A Condition Index for the Desert Tortoise (Gopherus agassizii)

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ABSTRACT. – We measured body masses and shell dimensions of free-ranging adult desert tortoises (*Gopherus agassizii*) through two years of above-average rainfall (1992–93) in the Mojave Desert of California. A condition index (CI), simulating a physical density value, was calculated as the ratio of body mass to estimated shell volume (carapace length x height x width). The highest CI determined for individual tortoises that were recaptured during all seasons was considered to be their prime CI. Prime CIs of individuals fell within a range of 0.6 to 0.7 g/cm³, and averaged 0.64 g/cm³. In general, prime CIs did not vary between sexes, between study sites in the eastern and western Mojave Desert, with variation in body size among adults, or with age. However, when adult males were examined separately, their prime CIs increased slightly but significantly with increasing body mass, and adult females in the western Mojave Desert had slightly lower prime CIs (0.62 g/ cm³). Changes over time in condition indices of three populations revealed seasonal and geographic variations that corresponded with the local availability of green forage plants and rainwater for drinking. Hatchling tortoises had very low CIs following five months of poor food availability and drought. We suggest that a prime CI value of 0.64 g/cm³ is a useful standard for evaluating the body condition of wild tortoises in the field.

KEY WORDS. – Reptilia; Testudines; Testudinidae; Gopherus agassizii; tortoise; condition index; body condition; Mojave Desert; California; USA

Among reptiles, desert-dwelling species show the greatest capacities for tolerating swings in body composition, especially water content, in response to seasonal periods of resource scarcity (Shoemaker and Nagy, 1977; Minnich, 1979, 1982; Bradshaw, 1986; Louw, 1993). Among desert reptiles, desert tortoises (Gopherus agassizii) have remarkably well-developed abilities to endure long-term imbalances in their water, energy, salt, and protein budgets (Nagy and Medica, 1986; Peterson, 1996; Bradshaw, 1997; Henen, 1997, 2002). This includes the storage of up to about 30% of their body mass as urine in their large urinary bladder, for use as a water reserve during droughts (Minnich, 1976, 1979). Being herbivorous, desert tortoises may also have much food material in their guts, and often females are gravid during the spring (Wallis et al., 1999). Thus, the body mass of an individual tortoise may vary considerably through a year, depending mainly on how much food and water it contains. Therefore, the ratio of body mass to a measure of shell length or volume should provide some indication of nutritional and hydration status of a tortoise.

Tortoises live inside rigid shells, which, in contrast to the situation in mammals, limits the extent to which their bodies can enlarge over short time periods. Thus, it is unlikely that a tortoise could become as obese as, say, a ground squirrel just before it enters hibernation. We have assumed that a wild tortoise is at its healthiest (nutritionally) when its body mass is at its highest point for a given shell size. In other words, we assumed that tortoises do not become "pathologically overweight" in the field the way they sometimes can in captivity.

The concept of condition index (CI) has been applied to many groups of animals, including fish (Neumann and Willis, 1994), mammals (Adamczewski et al., 1995), birds (Winkler and Allen, 1996), snakes (Bonnet and Naulleau, 1994), lizards (Bradshaw and De'ath, 1991), and the desert tortoise (Jacobson et al., 1993; Peterson, 1996). Usually, CI is calculated as body mass divided by an appropriate body length measurement, with the goal of correcting for size (length) differences between individuals in order to examine relative differences in body mass. We chose a volume measurement for the denominator (carapace length x height x width) in order to more accurately account for known or suspected differences in shell shape between sexes and among populations, and to render CI units into the more familiar units of density (mass per unit volume, as g/cm³). We avoided the more complicated regression equation methods of defining CI in order to have an index that can be used easily in the field to evaluate the condition of a tortoise in hand.

Our study had several goals. We wished to determine the CI value(s) representative of a fully-hydrated, well-fed wild tortoise. Does this "prime" CI value differ between sexes? Is it independent of variation in body size and age? Does it differ geographically? Are seasonal effects obvious? Do tortoises drop below their prime CI, and if so, how much, for how long, and at what times of year? We attempted to answer these questions by measuring body masses and shell dimensions of wild tortoises living in the Mojave Desert of California during two years having relatively high rainfall.

METHODS

In 1992 and 1993, we studied 98 free-ranging desert tortoises living in three study sites in California: in the eastern Mojave Desert at a site (35°22'N, 115°22'W) near Ivanpah and at another site (34°52'N, 115°10'W) near Goffs, and in the western Mojave Desert at the Desert Tortoise Natural Area (DTNA; in and around Section 12; 35°15'N, 117°52'W). Rainfall during winter was over three times greater than the long-term average for all three sites in both years (Henen et al., 1998). Most of the animals carried radiotransmitters weighing about 110 g, and were being monitored four times per year as subjects in a health and disease study (Christopher et al., 1999). Additional adult, subadult, and hatchling tortoises living in these sites were weighed and measured for CI data when encountered in the field. In October of 1993, we also measured 57 hatchling tortoises living at a study site (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.

Field measurements were made at each site during early spring (March), late spring (May), summer (July/August), and autumn (September/October) of 1992 and 1993. Captured tortoises were weighed as quickly as possible at the site of capture to avoid weight loss errors due to urination or defecation. In May of each year, we measured body masses (to \pm 5 g using a digital top-loading electronic balance), midline carapace length (CL, maximum, straight-line and midline distance from the anterior edge of marginal scute number 1 to the distal edge of the supracaudal scute, using C-shaped, adjustable aluminum calipers and a millimeter ruler, ± 1 mm), shell height (ventral to the heart at the intersection of the four humeral and plastral scutes to the top of the carapace directly above), and width (through the plane of the heart, the maximum distance between the crests of the left and right fifth marginal scutes). Body masses of radiotelemetered tortoises were corrected for the mass of the transmitter packages, which were measured when previously installed on the animals.

Originally, we measured the maximum width of tortoises, which was usually between the right and left marginal scutes number 8, over the hind leg openings. However, experience indicated that there was much variation between sexes, and especially between individual females, in this dimension. Thus, at the next opportunity, the width of each animal was measured at the junction of marginal scutes 6 and 7 (just forward of the hind leg openings). This dimension contained much less individual variation. In 1993, we decided to measure shell width as the distance between crests of right and left marginal scutes number 5, located at "heart" level, just behind the foreleg openings, in order to simplify the location of width and height measurements, and to normalize our measurements to those already gathered by other researchers studying desert tortoises. In May 1993, we measured widths of recaptured tortoises both ways (at scute number 5 [new method], and between scutes 6 and 7 [old method]), and calculated regression equations (new method vs. old method). These equations were then used to estimate "new" widths from "old" width measurements made during 1992, only for those tortoises that were not recaptured again in 1993.

Most tortoises we studied were adults, and did not grow much during this study, so we measured only their CL at the recaptures done in summer, autumn, and the following early spring. If CL remained the same as in May, we assumed that the width and height values also remained the same. When CL differed more than expected measurement error (± 2 mm), we estimated width and height using regression equations derived for this purpose from data for each site separately.

Statistical Analyses. — Results are presented as means, along with either standard deviation (SD, in the text) or 95% confidence interval (in the figures). Means were considered to be significantly different if p < 0.05. Student's and paired t-tests were used when samples were normally distributed, and rank sum tests were used otherwise. Either analysis of variance (ANOVA) or ANOVA on ranks (for nonparametric data) were used in comparisons of more than two groups. We followed parametric and nonparametric ANOVA with Student-Newman-Keul's and Dunn's post hoc analyses, respectively (all p < 0.05). Regression analyses were calculated using the linear least squares method.

RESULTS

Prime Condition Index. — Tortoises that were recaptured in all seasons sampled had their highest CI in May of either 1992 or 1993. Accordingly, if a tortoise was not sampled during May of 1992 or 1993, we did not use any of its CI values for estimating prime CI. For 31 adult females, prime CI averaged 0.647 ± 0.033 (SD) g/cm³, and the prime CI for 28 adult males averaged 0.635 ± 0.028 g/cm³. These means do not differ significantly ($t_{57} = 1.5$, p = 0.14) so we combined the sexes to obtain the overall mean of $0.641 \pm$ 0.031 g/cm³ (95% confidence interval of mean: ± 0.008).

Among adult females, there was no effect of body size on prime CI (F-test value for significance of regression = 0.001, p = 0.98), but among adult males, there was a small but statistically significant effect of size (F_{1,26} = 5.32, p =0.029). If the point for the smallest male (Fig. 1) is deleted, the regression for males becomes statistically insignificant (F_{1,25} = 2.51, p = 0.126). For females and males combined, there was no significant effect of body size on prime CI (F₁, $s_7 = 0.0004$, p = 0.984), even though the mean body size of adult females (2257 ± 414 g) was substantially lower than that of males (3721 ± 839 g; Mann-Whitney Rank Sum test, T = 1214, p < 0.0001).



Figure 1. Regressions of prime condition index (CI) on body size for adult female (large filled circles) and adult male (open squares) desert tortoises at three sites in the Mojave Desert of California. Regression lines are bounded by their 95% confidence intervals. Prime CIs for juveniles and hatchlings are shown as small filled circles.

Prime CI did not vary geographically among males (one-way ANOVA, $F_{2.25} = 1.81$, p = 0.185). However, females at the DTNA had significantly lower prime CIs (0.620 ± 0.38 g/cm³) than did females at Goffs (0.658 ± 0.025) and Ivanpah (0.657 ± 0.023). DTNA females did not have different prime CIs than did males combined ($t_{35} = 1.28$, p = 0.207).

Seasonal Variation. — We evaluated the influences of seasonal and geographic variation on the 98 adults studied at three sites. The CI values were expressed as percent of mean prime CI (0.641 g/cm³), to enhance clarity and comparisons. The CIs of female tortoises at Ivanpah (n = 10), Goffs (n = 19), and the DTNA (n = 9) changed substantially as the seasons progressed (Fig. 2). The CIs of adult males at Ivanpah (n = 17), Goffs (n = 22), and the DTNA (n = 13) also differed by season (Fig. 3). In all six cases (both sexes at three sites), ANOVA and post hoc analyses indicated highly significant differ-



Figure 3. Condition indices (mean CI \pm 95% confidence intervals) of adult male desert tortoises at three study sites in 1992 and 1993.



Figure 2. Condition indices (mean CI±95% confidence intervals) of adult female desert tortoises at three study sites through 1992 and 1993.

ences in relative CIs between different seasons. In both sexes, CIs were highest in late spring (May), and were generally lowest in late summer. The CI of tortoises declined by over 20% from spring to autumn.

Geographic Variation. — Females at the DTNA had lower CIs than did females at Goffs or at Ivanpah in spring of 1992 (Fig. 2). Similarly, males at DTNA had relatively low CIs in May of 1992 as well (Fig. 3). In summer and autumn, females at Ivanpah had higher (1992), or lower and higher (1993) CIs than females at other sites. Males at Ivanpah showed similar, but less extreme seasonal differences, compared to males at the other sites (Fig. 3).

Gender Differences. — In early spring of 1992, females had significantly lower CIs than did males (all sites combined; Fig. 4). Thereafter, CIs did not differ between the sexes. The apparent differences in summer and autumn of 1993 (Fig. 4) were not statistically significant (p > 0.05, ttests).



Figure 4. Condition indices (mean CI±95% confidence intervals) of adult desert tortoises at three sites in the Mojave Desert in 1992 and 1993.

Age Effects. - The CIs of a group of hatchling, juvenile, and subadult tortoises (n = 11) sampled in late April and May 1993 at the Goffs study site (average body mass = 411 \pm 354 g) ranged from 87 to 114% of prime CI (Fig. 1). These unmarked animals were not captured repeatedly to determine when their CIs were highest, so they were not included in the analysis of prime CI, but they were measured during the months of highest CIs in adults. These young tortoises did not differ significantly from the expected prime CI of 0.641 g/cm3. Moreover, there was no significant correlation of CI with body mass ($F_{1.8} = 0.038, p = 0.85$; Fig. 1). The two hatchlings in this group (60 and 75 g body mass) had CIs of 0.645 and 0.733 g/cm3 (101 and 114% of prime CI). In contrast, the 57 hatchlings (mean body mass = 38.0 ± 15.4 g) sampled at Fort Irwin in autumn had CIs averaging only 0.401 g/cm³ (62.5% of expected prime CI).

DISCUSSION

Prime Condition Index. - We suggest that a mean value of 0.64 g/cm3, with a 95% confidence interval of 0.63 to 0.65 g/cm3, is representative of a wild desert tortoise that is fully hydrated and well-fed (i.e., in prime condition) under field conditions during high-rainfall years in the Mojave Desert of California. This value appears to be independent of age and body size, although there was a small effect of body mass in males. If the tortoise is an adult female, then the range of prime CIs is 0.62 to 0.66, depending on location (lower in the western Mojave). It will be interesting to compare this estimate of prime CI with the prime CIs of Utah, Arizona, and Sonoran Desert populations (to evaluate possible geographic variation over a wider area), with zoo and pet tortoises (to see if "obesity" or "bloating" in tortoises is possible under protected conditions, and if CI differs in extremely old individuals), with captive tortoises known to be well-nourished at the Desert Tortoise Conservation Center near Las Vegas, Nevada (to evaluate effects of food provided ad libitum), and with wild tortoises diagnosed as having parasite infestations or diseases (to look for effects of diseases such as URDS; Jacobson et al., 1993).

Seasonal and Sexual Variation. - The occurrence of peak CI values in May (Figs. 2 and 3) was expected solely from a nutritional perspective, because spring was when green forbs were available. Following May, increasing temperatures and drought generated more arid conditions, and food plants dried and withered. Tortoises progressively lost body condition through summer, reaching their lowest CI values in August or October. We ascribe this decline mainly to loss of body water from tortoises (Nagy and Medica, 1986; Peterson, 1996), although reduced gut contents prior to hibernation may contribute to the lower body masses. At Ivanpah, tortoises increased their CI in late summer, most likely by drinking rainwater that feil on that site, but not on the other two sites, in both years (see below). Tortoises had relatively high CIs when they were first captured in early

spring (March; Figs. 3 and 4). They probably did not eat or drink during the winter hibernation period, and most tortoises captured in March had not yet emerged from winter burrows. Thus, it seems most likely that tortoises obtained food or water or both between the time we sampled them in October 1992, and the time they entered hibernation.

Hatchling tortoises at Fort Irwin had very low CIs, averaging less than 65% of prime CI. By October 1993, when the CI measurements were made, these tortoises had been losing weight for five months due to very dry conditions (Nagy et al., 1997). They had very low rates of water intake, indicative of either aphagia or consumption of very dry food, and analysis of relative water and food use indicated that they were quite dehydrated (Nagy et al., 1997). A CI of 65% of prime CI suggests that these hatchlings had lost about 35% of their body mass, indicative of the remarkable dehydration tolerance for which this species is known (Minnich, 1976; Nagy and Medica, 1986; Peterson, 1996). However, it would be useful to assess whether CIs change with age.

Geographic Variation. - The two main differences in CI between populations were the comparatively low CI values in DTNA tortoises (especially females) during spring of 1992, and the pattern of CI change during summer and autumn in Ivanpah animals. Both females and males at the DTNA attained high CIs in May of 1993, so the lower peak CIs they had in May of 1992 probably do not indicate an interpopulational difference in prime CI. We suspect that low food and water availability at DTNA in 1991 (Henen et al., 1998) put those tortoises at a lower condition level than at the eastern sites. Females may have been affected more than males due to their additional burden of reproduction (Henen, 1997). Similarly, greater water availability (and later, food availability from germinating forbs and sprouting perennials) from summer rain showers at Ivanpah probably accounted for the increase in CI between summer and autumn in both 1992 and 1993 at Ivanpah, but not at the other sites. Rainfall amounts during the period May to October in 1992 and 1993 were, respectively: 67.4 and 30.0 mm at Ivanpah, but only 0.8 and 1.2 mm at Goffs and 0.0 and 9.6 mm at the DTNA.

Age/Size Effects. — It is surprising that the CIs of the two hatchlings were close to the prime CI determined for adults, and that there was no demonstrable effect of body size on CI among the juvenile, subadult, and adult tortoises at Goffs in late spring. In many vertebrate species, including numerous squamate reptiles, there are changes in body proportions (shape) and especially in body fat content as individuals get older. These changes should be reflected in changing proportions of body mass to estimated volume. Either desert tortoises do not follow this pattern, or our method accounted for the changes that do occur with age. This apparent absence of a size effect is useful, because it simplifies the application of the prime condition index concept in the field ("0.64 g/cm³ is prime CI for all wild tortoises in the California Mojave Desert"). However, some of the data supporting this statement are thin, and the robustness of this conclusion should be verified, especially regarding hatchling tortoises.

Conclusion

Desert tortoises in "prime" nutritional condition had body condition indices (prime CIs) averaging 0.64 g/cm³. This value was generally representative of both females and males, of tortoises in both eastern and western portions of the Mojave Desert, and of all sizes (ages) of tortoises. We suggest that field workers can rapidly evaluate the body condition of tortoises they encounter by weighing them, and measuring midline carapace length, and shell width and height at the level of the heart. Dehydrated tortoises are expected to have CIs below about 0.45 g/cm³ (70% of prime CI).

Note Added in Proof. — Newly-available CI measurements from 24 neonate tortoises that were only 5–61 days old (hatched in September and October 2002 from eggs laid by captive females and kept in an incubator) averaged 0.641 ± 0.028 g/cm³. This is identical to the mean of 0.641 ± 0.031 g/ cm³ for 59 adults (above). Although these hatchlings were not from the field, this observation supports the suggestion that prime CI is independent of age and body size.

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