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DOES HIGH ADULT MORTALITY EQUAL A POPULATION CRASH FOR DESERT TORTOISES IN THE PIUTE VALLEY, NEVADA?

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Abstract. Apparent high mortality of adult desert tortoises (*Gopherus agassizii*) at the Piute Valley Permanent Study Plot in southern Nevada between 1979 and 1983 has not led to a decline in density. It did result in a significant decrease in mean carapace length (CL) and average age in 1983. Both mean CL and average age had increased by 1987. The stability of density at this plot seems to be due to increased juvenile survival of tortoises hatched after 1979 and immigration of tortoises from the surrounding area. The per capita mortality rate for 1979-1983 was estimated at 0.21/year, with adults being most affected. The per capita mortality rate for 1983-1987 was estimated at 0.08/year, affecting all ages evenly. Causes of the high rate of mortality between 1979 and 1983 cannot be determined, although this event seemingly was limited to a very small portion of the valley. Starvation, disease, and flooding may have contributed to tortoise deaths although all causes are speculative. Populations of desert tortoises seem to have the ability to withstand short periods of high rates of mortality, at least in areas of localized disturbance, and when high juvenile recruitment can offset adult loss.

INTRODUCTION

A large number of mortalities of desert tortoises (*Gopherus agassizii*) were found in a 2.59 km² (1 mi²) plot located in the Piute Valley of southern Nevada in 1983 (Mortimore and Schneider 1983). This study plot was established in 1979 at which time only a few mortalities were discovered (Karl 1979). It is therefore believed that this high number of deaths occurred between 1979 and 1983 and possibly resulted from a single event (Mortimore and Schneider 1983). We recensused this population of desert tortoises in 1987 to assess changes that might have taken place since 1979. Results of this census are presented elsewhere (Joyner and Germano in press). Here we compare our results to those of previous censuses and relate these changes to an understanding of responses of desert tortoises to disturbance.

METHODS

The plot is located in the Piute Valley of southern Nevada in the eastern Mojave desert (see Joyner and Germano in press for a description of this area). Densities in 1979 and 1983 were determined using the Schnabel estimator (Karl 1979; Mortimore and Schneider 1983). We reestimated density for 1983 using the Jolly - Seber estimator (Tanner 1978). This method takes into account losses and additions to the population. For 1987, we estimated density using a Lincoln index with May as the period of marking animals and August as the recapture period. Only 1/2 the plot was recensused in August due to time constraints. Therefore, the density of tortoises was computed for this half and then doubled to give an estimate of the number of tortoises for the whole plot.

Carapace lengths (CL) of each individual were plotted and mean carapace lengths computed for each year. Mean CLs of the total population, adults (>180 mm CL), and non-adults (<180 mm CL) were compared among years with two-tailed t-tests. We used Bonferroni adjustments to p-values using $p = 0.017$ as our significance value based on three comparisons within groups.

Ages of each individual were plotted and mean ages compared in a manner similar to carapace lengths. Ages of mortalities and 1987 live tortoises were determined for most individuals using scute annuli. This technique has been found to be accurate up to 20 - 25 years (Germano 1988; Germano and Fritts in press). Several individuals were determined to be older than the number of easily seen annuli based on scute edge beveling or non-growth since last capture. These individuals were categorized as > 25 years old. Ages were estimated for live tortoises found in 1979 and 1983 based on carapace lengths. The number of scute annuli is fairly well correlated to CL, especially for smaller individuals (Age = [CL - 36.52]/8.68, $r^2 = 0.823$, $n = 199$). 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 fell into this category from the 1987 live

and 1983 and 1987 shell groups.

Age-specific mortality rates were determined for 1979-1983 and 1983-1987 using the equation $qx = (k[fx])/gx$, where qx is the mortality rate per year for age x, k is the per capita mortality rate of the population, fx is the proportion of animals age x that are known to have died in the past year, and gx is the proportion of animals of age x in the preceding live population (Fryxell 1986). In order to compare mortality rates to age structures, 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 in order to obtain the yearly mortality rate for each time period.

Sex ratios were compared among live tortoises and shells. Sex was determined for tortoises >180 mm CL or, in some instances, for males >170 mm CL. Ratios were tested for deviation from a 1 to 1 sex ratio with Chi-square analysis.

Carapace length to weight regressions were constructed for 1979 and 1987 tortoises. Data for 1983 were not available. Regressions were based on the logarithmic transformation of both variables. Slopes were tested against 0 and against each other.

Individual growth was compared among 1987 live tortoises and mortalities in two ways. Growth rings of the second costal scute were compared among these 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 AW/estimated CL for the preceding year. The estimated CL is derived from the length of the ring, which are highly correlated ($r^2 = 0.96$, $n = 174$). Means of these two variables for each ring were compared among groups using the nonparametric Wilcoxon sign test.

We also tested the hypothesis that mortalities found in 1983 starved due to drought and long-term grazing pressure (Mortimore and Schneider 1983). We compared the mean AW of the last two growth rings for the shells found in 1983 to the mean AW of the 1980 and 1981 growth rings from live tortoises found in 1987 using t-tests.

Climate was analyzed using weather information from Searchlight, Nevada. Data were compared for three 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 these 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. We also compared the pattern of rainfall for these time periods using a predictability index (P) based on measures of constancy (C) and contingency (M) using log-transformed monthly totals (Colwell 1974). In areas with highest predictability of rainfall, $P = 1$. This could be due to either constant rainfall each month every year ($C = 1$), a regular pattern of monthly rainfall (seasonality) every year ($M = 1$), or a combination of the two.

RESULTS

Densities of desert tortoises were estimated to be 50/km² in 1979 (Karl 1979) and 72/km² in 1983 (Mortimore and Schneider 1983). Eighty-four tortoises were found in 1979 and 81 were found in 1983. We re-estimated the 1983 density to be 44 tortoises/km². An average of these two estimates for 1983 is 57.5 tortoises/km². We estimated the density in 1987 to be 59 tortoises/km² (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 four had been marked in May.

Carapace lengths (CL) of live tortoise populations varied significantly for each census (Fig. 1). Mean CL was significantly smaller in 1983 than in either 1979 ($t = 4.71$, 163 df, $p < 0.001$) or 1987 ($t = 3.25$, 127 df, $p < 0.01$). Mean CLs in 1979 and 1987 were not significantly different, however ($t = 0.695$, 130 df, $p > 0.10$, Table 1). No significant differences were found among mean CLs for adults (>180 mm CL). Adults made up 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 ($t = 4.28$, 84 df, $p < 0.001$), but was not significantly different than 1987 ($t = 1.44$, 68 df, $p > 0.10$, Table 1). The mean CL of non-adults was not significantly different between 1979 and 1987 ($t = 1.93$, 52 df, $p > 0.05$).

Thirty-seven mortalities were found in 1987 compared to 109 found in 1983 (Fig. 2). Ten shells were found in 1979 (Karl 1979). Carapace lengths of mortalities were not significantly different ($t = 1.959$, 143 df, $p > 0.05$), although mean CL in 1983 was larger than for 1987 (Table 1). Mean CLs of adult and non-adult mortalities were similar, but adults comprised 78% of the 1983 collection and only 49% of the 1987 collection. The mean CL of mortalities 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 ($t = 5.27$, 188 df, $p < 0.001$). Mean CL of mortalities from 1987 was not significantly different than mean CL of live tortoises.

Ages of tortoises varied significantly for years of censusing (Table 2). Changes in ages of live tortoise

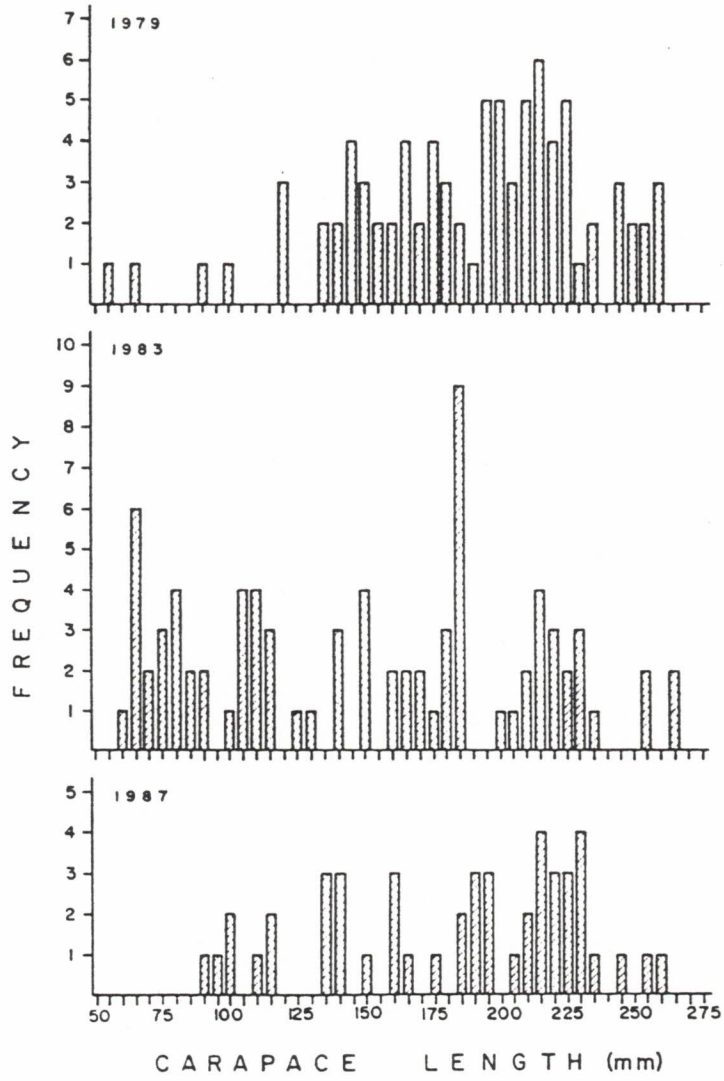

Figure 1. Carapace lengths of live desert tortoises from the Piute Valley Permanent Study Plot in 1979 (data from Karl 1979), 1983 (data from Mortimore and Schneider 1983), and 1987. Mean carapace lengths and sample sizes are given in Table 1.

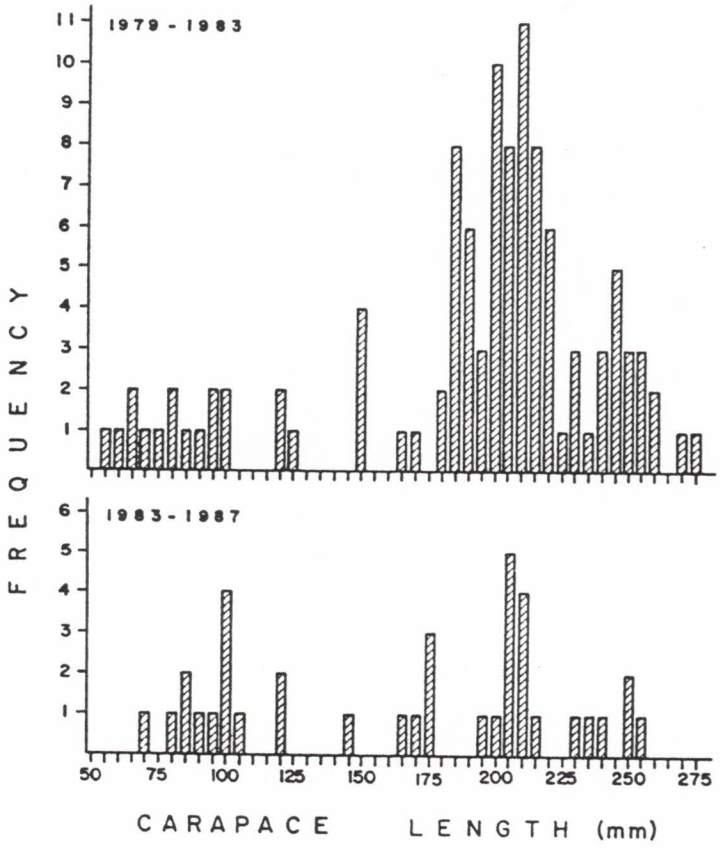

Figure 2. Carapace lengths of desert tortoises found dead in 1983 and 1987 from the Piute Valley Permanent Study Plot. Mean carapace lengths and sample sizes are given in Table 1.

Table 1. Mean carapace lengths (CL) and sample sizes of tortoises from the Piute Valley Permanent Study Plot.

Group	All Tortoises	>180 mm Cl	% of Total	<180 mm CL	%of Total
1979 live	186.8 mm (84)	217.1 mm (49)	58	144.5 mm (35)	42
1983 live	148.2 mm (81)	211.8 mm (30)	37	110.8 mm (51)	63
1987 live	181.1 mm (48)	213.8 mm (29)	60	125.8 mm (19)	40
1983 shells	197.6 mm (108)	212.9 mm (84)	78	106.4 mm (24)	22
1987 shells	165.4 mm (37)	216.3 mm (18)	49	117.2 mm (19)	51

Table 2. Mean ages and sample sizes of tortoises from the Piute Valley Permanent Study Plot in southern Nevada. Ages for 1979 and 1983 are estimates based on carapace length (see Methods).

	Ages (Years)			
Group	0 - 27	0 - 14	15 - 27	>25*
1979 live	16.6 (72)	10.9 (24)	19.5 (48)	- (12)
1983 live	12.1 (74)	7.5 (41)	18.8 (30)	- (7)
1987 live	14.1 (43)	11.3 (22)	17.0 (21)	- (5)
1983 shells	17.0 (94)	7.8 (22)	19.9 (72)	- (14)
1987 shells	14.0 (31)	8.4 (31)	19.3 (16)	- (6)

* Mean age cannot be determined.

populations are similar to the changes seen for CLs (Fig. 3). The estimated mean age for 1979 is significantly older than 1983 ($t = 4.59$, 144 df, $p < 0.01$) and 1987 ($t = 2.77$, 113 df, $p < 0.017$). Mean age for 1987 is not significantly different than 1983 ($t = 1.81$, 115 df, $p > 0.05$), but non-adults are significantly older ($t = 4.05$, 64 df, $p < 0.01$). Mean age of 1983 mortalities is significantly older than 1987 live tortoises ($t = 2.83$, 135 df, $p < 0.017$), but is not significantly different than 1987 mortalities ($t = 2.33$, 123 df, $p > 0.017$, Fig. 4).

Death rates were lower for 1983-1987 than for 1979-1983. Per capita mortality rate (k) for 1979-1983 was 0.21/year, using 130 tortoises for the plot as estimated in 1979, and was 0.08/year for 1983-1987, using 115 tortoises for the plot as we estimated for 1983. 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 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 is analyzed by size, 92% of tortoises >220 mm CL are males, whereas only 53% of tortoises 180-219 mm CL are males (Table 3). When analyzed by age, 63% of tortoises > 20 years are males, but 71% of tortoises of known sex between 13-19 years are males, a significantly higher proportion than females. The sex ratios of mortalities were not significantly different than 1 to 1 (Table 3).

Both the 1979 and 1987 regressions of weight against CL had significant slopes that were not significantly different from each other ($t = 0.90$, 122 df, $p > 0.10$). The regression equation for 1979 is weight $= 0.00031\ CL^{2.924}$ ($r^2 = 0.952$, $n = 73$) and for 1987 is weight $= 0.00051\ CL^{2.826}$ ($r^2 = 0.969$, $n = 53$).

No significant differences were found in a ring by ring comparison of growth between 1987 live tortoises and 1983 mortalities for either annual width (AW) or percent growth (G). When 1980 and 1981 rings are compared, no significant difference exists between the mean AW for the last two rings of 1983 mortalities ($X = 1.98$ mm, $n = 72$) and the 1980 and 1981 rings for 1987 live tortoises ($X = 1.92$ mm, $n = 79$; $t = 0.31$, 149 df, $p > 0.10$).

Average precipitation amounts were higher between July 1979 and July 1987 than for 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 (7.24 in) with seven of the ten years well below average (Table 4). When 1978 and 1979 are excluded, average precipitation drops to 129.3 mm (5.09 in), 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. Predictability analysis of rainfall showed similar and low predictabilities for 1970-1979 ($P = 0.347$, $C = 0.216$, $M = 0.131$) and 1980-1986 ($P = 0.397$, $C = 0.089$, $M = 0.308$).

DISCUSSION

The population of desert tortoises in the Piute Valley Permanent Study Plot experienced an apparent high rate of mortality, particularly of adults, between July 1979 and 1983. Related to this event was a significant decrease in the carapace lengths and ages of the population in 1983, which were returning to 1979 dimensions in 1987. The lower mean age in 1983 is probably a result of increased hatchling survival and increased immigration along with a disproportionate loss of adults. It is possible that the greater number of smaller tortoises found in 1983 could be due to better search effort for these sizes, but we do not believe that this is a total explanation. We censused the Piute Valley plot carefully in 1987, specifically looking for small tortoises, yet we found relatively few. While we do not doubt that some young are missed because of their inconspicuousness, we believe that the significant changes in carapace lengths and ages between 1979 and 1987 are real.

The CLs and estimated ages for 1983 indicate that smaller and younger tortoises came into this plot after the period of high mortality. Judging by the sex ratios, which have become biased towards males, immigration into this plot may have been by a high proportion of young males. The biased sex ratios are not due to higher adult male survival as can be seen by the equal proportions of males and females that died. Censuses in other parts of this valley in 1983 indicate that high mortality was localized to within and near this plot (Mortimore and Schneider 1983). Over time the sex ratios may equilibrate by movement of females into the plot from outside.

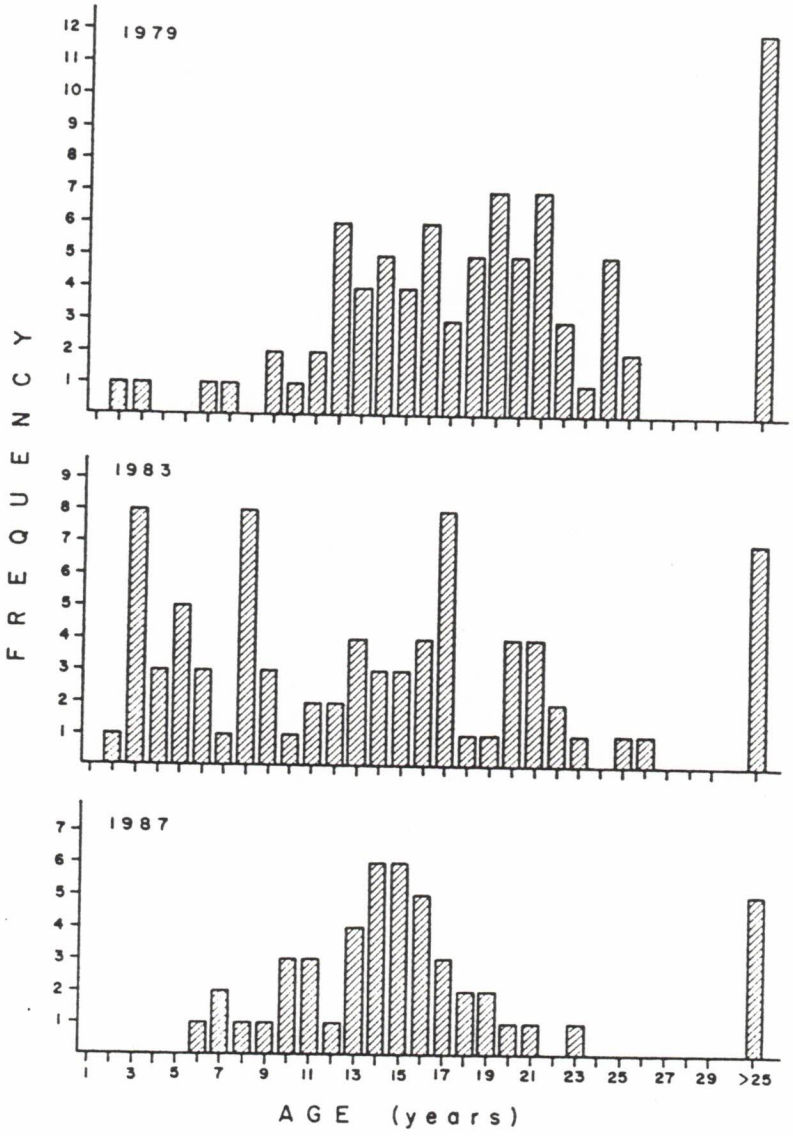

Figure 3. Ages of live desert tortoises from the Piute Valley Permanent Study Plot in 1979, 1983, and 1987. The 1979 and 1983 ages are estimates based on a carapace length to annuli number regression. A proportion of adults were placed in the >25 age category based on the proportion of adults in this category for which ages were assigned by annuli counts. 1987 ages are based on annuli counts.

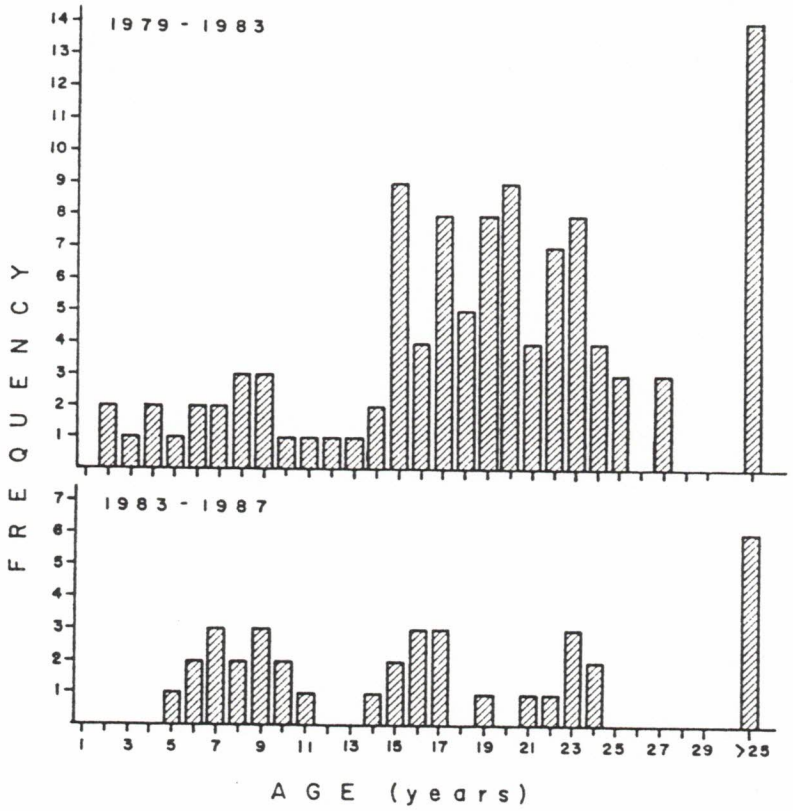

Figure 4. Ages of desert tortoises found dead in 1983 and 1987 from the Piute Valley Permanent Study Plot. Both 1983 and 1987 ages based on counts of annuli.

Table 3. Numbers of male and female desert tortoises from the Piute Valley Permanent Study Plot. Significant departures from a 1:1 sex ratio were determined by Chi-square analysis. The totals of live animals in 1987 were subcategorized by size and age.

Year	Males	Females	Ratio	X^2
1979 live	24	30	0.88 : 1	0.667
1979 shells	4	3	1.33 : 1	0.001
1983 live	22	11	2 : 1	3.667
1983 shells	35	41	0.85 : 1	0.474
1987 live (total)	20	9	2.22 : 1	4.172*
Size: 180-219 mm CL	9	8	1.13 : 1	0.059
>220 mm CL	11	1	11 : 1	8.330*
Age: 13-19 years	15	6	2.5 : 1	3.857*
>20 years	5	3	1.67 : 1	0.500
Shells	11	6	1.83 : 1	1.471

* Significant departure from 1:1 ration ($p<0.05$).

Table 4. Annual and winter precipitation (mm) for 1970-1987 and for three 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 three time periods. Precipitation in 1987 only includes the months January-July.

Year	Annual Total	Winter Total	Jan 1970-June 1979	July 1979-Dec 1982	July 1979-July 1987
1970	127.76				
		30.73	Annual Precipitation		
1971	68.83				
		17.02	170.9 (113.0)	281.2 (86.4)	256.5 (148.8)
1972	136.65				
		179.02			
1973	114.81				
		54.36			
1974	184.40		Winter Precipitation		
		100.08			
1975	132.08		104.4 (33.0)	139.4 (73.7)	161.0 (71.1)
		82.79			
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				

Densities may have decreased slightly since 1979, but it does not seem to have changed significantly over the eight year period, although we acknowledge 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, rendering 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 density estimates, though, are similar in magnitude and may indicate that the population has remained relatively stable since 1979. The population must have experienced a decline after 1979 because of the high number of mortalities found in 1983, but increased survival of young and immigration from adjacent non-affected areas seems to have quickly returned the density to 1979 levels.

Causes of the high rate of mortality are not apparent. Mortimore and Schneider (1983) cited long-term grazing confounded by a drought in 1981 as the reason for the high number of tortoise deaths. This hypothesis is not supported by growth analysis of annuli, size/weight regressions, or climate data. Growth did not differ significantly between tortoises that died before 1983 and those that survived to 1987. In addition, the overall health of the population seems stable. Although weights for 1983 were not available, 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 three 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 three very good years could lead to starvation. Estimates of adult death rates from 1972-1982 for a population only 42 km south of this site was 1.2% / year, in an area that has been grazed by livestock for 100 years (Berry and Nicholson 1984a). We do believe that grazing in desert habitats may have long-term harmful effects to the ecosystem in general, but, as Berry and Nicholson (1984b) have noted, the degree and effects of livestock grazing on desert tortoises remains unclear.

What is most unusual climatically for 1979-1983 is very high amounts of precipitation. This could have led to increases in disease and death due to floods. Diseases are known to affect other wild turtle species (Jacobson 1980a, 1980b). Several tortoises were found to have high numbers of ticks in 1979 (Karl 1979). Ticks can be vectors for disease (Frye 1973). No evidence of disease could be seen on shells collected in 1983, although shell morphology may not be affected by blood or visceral diseases. Also, other areas in this valley with similar population levels did not experience a die-off (Mortimore and Schneider 1983), which might be expected if disease were a factor. Flooding occurred on or near the plot in 1980 and 1982 (Jamrog and Stager 1987; Mortimore and Schneider 1983). The plot is bisected by numerous washes that are not prevalent in most of the valley. Desert tortoises have been killed as the result of flash floods (Woodbury and Hardy 1948; Coombs 1974).

It seems that the exact cause of the die-off will never be known. Starvation, disease, flooding, as well as predation may all have had an effect. No explanation is totally supported by the data available, all rely on circumstantial evidence. What does appear to be certain is that this population has undergone some major changes in size and age. Because of the localized nature of this event, the population seems to be returning to a level similar to before the high rate of mortality due to increased survival of young and increased immigration.

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