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Patterns of Burrow Use by Desert Tortoises (*Gopherus agassizii*) in Southcentral Nevada

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Abstract. – We monitored seasonal use of burrows and other cover by 113 radiomarked adult desert tortoises, *Gopherus agassizii*, at Yucca Mountain, Nevada, with 18,312 observations over 3 years. We found tortoises in burrows most often during the hottest and coldest months, and in pallets and away from cover most often during months with moderate temperatures. The number of burrows used annually (mean = 11.7, range = 4–23) differed among some years and differed between sexes in one year. Males and females used an average of 5 and 3 deep burrows (length > 1 m) per year, respectively. Tortoises used an average of 5 new burrows per year, which was, on average, 39 to 52% of the burrows used annually. Most new burrows (80%) were shallow (length < 1 m), which suggests a relatively high turnover of shallow burrows. Relative to females, males were observed in deep burrows more often, used a greater number of deep burrows, and were deeper in burrows. Males and females also used a different number of burrows and different types of cover during spring and fall. These seasonal differences probably were related to the annual reproductive cycle.

Key Words. – Reptilia; Testudines; Testudinidae; *Gopherus agassizii*; tortoise; ecology; behavior; burrows; thermoregulation; Nevada; USA

The desert tortoise (*Gopherus agassizii*) is found in parts of the Mojave and Sonoran deserts of North America and possesses numerous morphological, physiological, and behavioral characteristics advantageous for coping with the extreme temperatures, limited precipitation, and unpredictable availability of resources in this region (reviewed by Ernst et al., 1994). One important behavior exhibited by desert tortoises throughout most of their range is the use of burrows to avoid high temperatures during summer and low temperatures during winter (Woodbury and Hardy, 1948; McGinnis and Voigt, 1971; Zimmerman et al., 1994). Burrows also are important locations for social interactions, refuges from predators, and places to lay eggs (Ernst et al., 1994).

Because burrows are important for the survival of desert tortoises, understanding patterns of burrow use provides insight into the ecology of this species. Information on differences in depth and types of burrows used across the range of this species can further our understanding of how tortoises cope with variations in environmental conditions on spatial and temporal scales (e.g., Auffenberg and Weaver, 1969; Germano et al., 1994). Differences between males and females in the types of burrows used and their seasonal patterns of burrow use will help describe differences between sexes in habitat requirements and activity patterns. Also, because burrows are relatively persistent sign of tortoises, abundance of burrows and other sign has been used to estimate tortoise abundance (Luckenbach, 1982; Berry, 1986b). Thus, information on the number and variability of burrows used by tortoises could improve these estimates. Additionally, understanding burrow use may assist in conservation of desert tortoises. For example, if the availability of deep burrows limits the abundance of tortoises in an area (Woodbury and Hardy, 1948; Luckenbach, 1982), the loss of these resources to construction, livestock grazing, or off-road vehicles may jeopardize the existence or recovery of the species in those areas.

Desert tortoises have been studied extensively (Germano and Bury, 1994). However, relatively few studies have quantified burrow use, and most were either based on small sample sizes (Burge, 1978; Barrett, 1990; Bailey et al., 1995; Duda et al., 1999), penned animals (Nagy and Medica, 1986; Bulova, 1993), or of limited duration (Bulova, 1994; Bailey et al., 1995). We studied patterns of burrow use during three years by > 50 adult (i.e., > 180 mm carapace length) desert tortoises per year at Yucca Mountain, Nevada. Here we examine seasonal use of burrows and pallets (i.e., non-burrow cover) by adult desert tortoises; determine the number and types of burrows used annually; and examine differences in cover use among sexes, seasons, and years.

METHODS

Study Area. — Yucca Mountain (36°50'N, 116°25'E) is in Nye County, Nevada, approximately 150 km north of Las Vegas, and along the northern edge of the range of the desert tortoise (Bury et al., 1994). We studied tortoises that occupied the east side of Yucca Mountain and the alluvial fans of the adjacent Calico Hills at elevations of 950 to 1510 m; most tortoises monitored occupied elevations of 1000–1300 m.

The abundance of tortoises there is low relative to many areas in Nevada and California (Rautenstrauch and O'Farrell, 1998).

Soils were derived primarily from volcanic material and generally were secondarily calcareous, moderately alkaline, and well drained. On ridge crests and hill summits, soils generally were less than 0.25 m deep and situated on a thin caliche hardpan over bedrock. Textures were gravelly to cobbly with sands and sandy loams. The surface was dominated by large rocks. Soils on piedmonts and in canyons were moderately deep to deep above a caliche hardpan. These soils contained calcareous eolian sand and were sandy loams with a high proportion of rock fragments. Soils on alluvial fans were thick fine sands and sandy loams with abundant rock fragments.

Yucca Mountain is in a region of transition between the Mojave and Great Basin deserts. Two major floristic zones occurred in the study area. Vegetation was dominated by Mojave Desert plant communities below approximately 1200 m and by transitional plant communities having a mix of Mojave and Great Basin desert floras at higher elevations (Beatley, 1974, 1975). The most abundant shrubs in the area were creosotebush (*Larrea tridentata*), white bursage (*Ambrosia dumosa*), Anderson desert thorn (*Lycium andersonii*), blackbrush (*Coleogyne ramosissima*), and Nevada ephedra (*Ephedra nevadensis*).

From 1960 to 1995, average annual precipitation 13 km southeast of the study area was 13.9 cm (U.S. Department of Energy, unpubl. data). From 1986 to 1994, average daily minimum and maximum temperatures were 2 and 10°C, respectively, during December and 22 and 34°C, respectively, during July.

Methods. — Beginning in 1989, we radiomarked and monitored tortoises as part of a program to evaluate the impacts of U.S. Department of Energy activities on desert tortoises (Rautenstrauch et al., 1991). Most data reported here were from observations of adult tortoises during January 1992 through February 1995, when the greatest numbers of tortoises were located most frequently. We glued radiotransmitters, limited to < 4% of tortoise body weight, to the first pleural scute of females and the fourth pleural scute of males. We determined gender using external morphological characteristics (Woodbury and Hardy, 1948), or plasma testosterone levels (Rostal et al., 1994a).

We usually located radiomarked tortoises weekly or biweekly while they were hibernating (generally late October through early March [Rautenstrauch et al., 1998]), and twice per week thereafter. Approximately 25% of our observations were made during the four hours after sunrise, 25% during the four hours before sunset, and 50% during the remainder of the day. Each time we observed a tortoise, the type of cover it was using was classified as a burrow (underground chamber deeper than the length of the tortoise), a pallet (excavation less than the length of the tortoise, or a plant, rock, or other structure providing partial to complete concealment), or none (i.e., tortoise away from any cover). We tagged all burrows with a unique number, which was recorded each time a tortoise was found in that burrow, and measured the depth from the entrance to the end of the tunnel using a tape measure. We classified burrow depth as deep (depth > 1 m), shallow (depth < 1 m), or unknown (generally because a tortoise was blocking the burrow). We classified structures directly above each burrow entrance as shrub, caliche, boulder (rock > 1 m wide), none, or other. Each time we found a tortoise in a burrow during 1994, we measured the distance from the entrance of the burrow to the tortoise, or if the tortoise could not be seen, we measured the distance to the deepest observable point (the minimum depth).

Statistics. — To examine temporal and gender differences in use of cover types, we summed all observations of tortoises by sex, season, and year from March 1992 through February 1995 in each of four types of cover: deep burrow, shallow burrow, pallet, and no cover (burrows of unknown depth were recorded too infrequently to analyze). We classified seasons as winter (November–February), spring (March–May), summer (June–August), and fall (September–October). The resulting four-way contingency table (three years, four seasons, two sexes, and four cover types) was examined using hierarchical χ^2 tests (Fienberg, 1977; SYSTAT, 1992; Sokal and Rohlf, 1995). For three-way interactions that were significant, we analyzed separate three-way contingency tables by summing across non-significant factors. We also selected and analyzed some significant two-way interactions using two-way contingency tables to further clarify patterns. This hierarchical analysis resulted in about 100 χ^2 tests, so we used a Bonferoni-adjusted α of 0.0005 (0.05/100) to control the experiment-wise error rate (Rice, 1989).

We counted the number of burrows used per season and year by each tortoise as well as the number of new burrows (i.e., burrows in which an individual had not been found previously) used per tortoise annually. These counts were influenced by the number of times a tortoise was observed while out of hibernation (i.e., the active period), and counts of the number of new burrows used also was influenced by the number of times a tortoise was observed during previous years. Therefore, we used locally-weighted regression analysis (SYSTAT, 1992; Trexler and Travis, 1993) to calculate a best-fit curve of number of times located per active period and number of burrows used per tortoise. That curve reached an asymptote at about 50–60 active-period observations, indicating that 50 or more locations were required to achieve burrow-use estimates that were not influenced by the number of observations. Thus, we report number of burrows used per season and per year only for tortoises observed ≥ 50 times during an active period.

Similarly, we used locally-weighted regression analysis to evaluate the relationship between number of times a tortoise was located in previous years (to find previously used burrows) and number of new burrows it used in a year. That curve reached an asymptote at about 100 locations, indicating that an unbiased estimate of number of new burrows used during a year could only be determined for tortoises that had been located at least 100 times during the active periods of previous years. Thus, to estimate the number of new burrows used during a year, we used data only from tortoises located ≥ 50 times during the active period of that year and ≥ 100 times during the previous two or more active periods. Because many tortoises included in this study were first radiomarked in 1991, we estimated the number of new burrows used only for 1993 and 1994.

Annual estimates of burrow use were not independent because most tortoises were monitored in two or more years; therefore, we conducted separate t-tests for each year to examine differences between sexes in number of burrows, deep burrows, and new burrows used annually. To test for differences among years, we used repeated-measures analysis of variance on the subset of tortoises observed ≥ 50 times during all years; univariate tests were used for post-hoc comparisons between years, with α adjusted to 0.017 (0.05/3). Differences in the number of burrows used per season by males and females were assessed separately each year using repeated-measures analysis of variance, with season as the repeated factor. Because seasons differed in length, number of burrows used was divided by the number of months in each season. In all of these tests, we transformed the number of burrows used by the power of 0.75 to achieve normality and homogeneity of variances.

Measurements of the minimum depth of tortoises in burrows during 1994 were square-root transformed and we used analysis of variance to test differences in depth among sexes and seasons. The Tukey test (Sokal and Rohlf, 1995) was used for post-hoc comparisons among seasons.

RESULTS

We observed 113 adult desert tortoises 18,312 times from January 1992 through February 1995. These tortoises used 1558 burrows, of which 21.0% were deep, 70.2% were shallow, and 8.8% were of unknown depth. Deep burrows generally were under boulders (50.8%), caliche (25.7%), or shrubs (13.3%), although 9.2% were in the open and 1% were classified as other. Deep burrows were located throughout the study area, but tended to be under caliche or shrubs at lower elevations and under boulders on slopes and ridge tops. Most shallow burrows were under shrubs (51.4%), boulders (26.3%), or no structure (18.5%), but 2.0% were under caliche, and 1.8% were other.

Use of Cover. — We observed tortoises in burrows least often during April (29% of observations, years combined, Fig. 1). Use of burrows increased gradually from May (39%) through July (85%) and August (82%), and then decreased slightly in September (69%). From May through September, we found tortoises more often in shallow burrows than in deep burrows. Use of burrows, especially deep ones, then increased in October as tortoises began hibernating. During November–February, tortoises were found most often (74%) in deep burrows and were rarely found out of burrows (< 2%). We found tortoises in pallets most often during April (41%) and May (37%). We also found tortoises away from cover most often during April (30%) and May (25%), and we never found them away from cover during December–February (Fig. 1).

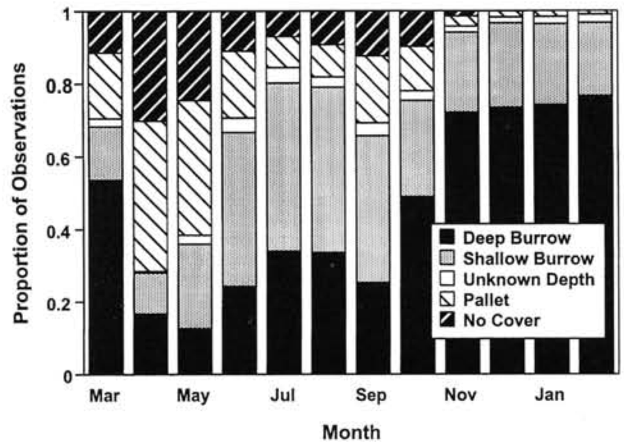

Figure 1. Proportion of observations of adult desert tortoises using different types of cover each month at Yucca Mountain, Nevada. Observations were summed over years, January 1992 – February 1995 (n = 18,312 observations).

Contingency table analysis revealed that sexes differed in use of cover, and that seasonal use of cover differed among years. The four-way interaction and two of the three-way interactions were not significant (Table 1). Season by year by sex was nonsignificant and was influenced solely by sampling efforts because it did not include the dependent variable of cover type. Non-significance of cover type by year by sex indicates that differences in cover use by sexes was independent of years and that differences in cover use among years was independent of gender.

The significant three-way interaction of cover type by season by sex (Table 1) indicates that males and females used cover differently within years. We found males in deep

Table 1. Results of hierarchical χ^2 tests of annual (1992–94) and gender differences in the use of four types of cover by desert tortoises at Yucca Mountain, Nevada. Only those individual components that contributed significantly ($p < 0.0005$) to interactions are shown ("+" = greater than expected use of a cover type, "–" = less than expected use).

Interaction Significant components	χ^2	df	p
Cover Type x Season x Year x Sex	14.88	18	0.670
Season x Year x Sex	29.44	24	0.204
Cover Type x Year x Sex	23.69	24	0.479
Cover Type x Season x Sex	185.21	27	<0.0001
+ Deep Burrows/Spring/Males	20.76	1	<0.0001
– Deep Burrows/Spring/Females	22.99	1	<0.0001
+ No Cover/Fall/Males	28.43	1	<0.0001
– No Cover/Fall/Females	25.43	1	<0.0001
Cover Type x Sex	417.83	3	<0.0001
+ Deep Burrows/Males	96.89	1	<0.0001
– Deep Burrows/Females	82.10	1	<0.0001
– Shallow Burrows/Males	128.98	1	<0.0001
+ Shallow Burrows/Females	109.30	1	<0.0001
Cover Type x Season x Year	129.78	36	<0.0001
+ Pallets/Summer/1992	13.07	1	0.0003
– Pallets/Summer/1994	21.38	1	<0.0001
Cover Type x Year	87.74	6	<0.0001
– Pallets/1992	20.92	1	<0.0001
+ Pallets/1993	34.40	1	<0.0001

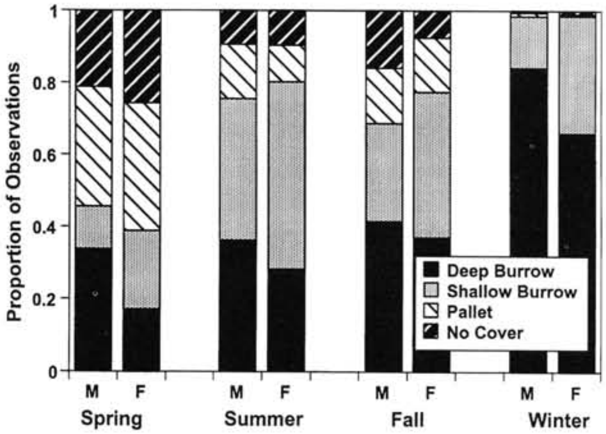

Figure 2. Proportion of observations of male and female desert tortoises using different types of cover each season at Yucca Mountain, Nevada. Observations were summed over years, 1992–94 (males, n = 8212; females, n = 9780).

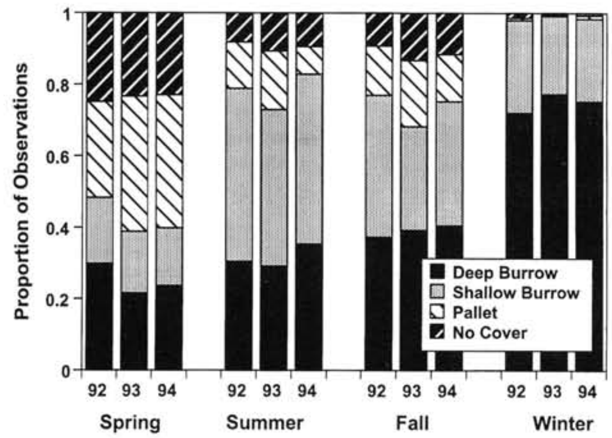

Figure 3. Proportion of observations of adult desert tortoises using different types of cover during each season and year, 1992–94, at Yucca Mountain, Nevada (1992, n = 5591; 1993, n = 6338; 1994, n = 6063).

burrows more often than females during all seasons (Fig. 2), but during spring, use of this cover type was disproportionately high by males and low by females (Table 1). In contrast, during fall, less than expected use of deep burrows by males ($\chi^2 = 8.14$, $p = 0.004$) and more than expected use by females ($\chi^2 = 9.98$, $p = 0.016$) approached significance. Also during fall, males were away from cover more often, and females less often, than expected (Table 1).

The types of burrows used by males and females also differed irrespective of season, as indicated by the significant two-way interaction of cover type by sex (Table 1). Males were more likely (44.2% of 8212 observations), and females less likely (31.6% of 9780 observations), to be found in deep burrows. In contrast, females were more likely to be found in shallow burrows (36.2%) than males (23.7%). The proportion of times males and females were found in pallets (16.9 and 17.6%, respectively) and away from cover (12.3 and 12.4%, respectively) were relatively equal. Although males at Yucca Mountain were, on average, about 20 mm longer than females (Lederle, 1999), differences in use of deep burrows probably were not caused by difference in size between genders (e.g., longer males not fitting into shallower burrows) because only burrows > 1 m long were classified as deep.

Cover use among years generally was similar (Fig. 3). The significant three-way interaction of cover type by season by year was primarily the result of greater than expected use of pallets during the summer of 1992 and less than expected use of pallets during the summer of 1994 (Table 1). Greater than expected use of deep burrows during the spring of 1992 ($\chi^2 = 8.12$, $p = 0.0044$) and less than expected use of pallets during spring 1994 ($\chi^2 = 10.96$, $p = 0.0009$) contributed to a lesser extent.

When summed across seasons, use of cover types was similar among years except for relatively small differences in use of pallets. The significant cover type by year interaction (Table 1) was the result of less than expected use of pallets during 1992 (15.4% of 5591 observations) and greater than expected use during 1993 (21.3% of 6338 observations). Use of pallets during 1994 (17.2% of 6063 observations) was not different from expected. The annual proportion of times tortoises were found in shallow burrows (1992 = 32.8%, 1993 = 28.8%, 1994 = 31.3%), deep burrows (1992 = 39.8%, 1993 = 37.4%, 1994 = 38.9%), and away from cover (1992 = 11.9%, 1993 = 13.4%, 1994 = 12.6%) were similar. Thus, tortoises were observed in burrows most often during 1992 (72.6% of all observations, including observations of tortoises in burrows of unknown depth), less often in 1994 (70.2%), and least often in 1993 (65.7%).

Number of Burrows Used. — Tortoises used an average of 11.7 burrows per year (SE = 0.28, range = 4–23, n = 179 sets of annual observations). Most tortoises (90%) used 7 to 17 burrows per year. Differences in the average number of burrows used per year by males and females were small, and were significant only in 1992, when males used an average of 2.2 more burrows than did females (Table 2). Based on 19 males and 22 females located ≥ 50 times in all three years, the number of burrows used differed among years ($F_{2,78} = 3.31$, $p = 0.042$). Post-hoc univariate comparisons among years revealed that the number of burrows used in 1992 ($\bar{x} = 12.6$, SE = 0.58) differed ($p = 0.007$) from the number used in 1994 ($\bar{x} = 11.2$, SE = 0.50). Burrow use in 1993 ($\bar{x} = 12.0$, SE = 0.63) did not differ ($p \geq 0.23$) from other years.

The number of deep burrows used differed between sexes in all years (all $p < 0.008$) but did not differ among

Table 2. Average number of burrows used by adult desert tortoises at Yucca Mountain, Nevada, during 1992 through 1994, and t-tests of differences between sexes annually. Number of burrows used annually was transformed to the power of 0.75 for analysis.

			Number of burrows used				
Year	Gender	n	$\bar{x}$	SE	Range	t	p
1992	Male	25	13.5	0.62	8–19	-2.24	0.029
	Female	27	11.3	0.78	4–22		
1993	Male	29	12.4	0.77	6–22	-0.73	0.466
	Female	33	11.7	0.67	7–23		
1994	Male	30	11.1	0.58	6–18	-0.53	0.599
	Female	35	10.7	0.57	6–20		

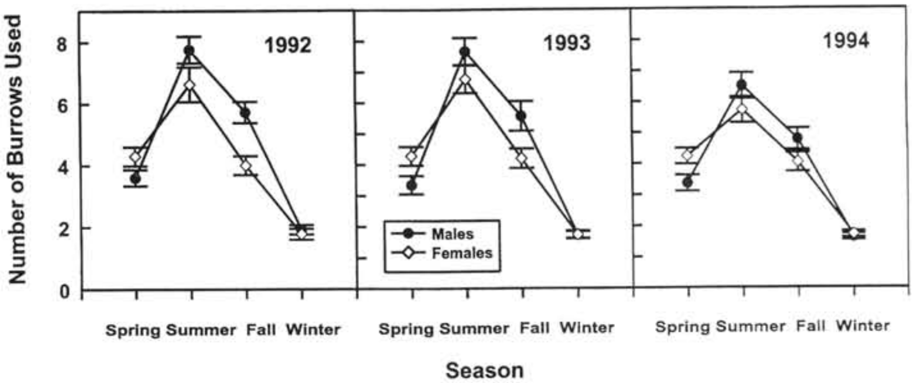

Figure 4. Average number of burrows used seasonally (± SE) by adult male and female desert tortoises at Yucca Mountain, Nevada, 1992–94.

years ($F_{2,78} = 0.36$, $p = 0.699$). Males used an average of 4.9 deep burrows (SE = 0.32, range = 0–13, $n = 84$ sets of annual observations) and females used an average of 3.0 deep burrows (SE = 0.21, range = 0–12, $n = 95$ sets of annual observations) per year. An average of 39% (SE = 2, range = 0–90%) and 27% (SE = 2, range = 0–75%) of the burrows used annually by individual males and females, respectively, were deeper than 1 m. Sixteen percent of tortoises used < 2 deep burrows in a year; most (80%) used 2 to 9.

The seasonal pattern of burrow use by males and females was similar among years (Fig. 4). In all years there was a significant season by sex interaction (all $p < 0.006$), resulting from females using more burrows than males during spring and males using more burrows than females during summer and fall. The within-subjects effect due to season (i.e., difference in number of burrows used per season) also was significant in all years (all $p < 0.001$). The average number of burrows used per season was lowest during winter and highest during summer. The between-subjects effect of gender (i.e., difference in number of burrows used by males and females) was significant in 1992 ($F_{1,50} = 5.92$, $p = 0.018$), but not in 1993 ($F_{1,60} = 1.56$, $p = 0.217$) or 1994 ($F_{1,63} = 0.51$, $p = 0.479$). The difference in 1992 was due primarily to males using more burrows than females during summer and fall.

Number of New Burrows Used. — Tortoises used an average of 4.8 new burrows each year (SE = 0.33, range = 1–15, $n = 68$ sets of annual observations). Only two tortoises used more than 9 new burrows in a year. The average number of new burrows used did not differ by gender in 1993 (t = -0.36, df = 18, $p = 0.639$) or 1994 (t = -0.79, df = 46, $p = 0.432$). However, the number of new burrows used by a subset of 18 tortoises (that were repeatedly measured a sufficient number of times during both years) differed between years ($F_{2,16} = 4.2$, $p = 0.048$). These tortoises used more new burrows in 1993 ($\bar{x} = 6.2$, SE = 0.76) than in 1994 ($\bar{x} = 4.8$, SE = 0.56). Averages of 52% (SE = 4%, range = 15–90%) and 39% (SE = 3%, range = 10–90%) of burrows used by these tortoises in 1993 and 1994, respectively, were new. These 18 tortoises were located 100–221 times prior to 1993 and 153–301 times prior to 1994.

Tortoises used an average of 1.0 (SE = 0.12, range = 0–4, $n = 68$ annual observations) new deep burrows per year. This was an average of 21% (SE = 3%, range = 0–100%) of new burrows and 9% (SE = 1%, range = 0–40%) of all burrows used per tortoise annually. The number of new deep burrows did not differ between sexes in 1993 (t = -0.68, df = 18, $p = 0.505$) or 1994 (t = -0.19, df = 46, $p = 0.852$) or between years ($F_{1,16} = 0.97$; $p = 0.347$).

Depth in Burrows. — The minimum depth that tortoises were in burrows during 1994 (the only year we measured depth in burrows) differed between sexes ($F_{1,3970} = 94.56$, $p < 0.001$) and seasons ($F_{3,3970} = 72.13$, $p < 0.001$). The interaction of sex by season also was significant ($F_{3,3970} = 15.27$, $p < 0.001$), indicating that relative differences in burrow depth between sexes varied seasonally. On average, males were deeper in burrows than females during spring (males: $\bar{x} = 87$ cm; females: $\bar{x} = 51$ cm), and less so during summer (males: $\bar{x} = 67$ cm; females: $\bar{x} = 51$ cm) and fall (males: $\bar{x} = 76$ cm; females: $\bar{x} = 66$ cm). Average minimum depth in burrows differed little during winter (males: $\bar{x} = 89$ cm; females: $\bar{x} = 85$ cm). Average minimum depth in burrows during winter and fall differed from other seasons (Tukey test, $p < 0.001$); the difference between spring and summer approached significance ($p = 0.062$).

DISCUSSION

Cover use by tortoises at Yucca Mountain generally followed the annual cycle of temperatures, although numerous differences in burrow use by males and females indicate that nutritional, reproductive, or other requirements influence their use of cover. Tortoises at Yucca Mountain use a relatively large number of burrows each year, including at least a few new burrows and deep burrows; therefore, burrows may not be a limiting factor in this population.

Annual Pattern of Cover Use. — We observed tortoises in burrows most often during the coldest and hottest months (Fig. 1), and in pallets or in the open most often when temperatures were moderate. This annual pattern is consistent with the assertion that burrows play a key role in behavioral thermoregulation by desert tortoises (McGinnis and Voigt, 1971; Zimmerman et al., 1994). This pattern also is similar to previous reports (Woodbury and Hardy, 1948; Burge, 1978; Nagy and Medica, 1986; Barrett, 1990; Bulova, 1994; Bailey et al., 1995), with the following two exceptions. First, tortoises in the Picacho Mountains, Arizona, used deeper burrows during summer than during other seasons (Barrett, 1990). In contrast, tortoises in our study at Yucca Mountain, Nevada, were deeper in burrows and were found in burrows > 1 m deep most often during winter, possibly because of the colder winter temperatures at Yucca Mountain. Second, tortoises at Arden, Nevada, used pallets most often during July (Burge, 1978), whereas our study animals used pallets most often during April and May. Less frequent use of pallets during spring at Arden may have resulted from cooler than normal spring temperatures during that study (Burge, 1978).

Tortoises at Yucca Mountain were found in burrows more often (Fig. 2) and used more burrows during summer than winter or fall (Fig. 4). This indicates that, although tortoises spent less time above ground during summer, they continued to move among burrows during that season.

Number of Burrows Used. — The number of burrows used each year ranged from 4 to 23, differed among sexes and years during part of the study (Table 2), and generally was similar to or greater than that reported elsewhere. Six desert tortoises at Arden, Nevada, used 11 to 20 burrows ($\bar{x} = 16.0$) during 13 months (Burge, 1978). Near Las Vegas, Nevada, 28 tortoises used 3 to 18 burrows and pallets ($\bar{x} = 9.1$) during June–October (Bulova, 1994). In southeastern Arizona, where desert tortoises are genetically and behaviorally different from those in Nevada (Ernst et al., 1994), 14 tortoises used 5 to 14 burrows ($\bar{x} = 7.6$) during 18 months (Barrett, 1990). At two locations in California where 29 and 9 tortoises were monitored, significantly more burrows were used during a productive year (males: $\bar{x} = 6.9$ and 13.8 at the two sites; females: $\bar{x} = 6.2$ and 11.6) than during a drought year (males: $\bar{x} = 3.8$ and 4.8; females: $\bar{x} = 3.1$ and 4.4) (Duda et al., 1999).

Tortoises at Yucca Mountain used 1 to 15 new burrows per year. The relatively high average proportion of new burrows used each year, 52% in 1993 and 39% in 1994, suggests that turnover and replacement of burrows is common. About 80% of the new burrows were < 1 m deep, suggesting that tortoises find or dig new shallow burrows more often than they find or dig new deep burrows. This probably was because most (70%) shallow burrows were under shrubs or in the open and therefore more likely to collapse than deeper burrows, 76% of which were under caliche or boulders. About half of the shallow burrows at Arden, Nevada, collapsed during one year (Burge, 1978), and Woodbury and Hardy (1948) stated that the shallow "summer holes" in southern Utah tended to collapse due to rain and rodent activity. Nagy and Medica (1986) reported that 11 tortoises within an enclosure excavated 68 new burrows during 15 months, mainly because many previously used burrows had collapsed due to rodent activity during winter.

The difference in the number of new burrows used in 1993 ($\bar{x} = 6.2$) and 1994 ($\bar{x} = 4.8$) may have resulted from tortoises having to replace more burrows after a wet winter (precipitation from November 1992 to February 1993 = 22.6 cm) than after a drier winter (November 1993 to February 1994 = 5.9 cm). Alternatively, this difference may have been due to tortoises having been located too infrequently prior to 1993 to find all old burrows, although we controlled for not finding all previously used burrows by considering only those tortoises observed ≥ 100 times in previous years.

Differences Between Sexes. — We found males deeper in burrows, using more deep burrows, and in deep burrows more often than females. These differences may have been due to thermoregulatory strategies or avoidance behavior. Bailey et al. (1995) speculated that female tortoises in Arizona may use shallow hibernacula so they can warm up and emerge from hibernacula earlier in the spring to begin acquiring nutritional resources needed to develop eggs. They also suggested that the cooler and more constant temperatures in deeper burrows used by males might help maintain normal testicular function and prevent sterility. Females at Yucca Mountain may have been shallower in burrows during spring and early summer to find warmer microhabitats and increase the rate of development of eggs prior to oviposition, although no data have been reported on optimal temperatures or thermoregulatory strategies for maximizing rate of egg development within female desert tortoises (Huey, 1982). Differences between sexes also may have been caused by females avoiding burrows occupied by courting males. Additional research is needed to test these possibilities and examine their causes.

The trend for males to be deeper in burrows and use deep burrows more often than females was most obvious in spring and less obvious in fall. During spring, we found females in deep burrows less often than expected. We also found females in shallow burrows and away from cover more often than males (Fig. 2), although these differences were not significant. In addition, the average number of burrows used by females during spring was larger than that of males (Fig. 4). This seasonal pattern appeared to be related, in part, to the annual reproductive cycle. Females lay eggs from May through early July, usually in or near the opening of burrows (Turner et al., 1986; Roberson et al., 1989; Rautenstrauch et al., unpubl. data). Thus, some differences may have been the result of females moving among burrows to find suitable nest sites. Also, differences may have been due to females foraging earlier or more often in the spring than males in order to meet the increased nutritional demands of egg production. However, no data have been presented to suggest that females spend more time foraging than males during spring. The greater number of times we observed males in deep burrows during spring likely was due in part to males exiting these hibernacula later than females (Rautenstrauch et al., 1998).

During fall, we found males away from cover more often than expected and in deep burrows slightly less often than expected. On average, males also used more burrows than females during fall. Most courtship behavior at Yucca Mountain was observed from mid-August through early October (Rautenstrauch et al., unpubl. data) and Rostal et al. (1994b) reported that testosterone levels peak in males during that period. Therefore, males may have been moving about (i.e., away from cover) and investigating more burrows during fall because they were seeking females. Berry (1986a) noted that male desert tortoises traveled to burrows used by females during the breeding season to court and mate. Near Las Vegas, Bulova (1994) observed that female desert tortoises used more shelters (burrows and pallets) and switched between them more than males during June, and that males used more shelters and switched between them more than females during August and September. Bulova (1994) attributed these differences to nesting and breeding activities. Differences between males and females during fall at Yucca Mountain also may have been caused in part by males entering hibernacula slightly later than females (Rautenstrauch et al., 1998).

Differences Among Years. — The pattern of burrow use generally was similar among years and the few significant differences we found were relatively small. For example, when cover use was summed across seasons, the only significant difference was a 6% increase in use of pallets from 1992 to 1993. The number of burrows used in 1992 and 1994 differed significantly, but the average difference of 1.4 burrows was small relative to the total number of burrows used.

Duda et al. (1999) reported that desert tortoises at two locations in California used approximately twice as many burrows in a productive year than during a year of drought. The few differences among years noted at Yucca Mountain do not appear to have been influenced by fluctuations in rainfall or forage production. Precipitation during 1992 (26.9 cm) and 1993 (26.6 cm) was about twice the long-term average (13.9 cm) and the timing of precipitation was similar in both years. Production of annual plants, sampled on 12 4-ha plots located throughout the study area, also was high both years (43 and 35 g/m^2, respectively [U.S. Department of Energy, unpubl. data]). Precipitation during 1994 (11.7 cm) was about half that of 1992 and 1993, and forage production was about 4 g/m^2. Therefore, if differences among years were directly influenced by precipitation or forage production, it would be expected that 1992 and 1993 would be similar, and 1994 different. However, none of the parameters we measured fit this pattern. For example, the proportion of times we found tortoises in burrows during 1994 was intermediate between that of 1992 and 1993 and the number of burrows used differed between 1992 and 1994, but 1993 did not differ from either year. It is likely that conditions in 1994 were not different enough to cause tortoises to change their burrow-use patterns.

Conservation Implications. — Woodbury and Hardy (1948) suggested that the availability of deep burrows limits the abundance of desert tortoises along the northern edge of this species' range; thus, loss of burrows from grazing, off-road driving, or other activities could detrimentally affect tortoise populations (but see Lovich and Daniels, 2000). While this may be true for other populations, tortoises at Yucca Mountain used a relatively large number of burrows each year, many of which they had not used in previous years of this study. Most tortoises (80%) used two or more deep burrows, although 4% were not observed using any deep burrows. Many burrows, especially shallow burrows, collapse naturally each year from weather or rodents (Woodbury and Hardy, 1948; Burge, 1978; Nagy and Medica, 1986), further indicating that tortoises normally must find or dig new burrows each year. This suggests that the loss of a few burrows, even deep burrows, may not have serious detrimental effects on the Yucca Mountain population because other burrows appear to be available, and burrows are replaced at a relatively high rate. However, it is possible that burrows with characteristics not considered in this study (e.g., extremely long burrows or burrows suitable for digging nest chambers) may be rare or difficult to replace. Thus, efforts should be made to protect burrows from destruction when possible.

Accurately monitoring changes in the abundance of desert tortoises has been identified as a critical management need for this species (U.S. Fish and Wildlife Service, 1994). Counts of tortoise burrows along transects or within plots, often in combination with counts of other sign (e.g., scat, carcasses), have been used to predict the absolute or relative density of populations of desert tortoises (Luckenbach, 1982; Berry, 1986b), as well as gopher tortoises (*Gopherus polyphemus*) (Burke and Cox, 1988). To compare counts of burrows among areas or through time, it must be assumed that the relationship between number of burrows and number of tortoises is constant among locations and periods compared. The results of this and other studies (e.g., Freilich et al., 2000) indicate that this assumption may not be valid. For example, tortoises at Yucca Mountain used more burrows than reported from some other areas (potentially inflating population estimates) and burrow use varied seasonally between males and females (creating seasonal variance in population estimates). Although differences among years were small in this study, at least one other study has reported a 50% decrease in the number of burrows used during a drought year (Duda et al., 1999). Such differences would result in yearly variance in population estimates. Therefore, counts of burrows must be considered as both site- and year-specific to be precise, and if conversion factors (i.e., number of burrows per tortoise) are not locally derived, then one must acknowledge and estimate potential sources of variance in the estimates of population size that are in addition to those associated with the population-estimate model used.

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