Effects of Climatic Variation on Field Metabolism and Water Relations of Desert Tortoises
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Effects of climatic variation on field metabolism and water relations of desert tortoises

Abstract We used the doubly labeled water method to measure the field metabolic rates (FMRs, in kJ $kg^{-1} day^{-1}$) and water flux rates (WIRs, in ml $H_2O kg^{-1} day^{-1}$) of adult desert tortoises (*Gopherus agassizii*) in three parts of the Mojave Desert in California over a 3.5-year period, in order to develop insights into the physiological responses of this threatened species to climate variation among sites and years. FMR, WIR, and the water economy index (WEI, in ml $H_2O kJ^{-1}$, an indicator of drinking of free water) differed extensively among seasons, among study sites, between sexes, and among years. In high-rainfall years, males had higher FMRs than females. Average daily rates of energy and water use by desert tortoises were extraordinarily variable: 28-fold differences in FMR and 237-fold differences in WIR were measured. Some of this variation was due to seasonal conditions, with rates being low during cold winter months and higher in the warm seasons. However, much of the variation was due to responses to year-to-year variation in rainfall. Annual spring peaks in FMR and WIR were higher in wet years than in drought years. Site differences in seasonal patterns were apparently due to geographic differences in rainfall patterns (more summer rain at eastern Mojave

sites). In spring 1992, during an El Niño (ENSO) event, the WEI was greater than the maximal value obtainable from consuming succulent vegetation, indicating copious drinking of rainwater at that time. The physiological and behavioral flexibility of desert tortoises, evident in individuals living at all three study sites, appears central to their ability to survive droughts and benefit from periods of resource abundance. The strong effects of the El Niño (ENSO) weather pattern on tortoise physiology, reproduction, and survival elucidated in this and other studies suggest that local manifestations of global climate events could have a long-term influence on the tortoise populations in the Mojave Desert.

Key words Physiological ecology · El Niño (ENSO) effect · Geographic variation · *Gopherus agassizii* · Resource availability

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Introduction

The ability of desert animals to obtain the pivotally important resources of water and food is a central aspect of their ecology (Louw and Seely 1982; Nagy 1994). Deserts, by definition, are dry, unpredictable habitats, so food and water supplies are often scarce (Nagy 1988). Desert tortoises (*Gopherus agassizii*) possess a variety of morphological, physiological, and behavioral characteristics which enable them to survive and reproduce in their harsh environment (Nagy and Medica 1986; Peterson 1994a; Henen 1997). Their former abundance in the Mojave Desert (Corn 1994; Berry and Medica 1995; but see Bury and Corn 1995) testifies to their success. Recent and rapid population declines (Fish and Wildlife Service 1994) have been attributed primarily to direct, deleterious human-related influences (cf. Garber and Burger 1995), such as introduced diseases (Jacobson et al. 1991), collection, and habitat reduction. However, climate patterns may also contribute to these declines. Knowing how climatic variation affects desert tortoise physiology, behavior, and demography is important to

the design, implementation, and success of conservation programs.

Three populations of desert tortoises in the Mojave Desert of California have been studied continuously for several years (Peterson 1994a,b, 1996a,b; Henen 1997). One of these years (1992) included an El Niño southern oscillation (ENSO) event (Glantz 1996). We were able to make nearly continuous measurements of energy metabolism and water intake rate on more than 60 free-living tortoises over 4 consecutive years, 2 of which were relatively dry, and one of which was comparatively wet (the ENSO year). This multiyear, multisite study of tortoise physiological ecology allowed us to evaluate (1) responses to seasonal and annual variation in climate, (2) the potential differences between populations along an east-west rainfall gradient that were suggested to exist from an earlier study (Nagy and Medica 1986), and (3) whether one sex might be more sensitive than the other to climatic variation, possibly influencing the reproductive strategies of the sexes.

Methods

Study sites

The three field sites were located in the Mojave Desert of California (for details see Peterson 1994a, 1996a; Henen 1997). The site in the western Mojave (at the Desert Tortoise Research Natural Area or DTNA, near California City; 35°15′N, 117°51′W) and one in the northeastern Mojave Desert (in Ivanpah Valley, about midway between Baker, California and Las Vegas, Nevada; 35°22′N, 115°21′W) were chosen to maximize the likelihood of observing differences in seasonal rainfall, while minimizing other climatic and physiographic differences (Peterson 1994a). They share similar plant communities (creosote bush-burro bush association), latitudes, elevations and average long-term annual rainfall. The third site (near Goffs in Fenner Valley, and also a creosote bush-burro bush community; 34°51′N, 115°09′W) was located in the eastern Mojave Desert about 60 km SSE of Ivanpah Valley, and historically is warmer and receives more summer rain than the other two sites.

Climate measurements

The range of shade air temperatures at each site was measured using minimum/maximum thermometers placed 1 m above the ground. Rainfall was monitored using two or more rain gauges at each site. Occasionally, our rain gauges did not yield accurate measurements for several reasons (e.g., overflow in heavy rains or animal disturbance). Rainfall data from nearby NOAA weather stations were highly correlated to on-site data (see Results), so we also calculated the average rainfall amounts for the two nearest NOAA stations to each site: Mojave and Randsburg for DTNA, Needles and Mitchell Caverns for Goffs, and Searchlight and Mountain Pass for Ivanpah. Temperatures and accumulated rainfall at each site were measured at approximately 4- to 20-week intervals, corresponding to sampling periods for doubly labeled water measurements.

Study animals

Field measurements at DTNA and Ivanpah were begun in 1989 on adult males only (10 at each site) and at Goffs on 10 adult females

only. In October of 1990, 10 adults of the opposite sex were added at each study site. Additional animals were added to the study as necessary to replace those few that died or disappeared. Ultimately, 12 males and 10 females at DTNA, 15 males and 12 females at Ivanpah, and 13 males and 18 females at Goffs were involved in the study. All animals carried radiotransmitters weighing approximately 110 g glued to their carapaces (see Peterson 1996a; Henen 1997 for details).

Field metabolic and water influx rates

The doubly labeled water method (Lifson and McClintock 1966) was used to measure field metabolic rate (FMR, as CO_2 production rate in 1 CO_2 kg^{-1} day^{-1}) and water influx rate (WIR, in ml H_2O kg^{-1} day^{-1}). Tortoises were injected with 37 MBq (1 millicurie) per kilogram body mass of tritiated water, and either 3 ml kg^{-1} (high level) or 0.16 ml kg^{-1} (low level) of 95 atom% ^{18}O water. After allowing a 14–18 h equilibration period for isotopes to mix thoroughly in body water (Henen 1997), initial blood samples were taken and tortoises were weighed and immediately released at the site of their capture. Tortoises were recaptured opportunistically at approximately 1- to 5-month intervals, when their weights were recorded and blood samples were taken (for details see Peterson 1996a; Henen 1997). Tortoises were reinjected as necessary to maintain accurately measurable enrichments of isotopes in their body water. Isotope concentrations in blood samples were analyzed at the University of California, Los Angeles, using liquid scintillation counting for tritium, proton activation analysis for high-level ^{18}O, and mass spectrometry for low-level ^{18}O (Nagy 1975, 1983, 1989). FMRs were calculated from isotope results using Eq. 2 of Nagy (1980) and the ^{18}O dilution space (or the corrected ^3H space: Peterson 1996a; Henen 1997) as an estimate of body water volume. WIRs were calculated using Eqs. 4 and 6 in Nagy and Costa (1980). FMR measurements, in units of CO_2 production, were converted to units of energy by multiplying by the factor 21.7 kJ l^{-1} CO_2 for seasons when animals were eating and 27.7 kJ l^{-1} CO_2 during winter when animals were presumably metabolizing fat (from Nagy 1983). The effects of body mass were accounted for by expressing all rates per kilogram of body mass, as shown to be appropriate for desert tortoises (Peterson 1996a,b).

Statistics

Correlations were evaluated with Pearson product-moment correlation analyses on untransformed data (semilog- or log-log-transformed data if untransformed data were heteroskedastic), or Spearman rank correlation analysis (for rainfall effects). Effects of sampling period (time), site and sex on FMR, WIR, and the water economy index (WEI) were evaluated with one-way (for within-site analyses) and two-way repeated-measures (for within- and between-site analyses), or standard analysis of variance when repeated-measures analysis of variance was inappropriate (i.e., analysis of sex effects due to infrequent repeat measures during the study). Two-way repeated-measures ANOVA did not allow comparisons of all periods due to gaps in the Goffs data set, so this statistic was used only for periods when data were available for all sites. Within-site analyses (one-way repeated-measures ANOVA) allowed the use of all data within each site. Analyses of variance were followed by Student-Newman-Keuls (SNK) pairwise multiple comparisons (q-test), paired or unpaired t-tests, or Mann-Whitney rank sum tests (T-test), as appropriate. When one-way repeated-measures ANOVA failed the normality assumption, a Kruskal-Wallis, one way ANOVA on ranks (H-test) was used. These analyses were done using Sigmastat 2.0 software. Results are shown as means and standard error (SE) or 95% confidence intervals (CI), and we used $P < 0.05$ as the criterion for significance.

Results

Rainfall

Simultaneous rainfall measurements made on site and at nearby NOAA stations were highly correlated ($P < 0.0001$). On-site rain accumulated during each 4- to 20-week measurement period and average nearby NOAA rain for the same period (excluding periods when on-site measurements were compromised) were correlated, with r values of 0.98 for DTNA, and 0.96 for Goffs. The data for Ivanpah were not normally distributed, but the log-transformed data were, and they indicated an r value of 0.89. Although NOAA data tended to overestimate on-site rainfall somewhat, apparently because at least one of the two NOAA stations used for each study site were at relatively higher elevations, we used the NOAA data in subsequent analyses because they were more complete, and they correctly reflected the seasonal and year-to-year patterns in rainfall at each site. Monthly rainfall values were used in Fig. 1 for illustrating variations in rainfall relative to long-term averages ("expected rainfall"), whereas NOAA rainfall totals for physiological measurement periods (4–20 weeks) were used in analyses of physiological data.

Winter rainfall (October through March) was low in 1988–1989 and 1989–1990 (23–37% of the long-term average at DTNA, 38–62% at Goffs, and 56–65% at Ivanpah; Fig. 1). The winter of 1990–1991 started out relatively dry, but a large rainstorm in March 1991 brought winter totals to above average at all three sites (124% at DTNA, 137% at Goffs, 110% at Ivanpah). In the winter of 1991–1992, rainfall totaled from 206% (DTNA) to 288% (Goffs, with Ivanpah intermediate at

Fig. 1 Monthly rainfall totals (mm) at the three study sites, expressed as the average of the two nearby NOAA stations (*vertical bars*) during our study, and as long-term (38- to 106-year) averages at the same two NOAA stations for each site (*running line*)

MOJAVE DESERT RAINFALL
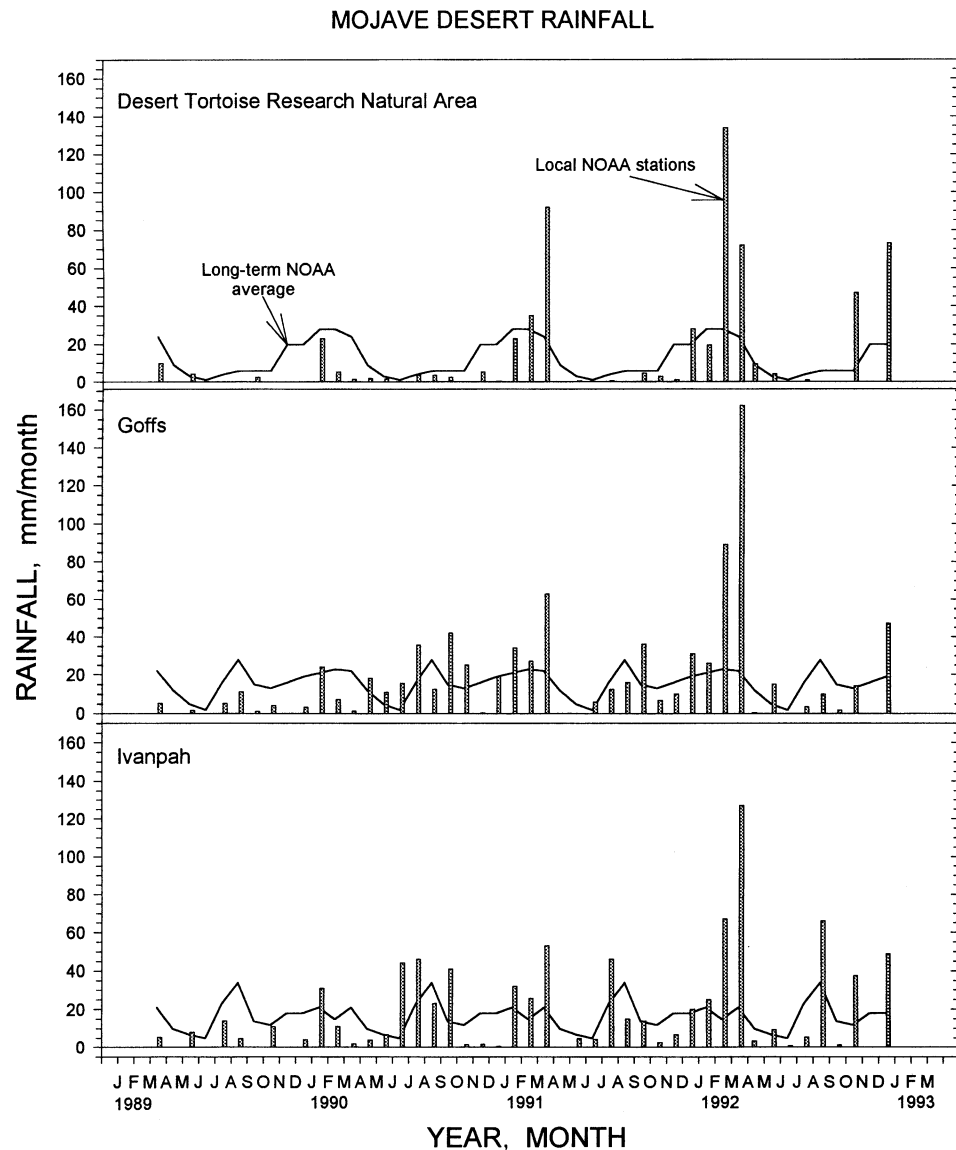
238%) of average, due to a strong El Niño (ENSO) event that affected much of southwestern North America (Polis et al. 1997).

Year-to-year variation was similar at all three sites, as indicated by highly significant ($P < 0.001$) correlations of measurement period rainfall (NOAA) between sites. However, the seasonal pattern of rainfall differed among sites ($P = 0.039$, one-way ANOVA followed by SNK pairwise multiple comparisons). Summer rainfall (June through September) was low at DTNA (the western site), averaging only 3.7% of annual rainfall (April through March total) during the 4 years of this study. The two eastern sites received 21.1% (Goffs) and 30.2% (Ivanpah) of their annual rain during the summer months.

FMR

Two-way repeated-measures ANOVA of FMR revealed highly significant effects on FMR of period ($F_{11,438} = 60.6$, $P = 9.4 \times 10^{-72}$), site ($F_{2, 438} = 32.0$, $P = 6.5 \times 10^{-12}$), and period-site interaction ($F_{22,438} = 13.7$, $P = 2.4 \times 10^{-34}$). This indicates that FMR (Fig. 2) varied over time, that average FMRs varied among the three sites, and that the seasonal pattern in FMR variation differed among sites. Subsequent SNK analyses (q-test, $P < 0.05$) indicated that the average FMR was significantly higher at Ivanpah (mean $\pm$ SE $= 23.0 \pm 0.9$ kJ kg^{-1} day^{-1}, $n = 145$) than at DTNA (13.6 ± 1.1 kJ kg^{-1} day^{-1}, $df = 111$, $q = 9.07$) or Goffs (13.5 ± 0.9 kJ kg^{-1} day^{-1}, $df = 181$, $q = 10.1$). One-way repeated-measures ANOVA of FMR within sites showed highly significant effects on FMR of period (all $F > 11.9$, $P < 3 \times 10^{-22}$, $df > 21,194$), with the highest FMRs occurring during the activity seasons (spring, summer), and the lowest FMRs occurring during the winter periods (SNK: all $q > 5.6$, $df \geq 12$ and $P < 0.05$). At DTNA, the yearly peak in FMR was significantly greater in 1992 than in 1989, 1990, or 1991 (SNK: all $q > 5.74$, $df \geq 17$, $P < 0.05$); at Goffs, 1991 > 1992 > 1989 (SNK: all $q > 3.4$, $df \geq 26$, $P < 0.05$); and at Ivanpah, 1991 and 1992 > 1989 and 1990 (SNK: all $q > 9.65$, $df \geq 14$, $P < 0.05$).

WIR

Rates of water influx showed similar seasonal, between-site, and between-year patterns as FMR (Fig. 3). Two-way repeated-measures ANOVA of WIR revealed that it varied over time (highly significant effects on WIR of period: $F_{17,687} = 217.8$, $P = 9.0 \times 10^{-232}$), among sites ($F_{2, 687} = 9.98$, $P = 8.8 \times 10^{-5}$), and that the seasonal pattern of WIR varied between sites (period-site interaction: $F_{34,686} = 41.9$, $P = 5.9 \times 10^{-130}$). Subsequent SNK analyses (all $P < 0.05$) showed that the average WIR was highest at Ivanpah (6.26 ± 0.19 ml kg^{-1} day^{-1}, $n = 243$; $q > 3.3$ and 6.3 for Goffs and DTNA
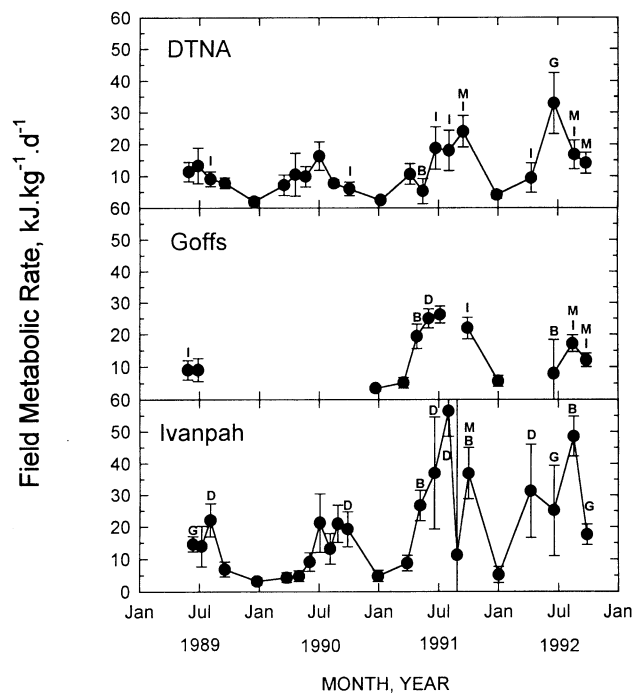

Fig. 2 Mean ($\pm$ 95% confidence interval or CI) field metabolic rate (*FMR*) of desert tortoises at three California sites in the Mojave Desert. Until October 1990, FMR [and water influx rate (WIR) and the water economy index (WEI) in subsequent figures] were measured only on males at the Desert Tortoise Research Natural Area (DTNA) and Ivanpah sites, and only on females at the Goffs site. Subsequently, FMR, WIR, and WEI were measured on males and females at all three sites. FMR and WEI were not measured at Goffs between February and October 1990, July to September 1991, and March to May 1992 (indicated by gaps here and in Fig. 4). The letters D (for DTNA), G (Goffs), and I (Ivanpah) label instances where the mean differs significantly from that of another site (or B for both other sites). M and F indicate periods having a significant difference between sexes, with the M or F indicating which sex had the higher mean

comparisons, respectively), intermediate at Goffs (5.62 ± 0.19 ml kg^{-1} day^{-1}, $n = 266$; $q > 3.46$ for DTNA comparison), and lowest at DTNA (4.86 ± 0.24 ml kg^{-1} day^{-1}, $n = 178$). One-way repeated-measures ANOVA within sites indicated that there were highly significant effects of time period on the WIR (all $F > 64.1$, $P < 1.6 \times 10^{-82}$, $df > 18,237$), with the highest WIRs occurring during the activity seasons of spring and summer, and the lowest rates occurring during winter (SNK: all $q > 1.4$, $df > 8$, $P < 0.05$). At DTNA, the peak WIR values in 1991 and 1992 (the wet years) were greater than in 1989 and 1990 (the 2 dry years; SNK: all $q > 15.1$, $df \geq 16$, $P < 0.05$); at Goffs, 1992 > 1991 > 1989 and 1990 (SNK: all $q > 1.2$, $d \geq 15$, $P < 0.05$); and at Ivanpah, 1992, 1991 and 1990 were greater than 1989 (SNK: all $q > 15.3$, $df \geq 16$, $P < 0.05$).

WEI

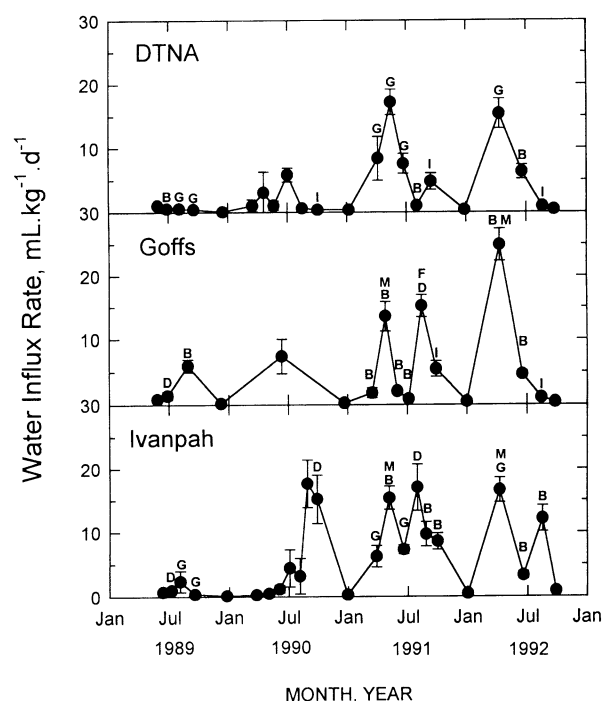The WEI is the ratio of water flux rate (ml day^{-1}) to FMR (kJ day^{-1}) and it expresses the amount of water

Fig. 3 Mean (±95% CI) water influx rate of desert tortoises at three California sites in the Mojave Desert. (see legend to Fig. 2 for further details)
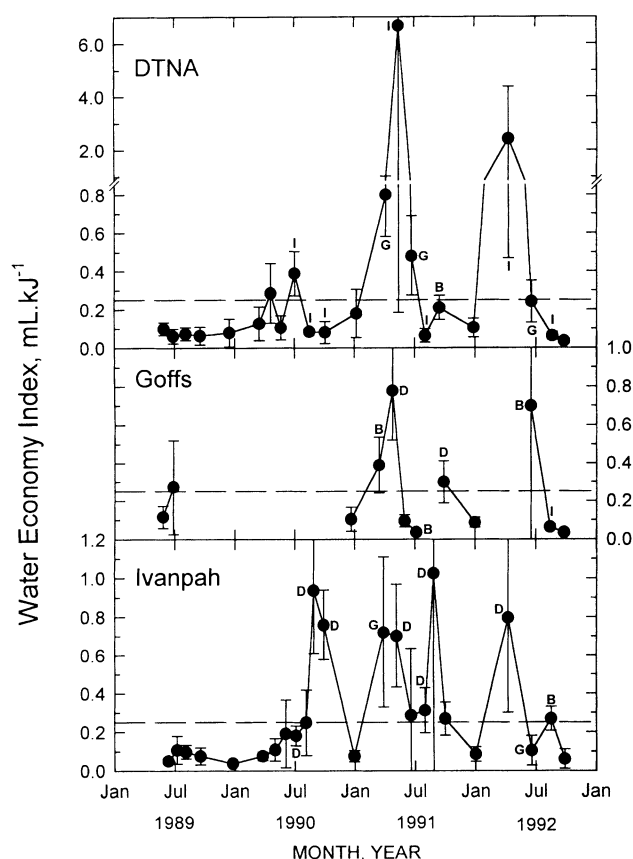

Fig. 4 Mean (±95% CI) water economy index (WEI) of desert tortoises at three California sites in the Mojave Desert (see legend to Fig. 2 for further details). WEI values higher than 0.25 (*dashed lines*) indicate probable drinking of free-standing water

used per unit of energy metabolized (ml kJ^{-1}; Nagy and Peterson 1988). We use WIR as our best estimate of water flux rate (which applies only to an animal in a steady-state condition, where influx = efflux = flux). The WEI adjusts the water intake rate for differences in metabolic rates due to differences in body size and season. The theoretical WEI for a given food can be calculated as its metabolic water plus preformed water yield divided by its metabolizable energy content (Nagy and Peterson 1988). Succulent desert plants have a WEI up to 0.25, so higher WEIs measured in tortoises would indicate that they had drunk rainwater. WEI values were low (<0.1 ml kJ^{-1}) during winter and during rainless periods in the activity seasons, and were high (approaching 1.0 ml kJ^{-1}) when rain fell during measurement periods when tortoises were active (Fig. 4). Two-way repeated-measures ANOVA of the WEI indicated significant effects of measurement period ($F_{11,43}$ = 13.8, P = 1.4 × 10^{-21}), site ($F_{2,433}$ = 10.8, P = 4.1 × 10^{-5}) and time-site interaction ($F_{22,433}$ = 7.90, P = 1.1 × 10^{-19}). However, this may have been due to one unusually high mean WEI value for DTNA. When it was deleted, the differences between sites were no longer significant. These results indicate that the WEI varied through time, and that the seasonal patterns of WEI variation differed between sites, but the evidence that mean WEI differed between sites was weak. One-way repeated-measures ANOVA of the WEI within sites showed highly significant effects of time period (all $F_{11,181}$ ≥ 5.17, P < 5.3 × 10^{-11}),

with the highest WEIs occurring during spring and summer activity seasons (SNK: all q > 0.0025, df ≥ 12, and P < 0.05). At DTNA, peak seasonal WEI values were highest in 1991, lower in 1992, even lower in 1990, and lowest in 1989 (SNK: all q > 0.018, df ≥ 11, P < 0.05); at Goffs, 1991 and 1992 > 1989 (SNK: all q > 4.01, df ≥ 12, P < 0.05); and at Ivanpah, 1990, 1991, and 1992 > 1989 (SNK: all q > 3.95, df ≥ 10, P < 0.05).

Sex effects

The expansion of physiological measurements in 1991 to include both male and female tortoises at the three sites allowed analysis of the effects of sex on FMR, WIR, and WEI over 2 years. There were insufficient repeat measurements on individuals to use repeated-measures ANOVA for testing the effects of sex. Two-way ANOVA of FMR within sites revealed significant effects of period (all P < 6.0 × 10^{-17} – see above), and sex ($F_{1,96}$ = 11.3, P = 1.2 × 10^{-3} for DTNA; $F_{1,164}$ = 4.46, P = 0.036 for Goffs; and $F_{1,134}$ = 9.11, P = 3.1 × 10^{-3} for Ivanpah), and no significant interaction (all F ≤ 1.6,

$0.6 > P > 0.12$, $df \geq 9{,}96$). The mean ($\pm$ SE) of males and females at DTNA (males: 14.3 ± 0.7 kJ kg^{-1} day^{-1}; females: 10.3 ± 1.0 kJ kg^{-1} day^{-1}), Goffs (males: 15.2 ± 0.6 kJ kg^{-1} day^{-1}; females: 13.2 ± 0.6 kJ kg^{-1} day^{-1}), and Ivanpah (males: 31.0 ± 1.7 kJ kg^{-1} day^{-1}; females: 24.4 ± 1.3 kJ kg^{-1} day^{-1}) differed by 39, 15, and 27%, respectively. SNK analyses indicated significant differences between sexes during several periods at all three sites (Fig. 2; all $q > 3.0$, $df > 10$, and $P < 0.05$), with males having higher FMRs than females in all instances. At DTNA, male FMRs were 52% higher than females in August and September 1991, 86% higher during August 1992, and 75% higher in September through October 1992. At Goffs, male FMRs exceeded those of females by 52% during August 1992, and by 68% during September through October 1992. At Ivanpah, male FMRs averaged 62% higher than female FMRs during September 1991.

Two-way ANOVA of WIR within sites yielded mixed results. No significant effects of sex were detectable for DTNA, but there were significant interactions of period and sex for Goffs ($F_{11,213} = 4.07$, $P = 2.3 \times 10^{-5}$) and Ivanpah ($F_{11,\ 177} = 3.19$, $P = 6.3 \times 10^{-4}$). Subsequent SNK analyses indicated that at Goffs, males had WIRs that were 28% higher than females in May 1991 and 24% higher in March through April 1992, but females had WIRs averaging 28% higher than males in July and August 1991. At Ivanpah, male WIRs averaged 29 and 38% higher than females in May 1991 and March through April 1992, respectively. These results indicate that seasonal patterns of WIR differences between sexes varied among study sites.

Rainfall effects

Peak FMR during the activity season (Fig. 2) was higher in years having higher rainfall ($r_s = 0.62$, $P = 0.035$, $n = 11$ for all sites combined, Spearman rank order correlation). However, within each site, FMR was significantly correlated with rainfall only at Ivanpah (correlation between active-season FMR and rainfall: $r_s = 0.21$, $P = 0.0028$, $n = 208$; correlation between spring FMR and rainfall for the previous winter, October through March: $r_s = 0.62$, $P < 0.00001$, $n = 67$). For all sites, activity season WIR was positively correlated with rainfall (DTNA: $r_s = 0.44$, $P < 0.001$, $n = 179$; Goffs: $r_s = 0.21$, $P = 0.0018$, $n = 214$; Ivanpah: $r_s = 0.39$, $P < 0.001$, $n = 251$) and spring WIR was correlated to rainfall for the previous winter (DTNA: $r_s = 0.80$, $P < 0.001$, $n = 52$; Goffs: $r_s = 0.71$, $P < 0.001$, $n = 73$; Ivanpah: $r_s = 0.83$, $P < 0.001$, $n = 75$). The WEI was significantly correlated with rainfall during the active season only at DTNA ($r_s = 0.54$, $P < 0.001$, $n = 165$) and Ivanpah ($r_s = 0.30$, $P < 0.001$, $n = 206$). Spring WEI was correlated with WIR ($r_s > 0.5$, $P < 0.005$, $n > 10$ for all sites) much more often and more strongly than with rainfall or with FMR.

Discussion

Habitat quality

Does it matter where a desert tortoise lives? Aside from the thermal requirements of the species for daily activity (body temperatures of 20–38 °C; McGinnis and Voigt 1971) and seasonal activity (Woodbury and Hardy 1948; Van Devender et al. 1976), desert tortoises require seasonal availability of food plants and especially drinking water to maintain typical activity and growth during a year. However, tortoises may experience shortages of food and water on a regular basis in at least some portions of their range (Medica et al. 1975; Nagy and Medica 1986; Peterson 1994b; Berry and Medica 1995). Our results indicate that rainfall events have pronounced effects on rates of water intake and possibly on energy utilization as well. Rain not only provides water for immediate drinking, but it also stimulates and sustains germination and growth of the plants tortoises eat (Beatley 1969, 1974; Nagy and Medica 1986). These plants provide considerable water (as succulence of their tissues) for tortoises during the period that they are green. Regional variation in rainfall is well known in the Mojave Desert (Shreve 1925; Rowlands et al. 1982), with winter rains being the major source of water in the western portion, but diminishing in importance toward the east, where monsoonal summer rains become important. This suggests that the western part of the Mojave should offer tortoises less rainwater for drinking during the activity seasons of the year, and hence be less benevolent to them.

Our results (Fig. 3) indicate that tortoises in the west (DTNA) were able to respond as exuberantly to a rainfall event (e.g., in spring 1991, by increasing WIR) as eastern tortoises. There were differences in the overall level of physiological performance between sites, but these were attributable to differences in timing and magnitude of rainfall events. Within sites, the highest WIR values were 145–165 times greater than the lowest average WIR values. A high WIR was associated primarily with opportunities to drink rainwater (23 of 28 instances of relatively high WIR were periods during which rain occurred), and seemed to be independent of geographic location (tortoises at all three sites were observed drinking water copiously when it was available during activity seasons). Peak WIRs were low during the dry years of 1989 and 1990, but were relatively high during 1991 and the ENSO year, 1992 (Fig. 3). These observations indicate that desert tortoises are heavily dependent on the timing and amounts of precipitation at their specific locale (see also Peterson 1996a,b).

Sex effects

The relatively high FMRs of male tortoises in the summer are not surprising. Male desert tortoises might

be expected to have high FMRs throughout most of the warm seasons because their home ranges are much larger than those of females (Berry 1986; O'Connor et al. 1994), and males court and attempt to mate with females at any opportunity (Rostal et al. 1994; Ruby and Niblick 1994; personal observations). Female desert tortoises do not appear to actively seek mates, and thus probably expend less energy in courtship and mating than males. However, the annual FMR of females was positively correlated with the number of eggs laid in spring 1988 and 1989 (Henen 1997), indicating that energy expenditures associated with reproduction (e.g., digging nests, producing the eggs, and increasing foraging effort to gather extra nutrients for producing eggs) are substantial. Thus, we hypothesize that males are less likely to have higher FMRs than females during spring when females complete egg production and nesting. Our results support this suggestion: only during the late summer and autumn of 1991 and 1992 did males have significantly higher FMRs than females.

Water can be a limiting resource for egg production, and water influx during summer and early fall can influence whether females produce any eggs the ensuing spring (Henen 1997). Therefore the wet conditions of 1991 and 1992 probably contributed to the relatively high egg production rates in 1992 and 1993 (I.R. Wallis, B.T. Henen, K.A Nagy, unpublished observations). It would have been prudent for males to expend extra energy in social interactions and courtship in autumn 1991 and 1992 to increase their chances of fertilizing many eggs. During the drier periods (1989 and 1990), both males and females had low FMRs and WIRs, which probably enhanced their chances for survival. This may have been associated with reduced reproductive behavior by both sexes during dry years.

On an annual basis, males had FMRs that were about 21% greater than those of females (21% for DTNA males, 16% for Goffs males, and 27% for Ivanpah males). This additional expenditure might be considered as part of male reproductive effort (RE). However, females also spent metabolic energy on reproduction during the year, as well as the chemical potential energy they channeled to eggs, so sexual differences in annual FMR do not facilitate a simple evaluation of male RE. Simultaneously measured, itemized field energy budgets (e.g., Henen 1997) for both male and female tortoises are needed for an accurate evaluation of RE.

Drought survival

Deserts are defined on the basis of having little precipitation, but they may also be characterized as having extremely variable temperatures (Louw and Seely 1982), levels of rainfall (Rowlands et al. 1982; MacMahon 1985), food quantity (i.e., plant productivity: Turner et al. 1986; Henen 1997), and food quality (see Peterson 1996b). Desert animals make physiological and behav-

ioral adjustments to survive and reproduce under such extremes, but different species may use different methods to succeed. The relatively low WIR and FMR of tortoises during droughts indicates that their feeding and activity levels were low, probably because they were spending much time in burrows, and not out foraging, mating, or fighting. Thus, desert tortoises use a conservative approach. Their retreat into burrows reduces water and energy expenditures which presumably enhances survival during harsh periods (Nagy and Medica 1986). The associated physiological capabilities of tolerating unusually high osmotic, electrolyte and urea concentrations in their blood (Peterson 1996a) facilitate endurance of long periods without food or water. This contrasts with the approach of carnivores: when food becomes more scarce, they forage more extensively (Lindstedt et al. 1986; Rolstad and Rolstad 1995; Gese et al. 1996; Quinn 1997).

Additionally, desert tortoises may temporally decouple the control of different physiological parameters such as energy, water, nitrogen, and electrolyte balance (Nagy and Medica 1986; Peterson 1996b). For example, desert tortoises can acquire energy surpluses while body water content (Nagy and Medica 1986; Peterson 1996b) and dry mass content (Henen 1997) are declining in summer and autumn when they are eating food low in water and protein (dry grass). They may also be able to accumulate protein while in a negative energy balance in spring (very succulent food provides less energy but more protein than required: Nagy and Medica 1986; Peterson 1996b). Moreover, between-year differences may be even more dramatic than seasonal differences. The enormous differences in FMR and WIR between the drier periods of 1989–1990 and the wetter periods of 1991 and 1992 further emphasize the remarkable capacity of desert tortoises to respond behaviorally and physiologically to their extremely variable environment, and emphasize the critical role of anhomeostasis (the ability to allow temporary, major increases in blood osmotic and ionic concentrations; Peterson 1996a) in helping desert tortoises endure harsh environmental extremes. For desert tortoises, behavioral and physiological plasticity is key to drought survival.

Weather patterns

In March 1991, following a third consecutive unusually dry winter, a large storm system yielded substantial rainwater over the entire Mojave Desert. Not only did this short but concentrated event enable tortoises to drink (Fig. 4), it also stimulated a major germination and bloom of "winter" annual plants across the Mojave Desert. Tortoises at all three sites exploited this food resource and all showed prolonged increases (compared to the 2 previous years) in FMR and WIR (Figs. 2, 3), indicating that large-scale widespread weather changes can reverse deleterious effects of previous local circumstances.

In the following year, 1992, another large-scale climatological event confirmed this observation. An El Niño (ENSO) event generated higher than average winter rainfall and concomitant high plant productivity the following spring. El Niño (ENSO) events are known to increase rainfall along the western coasts of both North and South America (Markham and McLain 1977; Barber and Chavez 1983; Glantz 1996), and to increase Mojave Desert rainfall in California by 37–44% above normal (NOAA 1998). Tortoises responded to this in unison at all three sites both behaviorally (drinking and foraging intensely) and physiologically (high FMR and WIR). In contrast, tortoise activity and physiological rates were low under drought conditions (Figs. 2, 3; Peterson 1996a,b; Henen 1997). Young desert tortoises also exhibit strong behavioral and physiological responses to extreme climate changes (Nagy and Medica 1986; Nagy et al. 1997).

Demography also appears to be rainfall dependent in desert tortoises. Reproductive output in 1983 (Turner et al. 1986) and in 1992–1993 (I.R Wallis, B.T Henen, K.A. Nagy, unpublished observations) was high following heavy winter rains associated with ENSO events, in contrast to very low reproduction following dry winters (F.B. Turner, K.H Berry, D.C Randall, G.C White, unpublished observations; Henen 1997). Drought conditions increase adult mortality (Turner et al. 1984; Peterson 1994b) and probably decrease recruitment of desert tortoises (Morafka 1994). It is unlikely that the parallel responses of desert tortoise behavior, physiology, and demographic parameters to climate conditions are coincidental. Evidence that ENSO events may have existed for at least the last 5000 years (Sandweiss et al. 1996) suggests that local manifestations of global climatic events may exert a large influence on the physiological ecology and demographic patterns of desert tortoise populations.

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