

# Changes in a Desert Tortoise (*Gopherus agassizii*) Population After a Period of High Mortality<sup>1</sup>

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**Abstract.**—An apparent high rate of mortality for desert tortoises at the Piute Valley in southern Nevada between 1979 and 1983 significantly decreased mean carapace length and average age of the population by 1983, but not density. By 1987, average size and age of the population had increased and density remained stable.

Chelonians, as a group, are characterized by high rates of adult survival, delayed maturity, and low rates of juvenile survival (Wilbur and Morin 1988). Many chelonians live a long time after reaching adulthood (Gibbons 1987), potentially leading to a long period of reproduction offsetting low juvenile survival (Wilbur and Morin 1988). The desert tortoise (*Gopherus agassizii*) (fig. 1) is an herbivorous chelonian of the desert Southwest that exhibits these population traits (Berry 1986, Luckenbach 1982, Osorio and Bury 1982, Turner et al. 1984, 1986). In 1983, a large number of desert tortoise skeletons were collected from a study plot located in southern Nevada and deaths were believed to have occurred since the initial census in 1979 (unpublished report, C. Mortimore and P. Schneider, Nevada Department of Wildlife, Las Vegas, NV). It was reported that since 1979, mean carapace length of the population decreased, sex ratio had become male biased, and that population density



Figure 1.—A large male desert tortoise (*Gopherus agassizii*) from the Piute Valley permanent study plot.

decreased, and that these changes occurred because long-term grazing of this plot by cattle weakened tortoises to such a degree that decreased forage production resulting from below-average rainfall in 1981 killed many individuals (unpublished report, C. Mortimore and P. Schneider, Nevada Department of Wildlife, Las Vegas).

We recensused this population in 1987 in order to determine changes that might have taken place since 1983 in age distribution, size distribution, sex ratios, and population density in order to address the following questions: Of what significance are such periods of high mor-

tality to the populations' probability of survival? How do desert tortoise populations respond to high rates of mortality? Are changes in population demographics long-lasting? Can we predict future changes in desert tortoise populations? We also reassess possible causes of the high rate of mortality between 1979 and 1983.

## METHODS

### Study Area

The 2.59 km<sup>2</sup> plot is located in the Piute Valley of southern Nevada in

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the eastern Mojave desert (fig. 2). Vegetation is Mojave desert scrub dominated by creosote bush (*Larrea tridentata*) and white bursage (*Ambrosia dumosa*) over the southeastern 2/3 of the plot grading into an area with an overstory of Mojave desert yucca (*Yucca schidigera*) in the northwestern third (fig. 3).

### Field Methods

The population was censused between April and June 1979 by the Bureau of Land Management (unpublished report, A. Karl, BLM, Las Vegas, NV) and again between April and June 1983 by the Nevada Department of Wildlife (unpublished report, C. Mortimore and P. Schneider, Nevada Department of Wildlife, Las Vegas, NV). Each tortoise encountered was measured, weighed, marked, its sex determined, and its location, behavior and general

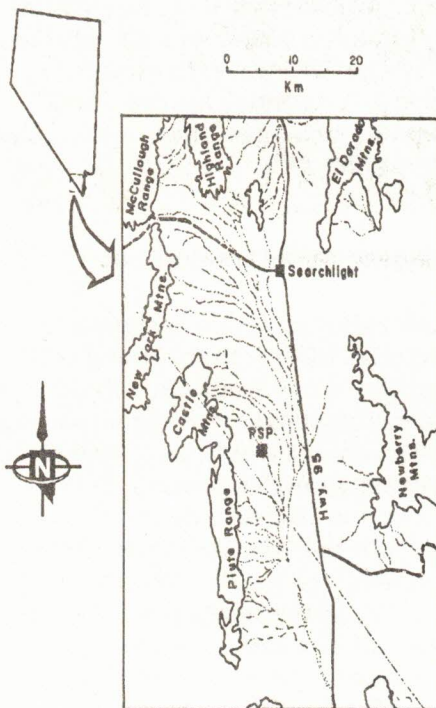


Figure 2.—The location of the desert tortoise permanent study plot (PSP) in the Piute Valley of southern Nevada. The dashed and dotted lines show major washes.



Figure 3.—Creosote bush and white bursage are the most conspicuous plants of much of the study plot (top) with Mojave yucca abundant in the northwestern portion (bottom). Other abundant plants at this site are California buckwheat (*Eriogonum fasciculatum*), rayless goldenhead (*Acaulopappus sphaerocephalus*), *Opuntia* spp., bush muhly (*Muhlenbergia porteri*), glg galleta (*Hilaria rigida*), six-week fescue (*Festuca octoflora*), filaree (*Erodium cicutarium*), desert dandelion (*Malacothrix glabrata*), and *Chaenactis* spp.

condition noted. Shells were collected and are catalogued in the Museum of Southwestern Biology, University of New Mexico, Albuquerque.

We recensused the plot 13-27 May and 18-25 August 1987. We collected similar data on tortoises, but included making casts of the second costal scute using dental casting ma-



terial (Galbraith and Brooks 1987). Measurements of growth rings from the impressions on the casts were taken.

Growth rings of desert tortoises have been found to be valuable for determining age and growth histories of many individuals (Germano 1988). Shells were collected and deposited in the Museum of Southwestern Biology.

## Data Analysis

### Density

Densities in 1979 and 1983 were determined by the investigators who conducted the censuses using the Schnabel estimator. This method involves making periodic estimates of density during the census based on the number of marked and unmarked animals found (Tanner 1978). Because of immigration into the plot, we reestimated density for 1983 using the Jolly-Seber estimator (Tanner 1978), which does not assume a closed population.

As a first approximation of density for 1987, we used a simple mark-recapture estimator with May as the period of marking animals and August as the recapture period. Only 1/2 the plot was recensused in August because of time constraints. Density was computed for this half of the plot.

### Carapace Length Distributions

Carapace lengths (CL) of individuals were plotted and mean CLs computed for live tortoises and remains for each census year. Mean CLs of the total population, tortoises >180 mm CL, and tortoises ≤180 mm CL were compared among years using anova with comparisons among means using Scheffe's multiple comparisons test.

### Age Distributions

Ages of individuals were plotted for live tortoises and remains and mean ages compared in a manner similar to CLs. Ages of skeletons and 1987 live tortoises were determined for most individuals using scute annuli, a technique that is accurate up to 20-25 years (Germano 1988). Several individuals were considered to be older than the number of easily seen annuli based on non-growth since last capture, or scute edge beveling, which indicates continued slow growth. These individuals were categorized as >25 years old.

Ages were estimated for live tortoises found in 1979 and 1983 using an age-CL regression ( $\text{Age} = 0.106 \text{ CL} - 3.82$ ). The number of scute annuli is well correlated with CL ( $r^2 = 0.908$ ,  $n = 150$ ), although the relationship is less accurate in larger individuals. We corrected for the presence of older individuals in our estimates by assigning a portion of adults of various sizes to the >25 age category based on the percentage of adults that were into this category from the 1987 live and 1983 and 1987 shell groups.

### Mortality Rates

Age-specific mortality rates were determined for 1979-1983 and 1983-1987 using the equation  $q_x = (k [f_x]) / g_x$ , where  $q_x$  is the mortality rate per year for age  $x$ ,  $k$  is the per capita mortality rate of the population,  $f_x$  is the proportion of animals age  $x$  that are known to have died in the past year, and  $g_x$  is the proportion of animals of age  $x$  in the preceding live population (Fryxell 1986). In order to compare mortality rates to age distributions, we determined mortality rates for age groups 0-14 years, 15-27 years, and >25 years. The per capita mortality rate was divided by 4 to obtain the yearly mortality rate for each time period.

### Sex Ratios

Sex ratios were compared among live tortoises and shells. Sex was assigned to tortoises ≥180 mm CL based on secondary sex characteristics or, in some instances, for males >170 mm CL when plastron concavity was obvious. Sex can be determined reliably in desert tortoises based on shell characters after 180 mm CL (unpublished report, F. Turner and K. Berry, Southern California Edison Co., CA) and female tortoises in this part of the Mojave desert reproduce at 189 mm CL (Turner et al. 1986), indicating that sexual maturity probably occurs between 180-190 mm CL. Ratios were tested for deviation from a 1:1 sex ratio with Chi-square analysis ( $p < 0.05$ ).

### CL/Weight Regressions

Carapace length to weight regressions were constructed for 1979 and 1987 tortoises based on the logarithmic transformation of both variables. Data for 1983 were not available. Slopes were tested against 0 and against each other using  $t$ -tests (Sokal and Rohlf 1981).

### Growth Rate Comparisons

Individual growth was compared among 1987 live tortoises and shell groups in two ways. Growth rings were compared among groups using mean annual widths (AW) and mean percent growth for rings 1-24 (See Germano 1988 for a description of growth ring measurements). Percent growth for a ring is  $\text{AW} / \text{estimated CL for the preceding year}$ . CLs were estimated using the length of growth rings from the second costal scute, which are highly correlated to CL ( $r^2 = 0.96$ ,  $n = 174$ ). Growth estimates based on annuli have been found to accurately reflect carapace growth in gopher tortoises (Landers et al. 1982) and desert tortoises (Germano In



Press). Means of these variables for each ring were compared among groups using the nonparametric

Wilcoxon sign test. We also compared the mean AW and mean percent growth of the last two growth rings for the shells found in 1983 to the mean AW and mean percent growth of the 1980 and 1981 growth rings from live tortoises found in 1987 using *t*-tests.

## Climate Analysis

Climate was analyzed using weather information from Searchlight, Nevada. Data were compared for 3 time periods; 1970-June 1979, July 1979-1982, and July 1979-July 1987. Means and variances of rainfall, both annual and winter, were compared among time periods. Mean monthly temperatures were compared among time periods and temperatures below freezing were analyzed for duration and relation to unusually warm winter daily highs.

## RESULTS

### Density

Tortoise density was estimated to be 50/km<sup>2</sup> in 1979 and 72/km<sup>2</sup> in 1983 by the authors of these censuses. Eighty-four and 81 tortoises were found in 1979 and 1983, respectively. We reestimated the 1983 density to be 44 tortoises/km<sup>2</sup>. We estimated the density in 1987 to be 59 tortoises/km<sup>2</sup> (95% confidence intervals, 19-173). We found 48 tortoises in 1987, 33 in May and 19 on the southern half of the plot in August, of which 4 had been marked in May.

### Carapace Length Distributions

Distributions of CLs of live tortoise populations varied significantly for each census (fig. 4). Mean CL was significantly smaller in 1983 than in either 1979 ( $p < .05$ ) or 1987 ( $p < .05$ ). Mean CLs in 1979 and 1987 were not significantly different, however ( $p > .05$ , table 1). No significant differences were found among mean CLs for adults ( $\geq 180$  mm CL). Adults comprised 58% of the 1979 population, 37% of the 1983 population, and 60% of the 1987 population. The mean CL of non-adults ( $< 180$  mm CL) was significantly smaller in 1983 than 1979 ( $p < .05$ ), but was not significantly different than 1987 ( $p > .05$ ,

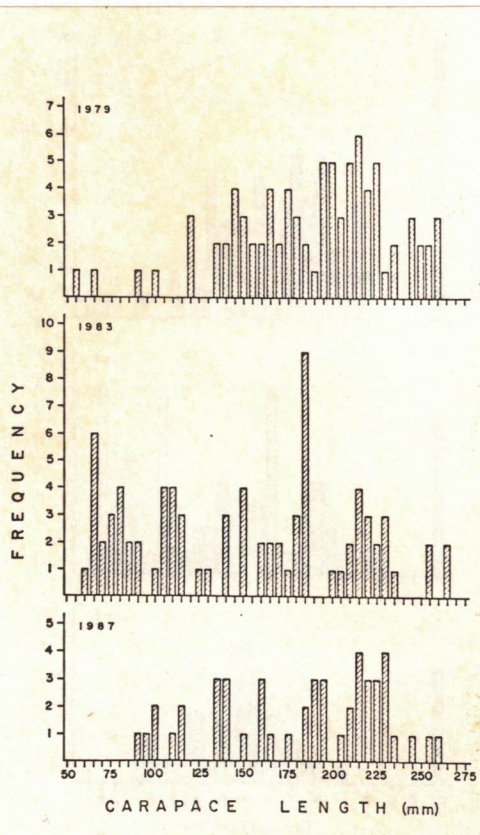


Figure 4.—Population size distributions for live desert tortoises from the Piute Valley permanent study plot. Mean carapace lengths and sample sizes are given in table 1.

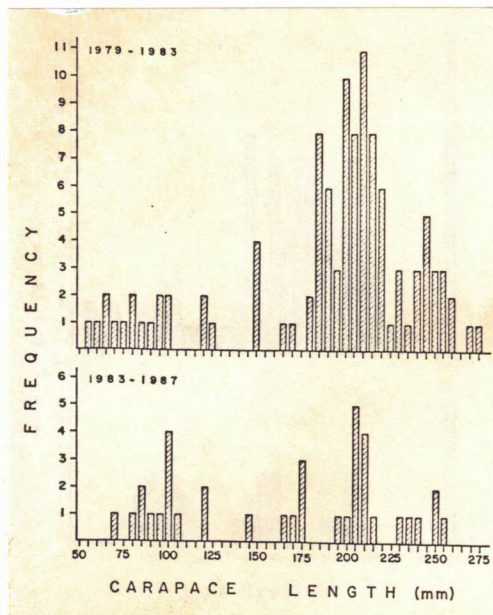


Figure 5.—Population size distributions for desert tortoises found dead in 1983 and 1987 from the Piute Valley permanent study plot. Mean carapace lengths and sample sizes are given in table 1.

Table 1.—Mean carapace lengths (mm) of tortoises from the Piute Valley permanent study plot. Standard deviation and sample size are given below the mean.

Group	All tortoises	>180 mm CL	% of total	<180 mm CL	% of total
1979 live	186.8 (44.0, 84)	217.1 (21.0, 49)	58	144.5 (30.8, 35)	42
1983 live	148.2 (59.6, 81)	211.8 (24.9, 30)	37	110.8 (38.3, 51)	63
1987 live	181.1 (46.6, 48)	213.8 (20.0, 29)	60	125.8 (37.8, 19)	40
1983 shells	197.6 (93.3, 108)	212.9 (22.6, 84)	78	106.4 (39.0, 24)	22
1987 shells	165.4 (58.1, 37)	216.3 (19.4, 18)	49	117.2 (36.9, 19)	51



table 1). The mean CL of non-adults was not significantly different between 1979 and 1987 ( $p > .05$ ).

Remains of 37 tortoises were found in 1987 compared to 109 found in 1983 (fig. 5). Ten shells were found in 1979. CLs of remains were not significantly different ( $p > .05$ ), although mean CL in 1983 was considerably larger than for 1987 (table 1). Mean CLs of adult remains in 1983 and 1987 were similar, as were non-adult CLs, but adults comprised 78% of the 1983 collection and only 49% of the 1987 collection. The mean CL of remains from 1983 was not significantly different from the mean CL of live tortoises in 1979 or 1987, but was significantly larger than live tortoises in 1983 ( $p < .05$ ). Mean CL of remains from 1987 was not significantly different than any live tortoise means.

### Age Distributions

Ages of tortoises varied significantly among years (table 2). Changes in age distributions of live tortoises were similar to the changes seen for CLs (fig. 6). The estimated mean age for 1979 was significantly older than 1983 ( $p < .05$ ) but not 1987 ( $p > .05$ ). Mean age for 1987 was not significantly different than 1983 ( $p > .05$ ), but non-adults were significantly older ( $p < .05$ ). Mean age of 1983 remains was significantly older than 1983 live tortoises ( $p < .05$ ), but was not significantly different than 1987 live tortoises or remains ( $p > .05$ , fig. 7).

### Mortality Rates

Death rates for 1983-1987 were lower than for 1979-1983. Per capita mortality rate ( $k$ ) for 1979-1983 was 0.21/year ( $N = 130$ ) and was 0.08/year for 1983-1987 ( $N = 115$ ). Mortality rates dropped for all age classes after 1983. For 1979-1983 mortality rates were 0.145/year for 0-14 year olds, 0.247/year for 15-25 year olds, and 0.195/year for tortoises >25 years. For 1983-

1987 mortality rates were 0.061/year for 0-14 year olds, 0.093/year for 15-25 year olds, and 0.103 for tortoises >25 years. Mortality rates for all adults (15-25 years and >25 years) for 1979-1983 was 0.240/year and for 1983-1987 was 0.103/year.

### Sex Ratios

Sex ratios of live tortoises show an increasing proportion of males (table 3), although only 1987 showed a significantly biased sex ratio. When the 1987 sex ratio was analyzed by size, 92% of tortoises >220 mm CL were males, whereas only 53% of tortoises 180-219 mm CL were males (table 3). When analyzed by age, 63% of tortoises  $\geq 20$  years were males, but 71% of tortoises of known sex between 13-19 years were males, a significantly higher proportion than females. The sex ratios of dead tortoises were not significantly different than 1:1 (table 3).

### CL/Weight Regressions

The regressions of weight against CL had significant slopes for 1979 and

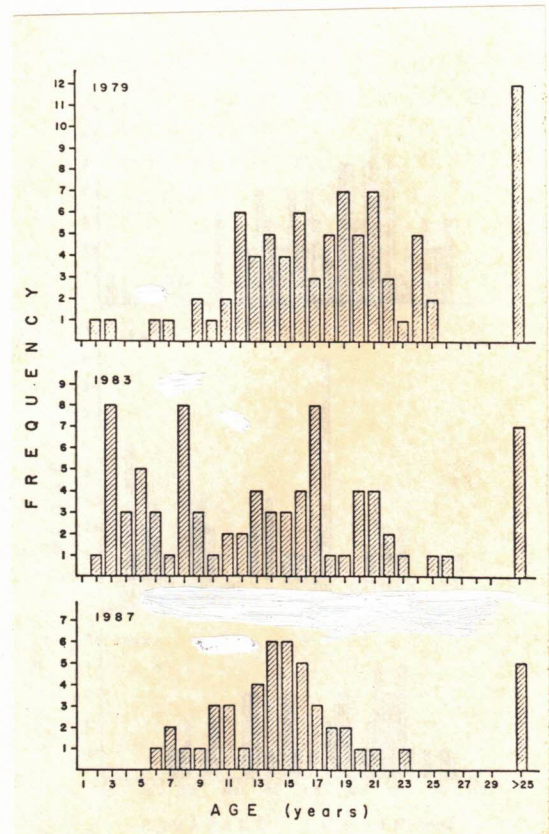


Figure 6.—Population age distributions for live desert tortoises from the Piute Valley permanent study plot. The 1979 and 1983 age distributions are estimates based on a carapace length to annulus number regression. A proportion of adults were placed in the >25 age category based on the proportion of adults in this category from the age distributions for which ages were assigned by annuli counts. The 1987 age distribution is based on annuli counts.

Table 2.—Mean ages of tortoises from the Piute Valley permanent study plot in southern Nevada. Standard deviation and sample size are given below the mean. Ages for 1979 and 1983 are estimates based on carapace length (see Methods).

Group	Ages (years)			
	0-27	0-14	15-27	<sup>1</sup> >25
1979 live	16.6 (5.1, 72)	10.9 (3.4, 24)	19.5 (2.9, 48)	— (12)
1983 live	12.1 (6.6, 74)	7.5 (3.7, 41)	18.8 (3.0, 30)	— (7)
1987 live	14.1 (3.8, 43)	11.3 (3.2, 22)	17.0 (2.2, 21)	— (5)
1983 shells	17.0 (6.2, 94)	7.8 (3.6, 22)	19.9 (3.3, 72)	— (14)
1987 shells	14.0 (6.2, 31)	8.4 (2.6, 15)	19.3 (3.5, 16)	— (6)

<sup>1</sup>Mean age cannot be determined.



1987 (fig. 8). The regression equation for 1979 is gram weight =  $0.000317 \text{ CL}^{2.924}$  ( $r^2 = 0.952$ ,  $n = 73$ ) and for 1987 is gram weight =  $0.000505 \text{ CL}^{2.826}$  ( $r^2 = 0.969$ ,  $n = 53$ ). Regression slopes were not significantly different from each other ( $p > .10$ ).

### Growth Rate Comparisons

No significant differences were found in a ring by ring comparison of growth between 1987 live tortoises and 1983 remains for either annual widths (AW) or percent growth.

When 1980 and 1981 rings were compared, no significant difference existed between the mean AW for the last two rings of 1983 mortalities ( $X = 1.98\text{mm}$ ,  $n = 72$ ) and the 1980 and 1981 rings for 1987 live tortoises ( $X = 1.92\text{mm}$ ,  $n = 79$ ;  $p > .10$ ).

### Climate Analysis

Average precipitation were higher between July 1979 and July 1987 than the previous 10 years (table 4). The highest average precipitation was recorded between July 1979 and December 1982. Winter rainfall (October-March) followed the same pattern, with both 1979-1987 and 1979-1982 averages higher than 1970-1979 (table 4). The period 1970-1979 was a drought period with average rainfall 7% below the long-term average of 183.8 mm and 7 of the 10 years were well below average (table 4). When 1978 and 1979 are excluded, average precipitation drops to 129.3 mm, 30% below the long-term average. July 1979-December 1982 averaged 40% higher rainfall than the long-term average with only 1981 experiencing below-average rainfall. Mean monthly high and low temperatures were similar among time periods. No extended periods of freezing temperatures were found for daily readings between 1979 and 1983.

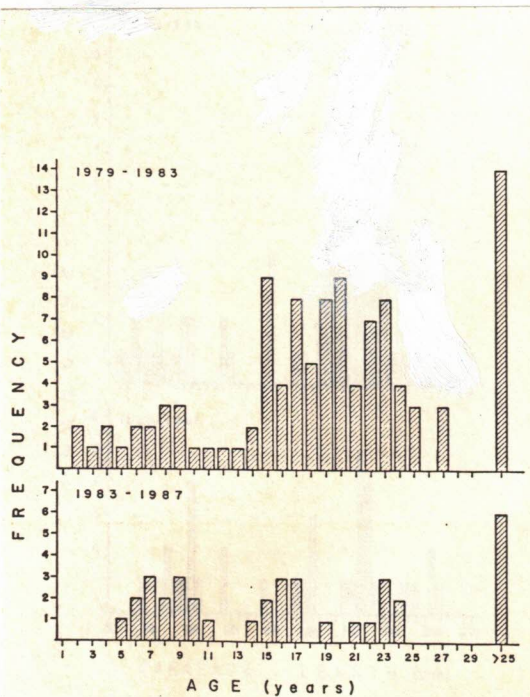


Figure 7.—Population age distributions for desert tortoises found dead in 1983 and 1987 from the Piute Valley permanent study plot. Both the 1983 and the 1987 age distributions are based on counts of annuli.

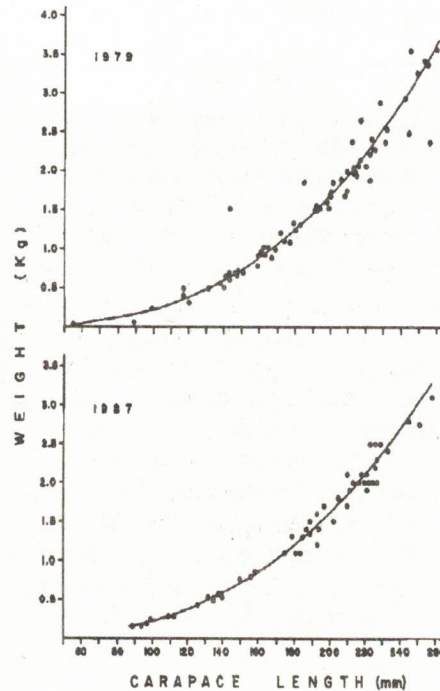


Figure 8.—Regressions of carapace length to weight for desert tortoises found in 1979 and 1987. Slopes of both regressions are significantly different from 0 but not from each other.

Table 3.—Numbers of males to females for desert tortoises from the Piute Valley permanent study plot. Significant departures from a 1:1 sex ratio were determined by Chi-square analysis. The 1987 live totals were sub-categorized by size and age.

Year		Males	Females	Ratio	$\chi^2$
1979	live	24	30	0.88:1	0.667
	shells	4	3	1.33:1	0.001
1983	live	22	11	2:1	3.667
	shells	35	41	0.85:1	0.474
1987	live (total)	20	9	2.22:1	<sup>1</sup> 4.172
	size: 180-219 mm CL	9	8	1.13:1	0.059
	>220mm CL	11	1	11:1	<sup>18</sup> 8.330
	age: 13-19 years	15	6	2.5:1	<sup>13</sup> 8.857
	>20 years	5	3	1.67:1	0.500
	shells	11	6	1.83:1	1.471

<sup>1</sup>Significant departure from 1:1 ratio ( $p < .05$ ).

### DISCUSSION

#### Population Parameters

The desert tortoise population in the Piute Valley study plot experienced a high rate of mortality, particularly of adults, between July 1979 and 1983. Related to this event was a significant decrease in the size and age distributions of the population in 1983, although both were returning to 1979 dimensions by 1987. The lower mean age in 1983 is probably a result of increased survival of hatchlings and increased immigration. The increased



survival of hatchlings, as shown by the significant increase of tortoises in the 1-4 age group in 1983, may be due to more favorable conditions because of lower densities just after the high rate of mortality, or to optimal climatic and habitat conditions.

It is possible that the greater numbers of smaller tortoises found in 1983 could have resulted from better search effort for these sizes (Berry and Turner 1984), but we censused the plot carefully in 1987, specifically looking for small tortoises, yet we found relatively few. While we do not doubt that young are missed because of their inconspicuousness, we believe that the changes in size and age distributions between 1979 and 1987 reflect actual population changes.

The size and estimated age distributions for 1983 indicate that a significant number of smaller and younger tortoises came into the plot between 1979 and 1983. Judging by the male-dominated sex ratio after 1979, immigration largely has been by young males. The biased sex ratios are not due to higher adult male survival since equal proportions of males and females died. Most of the males in the present population are fairly young, although they are large. Male turtles are known to disperse greater distances than females (Gibbons 1986).

Although many turtle populations have biased sex ratios, evolutionary theory indicates that these ratios should be under selective pressure to be relatively even, in most instances (Fisher 1930, Trivers 1972). However, desert tortoise age to maturity is ca. 15 years (Germano In Press, Woodbury and Hardy 1948), therefore a reproductive solution mediated by selection would require hundreds of years.

Censuses in other parts of this valley in 1983 indicate that this high rate of mortality was confined to this plot and areas close by (unpublished report, C. Mortimore and P. Schneider, Nevada Department of Wildlife, Las

Vegas, NV). Differences in sex ratios at this plot may be more a reflection of higher male movement rates compared to females and not to a real difference in numbers of males and females in the population as a whole. Over time the sex ratios may change by movement of females into the plot from outside.

Density may have decreased slightly since 1979, but it does not appear to have changed significantly over the 8 year period, although we recognize the imprecision of these density estimates. The number of tortoises found has decreased in each census, but investigators and time periods in the field have varied, ren-

**Table 4.—Annual and winter precipitation (mm) for 1970-1987 and for 3 time periods from the Searchlight, Nevada NOAA Station. Winter precipitation is defined by the months October-March. Means and standard deviations are given for the 3 time periods. Precipitation for 1987 only includes the months of January-July.**

Year	Annual total	Winter total	Time period		
			Jan. 1970- June 1979	July 1979- Dec. 1982	July 1979 July 1987
1970	127.76	30.73	Annual precipitation		
1971	68.83	17.02			
1972	136.65	179.02	170.9 (113.0)	281.2 (86.4)	265.5 (148.8)
1973	114.81	54.36	Winter precipitation		
1974	184.40	100.08			
1975	132.08	82.79	104.4 (33.0)	139.4 (73.7)	161.0 (71.7)
1976	161.80	52.58			
1977	107.70	183.90			
1978	473.71	249.43			
1979	256.54	260.10			
1980	313.44	67.06			
1981	162.81	101.09			
1982	366.10	216.15			
1983	376.68	61.47			
1984	300.48	191.52			
1985	149.35	91.69			
1986	166.88	126.24			
1987	73.66				



dering this comparison unreliable. We believe that the lower number of live tortoises found in 1987 is due to inexperienced field personnel and the shorter duration of time in the field. The most valid of these density estimates is the Jolly-Seber estimate of 44 tortoises/km<sup>2</sup>, because more assumptions are met with this technique. Unfortunately, estimates cannot be made for the first or last census with this technique. Density estimates, though, are similar in magnitude and we believe this indicates that density has remained relatively stable since 1979. The population must have experienced a decline after 1979 but we believe that increased survival of young and immigration from adjacent non-affected areas has quickly returned the density to 1979 levels.

### Mortality Factors

Causes of the high rate of mortality have not been demonstrated. The hypothesis that long-term grazing confounded by a drought in 1981 was the cause of the high number of tortoise deaths is not supported by growth analysis of annuli, CL/weight data, or climate data. Growth did not differ significantly between those that died before 1983 and those that survived to 1987. In addition, the weight to size regressions for 1979 and 1987 were the same and both were almost identical to the regression for tortoises from an ungrazed plot in Nevada (Medica et al. 1975). As for a drought in 1981, average rainfall was only 9% below the long-term average (up to 1987) and was actually at the average, up to 1981, given the drought in the 1970s. Preceding 1981 were 3 years of exceptionally high rainfall. In contrast, rainfall in 1977 was 41% below average and followed many drought years (table 4).

Desert tortoises are known to store water (Nagy and Medica 1986) and may be able to store fat. It seems

doubtful that one average year of rainfall after 3 very good years could cause starvation or lethal dehydration. The 2 years preceding our census in 1987 were below average in precipitation, yet mortality rates dropped. The period 1970-1977 was a drought, yet only 10 shells were found in 1979. If these low rainfall years didn't produce a high rate of mortality that could be detected in 1979, it is hard to imagine that one average year after 3 good years would result in excess mortality. Estimates of yearly adult death rates from 1972-1982 for a population only 42 km south of this site was 1.2%, in an area that has been grazed by livestock for 100 years (Berry and Nicholson 1984a).

Other possible causes for this mortality could have been disease, predation, or flooding. Diseases are known to affect other turtle species in the wild (Jacobson 1980a,b), but no evidence exists for disease as a factor. Many of the shells show signs of chewing by carnivores, although whether this indicates predation or scavenging cannot be determined. Flooding occurred in or near the plot in 1980 and 1982 (unpublished report, J. Jamrog and R. Stager, BLM, Las Vegas, NV). The plot is dissected by numerous washes that are most prevalent in this part of the valley (fig. 2).

The exact cause of the high rate of mortality may never be known. Starvation, disease, flooding, and predation may have all had an effect. No singular explanation is supported by the data. Whatever the causative agent, the population appears to be returning to a density and population structure as occurred before the period of high mortality.

### Management Implications

As a long-lived reptile, the desert tortoise is more vulnerable to fluctuations in adult mortality than to similar fluctuations in younger age

groups. Many desert tortoise populations consist of adult segments that usually have yearly survivorship rates of 95-98% (Berry and Nicholson 1984b). High adult survivorship is often coupled with low juvenile survivorship (Wilbur and Morin 1988) and part of the concern for tortoise populations is that they may not have the ability to withstand disturbance because of low juvenile survivorship. Female desert tortoises in the eastern Mojave desert have the ability to lay 2-3 clutches in a season (Turner et al. 1986). The significant increase in 1983 of tortoises 1-4 yr of age suggests more hatchlings have survived between 1979-1983 than previously. As with any other population parameter, juvenile survivorship can vary, and this may lead to periodic additions of greater numbers of young surviving to adult age.

It appears that desert tortoises have the ability to recover from disturbance in some instances. This appears to be what is happening at the Piute plot. Increased juvenile survivorship and immigration are holding the population density stable and the age and size distributions are returning to 1979 dimensions. This kind of recovery may not occur if a disturbance is prolonged or is widespread. Those managing desert tortoises must be aware of the dynamics of each population, but it is apparent that tortoise populations can recover from short-term high mortality.

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