

Young Desert Tortoise Survival: Energy, Water, and Food Requirements in the Field

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ABSTRACT.— Young desert tortoises (*Gopherus agassizii*) which hatched in large fenced enclosures in their natural habitat were studied during the first two years of their life. We measured rates of growth (body mass changes) and rates of energy metabolism (CO₂ production) and water flux (both by using doubly labeled water) from spring 1992 to spring 1994. We calculated rates of food consumption from energy budgets, and estimated water intake from the diet and from drinking rain water. When active, young tortoises used energy and water at rates similar to those expected for desert reptiles of their size, but they can conserve water and energy very effectively during dry seasons. They grew during the two-year study, having a 30% increase in body mass each year. Neonates and 1-year-olds showed substantial variation in rates of physiological processes between months within seasons, between seasons within years, and between years as well. The primary environmental factors cueing this variation apparently were temperature, rainfall, and the presence of green, succulent plant food. Metabolic rates peaked in late spring, and rates of water intake were highest either when green annual plants were available in spring or when rain fell in summer. During winter hibernation deep in burrows, tortoises were relatively inert, having very low rates of energy metabolism and water loss, and they lost little body mass. Rainless periods in summer appeared to be the most stressful times, as youngsters lost mass rapidly and their Water Economy Index values indicated a water deficit, even though they reduced their energy and water requirements by retreating into their burrows. During its first two years of life, a typical young tortoise used a total of about 175 g (dry matter) of food, equivalent to about 350 g fresh vegetation (3/4 of a pound) while growing from 34 to 55 g body mass. Neonate and 1-year-old survival may be threatened in dry years, when few annual plants germinate and summer rains are unavailable. Conservation efforts that improve availability and abundance of annual plants can benefit young tortoises.

KEY WORDS.— Reptilia; Testudines; Testudinidae; *Gopherus agassizii*; tortoise; physiological ecology; energetics; food requirements; water balance; behavior; hatchling survival; diet selection; drinking behavior; doubly labeled water; field metabolic rate; California; USA

The Mojave Desert populations of the desert tortoise, *Gopherus agassizii*, are listed as Threatened under the U.S. Federal Endangered Species Act. Presently available population data for chelonians indicate that neonate survival generally is very low (Congdon and Gibbons, 1990; Congdon et al., 1993). Among North American tortoises, mortality of young gopher tortoises (*G. polyphemus*) and Bolson tortoises (*G. flavomarginatus*) can be well above 50% per year (Morafka, 1994; Tom, 1994; Wilson et al., 1994). Mortality in young desert tortoises is presumed to be high as well (Germano, 1994; Fish and Wildlife Service, 1994). Although mortality in the egg phase may be relatively low for desert tortoises (Spotila et al., 1994), nest predation may be high (Turner et al., 1986). Adult mortality is about 2% per year (Fish and Wildlife Service, 1994). Thus, the period from before hatching to subadulthood seems to incorporate the most risk. It is important to know the causes of high youngster mortality in nature, because increases in survivorship at this stage of life can mean large changes in the population levels of this long-lived species (Congdon et al., 1993). Knowledge of mortality causes can be central to human efforts to improve neonate survival in the field,

which might be a promising way to conserve and restore this species.

This study was designed to provide details about the resource requirements, especially for energy, water, and food, of neonate (first year) and 1-year-old (between one and two years old) desert tortoises in the field. Neonates that were born inside a large fenced enclosure located in the central Mojave Desert were studied during each season to evaluate their physiological ecology through an entire year. The doubly labeled water method was used to measure rates of energy metabolism and water gain and loss.

MATERIALS AND METHODS

Study Site.— The 0.46 ha (1 acre) fenced enclosure was built in an otherwise undisturbed area (35°08'N, 116°30'W) in the southeast corner of the Fort Irwin National Training Center (U.S. Army), about 58 km northeast of Barstow, San Bernardino County, California. The vegetation at this site near the center of the Mojave Desert comprises a typical creosote bush (*Larrea tridentata*) and burro bush (*Ambrosia dumosa*) association. Rainfall was measured at a weather



Figure 1. Young desert tortoise (*Gopherus agassizii*) at the Mojave Desert field study site during autumn. The vegetation has been dead and dry for months, a situation commonly encountered by young tortoises.

station at Bicycle Dry Lake, about 21 km northeast of the site. Measurements were made during spring (March, April) and summer (July, August) of 1992, during spring (March), summer (June, July), and autumn (September) of 1993, and over winter from September 1993 to March 1994.

Animals. — The young tortoises in the enclosure in March 1992 had hatched the previous autumn from eggs produced by gravid females captured locally and placed in the enclosures for laying. All hatchlings were captured shortly after emerging from their nests, and identifying numbers were painted on their carapaces (Fig. 1).

Field Procedures. — Tortoises were captured by hand, weighed to 0.1 g, and given intramuscular injections (in the forelimb) of 0.15 ml of distilled water containing 97 atoms ^{18}O per 100 atoms oxygen and 0.33 millicuries (mCi) (equal to 17×10^6 Becquerels) of ^3H per ml. After waiting at least two hours for isotopes to mix completely in body water (Nagy, 1983), blood samples (about 120 μl) were taken from a jugular vein into heparinized glass capillary tubes, which were flame-sealed and placed on ice for transport to the University of California, Los Angeles, for analysis. The tortoises were immediately released where captured. Two uninjected tortoises were sampled to measure natural (background) abundances of the isotopes. Body water volumes at the time of injection were estimated from the dilution principle, using the ^{18}O isotope (Nagy, 1983). Recaptures of injected tortoises were attempted after 2 to 4 weeks. In spring and summer of 1992 injected tortoises were caught a second time, after another 2 to 4 weeks, to evaluate within-season variation. When animals were recaptured, their body mass was recorded, a urine (preferred) or blood sample was taken, and they were released again. If we captured a tortoise at the beginning of a new measurement period that had been

injected the previous season, we took a urine or blood sample before reinjecting it so that we could correct for existing isotopes when calculating body water volume. Fortunately, some previously injected animals still contained enough isotope to allow determination of flux rates between seasons, but we had only a small sample size for some seasons.

Laboratory Procedures. — Pure water was distilled from blood and urine samples under vacuum (Nagy, 1983). Aliquants were analyzed in duplicate for ^3H activity by liquid scintillation spectrometry, and in triplicate for ^{18}O concentration by proton activation analysis (Wood et al., 1975). Body water volumes, necessary for the field metabolic rate (FMR) and water flux calculations, were estimated for the times of injection from the dilution volumes of injected ^{18}O (Nagy, 1983). Body water volumes at recapture were estimated from body mass, assuming individuals maintained the same fractional body water content during the study. Rates of water influx and efflux were calculated using equations (4) and (6) in Nagy and Costa (1980), which account for linear change in body mass over measurement periods (see Appendix for all numbered equations). Field metabolic rates were calculated using equation (2) in Nagy (1980), as modified from Lifson and McClintock (1966). Rates of CO_2 production were converted to units of energy (J or joules) using the relationship 21.7 J/ml CO_2 produced for a herbivorous diet, and 27.7 J/ml CO_2 for winter periods, when tortoises were metabolizing mainly fat (Nagy, 1983). Feeding rates were calculated from FMR assuming desert annual plants contain 16.6 J/mg dry matter, of which 51.4% is metabolizable by tortoises (Nagy and Medica, 1986). Metabolic water production was calculated from FMR values assuming 0.637 ml H_2O produced per liter CO_2 produced (Nagy and Medica, 1986). Preformed dietary water intake was calculated from estimated dry matter intake (above) along with the value of 2.2 g water per g dry matter in the spring diet, as determined for desert tortoises in Nevada (Nagy and Medica, 1986). The sum of metabolic water produced plus dietary water consumed was compared to total water intake measured isotopically to evaluate drinking water intake and water vapor exchange. We estimated growth rates (in kJ/d) from changes in body mass, assuming a body energy content for growing tortoises of 23.9 kJ/g dry matter (Nagy and Medica, 1986).

Statistics. — Mean values are given along with standard deviations. Differences between means or medians were tested for statistical significance using a two-tailed *t*-test (paired where appropriate), or a Mann-Whitney *U*-test when variances were heterogeneous. Correlations between variables were evaluated using the method of least-squares regression analysis (Dixon and Massey, 1969) or polynomial regression using Sigmaplot version 1.00 (Jandel Scientific Software) statistical software. Analysis of variance (ANOVA) or Kruskal-Wallis analysis of variance on ranks was used to test for differences between three or more groups, followed by pairwise comparisons via Student-Newman-Keuls or Dunn's method. Statistical significance was accepted at $p \leq 0.05$.

Table 1. Seasonal changes in body mass, water influx rate, and field metabolic rate of young desert tortoises (*Gopherus agassizii*) through the first two years of life.

Season or month, year	Body Mass				Water Influx Rate		Field Metabolic Rate		
	mean, g	(SD, n)	change, %/d	(SD, n)	ml H ₂ O/d	(SD, n)	ml CO ₂ /d	(SD, n)	kJ/d (SD, n)
SPRING, 1992									
(March)	34.4	(6.6, 18)	+0.62	(0.21, 18)	1.43	(0.59, 18)	131	(53, 18)	2.85 (1.14, 18)
(April)	37.0	(6.4, 16)	+0.33	(0.33, 16)	1.35	(0.53, 16)	230	(135, 16)	5.00 (2.93, 16)
(March and April)	35.1	(6.1, 22)	+0.50	(0.23, 22)	1.40	(0.56, 22)	174	(73, 22)	3.77 (1.58, 22)
SUMMER, 1992									
(July)	35.0	(6.2, 11)	-0.68	(0.49, 11)	0.13	(0.04, 11)	68	(39, 10)	1.48 (0.85, 10)
(August)	35.0	(6.3, 10)	+0.35	(0.40, 10)	0.42	(0.17, 10)	79	(55, 8)	1.70 (1.18, 8)
(July and August)	40.5	(14.3, 17)	-0.14	(0.32, 17)	0.33	(0.18, 17)	71	(54, 17)	1.54 (1.17, 17)
WINTER, 1992									
(August 92 to March 93)	42.5	(12.8, 5)	+0.06	(0.04, 5)	0.19	(0.06, 5)	21	(7.7, 5)	0.59 (0.21, 5)
SPRING, 1993									
(March)	43.8	(10.5, 15)	+0.64	(0.51, 15)	1.26	(0.94, 15)	144	(0.99, 14)	3.13 (2.15, 14)
SPRING to SUMMER, 1993									
(March to June)	51.1	(19.6, 6)	+0.24	(0.09, 6)	1.25	(0.70, 6)	238	(211, 6)	5.16 (4.58, 6)
SUMMER, 1993									
(June and July)	52.2	(11.1, 7)	-0.22	(0.27, 7)	0.31	(0.10, 7)	119	(39, 7)	2.60 (0.84, 7)
SUMMER to AUTUMN, 1993									
(July to September)	53.8	(24.6, 4)	-0.33	(0.12, 4)	0.13	(0.11, 4)	62	(24, 4)	1.35 (0.52, 4)
AUTUMN, 1993									
(September)	50.1	(17.8, 10)	-0.39	(0.13, 10)	0.16	(0.11, 10)	97	(68, 10)	2.10 (1.48, 10)
WINTER, 1993									
(September 93 to March 94)	54.7	(16.0, 12)	+0.01	(0.07, 12)	0.09	(0.06, 12)	19	(10, 12)	0.53 (0.28, 12)

RESULTS AND DISCUSSION

The mean body masses of the tortoises we sampled increased from 34 g at the beginning of the study to 55 g two years later (Table 1). The individuals comprising each seasonal sample were collected opportunistically, so samples were a mixture of individuals studied previously along with naive individuals. Thus, the mean body mass values in Table 1 represent the population rather than individuals. The increase in variability of body mass through time (SD for mass increased from 6 to near 20; Table 1) was due in part to recruitment of newly hatched tortoises in summer 1993, and in part to large variation in the 1992 cohort. Some frequently recaptured individuals increased their mass nearly 50% per year, while a few others showed no gain or even mass loss during the entire two years.

Body water volumes, expressed as percent of body mass, did not change significantly from spring 1992 through summer 1993, and averaged 82.7% (\pm SD = 4.2, n = 44). However, water volume dropped to 76.6% (\pm 2.9%, n = 9) in September 1993.

Young tortoises gained weight most rapidly during spring of both years, and lost mass during both summers (Table 1). Interestingly, mass change over winter was negligible (Fig. 2). Rates of water intake, on a whole-animal basis, were high in spring and low during summer and winter. Water influx rate tripled between July and August 1992, in conjunction with rains in August. Field metabolic rates were highest during late spring and early summer, and lowest during winter.

Body Size Effects. — Energy and water needs depend on body size, and body masses of the young tortoises we studied varied between seasons (Table 1). Thus, before comparing results for different seasons, it is important to correct for

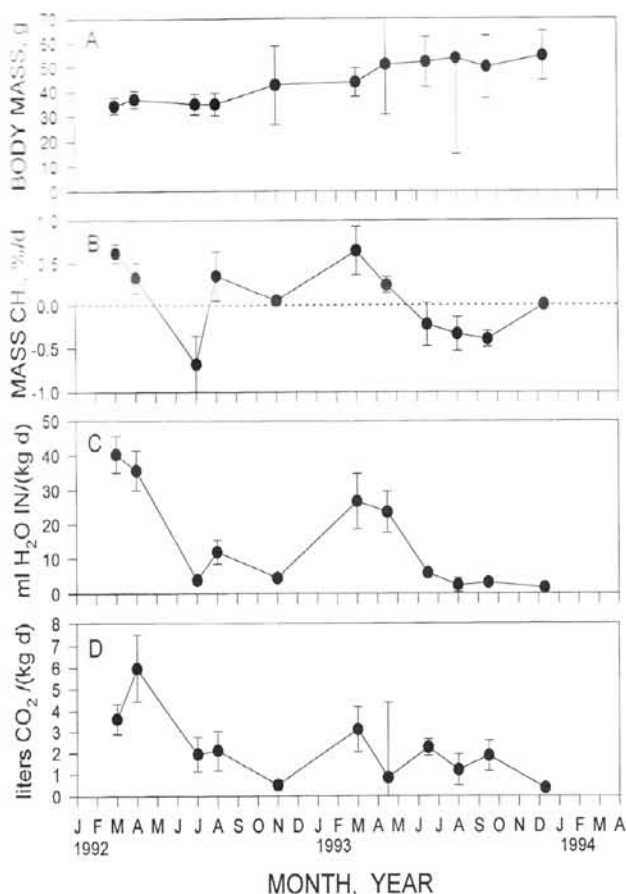


Figure 2. Monthly, seasonal, and yearly changes in body mass (A), daily rate of body mass change (B), and mass-specific daily rates of water influx (C) and CO₂ production (D) in a cohort of young desert tortoises (*Gopherus agassizii*) living in a large field enclosure during the first two years of life. Symbols indicate means \pm 95% confidence intervals.

variation in body mass. However, the relationship between increased need for energy and water and increased size is often not one-to-one. To determine this relationship for young tortoises, we regressed rates of energy and water flux (whole-animal basis, Table 1) on body mass on \log_{10} coordinates. Within each of the 13 study periods listed in Table 1, \log of field metabolic rate ($\text{ml CO}_2/\text{d}$) was significantly correlated with \log of body mass (g) in seven cases. Small sample size was a factor in four of the six non-significant cases. Thus, we combined all data for active seasons, and found a significant regression (Fig. 3), having the relationship: $\text{ml CO}_2/\text{d} = 2.2 \text{ g}^{1.02}$ ($p = 0.0003$, $r = 0.40$, SE of slope = 0.27). The slope of this allometric regression does not differ significantly from 1.0 (a one-to-one relationship), which justifies correcting for body mass effects by simply dividing by mass to yield units of $\text{ml CO}_2/(\text{kg d})$ or $\text{kJ}/(\text{kg d})$. For the water influx rate data, 8 of the 13 study periods yielded significant correlations, most of which had slopes somewhat higher than, but statistically indistinguishable from, 1.0. Surprisingly, the combined data for all active seasons showed no significant correlation ($p = 0.31$, $n = 80$). However, water influx rate was linearly related to field metabolic rate for all data combined ($p < 0.0001$, $r = 0.68$, 95% confidence interval of log-log slope included 1.0). Thus, we assumed that a slope of 1.0 was also appropriate for water influx rate, and corrected these results to units of $\text{ml H}_2\text{O}/(\text{kg d})$ for subsequent calculations.

Season Effects. — Monthly variation was examined statistically using paired t -tests on results from tortoises recaptured in both March and April 1992 and in both July and August 1992. In spring, significant monthly differences occurred in mean body mass, rate of mass change, and field metabolic rate, but not in water influx rate (Fig. 2). During summer, significant monthly differences occurred in rates of mass change and water influx, but not in mean mass or field metabolism. These differences correspond to environmental differences between months. In March, ambient temperatures and metabolic rates were lower than in April, but food plants were more succulent in March, and tortoises had higher water intake rates and grew faster. July was hot and dry, and tortoises had low water intake rates and lost body mass, but there was rain in August and they had higher rates of water intake and gained mass, apparently because they drank rain water. (We have seen neonates in the field place their noses to the substrate during rains, just as captive desert tortoises do when offered water in a pan, but we only surmise that neonates were drinking.) Thus, the physiological responses and needs of tortoises can change on a monthly basis depending on the status of their habitat.

Seasonal differences were also evident (Fig. 2). For this analysis, we used overall results for spring and summer, obtained by ignoring the data for the recaptures made at the midpoint of the two-month study intervals and calculating rates from initial and final samples alone. We did not combine results by season from the two years because of significant differences between years (see below). In 1992, significant seasonal differences existed in rates of body mass

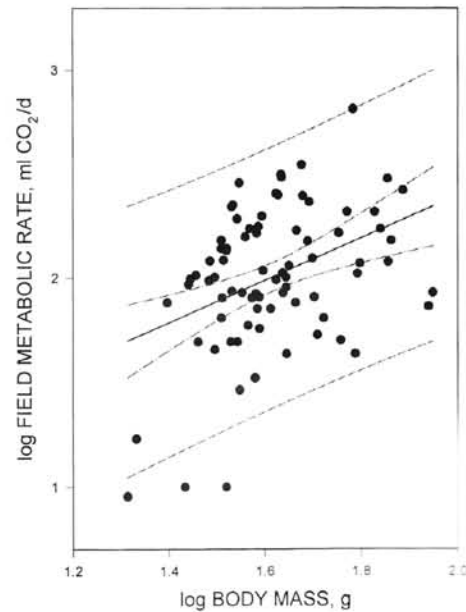


Figure 3. Relationship between whole-animal field metabolic rate ($\text{ml CO}_2/\text{d}$) and body mass (g) of young desert tortoises on logarithmic coordinates. The regression (solid line) is significant ($p = 0.0003$), and has the equation $\text{ml CO}_2/\text{d} = 2.24 \text{ g}^{1.02}$, ($r = 0.40$; d.f. = 1,79; SE of the slope = 0.27). The long-dashed lines indicate the 95% confidence intervals of the regression and the short-dash lines show the 95% confidence intervals of the prediction.

change, water influx, and field metabolism. For all three parameters, rates during spring were higher than during summer or winter. The situation in 1993 was similar, with mass change rate being greater during spring than during autumn or summer, water influx rate being greater in spring than in autumn or winter and greater in summer than in winter, and with field metabolic rate being lower in winter than in spring, summer, or autumn. These results are consistent with expectations based on changing environmental variables, especially temperature (hot summers and cool winters), rainfall (rain during winter inactivity periods and spotty thundershowers in late summer), and food availability (spring). Tortoises were active in the warmth of spring, eating and growing. The summer heat and drought elicited reduced above-ground diurnal activity and feeding, but thundershowers provided rain water which many tortoises drank. Winter cold reduced activity, including feeding, and tortoises spent most of their time hiding in burrows.

Adult desert tortoises also reduce above-ground activity during summer droughts, but the arrival of summer thundershowers triggers increased activity and drinking behavior (Nagy and Medica, 1986; Peterson, 1996a). Neonates and adults apparently share the ability to perceive the availability of rainwater in summer (Medica et al., 1980). Drinking rain water is critically important for adults to obtain adequate supplies of other nutrients (energy, protein) during the year (Peterson, 1996a, 1996b).

Variation between years was analyzed by comparing results for March 1992 with March 1993, results for summer 1992 with summer 1993, and results for "winter" (actually autumn and winter) 1992–3 with winter 1993–4. A paired t -

test ($n = 7$) indicated that during March of 1992, tortoises had lower body masses but higher mass-corrected rates of water influx and energy metabolism than they did in March of the following year. Similarly, tortoises in summer of 1992 ($n = 17$) had lower body masses but higher rates of water influx than did tortoises ($n = 7$) in summer of 1993. The only significant difference between means for winter 1992–3 ($n = 5$) and winter 1993–4 ($n = 12$) was for water influx rate, which was three times higher during 1992–3 than during 1993–4. These differences between years preclude combining the seasonal data for different years. The differences in body mass are expected for growing animals, but the differences in mass-specific physiological rates are most likely due to the differences in rainfall regime between years, with tortoises using more drinking water during 1992 (see below).

Comparative Physiology. — The field metabolic rate expected for a free-living reptile during its activity season may be estimated using the allometric equation describing results for iguanid lizards (Nagy, 1982, 1987; see Appendix). For a 45 g animal this relationship yields a value of 4.69 kJ/d, which for a herbivore is equivalent to 0.216 liter CO_2 /d, or 4.80 liter CO_2 /(kg d). Thus, the expected metabolic rate for a reptile is virtually identical to the actual field metabolic rate of young tortoises during spring of 1992 (Fig. 2). However, neonates and 1-year-olds had energy expenditures that were less than half of the expected value in summer 1992, and throughout the active season of 1993. Clearly, young tortoises can conserve much energy by reducing metabolic expenditures during spring, summer, and autumn. In winter, field metabolic rates were only about 10% of those expected for an active reptile.

Water influx rate can also be predicted from empirical allometric equations (Nagy and Peterson, 1988; see Appendix). A free-living 45 g reptile would be expected to have an influx rate of 23 ml H_2O /(kg d), and a desert reptile of the

same body mass has an expected influx rate of 17 ml H_2O /(kg d). Young tortoises in spring of 1992 were obtaining about twice as much water as expected (Fig. 2) and they also obtained more water than expected in spring of 1993. This comparison reveals an important desert adaptation possessed by young tortoises: the ability to obtain large amounts of water. They do this by selecting and eating large quantities of succulent foods in spring and by drinking available rain water in summer.

Tortoises that are gaining weight might be expected to have relatively high rates of water influx and energy metabolism due to feeding activities, while those that are losing weight might be less active and have reduced feeding rates. These predictions can be tested by regressing rates of water influx or field metabolism on rates of change in body mass. A significant relationship would lend support to the hypothesized explanation. Also, the intercept of a statistically significant regression can serve as an estimate of the rate of water influx or energy metabolism required by a young tortoise just to maintain itself with constant weight. The regression of water influx on body mass change for the active seasons (Fig. 4) was significant ($p < 0.0001$) and had the equation: ml H_2O influx/(kg d) = $16 + 24.3$ (% mass change/d), with $r = 0.72$ and d.f. = 1,79. The intercept indicates that an active (non-hibernating) neonate or 1-year-old tortoise needs a water influx rate of 16 ml/(kg d) to maintain water balance in the field. This is a little lower than the 17.2 ml/(kg d) predicted above for a desert reptile in general, suggesting that young desert tortoises possess good water-conserving abilities, as do other desert reptiles. In fact, the relationship shown in Fig. 4 looks like it would be better represented by two lines (as is the case for adult tortoises; Peterson, 1996b) and the zero mass change intercept might be closer to 7 ml/(kg d). If correct, this would indicate an unusually good ability of young tortoises to conserve water. More data are needed to address this possibility. Large adult males can maintain body mass in the field in the absence of drinking water with a water influx rate of only 1.5 ml/(kg d) (Peterson, 1996b).

The regression of metabolic rate on change in mass was also significant ($p < 0.0001$) and had the equation: liters CO_2 /(kg d) = $2.81 + 1.79$ (% mass change/d), with $r = 0.43$ and d.f. = 1,79. The intercept of 2.81 liters CO_2 /(kg d) for a steady-state young tortoise is only 58% of the rate of 4.80 liters CO_2 /(kg d) expected for a 45 g reptile. Thus, it appears that young tortoises have unusually low energy requirements, and this should enhance survivorship in a desert habitat, where plant productivity is lower than in other habitats.

Water Economy Index. — The ratio of water influx rate to field metabolic rate indicates the amount of water an animal uses per unit of energy it processes, and is termed the water economy index (WEI). A low ratio in an animal that is maintaining weight (and is assumed to be maintaining water balance as well) indicates a low water requirement. It can be calculated that animals with no drinking water, but maintaining weight while eating green plant matter, should have a WEI between 0.15 and 0.25 (Nagy and Peterson,

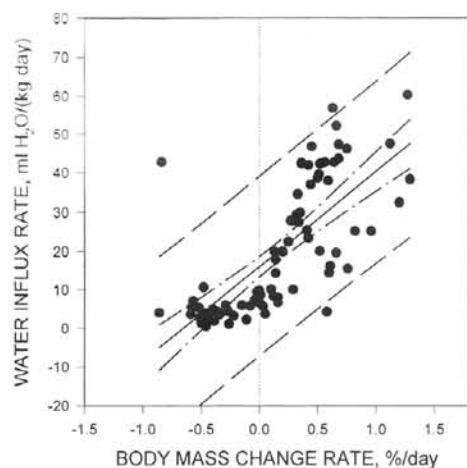


Figure 4. Relationship between water influx rate [mass-corrected units of ml/(kg d)] and rate of body mass change (as %/d) in young desert tortoises. The regression (solid line, $p < 0.0001$) has the equation: ml H_2O influx/(kg d) = $16.0 + 24.4$ (% change/d), with $r = 0.722$; d.f. = 1,80; SE of intercept = 1.36. The dash-dot lines indicate the 95% confidence intervals of the regression and the dashed lines show the 95% confidence intervals of the prediction.

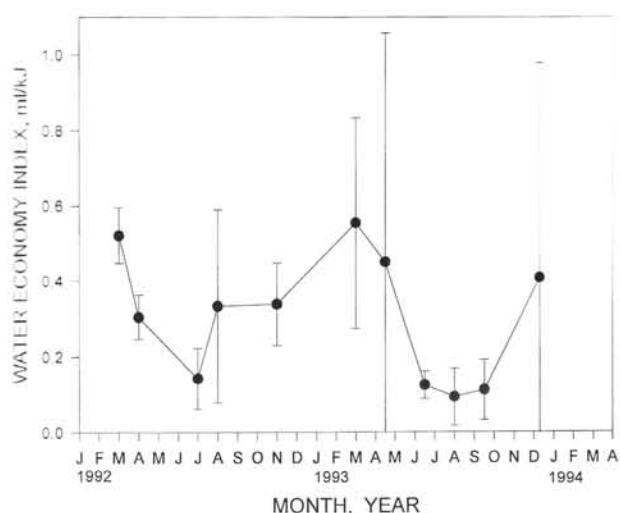


Figure 5. Seasonal changes in water economy index (WEI = ml H_2O influx per kJ energy metabolized) of young desert tortoises. Symbols represent mean \pm 95% confidence intervals.

1988). The WEI of young tortoises ranged from 0.09 to 0.55 ml H_2O /kJ (Fig. 5), with high values occurring during spring when tortoises were gaining weight and low values occurring when tortoises lost weight. To estimate WEI for youngsters maintaining constant body mass, we regressed WEI on mass change rate using means for each season. The regression (Fig. 6) was significant ($p = 0.0003$), and the equation for the line, $ml/kJ = 0.29 + 0.35 (\%/d)$, ($r = 0.88$, d.f. = 1,9), indicates a steady-state WEI value of 0.29 ml/kJ. This is a bit higher than that for a typical herbivore and is much higher than the value of 0.1 ml/kJ for non-drinking adult desert tortoises (Peterson, 1996b). This indicates two things: that baby tortoises may select especially succulent foods to eat and that they may drink rain water when available during their activity season. Thus, WEI values confirm the ability of tortoises to obtain much water from their habitat.

Food Requirements. — The rate at which young tortoises consumed metabolizable energy via food was estimated as the sum of energy allocated to metabolism (measured with doubly labeled water) and energy allocated to growth (estimated from mass changes). For a non-feeding tortoise, the rate of negative growth (indicating use of stored fat) would equal field metabolic rate. We did not observe this in our results (Fig. 7) for two main reasons. First, our measurement intervals all included periods when tortoises ate at least some food. Second, we could not resolve body mass changes into their component parts (i.e., change in water volume, lean body mass, and fat mass) so we lacked the resolution to permit more detailed analyses of energy budgets.

These estimates of feeding rates permit compilation of an energy budget for young tortoises during an entire year. We chose the period August 1992 to July 1993, during which we obtained continuous field measurements (Fig. 7), which corresponds approximately to the second year of life of a tortoise. During that year, a tortoise having an average body mass of 43.6 g catabolized 757 kJ of chemical potential

energy into heat energy, it added 69 kJ of chemical potential energy to its body substance via growth, and it consumed 826 kJ of metabolizable chemical potential energy in the form of food to accomplish this. Assuming a food gross energy content of 16.6 kJ/g dry matter and a digestibility of 51.4%, as for adults (Nagy and Medica, 1986), a youngster would consume 96.8 g of food (dry matter only) during its second year of life. Assuming an average diet water content of about 50%, the fresh food mass consumed in the second year of life is about 200 g, or a bit less than 1/2 pound of plant matter. We estimate that during its first year of life when its average body mass is about 35 g, a neonate would consume 78 g dry matter, or about 160 g fresh food. Thus, a young tortoise consumes an estimated 360 g (about 3/4 pound) of desert vegetation during its first two years of life, while increasing its body mass by about 60%.

Stress and Adaptation. — Young tortoises are apparently stressed by reduced availability of water in late spring and summer. They lost body mass during those periods in both years (Fig. 2), and though the energy budget analysis (Fig. 7) indicated that they were eating, their food plants were probably too dry by then to permit them to achieve water balance. Some shrubs still had green leaves, but the annual plants accessible to young tortoises as food were dead and dried. Young tortoises that are active above ground and feeding in July would be losing water by evaporation to the hot, dry air, as well as in the feces produced. If the food does not contain enough water to balance these losses, tortoises will lose body water and body weight, even though they maintain energy balance. Young tortoises could achieve water balance under these circumstances by drinking rain water, should it become available. They did just that in August 1992 (when no green, succulent plants were present

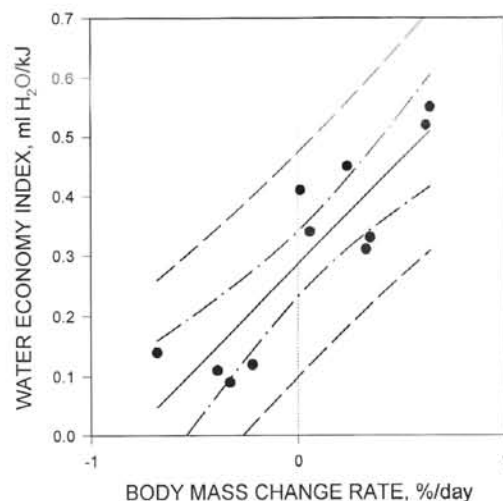


Figure 6. Relationship between water economy index (in ml H_2O influx per kJ energy metabolized) and daily rate of body mass change in young desert tortoises. The regression (solid line, $p = 0.0003$) has the equation: $ml/kJ = 0.286 + 0.350 (\%/d)$, with $r = 0.884$, d.f. = 1,9, SE of intercept = 0.025. The intercept indicates that young tortoises maintaining constant body masses would have a WEI of 0.286 ± 0.050 . The dash-dot lines indicate the 95% confidence intervals of the regression and the dashed lines show the 95% confidence intervals of the prediction.

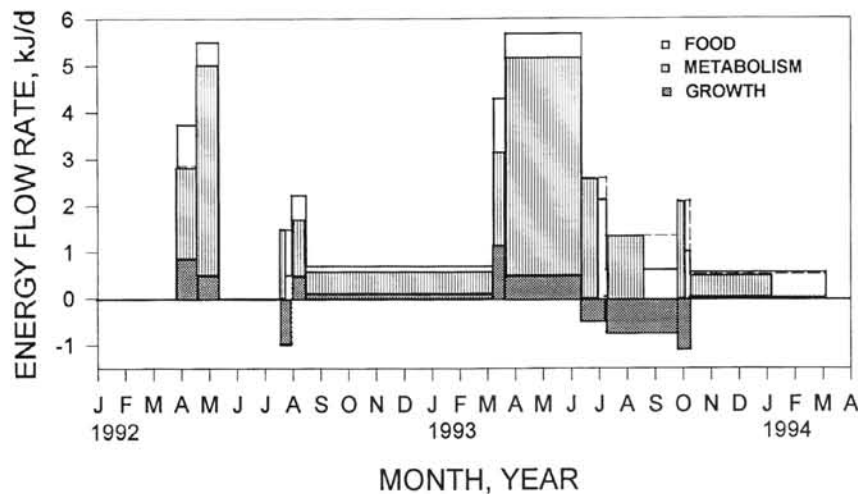


Figure 7. Seasonal changes in energy flux rates in young desert tortoises. Daily rates of food consumption (metabolizable energy intake in kJ/d, open boxes) were calculated as the sum of metabolic energy expenditure in kJ/d (vertical-lined boxes) and growth energy in kJ/d (hatched boxes).

in the habitat), as indicated by their increased water influx rates (Fig. 2), increased WEI (Fig. 5), and gain of body mass (Fig. 2). The itemized water budgets we derived from energy metabolism, food consumption, and diet composition values (Fig. 8) indicate that young tortoises tripled their intake of water in August 1992, compared to the preceding July, mainly by drinking rain water. If no rain falls, tortoises can reduce their rate of dehydration by not feeding and by remaining inactive in their burrows. Youngsters apparently did this to a large extent during the rainless summer of 1993,

as indicated by their low metabolic and water influx rates (Fig. 2) and low estimated feeding rates (Fig. 7). As a result, they lost mass much more slowly than they did during July of the previous year. However, the burrows in summer must be much drier than they are in winter, when the soil is moist from winter rains. During winter, young tortoises were apparently able to avoid dehydration and weight loss (Fig. 2) by staying in humid burrows, as do adults (Nagy and Medica, 1986). Thus, the main behavioral adaptations of young desert tortoises seem to be selection of a succulent

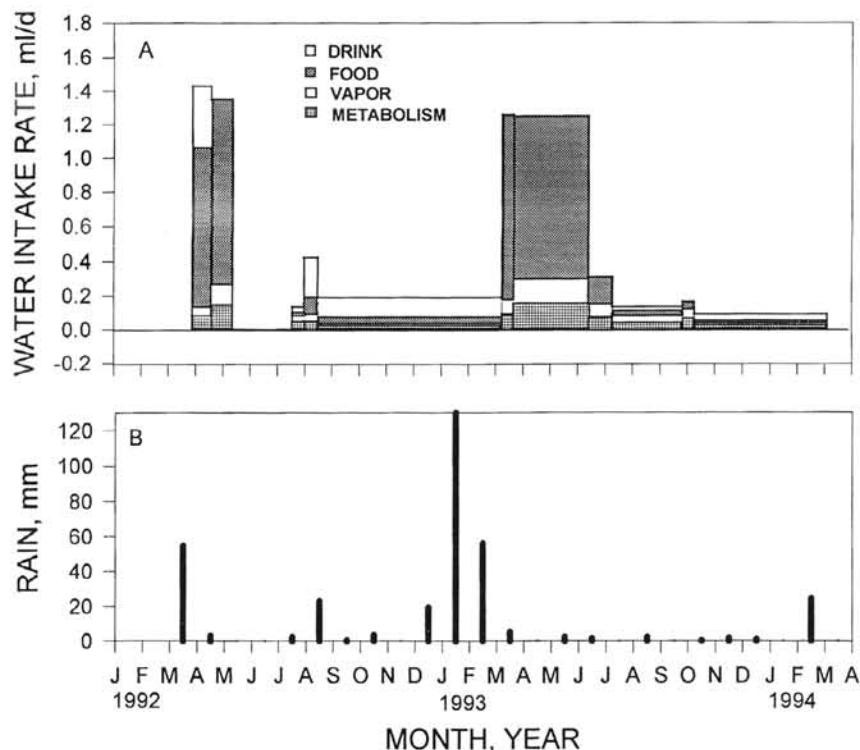


Figure 8. Seasonal changes in (A) estimated water budgets of neonate and 1-year-old desert tortoises, and (B) rainfall amounts. Total water intake rates were measured with doubly labeled water, metabolic water production and water vapor diffusional influx were calculated from field metabolic rates, water intake via the diet was estimated from food consumption calculations (Fig. 7), and drinking water intake was estimated by calculating the difference.

diet, drinking rain water when available during their activity season, and retreating to burrows to avoid hot, dry conditions in summer and to a lesser extent cold conditions in winter.

Conservation Implications

In the long-lived Blanding's turtle, Congdon et al. (1993) found that population stability was most sensitive to changes in adult or juvenile survival. It seems likely that desert tortoise populations are similarly sensitive to adult and juvenile survival. Although the major cause of mortality of young desert tortoises is probably predation, our results indicate that resource shortages, especially water in the form of rain or succulent vegetation, can be life-threatening as well. It follows from these conclusions that young tortoises should benefit from any action that increases or prolongs the availability of growing annual plants in their habitat. Similarly, their survival may be jeopardized by management actions that reduce the standing biomass, or shorten the period of availability, of annual plants in the tortoise habitat.

The availability of rain water in the warm seasons can be quite beneficial to the physiological well-being of neonates and 1-year-olds. Although rainmaking on a large scale is probably not a reasonable management option, small-scale efforts (occasional sprinkler irrigation in selected plots) may be feasible. One or two short periods of drinking water availability per year can be of great benefit to desert tortoises, both young and adult alike.

Burrows are clearly critically important for providing relatively humid and cool microenvironments for young tortoises. Burrow use reduces daily water requirements substantially during warm seasons, and during winter, it permits young tortoises to remain in water balance (maintain constant weight) for long periods of time. Thus, the availability of soils that permit burrowing and have the structural integrity to allow burrows to persist should benefit young tortoises as well. Activities that disrupt soil structure or alter the distribution of soil particle sizes may be deleterious.

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APPENDIX

Equations used for calculating body water volumes from equilibrium concentrations of injected isotopes, and field metabolic rates and water flux rates from isotope concentration changes, along with allometric (scaling) relationships used for predicting rates of energy metabolism and water intake in free-living reptiles.

Total Body Water (W):

$$W = \frac{(^{18}\text{O}_{\text{dil}} - ^{18}\text{O}_{\text{dis}})(V_{\text{dis}} / V_{\text{inj}} + V_{\text{inj}})}{(^{18}\text{O}_1 - ^{18}\text{O}_{\text{bg}})}$$

where W is in ml; $^{18}\text{O}_{\text{dil}}$ is concentration of ^{18}O , in units of atom % or parts per million (PPM), in the dilution of the injection solution; $^{18}\text{O}_{\text{dis}}$ is ^{18}O concentration in the distilled water used to dilute the injection solution; V_{dis} is volume (ml) of distilled water used to dilute the injection solution; V_{inj} is the volume (ml) of the injection solution in the dilution; V_{inj} is the volume of the injection administered to the animal; $^{18}\text{O}_1$ is the ^{18}O concentration in the initial blood sample (after equilibration of the injected isotope); and $^{18}\text{O}_{\text{bg}}$ is ^{18}O concentration in an uninjected animal (natural abundance, or background) (Nagy, 1983).

Field Metabolic Rate (FMR):

$$\text{FMR} = \frac{51.86 (W_2 - W_1) \ln(^{18}\text{O}_1 \cdot \text{H}_2 / ^{18}\text{O}_2 \cdot \text{H}_1)}{(M_1 + M_2) \ln(W_2 / W_1) t}$$

where FMR is in units of ml $\text{CO}_2/(\text{g h})$; W is body water volume (ml); ^{18}O is concentration in atom % or PPM (corrected for background); ^3H is tritium specific activity in counts per minute (CPM) per five μl (corrected for background); M is body mass in g; t is time elapsed in days; ln signifies natural logarithm; the subscripts 1 and 2 represent initial and final values; and the factor 51.86 incorporates conversion factors for various units (equation 2 in Nagy, 1980, for situations where body water volume changes linearly through time).

Water Influx Rate (WIR):

$$\text{WIR} = \frac{2000 (W_2 - W_1) \ln(^3\text{H}_1 W_1 / ^3\text{H}_2 W_2)}{(M_1 + M_2) \ln(W_2 / W_1) t} + \frac{2000 (W_2 - W_1)}{(M_1 + M_2) t}$$

where WIR is in units of ml $\text{H}_2\text{O efflux}/(\text{kg d})$ and the factor of 2000 converts from g to kg and is involved in calculating mean body mass (condensed from equations 4 and 6 in Nagy and Costa, 1980, for situations where body water volume changes linearly through time).

FMR Prediction (FMR_p):

$$\text{FMR}_p = 0.224 M^{0.799}$$

where FMR_p is in units of kJ/d and M is body mass in g (equation 38 in Nagy, 1987, the empirical allometric equation describing the relationship between FMR and body mass measurements in free-living iguanid lizards).

WIR Prediction (WIR_p):

$$\begin{aligned} \text{All reptiles: } \text{WIR}_p &= 0.065 M^{0.726} \\ \text{Desert reptiles: } \text{WIR}_p &= 0.038 M^{0.792} \end{aligned}$$

where WIR_p is in units of ml/day and M is body mass in g (equations 18 and 19 in Nagy and Peterson, 1988, the empirical allometric equations for measured WIR in free-living reptiles).

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