Energy and Water Balance, Diet, and Reproduction of Female Desert Tortoises (*Gopherus agassizii*)

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Abstract. – Long-term chronic impacts upon the diet and nutrition of female desert tortoises can decrease fecundity and cause local extinctions. In this synthesis, I analyze energy budgets, water budgets, and diets to evaluate the impact of environmental variation upon reproductive output. Female desert tortoises relax homeostatic regulation of many nutrient budgets (e.g., water, energy, nitrogen, and minerals) in order to endure the extremely harsh and variable conditions of their desert clime. Their diets also reflect adjustments to the variable abundance and nutritive value of desert plants, especially winter annuals. The relaxed approach to homeostasis helps desert tortoises survive and helps females muster the resources (nutrients) to produce eggs in most years. Female desert tortoises use an approach intermediate to capital and income breeding, relying upon body reserves and spring food consumption to produce eggs. Despite the extreme tolerances effected by relaxing homeostasis, desert tortoises are vulnerable to extreme desert conditions. Extended droughts preclude drinking and greatly reduce the availability of nutritive dietary plants, decreasing survivorship and egg production. Global environmental change could exacerbate these extreme conditions, adding another anthropogenic impact upon the Threatened desert tortoise.

Key Words. – Reptilia; Testudines; Testudinidae; *Gopherus agassizii*; tortoise; ecology; diet; eggs; energy; homeostasis; reproduction; water; USA

Drastic declines in chelonian populations worldwide have threatened or endangered many chelonian species with extinction and generated a critical need for chelonian conservation (IUCN, 2000; Klemens, 2000). In many instances, the effectiveness of chelonian conservation efforts would be improved with fundamental knowledge about the species' life history traits (Heppell, 1998; Congdon et al., 2000). Chelonian life history patterns usually include high adult survivorship, high egg and juvenile mortality (relative to adult mortality), delayed sexual maturity, and iteroparity. Consequently, one adult chelonian is often more valuable *per capita* to population stability than is one egg or hatchling (Frazier, 1992, 1993; Heppell, 1998). Under these circumstances, human intervention may be more effective by increasing adult survivorship (e.g., via use of Turtle Excluder Devices in shrimp nets).

This strategy may be effective if adults comprise the largest proportion of a population. If juveniles comprise the largest proportion of the population, stability of the population may be influenced more through the juvenile cohort than through the adult cohort (Heppell, 1998). Under these circumstances, conservation efforts aimed at juvenile survivorship can be the most effective. Conservation efforts aimed at juvenile and adult survivorship will typically be more effective than efforts to enhance fecundity (Heppell, 1998; Congdon et al., 2000). However, population models (e.g., U.S. Fish and Wildlife Service, 1994) suggest that long-term, chronic im-

pacts upon fecundity can cause local extinctions for chelonians. Given mounting concerns about global warming and its long-term impact upon ecosystem flora and fauna, it would be useful for managers and conservation biologists to understand the degree to which chelonian fecundity is affected by environmental variation.

Deserts are characterized by low primary productivity (Pianka, 1978) and extreme environmental variation (Louw and Seely, 1982), which exacerbates the limiting nature of resources available to desert organisms. Although desert tortoises have many adaptations or exaptations for desert survival (Minnich, 1977; Medica, et al., 1980; Nagy and Medica, 1986; Peterson 1996a, and many others), man threatens desert tortoises in many ways (U.S. Fish and Wildlife Service, 1994; Berry and Christopher, 2001). For desert tortoises there is an increasing body of literature regarding survivorship (e.g., Turner et al., 1984; Nagy and Medica, 1986; Peterson, 1994; Berry et al., 1996) and fecundity (Turner et al., 1986; Henen, 1994a,b, 1997; Murray et al., 1996, Mueller et al., 1998; Henen and Oftedal, 1999; Wallis et al., 1999, Averill-Murray et al., 2002). Our ability to develop accurate demographic models and conservation plans for the threatened Mojave Desert tortoise would benefit from a greater understanding of the relationships between 1) female nutrient budgets, 2) food abundance, 3) female tortoise diets, and 4) reproductive output. Here I present a synthesis of such relationships.

NUTRIENT BUDGETS

Energy Budgets and Diet

Field Site and Methods. — The influence of energy storage and use upon egg production was evaluated for 9 wild female *G. agassizii* at Goffs, California (34°52'N, 115°10'W) from July 1987 through July 1989 (see Henen, 1997, for details). This period coincided with two annual reproductive cycles, with females laying their eggs by early July each year. I considered spring to consist of an early spring period (from emergence in late February to early March until mid-April) and a late spring period, extending from mid-April until the summer solstice (June 21). Females forage and drink in early spring, and body mass often peaks by mid-April, about the time females ovulate their first clutch of eggs (Henen, 1997; Henen and Oftedal, unpubl. data; see also Rostal et al., 1994). During late spring at Goffs, ambient temperature increased substantially and most annual plants matured, senesced, dried, and died by late May. Female activity gradually declined as late spring progressed. I considered summer to extend from the solstice to the autumnal equinox (i.e., June 21 to September 21). Summers were hot, with mid-day air temperatures regularly exceeding

37°C. However, summer monsoons (*chubascos*) in the eastern Mojave Desert occasionally brought substantial rain to Goffs. The heavy summer rains stimulate the germination of summer annuals which tortoises eat. Autumn extended from the autumnal equinox to the time tortoises entered winter dormancy or brumation (i.e., late October or early November). Based upon field metabolic rates and qualitative assessment of activity, females appeared to brumate early in 1988 (ca. late September). Brumation lasted until late February or early March, varying among individuals, when females emerged from their winter burrows (dens).

I used three methods, gas dilution, doubly labeled water, and X-ray radiography, to accurately measure the energy budgets (Henen, 2002). Cyclopropane, a lipid soluble gas, was used to measure the lipid mass (g), nonlipid mass (= body mass – lipid mass, in g), and nonlipid dry mass (= nonlipid mass – total body water, in g; see body water determinations below) of each female on 10 occasions (Fig. 1). This method is currently the most accurate, nondestructive method for estimating lipid masses (within 10% error of absolute lipid mass) and it accurately estimates nonlipid mass by difference (within 5% of absolute nonlipid mass; Henen, 1991, 2001). I used lipid mass and the energy density of lipid extracts (mean = 37.5 kJ/g, from carcasses of 6 female desert tortoises) to calculate the lipid energy content (= lipid mass x 37.5 kJ/g) of each female for the 10 dates. Similarly, I calculated nonlipid energy content using nonlipid dry mass and its energy density (9.8 kJ/g, n = 6; body nonlipid energy = 9.8 kJ/g x nonlipid dry mass). These static measures were then compared across time to calculate lipid and nonlipid energy fluxes (kJ/d) for each female in each of the 9 periods.

I used the doubly labeled water (DLW) method to quantify field metabolic rates (FMR) as liters CO_2 produced per day. The CO_2 production rates were converted to energy units using 21.7 joules/ml CO_2 for tortoises during active periods (supporting metabolism by eating plants). I used a factor of 27.7 joules/ml CO_2 for brumation periods when tortoises fueled metabolism with body lipids (see Nagy and Medica, 1986). The DLW method is typically accurate to within 2 to 8% for terrestrial vertebrates (Nagy et al., 1999). Females were initially injected intramuscularly with DLW (4 ml/kg body mass of 95 atom% ^{18}O-labeled water containing 1 mCi of tritiated water). Upon recapture, females were injected with singly labeled water (0.9 ml of 0.25 mCi tritium/ml water) or DLW to increase isotope concentrations enough for accurate determination of field metabolic rate (FMR) and water flux rates (see Water Budgets). I radiographed females every two weeks from mid-April to mid-July to quantify fecundity (annual egg production). Using fecundity and the energy content of captive-tortoise eggs (mean ± SD = 142.4 ± 41.2 kJ/egg, n = 6; via microbomb calorimetry), I calculated the kilojoules of energy in the eggs produced (ovulated and laid). Energy allocations to eggs are determined primarily by the number of eggs produced (Henen, 1997; but see Wallis et al., 1999), which can be determined with 100% accuracy using radiography (see review by Kuchling, 1999).
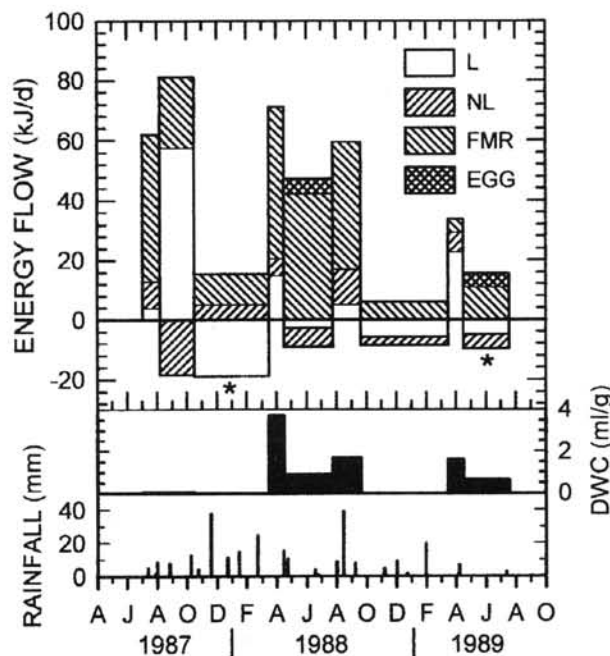

Figure 1. Seasonal energy flux rates (mean, kJ/d) of female desert tortoises at Goffs, California (Henen, 1994a, 1997). Energy was allocated to eggs (committed at ovulation in spring), to energy metabolism (field metabolic rates, FMR), and to or from body lipid (L) energy or body nonlipid (NL) energy. The anabolism and catabolism of body energy substrates (L or NL) are indicated by positive and negative values respectively. The asterisks indicate periods when females experienced energy deficits (i.e., females had statistically significant loss of body energy, L + NL energy flux <0) (n = 9 for the first six periods, 7 for periods seven and eight, and 8 for the ninth period). The water content of the diet (DWC: ml H_2O/g dry matter) was calculated, for the periods of the energy budgets, from DWC values measured throughout the two year period (Tables 1 and 2). Accrued rainfall (mm) was measured approximately once per month at the site.

Table 1. Diet of female desert tortoises at Goffs, California, during two annual cycles (July to July, with early July being the end of the egg-laying period). Values indicate the percentage of bites taken by tortoises per sampling trip (n = number of tortoises observed, number of animal days of observation). Items are ranked by their percentage of the total number of bites, which was 7545, except dry and moist forms of a species are listed in adjacent rows. Plants were categorized as annual (A) or perennial (P), including *Allionia incarnata*, which germinated in response to heavy summer rains in 1988 but did not survive to spring 1989 (see also Oftedal 2002). Data from Henen (1994a).

Diet item	A/P	1987 3-Jul 1,1	7-Aug 5,5	16-Sep 1,1	1988 16-Mar 3,3	15-Apr 4,6	5-May 7,7	22-May 5,7	19-Jun 4,4	4-Jul 4,4	23-Jul 4,7	18-Sep 3,4	1989 15-Mar 1,1	15-Apr 4,7	11-Jun 3,4	18-Jul 6,6	Total %
Schismus barbatus[1]	A	99.2	93.4	98.0		24.5		13.1	74.1	97.1	96.4			46.3	89.7	73.3	63.80
S. barbatus[2]	A					0.9	20.6	28.0				20.6		0.5			5.18
Allionia incarnata	A											69.9					7.93
Cryptantha angustifolia[2]	A				4.3	54.5	26.8	24.7									5.53
C. angustifolia[1]	A		3.6					1.9		2.5	2.7			3.2	2.1	0.6	1.59
Pleuraphis rigida[2]	P		2.7				20.3	32.4	4.6				100.0	3.2			4.04
P. rigida[1]	P								1.0	0.3				14.3	2.6	21.8	2.19
Pectocarya spp.[4]	A		0.1	2.0	18.5		27.6		3.8	0.2	0.7	0.6		2.8			2.48
Lotus strigosus	A				49.4	2.6											1.64
Opuntia ramosissima	P		0.1						16.0		0.1				1.5	1.6	1.30
Soil						16.4											0.76
Chamaesyce micromera	A											5.7			0.4		0.68
O. basilaris	P						0.3							15.2		0.4	0.48
Scat[3]														6.2	3.7		0.44
Lupinus concinnus	A				14.2												0.44
Boerhavia spp.	A											3.2					0.36
Erodium cicutarium	A				6.9		0.5										0.24
Camissonia boothii	A				6.9												0.21
Cryptogamic soil[5]														6.0			0.17
Other		0.8	0.2				1.2	3.8		0.6				2.3		2.3	0.56
Bites observed		244	1194	197	233	347	369	482	501	1170	674	855	12	217	536	514	100.00

[1]Relatively dry (often dead) matter compared to other bites of the same species. [2]Plants or plant parts high in moisture. [3]Scats from desert tortoises, lizards, and wood rats (*Neotoma lepida*). [4]*Pectocarya* spp. observed eaten by female tortoises may have included *P. heterocarpa*, *P. platycarpa* and *P. recurvata* although voucher specimens of plants were identified as *P. recurvata* (B. Prigge, UCLA). [5]The fungi (Division Ascomycota) in the lichens included *Collema coccophorum* and *Peltula* spp. Other items included *Amsinckia tessellata*, woody portions of *Pleuraphis rigida*, *Eriogonum trichopes*, *Chorizanthe brevicornu*, dry portions of *O. basilaris*, and *Loiseliastrum schottii*.

Diet was measured by observing the number of bites females consumed (not bite attempts) of plants and other items for three consecutive years (June 1986 to July 1989). Females often consumed many parts of plants, especially those of small annual plants (e.g., *Schismus barbatus*, *Cryptantha angustifolia*, and *Lotus strigosus*, Table 1), making it difficult to document which parts of small plants were consumed. However, for larger species (e.g., perennials like *Opuntia basilaris*, *O. ramosissima*, and *Pleuraphis rigida*), or plants with distinct reproductive and vegetative structures (e.g., the flowers and leaves of *Camissonia boothii*), I noted whether tortoises ate inflorescences, leaves (or clades of *O. basilaris*), or stems. I also qualitatively assessed whether the plant or other dietary matter was a) fresh with a high moisture content (e.g., new green leaves), b) dry with a very low water content (e.g., dead, old annuals), or c) of intermediate or moderate water content (e.g., senescing annuals). Functionally this translated to dietary water contents (DWC, g water per g dry matter, Table 2) that were a) high (ca. 1 or higher), b) very low (< 0.15), or c) intermediate (ca. 0.15 to 1). Some *Pleuraphis rigida* leaves that appeared brown on the outside had green centers and intermediate water contents, suggesting tortoises had keen foraging skills.

Within 24 hrs of the last feeding observation on each sampling trip, I collected representative samples of dietary items. This included sampling representative species, plant parts and phenological stages or conditions (e.g., approximate moisture contents), for determination of DWC by drying to constant mass at 60°C. However, Tables 1 and 2 specify only the species, annual-perennial category, condition or DWC of dietary items. I did not have a more rigorous analysis of plant part consumption and nutrient composition (see Oftedal, 2002; Oftedal et al., 2002). *Allionia incarnata* was considered an annual because it germinated in summer 1988 but did not survive through winter 1988–89. *Allionia incarnata* may be an annual in the Mojave Desert (e.g., Goffs) but a perennial in the Sonoran Desert (Oftedal, 2002; Van Devender et al., 2002). Dietary water contents were summarized only for the two years coinciding with the energy and water budget analyses. Some seasons had more than one set of feeding observations (e.g., late spring 1988). For each set of observations, I calculated "overall" DWC as the weighted average for all bites of organic matter (bites of soil were excluded from the April 1988 DWC calculation; Table 2). For example, using the percentages from Table 1 and specific DWC from Table 2, the overall DWC for 3 July 1987 = (0.992 x 0.030 g/g) + (0.8 x 0.034 g/g) = 0.030 g water/g dry. Except for brumation periods, the overall values were used to calculate a time-weighted average DWC for the nine periods of energy and water flux measurements (Figs. 1 and 2). For example, the DWC for late spring 1989 = 0.621 g water/g dry = [(57 days x 0.986 g/g) + (37 days x 0.087 g/g)]/94 days, where 0.986 and 0.087 equal the arithmetic average DWC for the two time periods of late spring, 57 and 37 are the number of days in these two periods, and 94 days is the number of days in late spring 1989.

Table 2. Water content (g water per g dry matter) of items eaten by female desert tortoises at Goffs, California. Data are listed according to the sequence of Table 1. For each sampling trip, the overall water content was calculated as the weighted average for organic matter in the diet; bites of soil were excluded from the April 1988 calculation. Data from Henen (1994a).

Water content (g water/ g dry matter)

Diet item	1987 3-Jul	7-Aug	16-Sep	1988 16-Mar	15-Apr	5-May	22-May	19-Jun	4-Jul	23-Jul	18-Sep	1989 15-Mar	15-Apr	11-Jun	18-Jul
Schismus barbatus*	0.030	0.045	0.037		0.096		0.067	0.069	0.029	0.033			0.015	0.021	0.021
S. barbatus					0.830	2.012	0.795				3.486		2.012		
Allionia incarnata											3.348				
Cryptantha angustifolia				4.038	0.829		2.349	2.137							
C. angustifolia		0.013					0.102		0.010	0.025			0.013	0.020	0.048
Pleuraphis rigida*		0.716				2.346	1.985	1.985				1.285	1.285		
P. rigida*								0.614	0.614				0.454	0.334	0.265
Pectocarya spp.		0.036	0.016	3.969		2.793		0.077	0.011	0.024	0.005		0.040		
Lotus strigosus				8.824	1.242										
Opuntia ramosissima*		0.078						0.078		0.078				0.009	0.076
Soil					0.010										
Chamaesyce micromera											3.409			0.021	
O. basilaris						10.207							11.960		2.880
Scat													0.006	0.006	
Lupinus concinnus				5.889											
Boerhavia spp.											2.937				
Erodium cicutarium				3.776		5.448									
Camissonia boothii				7.532											
Cryptogamic soil*													0.010		
Other*	0.034	0.034			2.432	2.946		0.073					0.022		0.029
Overall	0.030	0.062	0.037	6.871	0.542	2.462	1.403	0.164	0.030	0.033	3.347	1.285	1.944	0.029	0.087

*Some items were sometimes scarce or samples were lost, so the water contents for some items (indicated in italics) were assumed equal to that measured in an adjacent time period or at the same time of the previous year. Specifically, the value for a) dry *S. barbatus* in June 1989 was used for July 1989, b) high moisture *Pleuraphis rigida* on 5/22/88 was used for June 1988, c) high moisture *P. rigida* in March 1989 was used for April 1989, d) partially dry *P. rigida* in July 1988 was used for June 1988, e) dry *Opuntia ramosissima* in June 1988 was used for August 1987 and July 1988 (when *O. ramosissima* was scarce), f) dry lizard or wood rat scats (scarce) in April 1989 was used for June 1989, g) soil in April 1988 was used for cryptogamic soil in April 1989, and h) for *Loiseliastrum schottii* in July 1987 was used in August 1987.

Results. — Female desert tortoises demonstrated extreme physiological tolerance to changes in body condition and extreme flexibility with the remainder of their energy budgets (Fig. 1). High lipid storage rates in summer 1987 caused lipid contents to increase from 2 to 8% of body mass (Henen, 1997). These stores supported metabolism in winter 1987–88 and, with lipids accumulated in early spring 1988, enabled females to achieve an energy surplus for the first study year. Despite this surplus, female nonlipid energy declined 21% during the first study year (i.e., July 1987 to July 1988; Henen, 1997) due to large losses in summer 1987 (> 20% decline) and late spring 1988 (15% decline). In late spring 1988, the allocation of nonlipid matter to eggs explained 37% of the late spring declines in body nonlipid matter. Yet, egg production in 1988 was low relative to earlier measures on many of the same individuals (Turner et al., 1986). The combination of low egg production, declines in body nonlipid matter, and an energy surplus suggests that the acquisition and use of nonlipid matter (probably protein), and not energy per se, limited egg production in 1988 (Henen, 1997).

The second year of study (July 1988 to July 1989) included a very dry winter (35 mm of rainfall from 15 September 1988 to 15 March 1989) and the lowest springtime biomass of annual plants measured at Goffs, California (0.0558 g m^{-2}; Henen, 1997). In this year, females maintained a balance in total body energy, lipid energy, and nonlipid energy. To meet these balances, however, lipid anabolism in early spring 1989 compensated for lipid ca-

tabolism in winter 1988–89. Lipid metabolism in late spring 1989 was highly variable among individuals, so mean lipid flux did not differ from zero (i.e., there was no net anabolism or catabolism statistically). Also, nonlipid anabolism in summer 1988 compensated for the nonlipid catabolism, and nonlipid allocations to eggs, in late spring 1989. Mean nonlipid metabolism in winter 1988–89 and early spring 1989 did not differ from zero (Henen, 1997). Furthermore, the FMR of early spring and late spring 1989 were lower (91% and 74%, respectively) than the FMR of the respective periods of 1988. These energy savings in 1989 probably helped females conserve body energy, which probably helped most females to produce eggs in 1989. As in late spring 1988, contributions of nonlipid matter (or energy) to eggs accounted for a substantial (44%) portion of the decreases in body nonlipid matter in late spring 1989. Thus, lipid energy can be stored and subsequently used to support winter metabolism and probably egg production (Henen, 1997). However, nonlipid matter can also be stored for subsequent allocations to eggs or metabolism (Fig. 1 and Henen, 1997).

In the second study year, egg production was low, as in 1988, and three of the nine females did not produce eggs. This high level of nonreproducing mature females appeared unusual for the population (Turner et al., 1986). However, the energy budget differences between reproducing and nonreproducing females in the second study year reinforced the concept that protein was a limiting resource for reproduction. Nonlipid energy increased for females forgoing egg production in 1989 but tended to decrease for the reproduc-
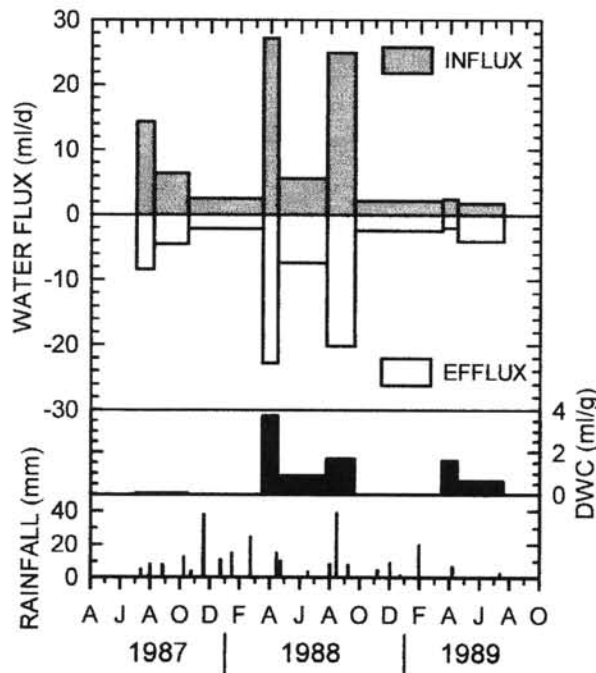
Figure 2. Seasonal water influx and efflux rates (mean, ml/d; positive and negative values, respectively) of female desert tortoises at Goffs, California, measured using doubly labeled water (Henen, 1994a). The water content of the diet (DWC) and rainfall were measured as indicated in Fig. 1.

tive females (a significant difference between the two groups). Additionally, changes in total body energy differed significantly between nonreproductive and reproductive females (tending to increase and decrease, respectively; Henen, 1994a, 1997).

Recent evaluations of the effects of nutrition on reproduction (Henen and Oftedal, 1999; and B.T. Henen and O.T. Oftedal, unpubl. data) have also demonstrated the importance of crude protein (or nitrogen) to egg production of captive females. In this study, female reproductive output (e.g., the number or total mass of eggs produced) was highly correlated to the amount of nitrogen consumed during the year leading to the reproductive season. Additionally, the correlation between reproductive output and nitrogen consumption prior to brumation was greater than the correlation of reproductive output to annual nitrogen consumption. These results are consistent with 1) energy and water budgets demonstrating that nutrient reserves stored before brumation may contribute to egg production the following spring (Henen, 1994a, 1997), plus, 2) ultrasound data demonstrating that females can develop egg follicles to full size prior to entering brumation (Rostal et al., 1994; Henen and Oftedal, 1999). Also, egg yolks, which are derived from follicles, contain about 90% of the nitrogen in desert tortoise eggs (Henen and Oftedal, 1999; B.T. Henen and O.T. Oftedal, unpubl. data).

Females exhibited energy deficits only during winter (Fig. 1). For the two-year field study (Henen, 1994a), female lipid and total body energy increased by 1.08 and 0.51 megajoules (MJ), or 113% and 11%, respectively. However,

nonlipid energy decreased by 0.57 MJ, or 12%. Tolerance to such large changes in body composition are consistent with similar physiological tolerances observed in the energy and water relations of juvenile (Nagy and Medica, 1986; Nagy et al., 1997) and male (Peterson, 1996a,b) desert tortoises. Subsequent FMR and water flux analyses on males and females in drought and wet (El Niño Southern Oscillation [ENSO]) years indicate extreme seasonal (up to 28 fold) and annual (up to 6 fold for similar seasons) differences in FMR (Henen et al., 1998). Desert tortoises may relinquish (Nagy and Medica, 1986), relax (Henen, 1994, 1997), and perhaps temporarily abandon (Peterson, 1996a), homeostatic regulation of water, electrolyte, energy, nitrogen, or other nutrient levels in the body. This ability would allow desert tortoises to 1) opportunistically acquire and store nutrients when they become available (Henen, 1994a, 1997; Henen et al., 1998) and 2) utilize those resources to survive, grow, or reproduce (Henen, 1994a, 1997). It would also allow desert tortoises to become extremely conservative with these resources and reserves during unfavorable periods (e.g., droughts; Henen, 1994a, 1997; Henen et al., 1998).

Water Budgets

The low and unpredictable levels of rainfall and primary productivity of deserts (Louw and Seely, 1982) suggest that water may be a limiting resource for desert tortoises. Nonetheless, female desert tortoises survive and produce eggs even in years of severe drought (e.g., 1989). Using doubly labeled water also enabled me to measure the water content (total body water or TBW in ml, from isotope dilution spaces), water influx and efflux rates, and water balance (= influx – efflux, in ml/d) of these nine females (Fig. 2). The quantity of hydrogen isotope in body water declines when water leaves the body (e.g., via urine, feces, eggs, secretions, exhaled water vapor, and evaporation from the skin and eyes). The concentration of hydrogen isotope in the body declines with water inputs (e.g., drinking, inhalation of water vapor, preformed water in food, and catabolism of foodstuffs). By tracking changes in hydrogen isotope concentration and quantity (TBW x concentration), I was able to calculate total rates of water efflux and influx for each female using equations 4 and 6, respectively, of Nagy (1980). As a group, females achieved water balance for a time interval when mean water balance did not differ significantly from zero (so TBWs were essentially constant). A water surplus was achieved when mean water balance was significantly higher than zero (TBW increased), and a water deficit occurred when mean water balance was significantly lower than zero (TBW decreased; all by Student-t tests, $p < 0.05$).

As for energy, desert tortoises appear to have relaxed homeostatic control of their water balance, accumulating water by drinking rainwater or consuming fresh annual plants (Fig. 2 and Table 2). During dry periods, females became extremely conservative with their water as indicated by their low efflux rates (Fig. 2, Henen, 1994a, and Henen et al., 1998). These low rates were achieved primarily through

reduced activity levels on the surface (see FMR for 1989, Fig. 1). Daily surface activity would expose tortoises to lower humidities than encountered deep within the burrows, and would increase tortoise ventilatory rates. Both factors would exacerbate respiratory water losses, and the low humidities aboveground would exacerbate cutaneous water loss. Reducing water losses should work synergistically with the relaxed control of body fluid volumes and concentrations (see also Minnich, 1977; Nagy and Medica, 1986; Peterson, 1996a) in extending desert tortoise tolerances to drought conditions (i.e., reducing mortality rates; see Peterson, 1994).

Total water influx and efflux rates showed tremendous seasonal variation during the two years (Fig. 2). Drinking and dietary water influxes comprised most (77 to 86%) of the annual water influx rates (Henen, 1994a). Seasonally, water efflux rates changed in parallel with water influx rates, suggesting that water use or efflux was constrained by the availability and influx of water. The highest total water influx and efflux rates occurred when females drank rainwater (summer 1987, summer 1988, and early spring 1988; Fig. 2). The lowest rates occurred when females could not drink rainwater or eat annual plants with high water contents, which occurred during brumation periods and all of spring 1989.

Statistically, these females achieved water balances (i.e., water influx = water efflux, and TBW did not change) during brumation. Being inactive and remaining in winter dens prevented females from drinking fallen rain or consuming new winter annuals (primarily in winter 1987–88), so water influxes (water vapor and metabolic water inputs) were small. Conversely, remaining inactive and in winter dens protected tortoises from cold winter temperatures (and predators) and kept water losses (e.g., urinary, fecal, respiratory and cutaneous) at low levels, especially during the dry winter of 1988–89. Little rain fell during early spring 1989, so females did not drink. Females also had little access to new (high water content) plants at that time. By reducing surface activity (and FMR, Fig. 1) and consuming perennial plants high in moisture content (*Pleuraphis rigida* and *Opuntia basilaris*), females managed to achieve water balance during early spring 1989.

Females achieved large water surpluses when they drank (i.e., summer and autumn 1987, early spring 1988, and summer 1988). Water influx rates were also very high in two of these periods (early spring 1988 and summer 1988; Fig. 2). This was probably because females also consumed many new winter annuals and new summer annuals, respectively (see DWC, Fig. 2 and Table 2).

During both egg-laying periods, females invested water in eggs (mean = 85 and 71 ml per female in late spring 1988 and late spring 1989, respectively; Henen, 1994a). In addition, females did not drink then because rainfall was scarce (Fig. 1). In late spring 1989, despite eating perennials with moderate (*Pleuraphis rigida*, DWC = ca. 0.3 g water/g dry) to high (*Opuntia basilaris*, DWC = ca. 3 g/g; Table 2) water contents, females had water deficits on average. This is not surprising given the drought conditions of 1989. The available annual plants in 1989 were dead, dry remainders from 1988. However, rainfall for winter 1987–88 (158 mm) was about the average for the Goffs study site (Henen, 1997), and new winter annuals were much more abundant than in 1989. Annuals with moderate to high water contents were readily consumed by females in early spring and late spring 1988. These water contents declined rapidly with senescence through late spring and summer (see *Pectocarya* spp. DWC, Table 2). Despite the consumption of plants with high or moderate water contents in late spring 1988, females also had water deficits in late spring 1988. This result, plus the water deficit for spring 1989, reinforces the idea that water is important to the reproductive success of female desert tortoises (see below).

Water appeared most limiting during severe droughts. Annuals with high moisture contents were scarce in early and late spring 1989, but were available and consumed in early and late spring 1988 (Table 2). Water flux rates in early and late spring 1989 were 10 and 50%, respectively, of corresponding rates in 1988 (Fig. 2). From July 1988 to July 1989, rainfall at Goffs was below average and water efflux exceeded water influx, so TBW decreased about 10% or 90 g during the year (Henen, 1994a). During these 12 months, females that produced eggs forfeited body water while females that abstained from egg production tended to increase their TBW (i.e., the annual change in TBW differed between reproducing and nonreproducing females; Henen, 1994a). From July 1987 to July 1988, annual rainfall was close to average and females achieved a water surplus equal to 10% of their TBW in July 1987. Thus water and protein appeared to be limiting resources for egg production during the drought year.

Water is essential for digestion. During summer 1987, females consumed principally dry annual plants (Tables 1 and 2), but lipid anabolism and nonlipid body metabolism changed dramatically from July 1987 to late summer and autumn (Fig. 1). This switch in metabolism coincided with summer rains (Henen, 1997). In early August, females emerged from their burrows to drink rainwater equaling, on average, one third of their mass (means: 460 ml water, 1389 g body mass; $n = 9$; see Henen, 1994a). This was matched in proportion in early spring 1988 when females drank, on average, 536 ml water (1644 g body mass, $n = 9$). Other studies (Nagy and Medica, 1986; Meienberger et al., 1993; and Peterson, 1993; Nagy et al., 1998) have shown how high TBW values or drinking enable desert tortoises to consume and digest dry diets. The summer drink in 1987 enabled females to store lipids to support winter metabolism but compromised female nonlipid content (Fig. 1 and Henen, 1997), TBW stores (Henen, 1994a), and probably their 1988 reproductive output. Digestion trials (Meienberger et al., 1993, Nagy et al., 1998) have suggested that body proteins and TBW are forfeited to support the digestion of dry grasses. However, the digestion of these grasses enabled females to store considerable lipid (Fig. 1), ultimately reducing the amount of body nonlipids catabolized during winter 1987–88 (Henen, 1997).

The critical nature of water to desert tortoises is also reflected in their drinking-related behaviors. Desert tortoises dig basins in the soil and when rainstorms occur in the active season, tortoises quickly emerge from their burrows to revisit these basins to drink pooled rainwater (Medica et al., 1980; BTH, pers. obs.). Multiyear analyses on male and female rates of water influx demonstrated a 237 fold range in water influx rates (ca. 150 fold within sites), with annual conditions (i.e., drought versus ENSO conditions) contributing 10 to 15 fold to these differences (Henen et al., 1998). Thus tortoises can capitalize upon rainwater or dietary water, if available during active periods, or become conservative during droughts. This facilitates storing large quantities of water and drawing upon these reserves to produce eggs (Henen, 1994a) and endure harsh, dry seasons and years (Nagy and Medica, 1986; Peterson, 1994, 1996a,b; Henen et al., 1998).

FOOD ABUNDANCE AND REPRODUCTIVE OUTPUT

The reproductive output of desert lizards (Turner et al., 1982) and desert rodents (Beatley, 1974; Kenagy and Bartholomew, 1985) depends upon winter rainfall or consequent levels of primary or secondary productivity. From 1983 to 1985, egg production by female desert tortoises at Goffs, California (Turner et al., 1986) was not correlated to winter annual biomass ($F_{1,60} = 0.00$, $p = 1.0$), but was inversely correlated to winter rainfall ($F_{1,60} = 6.19$, $p = 0.02$). Turner et al. (1986) hypothesized that tortoises may store resources (e.g., energy) before brumation and use these reserves the ensuing spring to help produce eggs. This could make egg production seem independent of winter rainfall and annual biomass. Evidence of nutrient storage for later allocation to egg production was supported by the energy and water budget analyses (Henen, 1994a, 1997) and measures of follicular development (Rostal et al., 1994; Henen and Oftedal, 1999, B. T. Henen and O. T. Oftedal, unpubl. data).

Results from subsequent studies on clutch frequency, egg production, and winter annual biomass (Turner et al., 1987; Henen, 1993, 1997; Mueller et al., 1998; Wallis et al., 1999; BTH, unpubl. data; C.R. Tracy, *pers. comm.*) are consistent with both the "storage" hypothesis and the "winter rainfall-plant biomass" hypothesis (i.e., capital versus income breeding, Drent and Daan, 1980). The desert tortoise strategy appears mixed between, or intermediate to, the capital and income strategies (Henen, 1997, 2002). Mean clutch frequency (Turner et al., 1987) and egg production (Henen, 1993, 1994b) at Goffs (eastern Mojave Desert) were correlated to the logarithm of winter annual biomass (g dry/m²). Data from the western Mojave Desert (Wallis et al., 1999) and northeastern Mojave Desert (southern Nevada, Mueller et al., 1998; Utah, C.R. Tracy, *pers. comm.*) also fit these relationships. Additionally, computer models suggest that a low biomass of winter annuals may retard growth to sexual maturity, decrease egg production, and cause declines in population size (Tracy, 1993).

The semilogarithmic nature of these data makes reproductive output a complicated issue. Egg production and clutch frequency are highly correlated to winter annual biomass at low levels of winter annual biomass (ca. 0 to 2 g dry/m²; Henen, 1994b). At higher biomass values (ca. 4–40 g dry/m²) however, egg production and clutch frequency tend to approach an asymptote or increase less rapidly than at lower biomass values. This pattern implies that other factors may limit egg production at high biomasses of winter annuals (Henen, 1993; Wallis et al., 1999). Some factors that may limit egg production at high annual biomasses include: 1) low body reserves before brumation, and 2) female body size, which may physically limit how many vitellogenic follicles or eggs the body can hold at one time. Wallis et al. (1999) suggested that home range quality, genetics, immaturity or sterility, senescence, or mating opportunities may also contribute to variation in reproductive output.

Furthermore, the biomass of winter annuals is only a gross indicator of nutrient availability to desert tortoises. The biomass of all winter annuals does not directly translate to the availability of dietary species or the availability of specific nutrients because tortoises are selective eaters (Nagy and Medica, 1986; Henen, 1993, 1994a; Esque, 1993, 1994; Oftedal et al., 2002). This is supported by the relative importance of winter forbs and grasses to the fecundity or annual egg production of Goffs tortoises. Fecundity was correlated to the biomass of winter forbs (i.e., log-log: $F_{1,5} = 7.05$, $p = 0.045$, $r^2 = 0.585$), but not to the biomass of winter annual grasses ($p > 0.1$ regardless of transformation; B.T. Henen and H.W. Avery, unpubl. data;). However, future reproduction may be influenced by the consumption of dry annual grasses in the summer and fall (see Energy Budgets and Diet).

Also, the digestibility of nutrients probably varies among plant species. High biomass values may include annuals with 1) low nutrient (e.g., protein or water) concentrations during certain phenological stages, 2) compounds or structures (hair or spines) that reduce plant palatability or digestibility, 3) heterogeneous spatial distributions, or 4) potentially toxic compounds (e.g., potassium, Minnich, 1977; Nagy and Medica, 1986). The high potassium levels in many desert plants requires tortoises to excrete large amounts of uric acid, water, or both to prevent deleterious effects (Nagy and Medica, 1986; Oftedal et al., 1994). Oftedal et al. (1994) demonstrated that high potassium diets can reduce growth, presumably by diverting nitrogen from protein synthesis to the excretion of potassium with uric acid. Thus, the high potassium levels of some plants effectively reduce the amount of dietary protein (nitrogen) and water retained when eating these plants.

FEMALE TORTOISE DIET

Apart from lists of dietary plants, we understand very little about the nutritional ecology of desert tortoises. First-level analyses of tortoise nutrition are based on extensive observations (i.e., bite count analyses; Table 1 and Avery,

1993; Esque, 1994; Snider, 1996) of tortoises foraging in the wild. Fecal analyses are also important sources of dietary information (Hansen et al., 1976; Van Devender et al., 1996). My analysis of 13,743 bite counts by female desert tortoises at Goffs, California (June 1986 to July 1989) pales in magnitude to the > 100,000 bite counts recorded elsewhere for desert tortoises (Esque, 1994). Also, my analysis can not match the more recent and detailed plant part, phenology, and nutrient analysis for desert tortoise diets (Oftedal et al., 2002). My sample sizes were not large (e.g., early spring 1989, Table 1), precluding robust generalizations about seasonal diets (e.g., early spring 1989) and differences among years. Additionally, my study period lacked an ENSO event, which brings extremely high rainfall, particularly in winter and spring (Henen et al., 1998), high biomasses of winter annuals (Turner et al., 1986; Henen, 1997; Wallis et al., 1999), a high plant species richness, and high fecundity (Wallis et al., 1999). The impact of ENSO events upon tortoise FMR and water flux rates is phenomenal (Henen et al., 1998), but ENSO effects upon nutritional ecology are not yet clear. Nonetheless, the 1986–89 data provide several insights into the dietary preferences of female desert tortoises, and seasonal and annual variations in tortoise diets.

Annual Plants

Desert tortoises consume many plant species, but most bites are of a few plant species (Nagy and Medica, 1986; Avery, 1993; Henen, 1993; Jennings and Fontenot, 1993; Esque, 1994; Oftedal et al., 2002). During spring, summer, and autumn, females at Goffs always took more bites of annual plants than of perennial grasses, cacti, or other material (Fig. 3). Of 13,743 bites consumed by females during these three years, 89.1, 6.8, and 4.1% of the bites were of annuals, perennials, and other material, respectively. Annuals comprised more of the diet in summer and fall (94 and 99%, respectively) than in spring (79%; Fig. 3). This was due to a) the high consumption of dry *Schismus barbatus*, an alien annual grass, in summer and autumn of 1987 and summer 1988, b) the high consumption of new summer annuals in autumn 1988, and c) the paucity of new winter annuals in 1989. Although consuming dry *S. barbatus* can cause negative water and nitrogen balance for desert tortoises (Nagy et al., 1998), consuming dry *S. barbatus*, in tandem with drinking, can greatly enhance energy balance and lipid stores (e.g., summer 1987; Fig. 1). This may help explain the high consumption of dry *S. barbatus* in each summer (1987, 1988, 1989) and autumn 1987. The relatively low consumption of annuals during spring was probably due to the fact that perennials can also be quite nutritious (see below) in spring; perennials are also abundant.

New summer annuals, which germinate in response to summer rains, were common to female diets in autumn 1988 (Table 1). Most of these annuals had very high water contents (Table 2) and at least one species, *Chamaesyce*
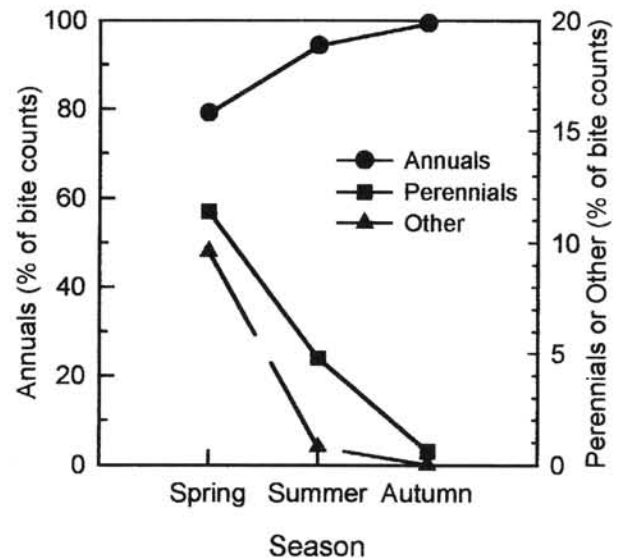

Figure 3. Seasonal levels (% of bite counts per season) of annual plant tissue (left axis), perennial plant tissue (right axis), and other material (right axis) in the diet of female desert tortoises at Goffs, California (Henen, 1994a). Diet was measured by counting consumed bites of food from June 1986 to June 1989 (n = 13,743 bites consumed). Other material included soil, scat (tortoise, lizard, and rodent), and cryptogamic soils (detailed in Table 1 or Henen, 1994a). Seasons were defined as a) spring (early and late spring) from emergence (ca. March) to summer solstice (ca. June 21); summer, summer solstice to autumnal equinox (ca. September 21); and autumn, autumnal equinox until brumation (late October to November).

micromera, can have high nitrogen levels at this time of year (Oftedal, 2002). The species consumed in autumn 1988, except *Pectocarya* spp., are known to have high water contents, high nitrogen (or crude protein) levels, and favorable levels of water and protein to potassium levels. Although all three nutrients are critical for desert tortoise metabolism, high potassium levels can be toxic. Water and nitrogen can be used to excrete excess potassium in urine (fluid or urate precipitates). Thus high levels of water and nitrogen are favorable for maintaining water, nitrogen, and potassium balance. High dietary levels of water, nitrogen, or both, relative to potassium, indicate a high potential to excrete excess potassium. Oftedal (2002) has derived an index of this potential (PEP index = potassium excretion potential index) and, with caveats, suggests that tortoises may prefer plants with high PEP indices. Three of the four plant species consumed in autumn 1988 are known to have moderate (*A. incarnata, S. barbatus*) to high (*C. micromera*) PEP indices before the plants senesce and die (Oftedal, 2002). The PEP index has not been assessed for *Boerhavia* spp. These four species of summer annuals may have had moderately to highly favorable PEP indices in September 1988. Consuming these species may have been highly favorable for female water, nitrogen, and potassium balance. PEP indices can change with phenological stage and due to leaching of potassium out of dead plants by rain (Oftedal, 2002). Perhaps potassium leaches out of dead *Schismus barbatus*, making such plants favorable for consumption by well-hydrated tortoises.

The high consumption of annuals appears consistent for much of the Mojave Desert (Avery, 1993; Esque, 1994; Snider, 1996; Oftedal et al., 2002), but the diet of Sonoran Desert tortoises contains more perennial plant matter (Van Devender et al., 1996, 2002). Perennial plants may be more common in the Sonoran Desert (Van Devender et al., 2002, Oftedal, 2002), which receives more consistent and intense summer rains relative to the western and central regions of the Mojave Desert. Goffs also receives more summer rain than does the western Mojave Desert (Wallis et al., 1999), so the Goffs' flora probably includes growth forms of some Sonoran Desert plants. The Goffs' site is located in the eastern Mojave Desert, in an ecotone of the Mojave and Colorado Deserts (K.H. Berry, *pers. comm.*). Thus the flora near Goffs includes elements from different deserts and may have a higher plant species richness than in other areas of the tortoise's distribution (e.g., the western Mojave Desert). One effect of the climate and flora of Goffs is that local egg size (small) and fecundity (high) seem to differ ecologically and evolutionarily from that of tortoises in the western Mojave Desert (Wallis et al., 1999; see also Mueller et al., 1998). The fecundity patterns and reproductive cycles in the Sonoran Desert also appear distinct from that of Mojave Desert tortoises (Murray et al., 1996; Averill-Murray et al., 2002; B.T. Henen, R.C. Averill-Murray, T.E. Christopher, and E. Stitt, unpubl. data); research on these topics continues.

Perennial Plants

Compared to summer and autumn, the consumption of perennials and other materials was high during spring (Fig. 3 and Table 1). This was probably due to several factors. First, the protein (nitrogen) levels of annuals and perennials tend to peak at the same time (Nagy and Peterson, 1991), providing alternatives for the tortoises. Perennials may also retain their elevated water and protein levels longer than do annuals in spring. The availability of summer annuals in 1988 (Table 1) probably reduced the consumption of perennials during autumn 1988; females probably preferred the summer annuals. The new growth of some perennials in response to summer and autumn rain may not occur before tortoises begin brumation. Additionally, the spring data include the 1989 data, which was when new annuals were extremely scarce and females were not very active, making it difficult to record foraging behaviors. Despite the absence of new winter annuals in 1989, females consumed more bites of annuals than bites of perennial plant matter (Table 1) by eating many dry, dead annuals that remained from 1988. In spring 1989, females also ate cryptogamic soils and many scats (Table 1), suggesting that females were desperate enough to sample new or different items.

The apparent preference for annual plants may be partially explained by the high protein concentrations of new annuals in spring (Nagy and Peterson, 1991), the high water content of new winter or summer annuals (Table 2, Oftedal, 2002), or the PEP indices of new or dead annuals. In addition, the consumption of annuals may be affected by the relatively high abundance of annuals to seemingly palatable perennials. Annual plant species, their phenologies, and their biomasses may differ considerably between sites (see Mojave-Sonoran Desert discussion above) as well as within sites showing elevation gradients (H.W. Avery, *pers. comm.*). Nonetheless, the annual and perennial plant dichotomy does not adequately express the complexity of the nutritive values of various plants to desert tortoises.

The availability of annual plants and the ability to relax energy and water homeostasis are critical to the survival and reproductive abilities of desert tortoises and thus are important considerations in conservation efforts. Avery (1998) has demonstrated that grazing cattle compete with tortoises for forage, especially important annuals like desert dandelion (*Malacothrix glabrata*). Additionally, wild and captive-bred tortoises should not be relocated or released if they are in poor body condition (Nagy et al., 2002). Knowledge about the biomass, nutrient composition, phenological changes in plant nutrient composition, and the nutritional value of desert plants (Nagy and Medica, 1986; Meienberger et al., 1993; Oftedal et al., 1994; Barboza, 1995a,b; Nagy et al., 1998; Oftedal et al., 2002) is recent. However, such information, for females, males, and juveniles, may be critical for 1) evaluating relocation sites, 2) managing the grazing of livestock, 3) improving disturbed tortoise habitat, and 4) evaluating efforts of temporary food supplementation.

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