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Sexing Young Free-Ranging Desert Tortoises (*Gopherus agassizii*) Using External Morphology

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ABSTRACT. – **The external morphology of *Gopherus agassizii* is sexually dimorphic with characteristics of the plastron useful for determining gender. However, these characteristics are associated with male secondary sexual characteristics, females being identified by the lack of such features, and therefore are less useful for assessing gender in young tortoises. We investigated whether these and other external characteristics could be used for determining gender of small tortoises by measuring 22 external characteristics on 105 tortoises (carapace length 52–299 mm) and analyzing these data using discriminant function analysis. The discriminant models were capable of unambiguously assigning gender to individuals as small as 140 mm carapace length, and by plotting the discriminant scores on carapace length, the model could be used to predict possible gender of even smaller tortoises.**

KEY WORDS. – **Reptilia; Testudines; Testudinidae; *Gopherus agassizii*; tortoise; sexual dimorphism; gender; morphology; discriminant function analysis; methodology; Mojave Desert; Nevada; USA**

Methods for using external morphology to determine the gender of large desert tortoises (*Gopherus agassizii*) have been well known for years, as both Miller (1932) and Grant (1936) referred to the sexes without comment. Woodbury and Hardy (1948) provided quantitative measurements of male and female tortoises and stated that the sexes generally can be identified using four characters. In males, the gular projection is longer, the plastral concavity is deeper, the tail is larger, and the overall size is greater than in females. However, overlap exists, and these characters are not entirely satisfactory: "by studying these four characters, adults can usually be distinguished with certainty and a large percentage of young tortoises can be placed satisfactorily, but even with careful study, there are a few that cannot be properly allocated" (Woodbury and Hardy, 1948:162).

Although using external morphology to determine sex of adult desert tortoises has generally been considered easy, the logic of current methods is potentially circular: males are thought to have a specific set of characters, therefore tortoises with those characters are male. Independent confirmation of gender (e.g., internal examination of gonads) generally is lacking.

Sexing juvenile desert tortoises is problematic because secondary sexual characters are used to determine gender, and these characters generally are not pronounced before males reach reproductive age (about 20 yrs for the females used in this study; Mueller et al., 1998) and a carapace length of about 180–200 mm. Therefore many biologists do not attempt to classify tortoises with carapace lengths smaller than about 180–200 mm. Sex of desert tortoises can be determined with a high degree of certainty using testosterone levels in the blood (Rostal et al., 1994a), laparoscopy (visual examination of the gonads; Rostal et al., 1994a), ultrasonography (Rostal et al., 1994b), or radiography of eggs (Turner et al., 1986), but these methods require techniques and laboratory facilities often not available to field researchers. The difficulty of determining gender of small tortoises using external characteristics was evidenced by the unsuccessful attempt of Burke et al. (1994) to determine the gender of captive-reared desert tortoise hatchlings.

The ability to easily determine the gender of wild juvenile desert tortoises using external morphology would aid researchers studying demographics and other sex-dependent topics that aid in conservation efforts. The objectives of this study were to determine whether juvenile male and female tortoises in the northern Mojave Desert differ in external morphology, and if they do, to use discriminant analysis to find a compact set of measurements that could be used in the field to determine gender before desert tortoises reach sexual maturity.

MATERIALS AND METHODS

As part of a tortoise monitoring and research program (Rautenstrauch et al., 1991) conducted at Yucca Mountain, Nevada, USA (36°51'N, 116°26'W), blood was drawn once per year (1993–95) and a few measurements of the carapace and plastron were recorded (1989–95). In 1992, 22 morphological measurements were taken on 105 tortoises. These measurements included: anal notch (AN), distance between the posterior edge of the plastron and the posterior edge of the carapace measured in the midline; minimum anal aperture (APER), estimated using circular cutouts of known diameter; anal width 1 (AW1), distance between the distal-most points on the two anal scutes; anal width 2 (AW2), distance between the lateral-most points of the suture between the anal and femoral scutes; carapace length (CL), maximum length of the carapace; foot widths (front-foot-right: FFR; front-foot-left: FFL; hind-foot-right: HFR; hind-

foot-left: HFL), distance between the medial side of the medial toe-nail to the lateral side of the lateral toe-nail; gular length (GULAR), distance from the middle of the seam between the gular and humeral scutes to the distal-most point of the longest gular; shell height (HGT), measured at the middle of vertebral scute 3; marginals 3–4 seam (M34), width of the carapace measured at the seam between marginal scutes 3 and 4; marginal 4 (M4), width of the carapace measured at the middle of marginal scute 4; marginals 7–8 seam (M78), width of the carapace measured at the seam between marginal scutes 7 and 8; plastral concavity (PC), depth of the femoral concavity measured by placing a straight-edge on the plastron along the midline and measuring the deepest point along the straight-edge; plastral notch length (PNN), midline length of the plastron measured between the anterior and posterior notches; plastral tip length (PTT), maximum length of the plastron; anal shield thickness (SHLD), thickness of the anal shield (xiphiplastron and anal scute) measured from the side immediately posterior to the leg; tail length (TL), measured from the posterior margin of the cloaca to the tip; tail width (TW), measured at the proximal base; mass (WT), total mass (in g); and maximum width (WTH), maximum width of the carapace. Except as noted, measurements were made using calipers and recorded to the nearest 1 mm for characters generally exceeding 70 mm, and 0.1 mm for shorter measurements.

In multivariate analyses, missing data were replaced with estimates generated by regressing the character of interest on the character with which it was most highly correlated. Most characters were highly correlated ($r > 0.95$) with at least one other character. Overall, 62 of 2310 data points (males: 38, 3.7%; females: 13, 1.4%; unknown gender: 11, 2.6%) were estimated. The majority of missing data were associated with male tails (TL: 10, TW: 14), female tails (TW: 4), and female gular lengths (4). In three cases, missing values were estimated based on measurements of the same animal in later years.

Gender was determined independently of external morphology for 35 females using testosterone levels in the blood, x-ray visualization of eggs, or observation of egg laying. Gender was determined for 13 males based on testosterone or observation of individuals engaged in male copulatory behavior. Larger individuals (CL > 200 mm) of uncertain gender were assigned to a gender category based on overall morphology that was similar to the morphology of individuals of known gender. Each character was evaluated separately in univariate plots, regression, and preliminary multivariate analyses, and this resulted in classifying 33 tortoises as male and 5 as female. For example, in a bivariate plot of carapace length versus plastral concavity, most individuals of known gender fell into one of two discrete regions, and most large (CL > 200 mm) individuals of unknown gender fell within the distribution of points defined by the individuals of known gender (Fig. 1). Nineteen smaller individuals of unknown gender were not assigned to gender *a priori*. This resulted in *a priori* classifications of our 105 study animals as 40 females, 46 males, and 19 of unknown gender.

Data were grouped by various categories (e.g., males, females, gender unknown, large males, large females, etc.) and examined for conformation to assumptions of normality (inspection of plotted residuals) and homogeneity of variance (F_{max} test) among groups. Regardless of grouping, data were approximately normal, particularly for data sets containing only larger or only smaller individuals. Equality of variances among groups was rejected for PC and SHLD in a data set containing all males and females, but these characters responded favorably to a square-root transformation. In a data set of larger animals grouped by gender, PC required a square-root transformation, and in a data set of smaller animals grouped by gender, AW1 and AW2 required an x^2 transformation. In these and other data sets, several characters approached significance ($\alpha = 0.05$), but no single transformation equalized the variances among groups. Rather than apply different transformations to various characters in the data sets, univariate differences were tested using the nonparametric Mann-Whitney U-test (Sokal and Rohlf, 1981).

Three data sets were analyzed using discriminant analysis: all animals ($n = 105$), only larger animals (CL ≥ 192 mm; $n = 78$), and only smaller animals (CL ≤ 217 mm; $n = 39$). A carapace length of 192 mm was chosen as the minimum size for the data set containing larger animals because by this size, sexually dimorphic characteristics such as depth of the plastral concavity (Fig. 1) were becoming apparent. A carapace length of 217 mm was chosen as the maximum size for the data set containing smaller animals because of sample size considerations and because it was not until this size that sexually dimorphic characteristics were fully developed (Fig. 1). For each data set, analyses were performed on untransformed data, and on various transformed data sets, using stepwise selection with prior probabilities set equal to group size (SPSS for the Macintosh; Norusis, 1990). Mass (WT) was not used in multivariate analyses. The test of equality of group covariance matrices (Box's M test) was rejected for the untransformed data set containing all animals ($p < 0.05$), but the F-statistic (2.98) was relatively small. Various transformations applied uniformly to the data did not improve the equality of variances. Equality of group covariances for large animals was also rejected ($p < 0.05$), but this F-statistic also was small (2.56), as was the F-statistic for the data set of only small animals ($F = 1.68$, $p = 0.05$). Departures from equality of group covariance matrices result in biases that, in the case of two-group discriminant analysis, fail to reject the null hypothesis of no difference between groups and tend to misclassify individuals by assigning too many observations to the group with the larger covariance matrix (Green, 1978). Because two-group discriminant analysis is believed to be robust to minor departures of equality of group covariances matrices (Green, 1978), the tests were conducted

Table 1. Sample size (n), mean ($\bar{x}$), standard error (SE), minimum (Min) and maximum (Max) of measurements of free-ranging large (CL ≥ 192 mm) desert tortoises (*Gopherus agassizii*) at Yucca Mountain, Nevada. Significance of size differences between females and males was tested using Mann-Whitney U-tests.

	Male					Female					U-test	
Character	n	$\bar{x}$	SE	Min	Max	n	$\bar{x}$	SE	Min	Max	Z	p
Anal Aperture (APER)	39	28.4	0.91	17.2	38.1	38	27.4	0.72	18.7	38.1	-0.88	0.381
Anal Notch (AN)	39	32.8	1.01	20.0	43.0	38	32.2	0.80	21.5	41.9	-0.46	0.647
Anal Shield Thickness (SHLD)	38	2.9	0.22	0.8	6.1	38	2.0	0.14	0.9	4.0	-3.03	0.002
Anal Width 1 (AW1)	39	51.9	1.56	31.5	70.7	38	43.7	0.84	29.9	52.8	-3.94	<0.001
Anal Width 2 (AW2)	39	68.6	1.31	52.6	84.5	38	62.6	1.00	49.0	78.0	-3.35	0.001
Carapace Length (CL)	39	252.9	4.25	199	299	38	240.0	3.24	192	275	-2.30	0.021
Front Foot Width, Left (FFL)	38	37.1	0.72	28.5	45.9	37	32.9	0.50	27.1	39.9	-4.14	<0.001
Front Foot Width, Right (FFR)	37	37.5	0.71	28.6	46.4	37	32.6	0.49	26.3	39.0	-4.75	<0.001
Gular Length (GULAR)	35	47.1	1.17	33.0	59.6	35	38.6	0.87	27.2	47.8	-4.80	<0.001
Hind Foot Width, Left (HFL)	39	34.2	0.73	23.5	42.5	37	30.8	0.57	22.8	36.8	-3.29	0.001
Hind Foot Width, Right (HFR)	39	34.3	0.74	25.6	43.2	37	31.0	0.58	23.9	38.1	-3.26	0.001
Plastral Concavity (PC)	39	10.1	0.60	2.9	17.2	37	1.8	0.16	0.0	3.9	-7.43	<0.001
Tail Length (TL)	39	30.1	1.01	17.1	40.7	31	22.2	0.80	9.2	32.5	-4.93	<0.001
Tail Width (TW)	35	20.7	0.84	10.4	32.2	28	20.0	0.62	13.5	27.2	-0.68	0.498
Height (HGT)	39	105.3	1.50	85	125	36	100.4	1.13	84	115	-2.33	0.020
M 3-4 Seam (M34)	39	173.5	3.16	131	209	37	161.1	2.16	131	186	-3.16	0.002
M4 (mid) (M4)	39	185.3	3.19	144	220	37	173.9	2.29	142	202	-2.87	0.004
Marginals 7-8 Seam (M78)	39	196.8	3.52	151	236	38	185.2	2.63	151	216	-2.69	0.007
Mass (WT)	38	2826.3	138.2	1376	4681	37	2330.8	80.7	1246	3371	-2.64	0.008
Maximum Width (WTH)	39	200.1	3.60	154	239	38	188.6	2.67	152	220	-2.64	0.008
Plastron Length (PNN)	39	235.4	4.42	176	295	37	222.1	3.29	175	265	-2.37	0.018
Plastron Length (PTT)	39	255.6	4.33	200	310	38	243.6	3.38	195	288	-2.23	0.026

using untransformed data, but the results were interpreted with caution.

RESULTS

In univariate analyses of larger (CL ≥ 192 mm) tortoises, the sexes differed (at the nominal rate of $p \leq 0.05$) for 19 of 22 characters (Table 1). If a Bonferroni adjustment to the alpha level was used ($\alpha = 0.05/22 = 0.002$; Rice, 1989), 11 tests would still be considered significant. Among the 11 significant tests were the three characters noted by Woodbury and Hardy (1948) as being useful for separating the sexes: gular length, plastral concavity, and tail length. For all characters, males tended to be larger than females, but there was overlap for every character. However, for larger animals (CL ≥ 192 mm), the plastral concavity of females never exceeded 3.9 mm, and in no case was a male's plastral concavity shallower than 2.9 mm (Table 1). If only the largest animals were considered (CL > 220 mm), then all would be correctly assigned to gender class based on depth of the plastral concavity (females ≤ 3.9 mm; males ≥ 4.8 mm).

Table 2. Sample size (n), mean ($\bar{x}$), standard error (SE), minimum (Min) and maximum (Max) of measurements of free-ranging small (CL ≤ 217 mm) desert tortoises (*Gopherus agassizii*) of known gender at Yucca Mountain, Nevada. Significance of size differences between females and males was tested using Mann-Whitney U-tests.

	Male					Female					U-test	
Character	n	$\bar{x}$	SE	Min	Max	n	$\bar{x}$	SE	Min	Max	Z	p
Anal Aperture (APER)	6	19.7	1.10	17.2	23.8	14	17.8	1.55	10.3	28.6	-1.03	0.303
Anal Notch (AN)	6	23.0	1.33	20.0	27.9	14	20.3	1.70	11.7	33.6	-1.07	0.284
Anal Shield Thickness (SHLD)	6	1.3	0.16	0.8	1.9	14	1.4	0.08	0.9	1.9	-0.17	0.869
Anal Width 1 (AW1)	6	36.5	1.33	31.5	40.4	14	30.9	2.11	18.1	44.2	-1.90	0.058
Anal Width 2 (AW2)	6	53.4	1.77	45.9	58.3	14	43.7	3.01	24.0	60.5	-1.77	0.076
Carapace Length (CL)	6	201.7	5.14	179	217	14	177.0	7.98	129	212	-1.49	0.138
Front Foot Width, Left (FFL)	6	29.0	0.97	25.4	32.8	14	24.4	1.11	17.4	31.0	-2.56	0.011
Front Foot Width, Right (FFR)	5	29.3	0.93	25.7	32.8	14	24.4	1.16	17.8	31.4	-2.04	0.042
Gular Length (GULAR)	5	33.9	2.62	23.3	43.4	14	29.2	1.44	21.7	37.7	-1.30	0.195
Hind Foot Width, Left (HFL)	6	25.9	1.18	21.4	29.0	14	22.4	1.24	14.2	30.8	-1.57	0.117
Hind Foot Width, Right (HFR)	6	25.9	0.88	22.0	28.5	14	22.4	1.25	14.5	29.3	-1.61	0.108
Plastral Concavity (PC)	6	3.5	0.71	0.8	5.9	13	1.2	0.23	0.0	2.8	-2.63	0.009
Tail Length (TL)	6	18.5	1.98	10.0	24.5	11	16.7	1.71	9.2	27.5	-0.10	0.920
Tail Width (TW)	5	14.6	1.62	10.4	20.3	9	14.8	1.13	9.7	22.5	-0.47	0.641
Height (HGT)	6	89.5	3.53	75	100	14	79.8	2.79	60	93	-2.02	0.043
M 3-4 Seam (M34)	6	134.5	5.23	111	148	14	120.4	6.01	85	158	-1.44	0.149
M4 (mid) (M4)	6	146.3	4.55	127	161	14	130.2	5.97	95	165	-1.44	0.149
Marginals 7-8 Seam (M78)	6	154.5	5.08	133	171	14	136.0	6.43	100	169	-1.49	0.138
Mass (WT)	5	1400.7	140.79	760	1783	14	1057.5	143.13	391	1882	-1.30	0.195
Maximum Width (WTH)	6	157.0	4.94	136	173	14	138.6	6.56	102	174	-1.44	0.149
Plastron Length (PNN)	6	186.0	7.19	164	212	14	165.9	7.80	118	206	-1.44	0.149
Plastron Length (PTT)	6	206.2	6.26	185	229	14	182.0	8.59	128	227	-1.49	0.138

Table 3. Unstandardized discriminant function coefficients that separate free-ranging male and female desert tortoises (*Gopherus agassizii*) at Yucca Mountain, Nevada. Three sets of discriminant coefficients are presented: one set for separating all animals (52 ≤ CL ≤ 299 mm), one set for separating only larger animals (CL ≥ 192 mm), and another set for separating only smaller individuals (CL ≤ 217 mm). The functions correctly classified 98, 100, and 100% of individuals of known gender, respectively.

Character	All Animals	Only Adults	Only Small Animals
Minimum anal aperture (APER)	-0.104	—	—
Anal width 1 (AW1)	-0.063	-0.055	—
Anal width 2 (AW2)	0.108	—	—
Front foot right (FFR)	0.315	0.242	0.608
Gular length (GULAR)	0.039	0.082	-0.254
Hind foot right (HFR)	—	0.101	-0.128
Carapace length (CL)	-0.046	-0.054	—
Anal notch (AN)	—	-0.105	—
Plastral concavity (PC)	0.420	0.498	1.171
Anal shield thickness (SHLD)	-0.364	-0.395	—
Plastron length (PTT)	0.026	—	—
Tail width (TW)	-0.056	-0.062	—
Tail length (TL)	—	—	-0.194
Maximum width (WTH)	-0.043	—	—
(Constant)	-1.003	3.289	-3.837

In univariate analyses of smaller (CL ≤ 217 mm) tortoises, the sexes differed (at the nominal rate of $p \leq 0.05$) for 4 of 22 characters (Table 2). If an adjustment were applied to the error rate ($p \leq 0.002$), then no tests would be significant. However, even for these small animals, plastral concavity approached significance ($p = 0.009$): female plastral concavity never exceeded 2.8 mm, and that of the males always exceeded 0.8 mm (Table 2).

In the trivial case of using discriminant analysis to identify the gender of larger animals (CL ≥ 192 mm), all individuals of known gender classified correctly. Although it is generally considered easy to classify adults based on external morphology, the model required nine characters to correctly classify all individuals (Table 3, "Only Adults"). The eigenvalue of this function was 5.674, and the canonical correlation was 0.922.

Using the data set composed of all animals of known gender, discriminant analysis selected 11 measurements and correctly classified all but one tortoise (male #493, Fig. 1). When the 19 small animals of unknown gender were classified using this discriminant function (Table 3, "All Animals"), 2 were classified as males and 17 were classified as females. Despite the apparent success of this model, it is likely that some small males were incorrectly classified as females because the sex ratio of adult tortoises at Yucca Mountain was approximately 1:1.

Although the sample size was small (n = 39), when small animals (CL ≤ 217 mm) were subjected to discriminant analysis, all 20 individuals of known gender classified correctly. When the 19 small individuals of unknown gender were classified with this discriminant function (Table 3, "Only Small Animals"), all tortoises fell cleanly into the two groups using only five characters (Fig. 2). The eigenvalue of this function was 3.056, and its canonical correlation was 0.868. The program estimated the probability of group membership, and most (13 of 19) were assigned to gender class with greater than 99% certainty; only one fell as low as 78%.

DISCUSSION

This study applies statistical rigor to long-standing assumptions about our ability to identify large male and female tortoises in the northern Mojave Desert using exter-

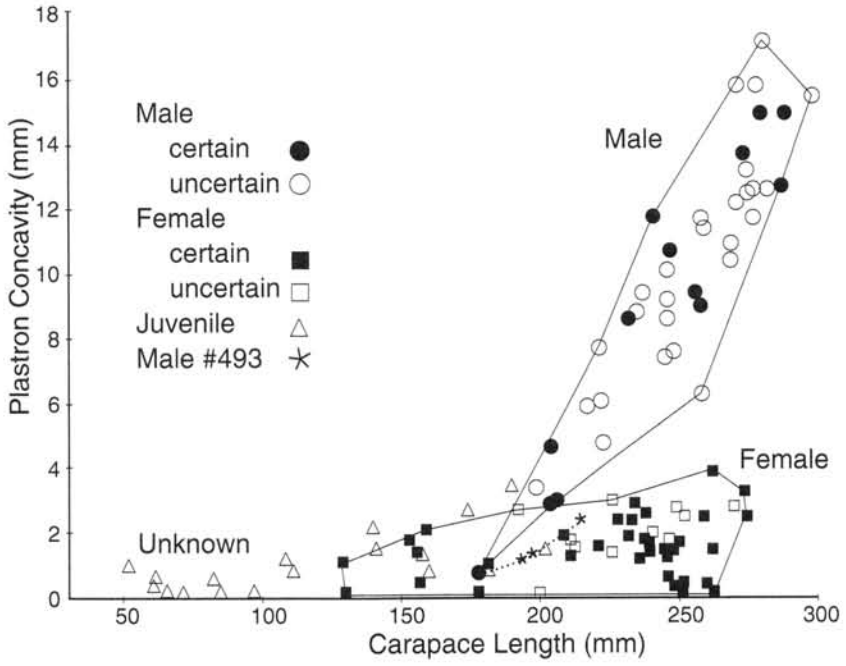

Figure 1. Depth of the plastral concavity in relation to size (carapace length) with *a priori* gender groupings. Individuals were assigned to gender category based on non-morphological criteria (gender certain) or based on morphology that was similar to morphology of known animals (gender uncertain). Smaller animals were not assigned to gender based on morphology (juvenile uncertain). The position (stars) and trajectory (dotted line) of male #493 is shown for each year from 1992 to 1995.

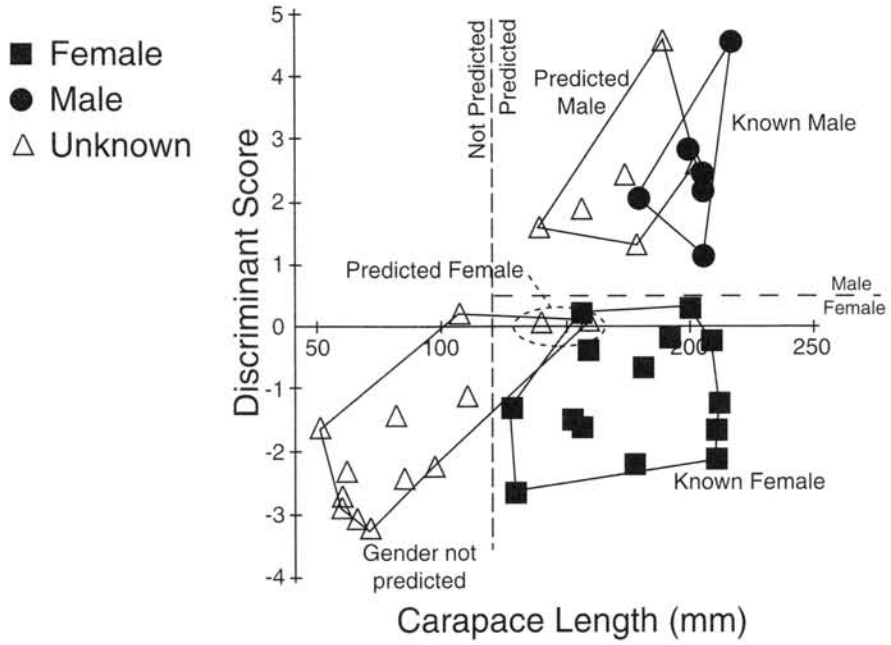

Figure 2. Distribution of discriminant function scores from the model using only small animals (CL ≤ 217 mm) in relation to size (carapace length). Young males and females (140 ≤ CL ≤ 217) of known gender classified correctly, but all smaller (CL < 140 mm) animals of unknown gender were assigned to the female class.

nal morphology, and it supports the conclusion that characters traditionally used (plastral concavity, gular length, and tail length) are useful and diagnostic. In univariate analyses, these characters have the largest Z-scores (Table 1). Two other characters, the distance between the posterior-most points of the anal scutes (AW1; Z = -3.94) and front-foot widths (Z ≤ -4.14), also may be useful characters. For larger animals (CL > 220 mm), the depth of the plastral concavity alone is sufficient to determine gender, and use of the other traditional characters can add support to decisions on gender determination.

However, in the northern Mojave Desert, it is not until animals reach a carapace length of about 220 mm that one can be certain of correctly identifying the gender of all tortoises using a few external characters. For example, when tortoise #493 (male, determined by testosterone level) was first measured in 1992, he had a carapace length of 179 mm, an unusually flat plastron (PC = 0.8 mm), and he looked like a female (Fig. 1). However, as he aged from 1992 to 1995, his plastral concavity rapidly deepened, and it is likely that by 1996, the depth of his plastral concavity would have exceeded that of most or all females.

Despite the apparent success of the model for smaller animals (CL ≤ 217 mm), when discriminant scores were plotted against carapace length (a proxy for age; Fig. 2), it appeared that "subadult animals" (140 < CL < 200) were properly classified, but smaller animals were only classified as females. While it was possible that all of the smaller animals were indeed female, it was more likely that some of these smallest animals (CL < 140 mm) were males that had not yet begun to acquire statistically significant secondary sexual characters. Despite the probable misclassification, when discriminant scores were plotted against carapace length (Fig. 2), the observed relationship invites speculation that it may be possible to predict gender in animals as small as 100–110 mm CL. One individual (CL = 108 mm) had a discriminant score of 0.19 (Fig. 2), a score that would appear to be relatively large for such a small size if it were a female; it is likely that as it ages, its score would continue to increase, and it would later be classified as a male. Another individual of similar size (CL = 111 mm) had a discriminant score of -1.14 (Fig. 2), a score that appears more reasonable for a small female.

Only three characters were important for separating males and females in all three data sets (Table 3). In each case, deep plastral concavities (always the largest coefficient) and wide front-right feet (always a large coefficient) were associated with males. Gular length was important in each case, but a long gular was associated with males only for the data sets containing all animals and large animals. Contrary to what may be expected, for the smaller tortoises used in this study, a long gular was associated with females. Four characters were selected in two cases. Wide tail and anal widths (AW1, AW2), and thick anal shields (always a large coefficient) were associated with females. Hind foot-width entered the model for small and large animals, but with different signs. For large animals, a wide foot was associated with males, but for small animals it was associated with females.

This study was based on desert tortoises from the northern edge of their range, and because the shape of the carapace is known to be influenced by environmental factors (Reiber and McDaniel, 1995), these results may not apply elsewhere. However, these models selected characters that are believed useful for determining gender throughout the

species' range, and others have shown that tortoise populations in the northern and eastern Mojave do not differ markedly from one another (Germano, 1993; Weinstein and Berry, in litt.); therefore, these models likely are useful over a wider area than just Yucca Mountain (i.e., at least the eastern Mojave Desert).

These results provide a tool for estimating the gender of small tortoises (CL ≤ 217) from the northern Mojave Desert that have not developed secondary sexual characteristics to a sufficient degree to allow easy gender determination in the field. To use this tool for small tortoises, researchers can measure the five important characters ("Only small Animals"; Table 3), multiply each measurement by its corresponding discriminant function coefficient, sum the products, and add the constant:

$$(FFR*0.608) + (GULAR*-0.254) + (HFR*-0.128) + (PC*1.171) + (TL*-0.194) - 3.837$$

If the resulting score exceeds 0.5, the specimen most likely is male; otherwise it most likely is female. For the smallest animals (CL < 140 mm), the score and carapace length can be plotted on Fig. 2 for comparison with the results of this model, possibly permitting a prediction to be made regarding gender identification. While the sample used to build the model was small, it correctly classified all mid-size small tortoises (140 ≤ CL ≤ 217) of known gender, and in posterior classification of individuals of unknown gender within this size range, it unambiguously and correctly assigned individuals to gender.

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