For each hatchling sighted, we recorded data on time-space utilization: time of day, degree of cloud cover, expo-

sure of the lizard to the sun (full sun, partial sun, shade), habitat type {yucca, blowouts (large wind-eroded depressions), sparse grass, dense grass}, substrate type (sand, grass, yucca), height above ground, and location on the grid in reference to markers placed at 30 m intervals.

Maximum consumption rate. To estimate the maximum consumption by free-ranging lizards, we collected 11 hatchlings from areas surrounding the mark-recapture grid. These animals, similar in size and body mass to our experimental animals, were housed outdoors in a plastic enclosure ~1.5 m in diameter. These hatchlings were fasted for three days and then individually offered a single prey item (small grasshopper) at 20 min intervals for one h and then at 30 min intervals over the next 3–4 h. We estimated the proportion of the total food consumption of field animals that was supplemented by calculating the ratio of the mean daily consumption of supplemental food by lizards in the field to the mass of prey eaten by fasted lizards in one day. Because the daily consumption rate of animals fasted for three days was likely higher than the consumption rate of free-ranging animals, our estimate of the proportion of supplemental food provided to free-ranging lizards was conservative.

Data analyses

Growth rate. Growth was measured as rates of length gain (mm d^{-1}) and mass gain (g d^{-1}). To minimize measurement error, all measurements were made by SMJ. Additionally, only those individuals captured throughout the entire treatment period were included in the analysis. We tested for differences in growth among treatment groups using an analysis of variance (ANOVA). This analysis is appropriate because the growth rate of juvenile lizards is high and approximates linearity (Andrews 1982). Additionally, a linear model provided a better fit for the growth of hatchlings in our study than non-linear models. An analysis of covariance (ANCOVA) of log body mass using log SVL as the covariate provided another index of growth. The ANCOVA, which defined the size-specific body mass (i.e. robustness) of hatchlings, was carried out using the mass and SVL of hatchlings at the end of the fall treatment period.

Survival. Survival was calculated over two time scales: (1) short-term survival from the initiation of treatment to the end of the fall study period and (2) overwinter survival from the end of the fall study period until May of the following year. To compensate for possible spring migration off the study area, the grid was extended 50 m on each side during the spring census. Chi-squared tests were used to test for differences in survival among treatment groups.

Time-space utilization. We used a stepwise discriminant analysis to test for differences in time-space utilization among treatment groups. Variables entered into the analysis were Julian day, time of day, sky conditions, exposure of the lizard to the sun, habitat type, substrate type and height above the ground. The minimum Mahalanobis distance method (SPSS, Nie et al. 1975) was used to discriminate among groups.

Home-range size was calculated using two methods: the minimum convex polygon method and the A_4 method (see

Jennrich and Turner 1969). Home-ranges were calculated only for individuals that remained on the grid a minimum of 20 days. Home-range size calculated by the minimum convex polygon method was not adjusted for the number of sightings because (1) home-range sizes for most animals were still increasing at the end of our study and (2) within our treatment groups, regressions of home-range size on number of sightings failed to produce any significant relationships. Home-range size calculated by the A_4 method is independent of the number of sightings (Jennrich and Turner 1969; Schoener 1981). Home-range size was logarithmically transformed to normalize variance and an ANOVA was used to compare home-range size among groups.

We calculated an index of activity for each hatchling by expressing the number of days an individual was sighted as a proportion of the total number of days it could have been active. The prevailing meteorological conditions permitted activity on only 25 out of the 45 days from the start of our experimental manipulations to hibernation. The 20 days we were unable to work were primarily the result of three periods of rain and low ambient temperatures. This inclement weather occurred toward the end of our study and each lasted approximately one week (i.e., 5/7, 7/7, and 6/7 days). The proportion of days active for each animal was transformed (arc sine square root) to normalize variance and an ANOVA with a priori contrasts was used to test for differences among treatment groups. Due to the intensity of our searching efforts, this analysis provides a reliable index of relative activity among treatment groups.

Results

Growth rate

There were no significant differences in mean initial SVL or body mass among the four groups. Pooled for all four groups, initial SVL was 36.6 ± 1.5 (95% CI) mm and initial body mass was 1.2 ± 0.1 g.

Neither supplemental feeding nor watering had a significant effect on growth rate in either length or mass or size-specific body mass at the end of the fall treatment period (Fig. 1). Lizards were treated, on average, once every 2.8 days. Given our sample sizes and observed standard deviations, we were 90% certain of detecting, as statistically significant (Sokal and Rohlf 1981), differences in growth in length as small as 0.066 mm d^{-1} and differences in growth in mass as small as 0.018 g d^{-1} .

Hatchlings fasted for three days consumed an average of 182 mg of wet food per gram of body mass per day ($\text{mg g}^{-1} \text{ d}^{-1}$). By comparison, hatchlings in the food only and food and water treatment consumed an average of 20 mg of supplemental food $\text{g}^{-1} \text{ d}^{-1}$. Thus, we supplementally provided a minimum of 11% of the total food a hatchling would have consumed in the field.

Hatchlings in the water only treatment consumed significantly more water (12 mg of water $\text{g}^{-1} \text{ d}^{-1}$) than those in the food and water treatment ($7 \text{ mg g}^{-1} \text{ d}^{-1}$). This is probably due to the fact that hatchlings in the latter group were always offered food first which may have reduced the amount of water they could consume. The water content of the arthropod prey in the field (determined by freeze-drying) averaged 68%. Assuming that the maximum rate of food consumption by hatchlings in the field is equal to that of fasted hatchlings, we estimate that we supplement-

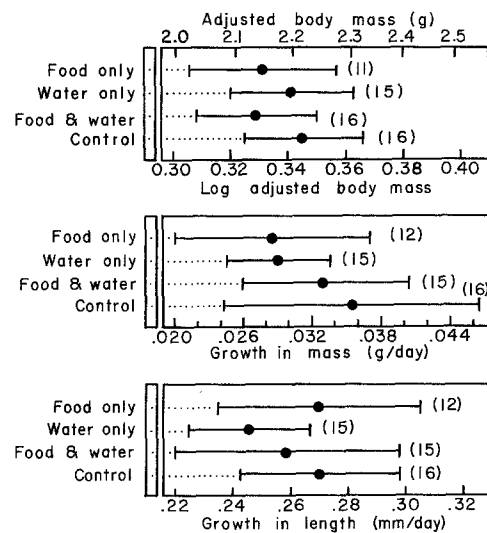


Fig. 1. Growth rate (bottom), rate of mass gain (middle) and size-specific body mass (top) ($\pm 95\%$ CI) for hatchling *Sceloporus undulatus*. The numbers in parentheses indicate sample size. There were no significant differences between treatment groups for any of the parameters

Table 1. Survival of hatchling *Sceloporus undulatus* throughout the treatment period (short-term survival) and through the winter (overwinter). There were no significant differences among treatment groups for either short-term ($\chi^2 = 2.39$; $P > 0.05$) or overwinter ($\chi^2 = 1.81$; $P > 0.05$) survival

	Survivors	Non-Survivors	Percent Survival
Short-Term Survival			
Food Only	12	4	75%
Water Only	16	3	84%
Food and Water	16	1	94%
Control	16	4	80%
Overall	60	12	83%
Overwinter Survival			
Food only	3	9	25%
Water Only	3	13	19%
Food and Water	5	11	31%
Control	2	14	13%
Overall	13	47	22%

tally provided a minimum of 4.5% (food and water group) to 7.5% (water only group) of the total water a hatchling would have consumed in the field.

Rates of growth within a treatment group were unaffected by individual variation in the amount of supplemental food or water consumed. This was tested by regressing both growth rate in length and rate of growth in mass against either the mass of supplemental food or the mass of supplemental water consumed. In all three treatment groups, these regressions were insignificant.

Survival

Supplemental food and water did not affect either short-term ($\chi^2 = 2.26$; $P > 0.05$) or overwinter ($\chi^2 = 1.81$; $P > 0.05$) survival (Table 1). Minimal survival during the 45 days between initiation of our study and hibernation

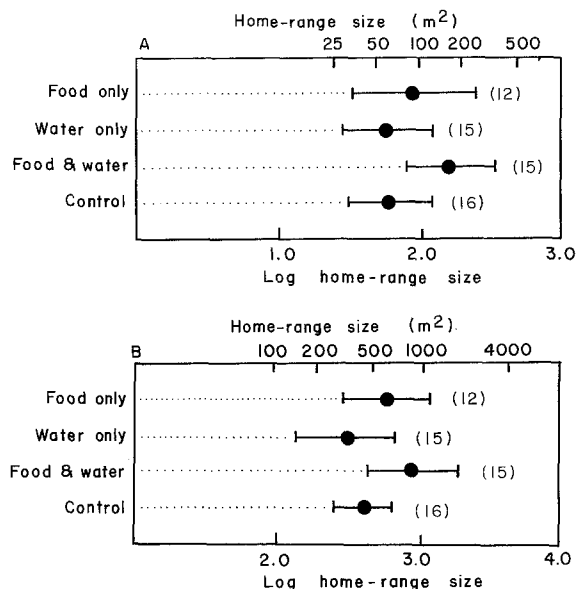


Fig. 2A, B. Home range size ($\pm 95\%$ CI) for hatchling *Sceloporus undulatus* as calculated by the minimum convex polygon method (A) and the A_4 method (B). The numbers in parentheses indicate sample size. There were no differences in home range size among treatment groups.

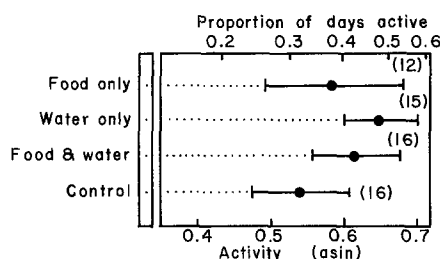


Fig. 3. Proportion of days active ($\pm 95\%$ CI) for hatchling *Sceloporus undulatus*. The numbers in parentheses indicate sample size. Treatment groups receiving water only and food and water were significantly more active than the control group.

was 83% (animals not recovered may have been lost through either predation or emigration). Minimum overwinter survival was 22%.

Time-space utilization

A stepwise discriminant analysis of the time-space variables failed to define any significant canonical discriminant functions and was thus unable to distinguish among the four experimental groups. Home-range size was also unaffected by any of our treatments. There were no significant differences in home-range size among treatment groups using either the minimum convex polygon or A_4 methods (Fig. 2).

There were, however, significant differences among groups in the proportion of days they were active. Hatchlings in the two groups that received supplemental water were active most often. The water only group was active significantly more often ($\bar{X}=37\%$, $P=0.02$) than the control group ($\bar{X}=27\%$) and the food and water group was marginally more active ($\bar{X}=34\%$, $P=0.08$) than the control group (Fig. 3).

Discussion

Variation in growth rates within populations of lizards has commonly been associated with variation in rainfall through its effect on food abundance in both desert (Dunham 1978; Ballinger and Congdon 1980) and semitropical (Schoener and Schoener 1978; Stamps and Tanaka 1981b) habitats. However, Stamps and Tanaka (1981a) and Jensen and Andrews (1984) have demonstrated that water availability can directly affect growth and that this effect is independent of food availability. In addition to its effect on growth, water availability can also alter activity (Stamps 1976; Minakami 1977; Stamps and Tanaka 1981b) and body temperature regulation (Ballinger et al. 1970; Bury and Balgooyen 1976). Consequently, periods of low water availability may not only restrict foraging time due to the high ambient temperatures that commonly occur during droughts, but also depress food abundance. In this study, we attempted to determine the effects of food abundance and water availability on growth and time-space utilization of hatchling *S. undulatus*.

Growth

At Arapaho Prairie, supplemental food did not increase the rate of growth in either length or mass of hatchling *S. undulatus*. One potential criticism of this result is that we did not provide hatchlings with sufficient supplemental food to significantly affect growth. Our estimate of 11% is conservative because fasted hatchlings probably consumed food at a higher rate than free-ranging animals. If juveniles consumed food at a rate equal to adults maintained in the laboratory ($46 \text{ mg g}^{-1} \text{ d}^{-1}$, unpubl. data), then we estimate that free-ranging hatchlings were supplemented with $\sim 43\%$ of their daily food intake. Forty-three percent may be an overestimate because adults may have a lower mass-specific consumption rate than do juveniles.

Despite consuming a mean of 20 mg of supplemental food $\text{g}^{-1} \text{ d}^{-1}$, supplementally fed hatchlings did not grow faster than controls. By comparison, an average of 14 mg of supplemental food $\text{g}^{-1} \text{ d}^{-1}$ caused an average increase in body mass of 27% in adult side-blotched lizards, *Uta stansburiana* (Waldschmidt 1983). Furthermore, Waldschmidt (1983) demonstrated a positive correlation between the amount of supplemental food consumed and mass gain. We found no significant relationship between growth in length or growth in mass when each was regressed on the mass of supplemental food consumed. Hatchling *S. undulatus* that consumed small amounts of supplemental food were still able to find enough food on their own to maintain growth rates comparable to hatchlings that consumed greater amounts of supplemental food.

In contrast to our results, growth rates of hatchling *S. undulatus* in Kansas (Ferguson et al. 1982) were significantly affected by supplemental feeding, but only during late fall when hatchling densities were high. The density of hatchling *S. undulatus* reported by Ferguson et al. (1982) was at least 5 times greater than the density of hatchlings in our study area. The extremely high densities in the Kansas population likely resulted in a shortage of food. Kansas hatchlings received supplemental food, on average, once every 4.1 days compared with once every 2.8 days in our study.

Growth of hatchling *S. undulatus* was also unaffected

by supplemental water. The lack of a significant effect of water on growth could mean that we did not provide hatchlings with sufficient water to affect growth. Although we know of no data indicating the mass of water required to affect growth, we believe that we provided enough supplemental water to affect growth if it had been limited by water. First, we conservatively estimate that we provided a minimum of 4.5% (food and water) to 7.5% (water only) of the total water consumed by hatchlings during our study. Using our laboratory estimate of maximum food consumption of adults, we estimate that we provided as much as 38% of the water consumed by the lizards. Although this mass of supplemental water had no effect on growth, it was sufficient to cause a significant increase in activity. Second, regressions of growth rate in length and mass on mass of supplemental water ingested were insignificant. We interpret this to mean that all hatchlings obtained enough water from the environment (prey, dewfall) to maintain growth. Water was not limiting even though the climatological data and personal observation indicated that 1984 was an extremely dry year. During the reproductive season (April–July 1984), precipitation (2.05 cm) was 0.65 cm below the 30 year mean for this area (NOAA Climatological Data). During the fall experimental period (August–October), precipitation (0.81 cm) was 0.35 cm below the 30 year mean.

We provided hatchlings with enough food and water to affect growth had these resources been limiting. What we have been calling supplemental feeding would more accurately be described as “replacement” feeding; the prey items we fed to hatchlings were not supplemental prey, but rather, were prey that hatchlings would have eventually eaten. We interpret the insignificant effects of supplemental feeding and watering on growth as evidence that food and water were not limiting at our study site. This conclusion is consistent with other studies of lizards at Arapaho Prairie. Jones et al. (1987) showed that fecundity of *S. undulatus*, which was variable from year-to-year, was unaffected by fluctuations in food abundance. They reported that food abundance over a four-year period averaged at least twice as high as levels typically reported in desert ecosystems. Additionally, Jones (1983) showed that there was no competition for food between *S. undulatus* and the ecologically similar and syntopic species, *Holbrookia maculata*, at Arapaho Prairie.

Comparing the growth rates of lizards among different field populations is difficult because the time intervals and physical environments during which growth is measured are often different. In comparison with other studies, the growth rates we report here are low because they were calculated over a relatively long period of time; we also included the two weeks prior to hibernation when ambient temperatures were low. Before the onset of cool, wet weather in late September, the growth rates in length of our hatchlings (0.37 ± 0.06 (95% CI) mm d⁻¹) equalled or exceeded the growth rates of hatchling *S. undulatus* maintained in the laboratory with abundant food and warm temperatures (Ferguson and Brockman 1980). The rate of growth in mass of hatchlings in our study also equalled or exceeded the rates of hatchlings maintained in the laboratory, even when we include growth during the period of cool weather (viz. $0.029\text{--}0.036$ g d⁻¹, our study vs $0.027\text{--}0.038$ g d⁻¹, Ferguson and Brockman 1980).

Ferguson and Brockman (1980) calculated field growth

rates (length) of hatchlings in Kansas and Texas that were similar to growth rates of our Nebraska hatchlings prior to the cool weather. Ferguson et al. (1980) and Tinkle and Ballinger (1972) stated that the growth of hatchlings in Kansas and Texas, respectively, was not limited by food. Similarly, our results suggest that food was not limiting during our study. High food abundance is typical in this area (Jones 1983, Jones et al. 1987) and the growth rates we report here are no higher than those reported for hatchling *S. undulatus* at this site by Jones and Ballinger (unpublished work). The abundance of grasshoppers (a major food item of *S. undulatus*) in 1984 likewise was not higher than normal (Joern 1982, unpubl. data). Thus, 1984 was not exceptional in terms of hatchling growth and food abundance.

Survival

There were no significant differences in survival between groups. The two groups receiving supplemental water were more active but had survival rates comparable to the groups that were active less often and presumably exposed to fewer predators. Hatchling survival appears to be very similar to adult survival. Jones and Ballinger (unpublished work) argued that predation at Arapaho Prairie is low and that mortality of adult lizards is density-independent and occurs primarily during hibernation. As with adults, the lowest survival for hatchlings at Arapaho Prairie occurred during hibernation (22% vs 83% during the 45 day fall treatment period). For comparison, Ferguson et al. (1983) reported that survival of hatchling *S. undulatus* in Kansas during their three-week treatment period was approximately 50%.

Time-space utilization

Evidence from several studies suggests that both supplemental food and water affect time-space utilization of lizards. Licht (1974), Simon (1975) and Ferguson et al. (1983) reported that lizards fed supplemental food decreased the size of their home-range. On the other hand, both Stamps and Tanaka (1981b) and Waldschmidt (1983) found no long-term changes in home-range size due to supplemental feeding. Other effects of supplemental food are increased rate of display (Stamps and Tanaka 1981b) and decreased rate of movement through the habitat (Waldschmidt 1983).

In Kansas, home-ranges of hatchling *S. undulatus* that received supplemental food were significantly smaller than home-ranges of control animals (Ferguson et al. 1983). Hatchlings on plots with natural food abundances likely foraged over larger areas to find sufficient food. However, if food is plentiful, home-range size should not be dependent on relative food abundance and supplemental feeding should have no effect on home-range size. This is exactly the result obtained in our study.

There have been few studies on the effects of supplemental water on time-space utilization. Stamps (1976) reported that hatchling *Anolis aeneus* decreased aggression and activity as rainfall decreased but, after receiving supplemental water, significantly increased activity and aggression. If supplemental water allows greater activity and higher levels of aggression, then we might expect individuals receiving supplemental water to have higher quality home-ranges. Fox (1978) and Fox et al. (1981) demonstrated that more aggressive juveniles (*U. stansburiana*) can, in some instances, obtain higher quality territories and home-ranges.

In studies to date, the effects of supplemental watering on reptiles have been to alter their habitat utilization, their activity, or both.

In our study, 12 mg of supplemental water $\text{g}^{-1} \text{d}^{-1}$ was sufficient to significantly increase the activity of the water only group and 7 mg $\text{g}^{-1} \text{d}^{-1}$ increased the activity of the food and water group to near statistical significance. Because water loss is greatly increased by the warmer body temperatures and greater activity (Mautz 1982), hatchlings that received supplemental water could be active more often without accruing a water deficit. Furthermore, the effect of water on activity was independent of its effect on growth. This suggests that growth was limited by factors other than the availability of food and water (e.g., rate of protein metabolism).

A discriminant analysis of the time-space variables failed to identify any significant discriminant canonical functions that could distinguish between the experimental groups. Thus, increased activity by the groups receiving supplemental water was not correlated with any differences in habitat utilization. The insignificant differences in home-range size and habitat use suggest that hatchlings that received supplemental water did not necessarily occupy or move into higher quality home-ranges but were simply active more frequently. Increased activity resulting from supplemental water conferred no detectable advantage in terms of growth or habitat use.

The aim of our study was to determine the effects of food and water on growth and time-space utilization of hatchling lizards. Supplemental watering increased the amount of time a lizard could be active. However, when active, hatchlings in all experimental groups utilized the habitat in a similar manner. We conclude that growth was not limited by either food or water during our study. We attribute this to the high food abundance and water availability at our study site. These results lead us to caution against the blanket assumption that lizards necessarily compete for food and high quality home-ranges or that growth is always limited by food and water.

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