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Seasonal Variation in Survivorship and Mortality of Desert Tortoises in the Sonoran Desert, Arizona

J. Daren Riedle,[1] Roy C. Averill-Murray,[2] and David D. Grandmaison

Arizona Game and Fish Department, 5000 West Carefree Highway, Phoenix, Arizona 85086 USA

Abstract.—We determined annual survivorship and causes of mortality at two Desert Tortoise, *Gopherus agassizii*, study sites in the Sonoran Desert, Arizona, based on radio-telemetry data. Annual survivorship was high (89–97%), did not differ between sexes, and was comparable to previous studies using mark–recapture methods. Survivorship between sexes differed seasonally at one site, based on differences in seasonal activity patterns and differential exposure to predation by mountain lions, *Puma concolor*. In the absence of mammalian predation, seasonal survivorship did not differ between sexes. The next leading cause of mortality was failure to right oneself after a fall or after being flipped during reproductive or combat events.

Adult Desert Tortoises (*Gopherus agassizii*) are long-lived iteroparous organisms of the southwestern United States that may experience significant extrinsic sources of mortality throughout life (Boarman, 2002). Sources of mortality include predation (Woodbury and Hardy, 1948; Peterson, 1994; Kristan and Boarman, 2003), drought (Longshore et al., 2003), disease (Peterson, 1994; Berry, 1997), roads (Hoff and Marlow, 2002; Boarman and Sazaki, 2006), and off-highway vehicle activity (Bury and Luckenbach, 2002). Different activity cycles associated with reproduction between males and females may expose each sex to different levels of mortality at different times during the year. Female *G. agassizii* in both the Mojave and Sonoran Deserts in Arizona tend to exit hibernation earlier than males (Bailey et al., 1995; Martin, 1995), allowing foraging that is critical to the construction of a clutch (Averill-Murray, 2002). Summer rains increase movements and social behavior (courtship and mating) in both sexes, but males range over larger distances than females (Averill-Murray et al., 2002a). Therefore, females may experience relatively high mortality early in the year, whereas males may experience relatively high mortality during summer. Ultimately, detailed information on the differential mortality between sexes could aid in understanding sex ratios and demography of a population and differential costs of reproduction that shape life histories (Shine, 1980).

The species is broadly distributed, and it occupies a range of habitat types. Therefore, variation in mortality, between sexes within populations, and between populations might be expected. The goal of our study was to examine survival of *G. agassizii* in relation to seasonal activity patterns based on two long-term radio-telemetry projects in the Sonoran Desert, a region where *G. agassizii* survivorship has received relatively little study. By using known-fate survival models, we quantified mortality and identified causes of mortality in two populations of the Sonoran Desert Tortoise. We expected that females would have higher mortality than males during the spring (Bailey et al., 1995; Martin, 1995) but that males would have high mortality relative to females during summer (Averill-Murray et al., 2002b).

Materials and Methods

The Sugarloaf Mountain study site is located on the Tonto National Forest, Maricopa County, Arizona. The site was characterized by elevations of 549–853 m with steep, boulder-strewn slopes bisected by many arroyos. Vegetation was classified as palo verde-mixed cacti series of the Arizona Upland subdivision of the Sonoran Desert (Turner and Brown, 1982). The site was bordered on the east by a state highway, but this area was not frequently used by tortoises and human use was generally minimal.

The Florence Military Reservation (FMR) study site, 80 km southeast of metropolitan Phoenix, occurred within both the Arizona Upland and Lower Colorado River Valley subdivisions of the Sonoran Desert (Turner and Brown, 1982). Geomorphology was characterized by gently sloping to flat alluvial fans in the north that were filled by unconsolidated to weakly consolidated silts, sands, clay, and gravel. The alluvial fans were bisected by deeply incised washes on the eastern portion of the reservation. We followed tortoises in both more typical boulder habitat and along alluvial fans. Precipitation at both sites usually occurs in late summer and winter, separated by dry periods in the fall and spring. Because of military and recreational activities at the FMR site, anthropogenic impacts were much greater at FMR than at Sugarloaf.

We attached radio transmitters (<5% body mass; Advanced Telemetry Systems, AVM Instrument Co., Telonics, or Wildlife Materials) to the anterior carapace using epoxy. At Sugarloaf, we located tortoises at least once per week between 1991–93 and 1996–2005. At FMR, we located tortoises 2–3 times weekly throughout the year from 2000–07. We followed 32 females and 11 males at Sugarloaf and 16 females and 13 males at Florence for a total of 292 and 84 ''tortoise years,'' respectively. We defined a tortoise year as one tortoise tracked for a period of one year.

[1] Corresponding Author. Present address: Department of Life, Earth, and Environmental Sciences, West Texas A&M University, Canyon, Texas 79016 USA; E-mail: macrochelys@hotmail.com

[2] Present address: United States Fish and Wildlife Service, Desert Tortoise Recovery Office, 1340 Financial Boulevard #234, Reno, Nevada 89502 USA

TABLE 1. Comparison of Kaplan-Meier endpoint survival estimates and 95% confidence intervals for censored = live and censored = dead scenarios between sexes of Desert Tortoises at Sugarloaf and the Florence Military Reservation (FMR).

	Censored = Live		Censored = Dead	
	Survivorship	95% CI	Survivorship	95% CI
Sugarloaf				
All tortoises	0.96	0.94–0.98	0.94	0.92–0.97
Male	0.97	0.92–1.00	0.95	0.90–1.00
Female	0.96	0.93–0.99	0.94	0.90–0.97
FMR				
All tortoises	0.96	0.92–1.00	0.88	0.81–0.94
Male	0.97	0.92–1.00	0.88	0.79–0.98
Female	0.95	0.9–1.00	0.87	0.78–0.96

We estimated survival for radio-tagged animals using the Kaplan-Meier product limit method modified for staggered entry (Pollock et al., 1989). We recorded the fate of tortoises as live, dead, or censored (unknown fate attributed to transmitter failure or emigration out of the study site). Output in Kaplan-Meier can be described as either a ''best case'' or ''worst case'' scenario. Censored tortoises were considered to be alive in the best case scenario and dead in the worst case scenario. We analyzed the data using code from White and Garrott (1990) developed for SAS (SAS Institute, Inc., Cary, NC, 1989). We compared the shape of the curves using Chi-square integrated into code developed by White and Garrott (1990). Cause of death for all individuals was determined, when possible, by inspection of the carcass.

RESULTS

Annual survivorship was high at both sites, and annual survival did not differ between males and females at either site (Table 1). At Sugarloaf, however, the shape of the survival curves differed significantly between sexes ($\chi^2_{df = 1} = 15.5$, $P < 0.01$), because female mortality occurred earlier in the year than male mortality (Fig. 1A). Time of mortality did not differ between sexes at FMR ($\chi^2_{df = 1} = 0.2$, $P = 0.663$; Fig. 1B). Annual survival did differ between Sugarloaf and FMR when censored tortoises were considered dead (Table 1). The shape of the curves also differed ($\chi^2_{df = 1} = 21.4$, $P < 0.01$), as FMR tortoises exhibited mortality earlier in the year and overall higher mortality throughout the year (Fig. 1C).

We found the remains of 10 radio-tagged tortoises at Sugarloaf and determined probable cause of mortality for seven individuals. We found one individual wedged between two boulders, probably the result of a fall. One male and two females were found dead and lying on their carapaces, but we could not determine the causes of their deaths because of advanced decomposition. Six tortoises showed signs of predation, with Mountain Lion, *Puma concolor*, responsible for five of those based on canine marks on the shell and tracks in the vicinity of the carcass. All tortoises depredated by lions had up to two-thirds of the carapace removed by the lions. We found the sixth carcass missing its head and limbs but were unsure as to whether this was caused by predation or by a scavenging event. Actual annual mortality of radio-tagged individuals ranged from zero to three per year, and any year where mortality was >1 included at least one predation event by lions. All predation events occurred during the primary activity season for tortoises (spring and late summer), suggesting random encounters between tortoises and lions. Three mortalities, none with signs of predation, occurred at FMR within our telemetry group. Two were found on their carapaces (resulting from falls), whereas the third was upright and known to be declining in health prior to its death.

DISCUSSION

Desert Tortoises in the Sonoran Desert exhibit high adult survivorship based on two independent survival estimation techniques, mark–recapture (94–97%; Averill-Murray, 2002; Averill-Murray et al., 2002b) and radio telemetry (88–96%; this study). Although the magnitude of anthropogenic effects on survivorship is unclear, predation and accidental falls may account for most adult mortality. Annual survival did not differ between sexes at our sites, but sex-specific activity patterns as reported by Averill-Murray et al. (2002a) do appear to influence differential exposure to predation.

Other than predation, general accidents may actually be the other major cause of mortality. Activities such as courtship and male–male combat could lead to a tortoise being overturned (Allard, 1939; Ruby and Niblick, 1994; Dodd, 2001). The steep terrain inhabited by *G. agassizii* in the Sonoran Desert can also cause tortoises to simply ''fall down'' and Desert Tortoises may find themselves in life-threatening positions. Detection and recovery of telemetered individuals at FMR may have affected overall estimates of survival for that site. Desert tortoises at FMR rely heavily on deep caliche caves within incised washes as shelter sites (Riedle et al., 2008), which can dampen radio signals considerably. Should an animal retire to caliche cave as its transmitter expires, it then becomes lost to the researchers unless fortuitously found later. Our large number of censored tortoises at FMR (eight tortoises over six years) resulted in an 8% difference in annual survival between censored = live and censored = dead Kaplan-Meier models (Table 1).

Gopherus agassizii populations in Arizona are currently the focus of a collaborative inter-agency conservation effort (Howland and Rorabaugh, 2002). As part of those planning efforts, understanding

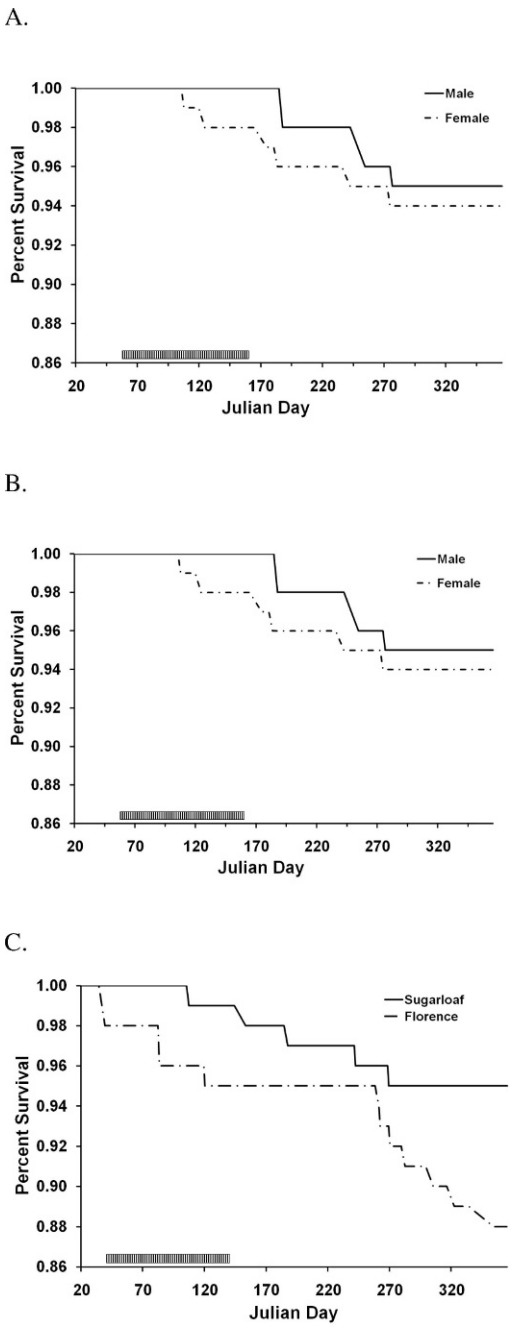

FIG. 1. Kaplan-Meier survival curves for Desert Tortoises in the Sonoran Desert, Arizona. All censored tortoises are assumed dead. Spring (March to June) indicated by bar above x-axis. (A) Male and female Desert Tortoises at the Sugarloaf study site. (B) Male and female Desert Tortoises at the Florence Military Reservation study site. (C) Comparison between the Sugarloaf and Florence Military Reservation study site.

factors influencing sex-specific mortality are of utmost importance. Results from these radio-telemetry studies will enable us to link previous studies on reproduction (Averill-Murray, 2002) and foraging (Oftedal, 2002), thus providing a more complete understanding of *G. agasszii* population dynamics in Arizona.

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