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Desert Tortoise (*Gopherus agassizii*) Survival at Two Eastern Mojave Desert Sites: Death by Short-Term Drought?

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ABSTRACT.—**Survival of adult Desert Tortoises (*Gopherus agassizii*) appears related to site-specific variation in precipitation and productivity of annual plants. We studied adult tortoise survival rates at two closely situated, but physiographically different, sites in the eastern Mojave Desert over a nine-year period (spring 1992 to spring 2001). Survival rates were initially derived from population surveys conducted over a three-year period and by radio-telemetry monitoring over a seven-year period beginning in 1994. After a period of initial stability, survival rates on the two sites diverged over the study period, and seven-year survival rates estimated from radio-telemetry monitoring were 0.900 and 0.269, respectively. A die-off in 1996 on the latter site appears to have been triggered by a period of drought, which began in the summer of 1995, coupled with a failure of annual vegetation production in 1996. Depressed survival rates on this site were associated with drought conditions during three of four years. Although the decline had the appearance of an epizootic, there were no clinical signs of disease. Relatively short-term drought, combined with little or no annual biomass, appears to have caused severe reductions in tortoise survival. If periods of drought-induced low survival are common over relatively small areas, then source-sink population dynamics may be an important factor determining tortoise population densities.**

Desert Tortoises *Gopherus agassizii* exhibit a remarkable capacity to respond behaviorally and physiologically to drought conditions (Nagy and Medica, 1986; Henen et al., 1998; Duda et al., 1999). During unfavorable periods, desert tortoises decrease surface activity and generally remain inactive or dormant within their burrows (Duda et al., 1999), reducing water loss and minimizing energy expenditures (Nagy and Medica, 1986). Desert tortoises can tolerate extreme variations in energy, nutrient, and water balance on seasonal, annual, and potentially longer time frames (Nagy and Medica, 1986; Peterson, 1996a,b; Henen et al., 1998). The ability of desert tortoises to tolerate drought conditions, however, has limitations. Their primary springtime diet of succulent annual vegetation appears to be osmotically stressful because of high potassium levels (Nagy and Medica, 1986; Oftedal and Allen, 1996). Tortoises must void these ions as urinary waste, but to minimize water loss, tortoises may accumulate ions and nitrogenous wastes in their large urinary bladders for months or longer (Nagy and Medica, 1986). Seasonal rainstorms, common during summer in the eastern Mojave Desert, allow tortoises to drink (Medica et al., 1980), which results in the replenishment of body water, voiding of concentrated urine, and regaining of water and electrolyte balance (Nagy and Medica, 1986; Peterson, 1996a,b; Henen et al., 1998). Without this rehydration, tortoises may not be able to take advantage of dry annual forage, which appears to be important for achieving long-term energy balance (Nagy and Medica, 1986; Peterson, 1996a). During years of low precipitation, the effects of little or no annual plant productivity may be compounded by the failure of seasonal rainstorms, which would preclude the rebalancing of water and electrolytes and the consumption of any available dry plants from the previous year.

The spatial and temporal variability of precipitation and primary productivity characteristic of the Mojave Desert (Beatley, 1974; Smith et al., 1997) may greatly affect survival rates of desert tortoises. High adult tortoise mortality associated with drought has been documented among years within a single site (Turner et al., 1984; Germano and Joyner, 1988; Peterson, 1994) and among sites between geographic regions (eastern and western Mojave Desert; Peterson, 1994). Desert tortoises appear susceptible to dehydration and starvation during periods of drought (Peterson, 1994), and tortoises suffering from potentially chronic diseases like upper respiratory tract disease (URTD) may be more vulnerable to lethal effects during a drought because

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of their poorer physiological condition (Jacobson et al., 1991). Furthermore, periods of drought may indirectly increase mortality through increased predation on adult tortoises as the result of a functional response (prey switching) of predators to a decrease in prey availability (Woodbury and Hardy, 1948; Peterson, 1994).

Predictions from a population viability model for tortoises in the Mojave Desert (Doak et al., 1994) indicate that population growth is much more sensitive to changes in adult survival rates, particularly in large adult females, than to either reproduction or size-specific growth rates. Consequently, decreases in adult tortoise survival rates are predicted to negatively affect population viability (Doak et al., 1994). Determination of how climatic and weather variability affects survival of adult tortoises over small geographic areas in undisturbed populations may be important to our understanding of regional population dynamics. We studied survival rates of adult tortoises from two relatively undisturbed, and physiographically different, sites over a nine-year period in the eastern Mojave Desert. Initial survival rates, as well as population estimates, were derived from population surveys over a three-year period. Radio-telemetry monitoring was commensurate with the latter part of the population surveys and extended over seven years. The sampling period covered a broad range of yearly precipitation amounts, and drought conditions were documented on both sites. We evaluated survival rates from these two sites and their relationship to site-specific measures of precipitation and aboveground winter annual biomass.

Materials and Methods

Study Area.—The two study sites were located 29 km apart on the Nevada side of the Lake Mead National Recreation Area and were either within or adjacent to an area identified by the U.S. Fish and Wildlife Service as critical tortoise habitat (Piute-Eldorado Desert Wildlife Management Area; U.S. Fish and Wildlife Service, 1994). Both sites were established in 1992 by the National Park Service for long-term tortoise monitoring and organized as 2.6-km^2 plots gridded into 100 square-cells using poles located at the corners of each cell. The Cottonwood site (northwest corner 706631E, 3928706N) was located about 1.5 km southwest of the Cottonwood Cove Marina on an undulating, alluvial bajada that descends gradually eastward toward Lake Mojave. Elevation ranged from 290–360 m. Perennial vegetation on this site was typical of the eastern Mojave Desert, being dominanted by *Larrea tridentata* and *Ambrosia dumosa*. The Grapevine site (northwest corner 709984E, 3900010N) was located on more rugged terrain on the east slope of the Newberry Mountains south of Grapevine Canyon and about 8 km west of Lake Mojave. Elevation ranged from 650–860 m, and the area consisted of small valleys and steep ridges interspersed with rock outcrops and boulders. Perennial vegetation at this site was of greater variety than at Cottonwood, with communities consisting of a *Larrea-Ambrosia* association and a mixed-shrub association dominated by *Eriogonum fasiculatum, Viguiera deltoidea, Ephedra nevadensis, Ambroia dumosa, Larrea tridentata*, and *Encelia* spp. (Holland, 1982).

Population Surveys and Radio-Telemetry.—As part of a monitoring program, population surveys of desert tortoises were conducted on the two study sites each spring from 1992 through 1995. Surveys generally conformed to a 60 person-day technique for mark-recapture estimation of desert tortoise populations with each site systematically searched twice a year from mid-March through May by trained personnel (see Berry et al., 1986). Starting in 1993, radio-telemetry monitoring began on these sites, and in spring 1994 this monitoring effort was expanded to estimate long-term survival rates. Radio-transmitters (MOD-225, Telonics Inc., Mesa, Arizona) were fitted on adult tortoises (Maximum Carapace Length, MCL $\geq$ 180 mm) and attached with epoxy gel to costal scutes (Boarman et al., 1998) either forward on the carapace to avoid interfering with mating (females and males) or near the rear (males). Capture efforts to place transmitters on tortoises were coincident with the population surveys but also included searches at other times and opportunistic encounters during radio-telemetry. Through 1999, transmitters were added to new tortoises or replaced on individuals before batteries were expected to fail or when signal strength weakened or failed. The number of radio-telemetry monitored tortoises varied over time with a range of 10–52 at Cottonwood and 10–48 at Grapevine with the maximum number at both sites occurring in summer 1995 (Table 1). All captured tortoises were measured, weighed, independently marked using a scute-notching scheme, and their health evaluated using a standard checklist (Berry and Christopher, 2001).

Mark-recapture population estimates for adult tortoises were calculated over two years using tortoises captured during one year as the marked cohort for the following year. This approach was used because recapture rates were low during any particular survey. Estimates focused on adults to mitigate variation in age-class capture probabilities (Schneider, 1980). The two separate searches of each site during a season (recapture events) were combined to calculate estimates using the closed joint hyper-

TABLE 1. Annual survival rates calculated using the Kaplan-Meier estimator (Pollack et al., 1989) for adult desert tortoises on the Grapevine Canyon and Cottonwood Cove study sites in Lake Mead National Recreation Area, Nevada. Sampling occasions correspond to six-month seasonal periods (winter–spring and summer–fall). Survival was assumed to be 100% at the beginning of each year. Monitoring for 2001 only occurred through spring.

	Cottonwood			Grapevine		
Year	Sampling occasion (at-risk/deaths)	Survival rate	95% C.I.	Sampling occasion (at-risk/deaths)	Survival rate	95% C.I.
1994	26/0, 26/1	0.962	0.889–1.034	10/0, 10/0	1.000	1.000–1.000
1995	33/0, 52/0	1.000	1.000–1.000	15/0, 48/2	0.958	0.903–1.014
1996	51/1, 50/15	0.686	0.580–0.793	46/0, 45/0	1.000	1.000–1.000
1997	35/0, 32/7	0.781	0.655–0.908	40/0, 39/0	1.000	1.000–1.000
1998	24/0, 23/3	0.870	0.742–0.998	38/0, 37/0	1.000	1.000–1.000
1999	20/2, 18/6	0.600	0.425–0.775	35/0, 35/0	1.000	1.000–1.000
2000	10/0, 10/0	1.000	1.000–1.000	34/0, 33/2	0.939	0.861–1.018
2001	10/0			27/0		

geometric maximum likelihood estimator (Bartmann et al., 1987; White and Garrott, 1990) as implemented by the program NOREMARK (G. C. White, Department of Fishery and Wildlife, Colorado State University, Fort Collins, 1995). The number of young tortoises encountered on each site during surveys was compared by Chi-square using the number observed each spring from 1992 through 1995. The assumption of demographic closure during the two-year sampling periods was investigated by evaluating the percentage of radio-monitored tortoises that remained on the study sites during consecutive spring survey periods between 1993 and 1995.

Survival Estimation.—The annual survival rate of tortoises on each study site was estimated as one minus the annual death rate for adults during the years when population surveys were conducted (1992–1995). Because surveys were conducted each year and because so few adult animals were determined to have died from spring 1992 through spring 1995, deaths could be assigned to particular years. Annual death rates were estimated as the number of documented deaths on each site during the study period divided by the respective median of the two-year population estimates.

Survival rates starting in summer 1994 and ending after the spring monitoring in 2001 were determined directly from radio-telemetry monitoring using the Kaplan-Meier product limit estimator (Kaplan and Meier, 1958) modified for use with staggered entry data (Pollock et al., 1989). Variances of the survival estimates were calculated using the alternative Cox and Oakes formula cited by Pollock et al. (1989). The survival function produced by this estimator is the probability of an arbitrary animal in a population surviving some number of time units from the beginning of the study period, with the function only changing at time points when deaths occur (Pollock et al., 1989). Differences between cumulative survival curves from the two study sites, and differences between the sexes within each study site, were evaluated using modified log-rank tests (i.e., χ^2_2; Pollock et al., 1989). Annual survival rates were derived in two ways from radio-telemetry monitoring data, as an average value over seven years and by specifically calculating rates assuming 100% survival at the beginning of the first of the two sampling periods each year.

Monitored tortoises were located every two weeks during spring and fall, and occasionally during summer and winter months in 1994 and 1995. Starting in 1996, sampling was conducted during spring and fall and only until the status (alive or dead) of each tortoise was determined. Thus, time-units for survival rate calculations were approximately six-month periods roughly corresponding to winter-spring and summer-fall seasonal periods (14 time-units total). On occasion, monitored tortoises could not be located during an active season or could only be located within a burrow or crevice without being observed. If the animal's status was determined during the following active season, the appropriate status was assigned to the missing sampling period during analyses. Animals that could not be found during the second active season were considered censored starting the period following the last documented movement or actual sighting. A few censored tortoises were eventually recaptured after several seasons and fitted with new transmitters. To avoid bias, these censored animals were treated as new additions to the monitored population at the time of recapture (Bunck et al., 1995). Near the end of the study, one censored tortoise was discovered dead, but the death could not be de-

TABLE 2. Mark-recapture population estimates and 95% confidence limits for adult tortoises on the Cottonwood and Grapevine study sites, Lake Mead National Recreation Area, Nevada. Population estimates were calculated over two years using tortoises captured one year as the marked cohort for the following year. The two separate searches of each site during a season were combined to calculate population estimates using the joint hypergeometric maximum-likelihood estimator (JHE).

Period	Sampling occasion	Marked available	Unmarked seen	Marked seen	JHE estimate	JHE 95% CI
Cottonwood						
1992–1993	1	18	11	5		
	2	18	8	2	66	42–133
1993–1994	1	23	11	4		
	2	23	9	8	61	45–97
1994–1995	1	26	12	12		
	2	26	9	7	54	44–73
Grapevine						
1992–1993	1	19	14	3		
	2	19	5	3	81	49–178
1993–1994	1	26	6	6		
	2	26	7	5	56	42–91
1994–1995	1	22	10	7		
	2	22	9	3	63	44–107

termined to a particular sampling period and was excluded from analyses to avoid bias.

Annual Biomass.—Production of above-ground winter annual biomass (henceforth referred to as annual biomass) was measured on the study sites each spring from 1992 to 2000 to provide a relative measure of available tortoise forage. Plots of 0.1 m^2, were established every 5 m along 50-m transects (10 plots per transect) in four locations on each of the study sites. Above-ground winter annual vegetation was harvested from each plot at the peak of the growing season, oven-dried, and weighed. Based on observations of annual plant distributions over the general area during spring 1992, a stratified random approach established transects so that, on each study site, two transects were in relatively higher-productivity areas, and two were in relatively lower-productivity areas. At Cottonwood, areas of high productivity were located on bajada (relict fan and secondary washes) within the *Larrea-Ambrosia* vegetation association, and the low-productivity areas were located in a large wash that bisected the site. At Grapevine, high-productivity areas generally were in flatlands and valleys where *Larrea-Ambrosia* dominated, and low-productivity areas were located on slopes.

Annual biomass was analyzed using repeated-measure analysis of variance (ANOVA; Von Ende, 2001) with year as the within-subject factor, study site and transect productivity as between-subject factors, and their interactions. Data from 1993 were excluded from the analysis because of a lost sample from one of the high-productivity transects at Grapevine. Data were evaluated for assumptions of normality and sphericity using Kolmogorov-Smirnov goodness-fit-test (Zar, 1984) and Mauchly's Criterion (Von Ende, 2001), respectively. Polynomial contrasts were used to compare biomass trends between years at each site and to examine the interaction between years and study sites. Contrasts were conducted as two overlapping analyses (1992–1998, 1995–2000) because of the limited degrees of freedom. Analyses were performed using SPSS (vers. 9.0) and SAS (vers. 8.2).

Weather Data.—A weather station at Cottonwood Cove Ranger Station was established in 1975, and precipitation data for the period of 1975 through 2000 were obtained from the National Park Service. On Grapevine, a solid-state weather station was installed in August 1993, and no site-specific weather data were available previous to this date. Precipitation data were summarized by month and plotted to reveal trends. Spearman nonparametric correlation analysis (SPSS) was used to explore the relationship between precipitation and annual biomass (Zar, 1984).

RESULTS

Population Estimates.—Using the median values of the two-year population estimates (Table 2) as the best estimate of the number of adult tortoises on each site from 1992–1995, approximately 61 adult tortoises occupied Cottonwood and 63 adult tortoises occupied Grapevine. The mean of the estimates suggests a slightly larger population at Grapevine (about 67 animals). These estimates seem reasonable given that 54

adult individuals were observed on each of these sites in 1995 during tortoise captures and radio-telemetry monitoring, and the total numbers of adult tortoises registered (first observation) at the sites from 1992–1995 were 59 at Cottonwood and 61 at Grapevine. The assumption of demographic closure necessary for two-year population estimates appeared to have been valid. Of 14 radio-monitored tortoises in spring 1993 and 33 radio-monitored tortoises in spring 1994, all but one tortoise spent time on their respective study site during the spring survey of the following year (mid-March through May). The population estimates and the observed numbers of adult tortoises suggest that these sites had similar adult population densities, with the population at Grapevine slightly larger than that at Cottonwood.

During years when population surveys were conducted (1992–1995), the Grapevine site appeared to have higher numbers of juvenile and immature tortoises (MCL < 180 mm) than the Cottonwood site. The total numbers of juvenile and immature tortoises registered during all the surveys were 30 on Grapevine and seven on Cottonwood. The number of young tortoises encountered during the surveys on the two sites was different than what would be expected assuming similar populations ($\chi^2 = 14.30$, df = 1, $P < 0.001$), and this difference was noticed in spite of the more difficult survey conditions on Grapevine.

Survival Rates.—Estimated survival rates were high from 1992 through 1995. During this period, three adult tortoises died at Cottonwood, although one of these may have died in 1991, and one adult tortoise died of natural causes at Grapevine. Annual survival rates (1 – death rates) for the period of spring 1992 through spring 1995 estimated from the population survey data were 0.983 for each year at Cottonwood, and 0.984, 1.0, and 1.0 at Grapevine, respectively. These high survival rates were generally consistant with the high estimated survival rates derived from radio-telemetry monitoring during 1994 and 1995 (Table 1, Fig. 1). The somewhat lower annual survival rate derived from radio-telemetry monitoring in 1995 at Grapevine (i.e., 0.958) resulted from two deaths attributable to the summer period of that year after the population survey had ended; thus, these deaths were not included in the estimate derived from the population survey data.

Survival rates derived from radio-telemetry data began to diverge at the two sites in 1996 with 15 deaths during the summer at Cottonwood (Table 1; Fig. 1). For the following three years, annual survival rates at Cottonwood were consistently lower than at Grapevine with most of the deaths occurring during summer months.

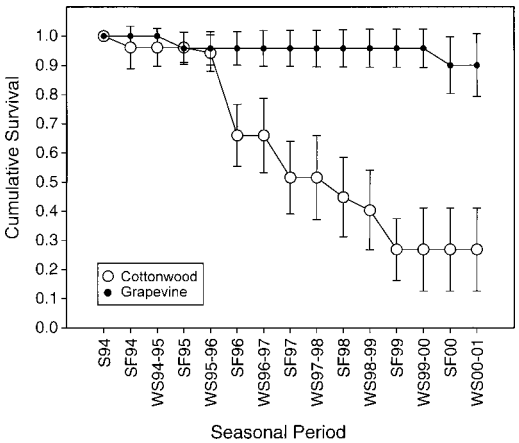

FIG. 1. Cumulative survival rates (with 95% confidence intervals) for adult desert tortoises at the Grapevine and Cottonwood study sites in Lake Mead National Recreation Area, Nevada. Survival rates were calculated using the Kaplan-Meier estimator, modified for use with staggered entry data. Time-units correspond to two sampling periods each year and approximately represent survival during periods winter-spring (WS) and summer-fall (SF). Sampling began in spring 1994, but this was not considered a complete sampling period; thus, these data were excluded from calculations.

This four-year pulse of low survival at Cottonwood resulted in large differences between survival curves at the two sites. The seven-year survival curves (summer 1994 to spring 2001) derived from radio-monitoring (Fig. 1) were different ($\chi^2 = 32.128$, df = 1, $P < 0.001$), with a survival probability over seven years of 0.269 (±0.143, 95% C.I.) at Cottonwood and 0.900 (±0.107, 95% C.I.) at Grapevine. This translates into average annual survival rates of 0.829 at Cottonwood and 0.985 at Grapevine. Seven-year survival probabilities based on sex were 0.218 (±0.189, 95% C.I.) for females and 0.319 (±0.211, 95% C.I.) for males at Cottonwood, and 0.933 (±0.005, 95% C.I.) for females and 0.869 (±0.006, 95% C.I.) for males at Grapevine. These translate to average annual survival rates of 0.804 and 0.849 at Cottonwood, and 0.990 and 0.980 at Grapevine for females and males, respectively. There was no difference in the seven-year survival curves between the sexes at either site (Cottonwood: $\chi^2 = 1.278$, df = 1, $P > 0.50$; Grapevine: $\chi^2 = 0.756$, df = 1, $P > 0.25$).

Environmental Variables.—Annual biomass was positively and highly correlated with growing season precipitation (September through March) at both Cottonwood ($r^2 = 0.85$) and Grapevine ($r^2 = 0.86$). Annual biomass data from the four transects at each site appeared normal (all $P > 0.5$). Production of annual biomass was higher

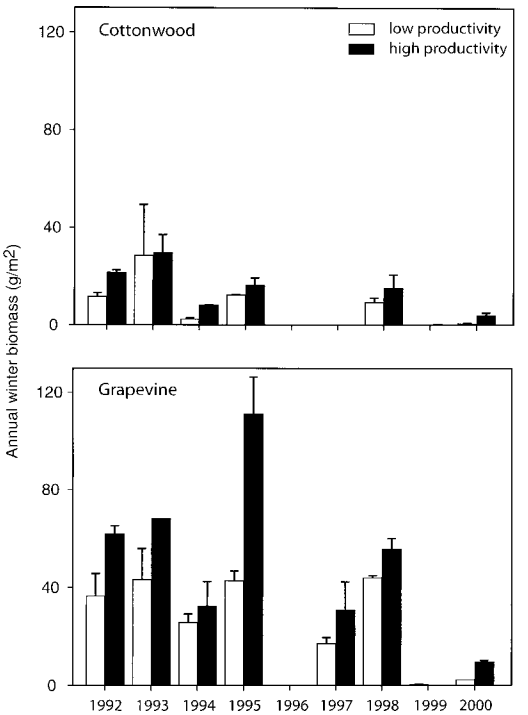

FIG. 2. Above-ground winter annual biomass (g/m^2) on the Cottonwood and Grapevine study sites, Lake Mead National Recreation Area, Nevada. Biomass measurements are the average biomass collected from two line-transects with standard error. At each site, two transects represented what were considered high- and low-productivity areas, respectively. A 1993 sample from one of the high-productivity transects at Grapevine was lost, and data from the remaining site is presented for visual interpretation.

at Grapevine than at Cottonwood over the entire study period ($F = 330.75$, $P < 0.000$). Excluding 1996, a year of drought when neither site had measurable productivity, annual biomass at Grapevine averaged more than three times that at Cottonwood (Fig. 2).

Tests for sphericity were significant (all $P < 0.01$), indicating that F-statistics for the within-subject factors and their interactions were inflated (Von Ende, 2001). Thus, we used P values from tests with Huynh-Feldt Epsilon adjustments for the degrees of freedom for within-subject tests. Annual biomass differed among years ($F = 20.43$, $P < 0.001$) and between sites among years (interaction effect: $F = 7.92$, $P < 0.001$). Polynomial contrasts indicate that annual biomass changed from each sampling to the next over the study period (all $F \geq 14.90$, all df = 1, all $P < 0.05$). Between 1992 and 1994, annual biomass decreased similarly within Cottonwood and Grapevine ($F = 1.45$, df = 1, $P = 0.282$), adjusting downward from highs associated with a period of high precipitation in the eastern Mojave Desert described as an El Niño event (Kousky and Bell, 2000). For each of the subsequent time periods, however, biomass increased or decreased at different rates at the two sites reflecting the generally higher productivity at Grapevine (all $F \geq 6.92$, all df = 1, all $P < 0.05$).

Annual biomass was either very minimal or absent from Cottonwood during the spring of 1996, 1997, and 1999, and from Grapevine in 1996 and 1999 (Fig. 2). The significant declines of annual biomass in 1996 at both sites corresponded to drought conditions that began in the latter part of 1995 (Fig. 3). Differences in local rainfall patterns during the 1997 growing season resulted in the continued failure of annual biomass on Cottonwood that year, whereas biomass increased significantly at Grapevine from the previous year (interaction effect: $F = 15.14$, df = 1, $P = 0.012$). Annual biomass productivity was again extremely minimal during 1999, showing declines at both sites from the previous year.

DISCUSSION

Long-term viability of desert tortoise populations appears critically dependent on longevity of adult tortoises (Doak et al., 1994). Although much of the modeling of desert tortoise demography remains unpublished, in relatively undisturbed Mojave Desert populations, annual survival rates of adult tortoises necessary for stationary or increasing populations have been estimated from models to be greater than about 0.95 (e.g., U.S. Fish and Wildlife Service, 1994). Grapevine and Cottonwood had similar adult population densities in the early 1990s, and based on population surveys, initial survival rates at both sites were within the range expected for maintenance or growth of each population. Average annual survival rates at Grapevine over the seven years of radio-telemetry monitoring (0.985) continued to be within the range expected for the maintenance or growth of that population. The annual survival rate at Cottonwood, however, averaged 0.829 over this period, which implies a sharp decline in the adult population at this site over the study period.

Observations at Cottonwood suggest that adult tortoise survival is highly dependent on precipitation and annual biomass production at this site. During the three years of no or very minimal annual biomass production on this site (1996, 1997, and 1999), adult tortoises experienced depressed survival. The die-off in 1996 (30% of the radio-monitored adults) followed a drought that began in the summer of 1995. When tortoises emerged at Cottonwood in

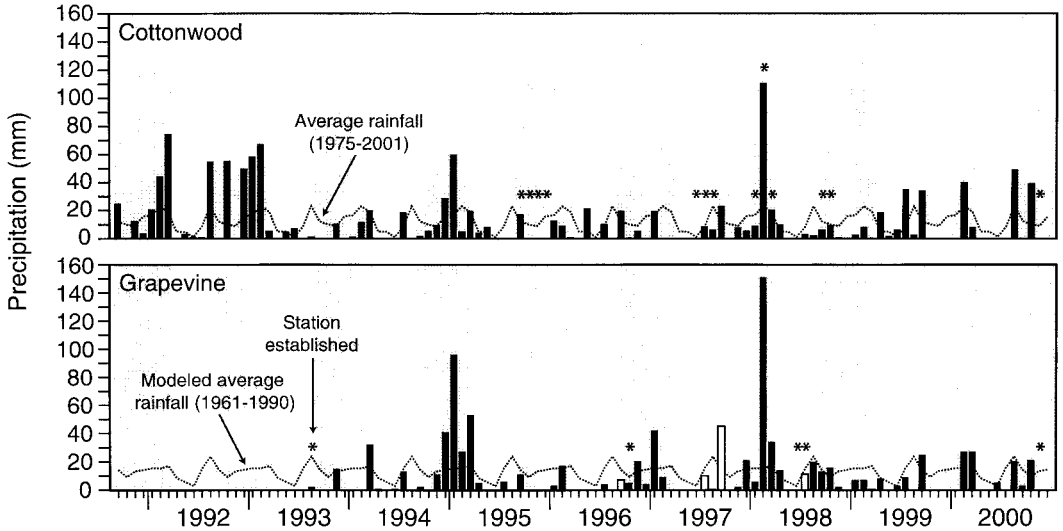

FIG. 3. Monthly precipitation for the Cottonwood and Grapevine study sites between September 1991 and December 2000. Asterisks indicate months for which less than 20 days of data were available. White bars indicate months for which no data were available from the Grapevine station, and data from a station at Katherine Landing (approximately 10 km east at 200 m elevation) were substituted. Correlation between precipitation at the two stations for months during which data were available was 0.717 (Spearman's rho, $P < 0.001$, $N = 75$). Shading indicates periods when rainfall is considered important for growth of winter annuals (Beatley, 1974; Turner and Randall, 1989). The long-term monthly average at Cottonwood was calculated using data from 1975–2001. A modeled long-term monthly average for Grapevine was derived from PRISM data covering the period 1961–1990 (Daly et al., 1994).

spring 1996, there were no succulent annual plants on which to feed and reestablish water balance, and deaths were concentrated during the following summer months. These deaths occurred during a single year of low rainfall and poor forage, and although we have no physiological evidence, these deaths likely resulted from dehydration. Drought conditions and low survival continued in 1997 at Cottonwood, but in 1998 precipitation was near the 25-year mean, and a moderate amount of annual biomass was available. Survival rates, however, remained low. Deaths that year were not concentrated during summer months and might relate to the poor condition of tortoises coming out of a two-year drought. Going into the poor forage year of 1999, tortoises at Cottonwood would have endured two of the previous three years with no annual biomass, and we speculate that starvation was likely. Although annual biomass was low again in 2000, survival rates were high, but the number of tortoises monitored was very small.

Tortoises at the Grapevine site did not experience depressed survival during the study period, and high biomass production on this site appears to mitigate the impact of short-term drought on adult tortoise survival. Tortoises at this site were likely in very good condition during the drought in 1996 based on biomass levels during the previous four years. Local rainfall patterns at this site resulted in annual plant production in 1997 that was substantial in comparison to the lack of annual biomass at Cottonwood that year. Forage conditions were also higher at Grapevine than at Cottonwood during 1998, which may have limited mortality on the former site during the poor forage conditions during 1999.

Although the die-off at Cottonwood has the appearance of an epizootic, all of the captured tortoises were evaluated for potential signs of disease (Berry and Christopher, 2001), such as URTD, and none appeared symptomatic. A few tortoises at Grapevine were recorded early in the study with minor nasal discharge, but the population at this site did not experience a die-off. Nevertheless, no laboratory diagnostics were undertaken, and clinical signs for diseases like URTD may not be readily manifested (Schumacher et al., 1997). Therefore, we cannot rule out the possibility that tortoises at Cottonwood were infected with some chronic disease that became more lethal or that increased the susceptibility of tortoises to starvation and/or dehydration during drought conditions. Predation did not appear to be a substantial factor in these deaths (only three recovered carcasses clearly showed marks from predators, which may have been signs of scavenging).

High mortality in adult desert tortoises appears to generally occur during relatively dry years, and drought conditions over two years have been demonstrated to induce starvation or dehydration, or both, in eastern Mojave Desert tortoises (Peterson, 1994). The limited rainfall at Cottonwood after the spring foraging period in 1995 through the summer of 1996, and a failure of annual plant growth in spring 1996, appears to have pushed almost one-third of the adult tortoises past their physiological limits during little more than a year. Although many of the Cottonwood tortoises survived this period, apparently even relatively short-term drought, coupled with little or no annual biomass production, can cause substantial reductions in adult survival rates. Whether this inability to withstand droughts of short duration is associated with recently introduced disease is not understood. If periods of drought-induced low survival have been common in the Cottonwood area, or have now become a feature of this system, then this area may function as a population sink supported by immigrants from neighboring, more productive areas. The possibility of increased immigration after a local die-off was suggested to have influenced the recovery of tortoise density at a site in the neighboring Piute Valley (Germano and Joyner, 1988). Grapevine, with its higher and more consistent rates of annual biomass production, higher adult survival rates, and higher number of juvenile and immature tortoises (thus higher recruitment potential) may represent a long-term source area for immigrants.

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Literature Cited

Bartmann, R. M., G. C. White, L. H. Carpenter, and R. A. Garrott. 1987. Aerial mark-recapture estimates of confined mule deer in pinyon-juniper woodland. Journal of Wildlife Management 51:41–46.

Beatley, J. C. 1974. Phenological events and their environmental triggers in Mojave Desert ecosystems. Ecology 55:856–863.

Berry, K. H., and M. M. Christopher. 2001. Guidelines for the field evaluation of desert tortoise health and disease. Journal of Wildlife Diseases 37: 427–450.

Berry, K. H., L. L. Nicholson, S. Juarez, and A. P. Woodman. 1986. Changes in desert tortoise populations at four study sites in California. Proceedings of the Desert Tortoise Council Symposium 1986:60–80.

Boarman, W. I., T. Goodlett, and G. C. Goodlett. 1998. Review of radio transmitter attachment techniques for chelonian research and recommendations for improvement. Herpetological Review 29: 26–33.

Bunck, C. M., C. L. Chen, and K. H. Pollock. 1995. Robustness of survival estimates from radio-telemetry studies with uncertain relocation of individuals. Journal of Wildlife Management 59:790–974.

Daly, C., R. P. Neilson, and D. L. Phillips. 1994. A statistical-topographic model for mapping climatological precipitation over mountainous terrain. Journal of Applied Meterology 33:140–158.

Doak, D., P. Kareiva, and B. Klepetka. 1994. Modeling population viability for the desert tortoise in the western Mojave Desert. Ecological Applications 4:446–460.

Duda, J. J., A. J. Krzysik, and J. E. Freilich. 1999. Effects of drought on desert tortoise movement and activity. Journal of Wildlife Management 63: 1181–1192.

Germano, D. J., and M. A. Joyner. 1988. Changes in a desert tortoise (*Gopherus agassizii*) population after a period of high mortality. *In* Management of amphibians, reptiles, and small mammals in North America, pp. 190–198. U.S. Department of the Interior, U.S. Forest Service, Ft. Collins, CO.

Henen, B. T., C. C. Peterson, I. R. Wallis, K. H. Berry, and K. A. Nagy. 1998. Effects of climatic variation on field metabolism and water relations of desert tortoises. Oecologia 117:365–373.

Holland, J. S. 1982. A floristic and vegetation analysis of the Newberry Mountains, Clark County, Nevada. Unpubl. master's thesis, Univ. of Nevada, Las Vegas.

Jacobson, E. R., J. M. Gaskin, M. B. Brown, R. K. Harris, C. H. Gardiner, J. L. Lapointe, H. P. Adams, and C. Reggiardo. 1991. Chronic upper respiratory tract disease of free-ranging desert tortoises (*Xerobates agassizii*). Journal of Wildlife Diseases 27:296–316.

Kaplan, E. L., and P. Meier. 1958. Nonparametric estimation from incomplete observations. Journal of the American Statistical Association 53:457–481.

KOUSKY, V. E., AND G. D. BELL. 2000. Causes, predictions, and outcomes of El Niño 1997–1998. *In* S. A. Changnon (ed.), El Niño 1997–1998: The Climate Event of the Century, pp. 28–48. Oxford Univ. Press, New York.

MEDICA, P. A., R. B. BURY, AND R. A. LUCKENBACH. 1980. Drinking and construction of water catchments by the desert tortoise, *Gopherus agassizii*, in the Mojave Desert. Herpetologica 36:301–304.

NAGEY, K. A., AND P. A. MEDICA. 1986. Physiological ecology of desert tortoises in southern Nevada. Herpetologica 42:73–92.

OFTEDAL, O. T., AND M. E. ALLEN. 1996. Nutrition as a major facet of reptile conservation. Zoo Biology 15:491–497.

PETERSON, C. C. 1994. Different rates and causes of high mortality in two populations of the threatened desert tortoise *Gopherus agassizii*. Biological Conservation 70:101–108.

———. 1996a. Ecological energetics of the desert tortoise (*Gopherus agassizii*): effects of rainfall and drought. Ecology 77:1831–1844.

———. 1996b. Anhomeostasis: seasonal water and solute relations in two populations of the desert tortoise (*Gopherus agassizii*) during chronic drought. Physiological Zoology 69:1324–1358.

POLLOCK, K. H., S. R. WINTERSTEIN, C. M. BUNCK, AND P. D. CURTIS. 1989. Survival analysis in telemetry studies: the staggered entry design. Journal of Wildlife Management 53:7–15.

SCHNEIDER, P. B. 1980. A comparison of three methods of population analysis of the desert tortoise, *Gopherus agassizi*. Proceedings of the Desert Tortoise Council Symposium 1980:156–162.

SCHUMACHER, I. M., D. B. HARDENBROOK, M. B. BROWN, E. R. JACOBSON, AND P. A. KLEIN. 1997. Relationship between clinical signs of upper respiratory tract disease and antibodies to *Mycoplasma agassizii* in desert tortoises from Nevada. Journal of Wildlife Diseases 33:261–266.

SMITH, S. D., R. K. MONSON, AND J. E. ANDERSON. 1997. Physiological ecology of North American deserts. Springer, New York.

TURNER, F. B., AND D. C. RANDALL. 1989. Net production by shrubs and winter annuals in southern Nevada. Journal of Arid Environments 17:23–36.

TURNER, F. B., P. A. MEDICA, AND C. L. LYONS. 1984. Reproduction and survival of the desert tortoise (*Scaptochelys agassizii*) in Ivanpah Valley, California. Copeia 1984:811–820.

U.S. FISH AND WILDLIFE SERVICE. 1994. Desert tortoise (Mojave population) recovery plan. U.S. Fish and Wildlife Service, Portland, OR.

VON ENDE, C. N. 2001. Repeated-measures analysis. *In* S. M. Scheiner and J. Gurevitch (eds.), Design and Analysis of Ecological Experiments, 2nd ed., pp. 134–157. Oxford Univ. Press, Oxford.

WHITE, G. C., AND R. A. GARROTT. 1990. Analysis of Wildlife Radio-Tracking Data. Academic Press, New York.

WOODBURY, A. M., AND R. HARDY. 1948. Studies of the desert tortoise, *Gopherus agassizii*. Ecological Monographs 18:145–200.

ZAR, J. H. 1984. Biostatistical Analysis. 2nd ed. Prentice-Hall, Emglewood Cliffs, NJ.

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