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Reproduction in a Desert Tortoise (*Gopherus agassizii*) Population on the Beaver Dam Slope, Washington County, Utah

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ABSTRACT. – Life history information including clutch size, clutch frequency, annual fecundity, egg dimensions, hatchling success, and home range size was collected in 1989 from the Beaver Dam Slope desert tortoise population, in southwestern Utah. The mean clutch size for both first and second clutches was 5.2 ± 0.50 eggs (n = 16). Mean clutch size of the first and second clutches did not significantly differ. Mean clutch frequency was 1.33 ± 0.14 clutches per reproductive female (n = 12). Carapace length was significantly correlated with mean clutch size and clutch frequency. Annual fecundity of tortoises ranged from 3 to 18 eggs. Mean annual fecundity was 7.0 ± 1.16 eggs and was significantly correlated with carapace length (n = 12). Carapace length was significantly correlated with egg width but not egg length. Reproductive tortoises had a smaller home range than non-reproducing tortoises; however, this difference was not significant. Compared with other Mojave desert tortoise reproductive studies, the Beaver Dam Slope population had a lower clutch frequency and percentage of reproducing females. In the past decade, the Beaver Dam Slope has experienced dramatic population declines due primarily to disease and habitat degradation and alteration.

KEY WORDS. – Reptilia; Testudines; Testudinidae; *Gopherus agassizii*; tortoise; reproduction; annual fecundity; clutch frequency; clutch size; egg length; egg width; hatching success; hatchling; Beaver Dam Slope; Utah; USA

Knowledge of a species' life history characteristics is fundamental to understanding the demographics of a population. Those traits associated with reproduction are critical to the long term success of a species (Gibbons and Greene, 1990). Chelonians have evolved several life history strategies to maximize their reproductive output, including longevity, delayed sexual maturity, low reproductive rate, and iteroparity, that is, repeated cycles of reproduction (Congdon and Gibbons, 1990a). Available life history information associated with desert tortoise (*Gopherus agassizii*) reproduction has been limited to several sites within the western Mojave (Wallis et al., 1999), eastern Mojave (Turner et al., 1984, 1986; Karl, 1998; Wallis et al., 1999), and northern Mojave Desert (Mueller et al., 1998), as well as a single locality within the Sonoran desert (Murray et al., 1996). Reproductive characteristics have not yet been reported for the Beaver Dam Slope population, Utah, at the northeastern extent of the desert tortoises' range.

In 1980, the Beaver Dam Slope tortoise population in southwestern Utah was listed as threatened under the U.S. Endangered Species Act of 1973, as amended (USFWS, 1980). In 1990, the entire Mojave population north and west of the Colorado River was listed as threatened (USFWS, 1990). Reasons for the declines of Mojave populations were attributed to habitat degradation and loss, collection for pets or other purposes, predation, disease, as well as the inadequacy of existing regulatory mechanisms to protect desert tortoises and their habitat (USFWS, 1994).

The objective of this study is to report baseline life history information from the Beaver Dam Slope desert tortoise population. This study focused on reproductive characteristics, including oviposition dates, clutch size and frequency, annual fecundity, egg dimensions, hatchling success, as well as home range. An understanding of life history parameters related to reproduction will assist management and conservation of desert tortoises on the Beaver Dam Slope.

METHODS

Study Area. — The study was conducted on the Beaver Dam Slope, along the western foothills of the Beaver Dam Mountains, in extreme southwestern Utah, Washington County. The 4.83 by 8.04 km study area lies approximately 1.61 km north of the Arizona – Utah state line and 1.61 km east of Beaver Dam Wash within three previously surveyed mark-recapture study plots: Beaver Dam Slope, Woodbury-Hardy, and Welcome Wash (NW: 37°02'11"N, 113°55'14"W; 823 to 1097 m elevation). The study area is characteristic of the northeastern Mojave Desert with low humidity, low precipitation, and a wide annual temperature range. Summer temperatures regularly exceed 38°C and often rise to 43°C, with winter temperatures falling as low as -7°C. Average annual precipitation is 187.96 mm, with the majority of rainfall occurring between December and February (National Oceanic and Atmospheric Administration [NOAA], 1961–90). Winter precipitation is characterized by low intensity frontal patterns of long duration, while summer precipitation is characterized by brief intense thunderstorms. May and June are normally the driest months.

A soil profile of the study area indicates a silt and clay top soil and a well-drained sandy loam layer, with smaller percentages of granular gravel and sand (Mortensen et al., 1977). Alluvial fans consist of top layers of gravel over coarsely textured soils. Limestone caliche layers, a calcium carbonate hardpan, are found along large drainages. Sandstone outcrops occur on steep hillsides and slopes. Numerous small southwest washes flow into several major drainage routes including Big Wash, Castle Cliff Wash, and Welcome Wash. Vegetation at the study area is classified in the Joshua Tree Series of the Mohave Desertscrub Biome (Turner, 1994). Dominant perennial species include creosote (*Larrea tridentata*), white bursage (*Ambrosia dumosa*), snakeweed (*Gutierrezia sarothrae*), Joshua tree (*Yucca brevifolia*), banana yucca (*Y. baccata*), winter fat (*Ceratoides lanata*), and ephedra (*Ephedra nevadensis*).

Study Animals. — Adult female desert tortoises were located by a team of field workers walking parallel transects within the study area. Females with a straight midline carapace length (CL) greater than 185 mm were used in the study. Tortoises were consecutively numbered using a unique series of scute notches (Cagle, 1939). Other data collected at time of capture included ambient/surface temperatures, general weather observations, and activity and behavior of the tortoise.

Tortoises were fitted with radiotransmitters (Telonics Model 125, Mesa, AZ), affixed above the left forelimb with five minute gel epoxy. Transmitters were attached below the highest point of the carapace to reduce interference in shelter sites. Receivers (Telonics TR-2) and Yagi directional antennae were used to relocate tortoises. Upon relocation, tortoises were transported bi-weekly to field vehicles where they were weighed, measured, radiographed, and released at the point of capture.

Tortoise egg production was monitored using radiography as described by Gibbons and Greene (1979). A portable X-ray unit (Kramex PX20N, Diagnostic X-ray units, Japan) with an operating voltage of 70 kV peak was used. Rare earth intensifying cassettes with Kodak X-omatic X-ray film (BXR 24x30; 0.16-sec exposure) were utilized with the X-ray source 80 cm above film. Egg dimensions (length and width) were corrected for magnification based on the geometric relationship of an actual egg to a magnified egg image (Graham and Petokas, 1989); egg centers were approximately 25 mm above the film.

Female tortoises were monitored closely during periods when egg deposition was expected. Clutches and oviposition dates were determined by positive followed by negative X-rays (zeroes) as well as clarity of shells in X-rays. All telemetered tortoises were weighed and located on a daily basis to determine exact day and location of egg deposition. Mesh exclosures were constructed around nest sites to prevent nest predation and to monitor hatchling emergence. Enclosures consisted of wire mesh (hardware cloth) encircling the nest. Rocks and dirt were placed around the bottom of the mesh to prevent predation. If the location of the nest was uncertain, exclosures were constructed around those areas used during the expected deposition period. Once exclosures were constructed, nests were monitored daily for signs of predator invasion and hatching activity.

Statistical Analyses. — The three year study on the Beaver Dam Slope was conducted from 10 June 1987 to 11 July 1989. However, we report only 1989 results since 1987 and 1988 data were collected after the nesting season began. Tortoises with two or less radiographs during the 1989 field season were excluded from analyses unless stated otherwise.

Tortoise locations were plotted on topographic maps, and 95% minimum convex polygon (MCP) home ranges were calculated using the statistical package HOME RANGE (Haynes, 1949). Consecutive observations were checked for autocorrelation (Swihart and Slade, 1985). Tortoises with over 25 independent locations were included in the home range analyses. Means are presented ± one standard error (SE). All analyses including clutch size, clutch frequency, and annual egg production are for egg-laying tortoises only. The two-sample t-test was used to compare the size of first and second clutches, as well as home range size between reproductive and non-reproductive females. Analysis of variance was used to compare the relationship between CL of reproductive females with the following dependent variables: mean clutch size, first clutch size, clutch frequency, annual egg production, mean egg dimensions, and CL of emerging hatchlings. In addition, analysis of variance was used to compare the relationship between mean clutch size and egg dimensions, as well as hatchling CL and egg dimensions. Statistical analyses were completed using Quattro Pro v.6.0 and considered significant at $p < 0.05$.

RESULTS

Clutch Size and Frequency. — Twenty-one tortoises were monitored from 20 April to 11 July 1989 (Table 1). Three tortoises (#584, #604, #896) deposited a split clutch into two or three egg laying events. The smallest reproductive tortoise on the Beaver Dam Slope had a CL of 192 mm. Seven female tortoises failed to produce any eggs. Due to incomplete reproductive data, three tortoises (#641, #649, #820) were not included in analyses unless otherwise noted. Carapace length of tortoises monitored throughout the season was 215.5 ± 4.75 mm (n = 18, range = 188–272). Females that laid eggs during the season (66.7%) laid their first clutch by late April (n = 6), early May (n = 4), or late May (n = 2). Of the females that laid eggs, 33.3% laid a second clutch of eggs by late May or early June. The earliest clutch was laid by 9 May 1989. The last clutch was last detected on 4 July 1989, except for tortoise #584 who had one egg impacted in its cloaca. Mean retention time from initial detection to oviposition was estimated to be 26.6 ± 2.41 days (n = 14, range = 12–43; Table 2). The interval between first and second oviposition was estimated at 24.8 ± 3.42 days (n = 4, range = 15–30).

Twelve tortoises produced a first clutch of eggs ranging from 2 to 8 eggs, with a mean of 5.2 ± 0.47. Four tortoises produced a second clutch of eggs ranging from 3 to 10 eggs

Table 1. Midline carapace length (CL); egg production, including clutch size and date; and number of clutches of desert tortoises at the Woodbury-Hardy Study Plot (WH), Welcome Wash Study Plot (WW), and the Beaver Dam Slope Study Plot (BDS) in 1989. Individual clutches are underlined. Three tortoises (#641, #649, #820) were not included in analyses due to incomplete reproductive data. Tortoise #584 was unable to deposit the final egg in its clutch due to an impacted egg in its cloaca. Dash symbol indicates tortoise was inaccessible and therefore not radiographed.

Tortoise number	Study Area	CL (mm)	April 20—21	April 24	April 28	May 8—11	May 23—24	May 25—26	June 7—8	June 21—22	July 3—4	July 11	# of Clutches
414	WH	203	0	—	—	0	0	—	0	0	—	—	0
508	BDS	208	6	—	—	6	0	—	0	0	—	—	1
548	WH	226	7	—	—	7	0	—	4	0	—	—	2
559	WW	212	0	—	—	4	4	—	0	0	—	—	1
560	WH	192	0	—	—	0	0	—	0	0	—	—	0
564	WH	198	0	—	—	0	0	—	0	0	—	—	0
566	WW	204	0	—	—	0	0	—	0	0	—	—	0
578	WH	221	5	—	—	5	0	—	0	0	—	—	1
582	BDS	188	0	—	—	0	0	—	0	0	—	—	0
584	BDS	192	0	—	—	0	—	3	3	3	1	1	1
604	WW	225	0	—	—	0	6	—	6	4	2	—	1
638	BDS	231				2	5[1]	—	5	0	—	—	2
641	WW	229				2	0	—	—	—	—	—	1
649	BDS	262				—	—	5	0	—	—	—	1
820	WW	205	0	—	—	0	—	—	—	—	—	—	0
873	WW	219	5	—	—	0	3	—	0	—	—	—	2
896	BDS	203	—	0	—	5	5	—	2	0	—	—	1
904	WH	224	—	0	—	5	5	—	0	—	—	—	1
905	WH	235	0	—	—	0	0	—	0	0	—	—	0
914	WH	226	6	—	—	6	0	—	0	0	—	—	1
1000	WH	272			8	0	10	—	10	0	—	0	2

[1]Very faint shells on radiograph.

with a mean of 5.5 ± 1.55. Mean clutch size of the first and second clutches did not differ significantly (t = -0.28, 14 df, p = 0.78). The mean clutch size when first and second clutches were combined was 5.2 ± 0.50 (n = 16, range = 2–10). Mean clutch size was significantly correlated with CL ($F_{1,10}$ = 13.40, p = 0.004, r^2 = 0.57). The mean clutch frequency was 1.33 ± 0.14 (n = 12, range = 1–2) clutches per reproductive female and was significantly correlated with CL ($F_{1,10}$ = 5.16, p = 0.05, r^2 = 0.34).

Annual Fecundity. — Annual fecundity of reproductive tortoises monitored throughout the season ranged from 3 to 18 eggs. Mean annual fecundity was 7.0 eggs ± 1.16 (n = 12) and was significantly correlated with carapace length ($F_{1,10}$ = 32.76, p = 0.0002, r^2 = 0.77; Fig. 1). The regression equation predicted an increase of one egg for each 5.55 mm increase in CL.

Egg Dimensions. — Normal eggs were elliptical to nearly spherical in shape on radiographs. The mean width and length, respectively, of the eggs were 37.2 ± 0.26 mm (n = 81, range = 33–43) and 44.3 ± 0.33 mm (n = 81, range = 34–52; Table 2). Carapace length was significantly correlated with egg width ($F_{1,12}$ = 13.48, p = 0.003, r^2 = 0.53) but

Table 2. Midline carapace length (CL); oviposition dates, including when eggs were first detected, last detected, and laid by; clutch size; mean egg width, mean egg length and standard error (SE); and hatching date and number of hatchlings for reproductive desert tortoises on the Beaver Dam Slope Study Area, Washington County, Utah, 1989. Tortoise #584 was unable to deposit an impacted egg in its cloaca. Dash indicates information was undetermined.

Tortoise Number	CL (mm)	Clutch #	Eggs			Clutch Size	Mean Egg Dimensions				Hatching Date	# of Hatchlings
			First detected	Last detected	Laid by		Width (mm)	SE	Length (mm)	SE		
508	208	1	4/21	5/08	5/24	6	35	0.5	41	0.5	8/22	3
548	226	1	4/20	5/08	5/23	7	38	0.8	46	0.6	—	—
		2	6/07	6/07	6/21	4	36	0.2	42	2.2	—	0
559	212	1	5/09	5/24	6/08	4	37	0.2	44	0.8	8/29	3
578	221	1	4/20	5/08	5/23	5	35	0.4	47	0.5	8/30	2
584	192	1	5/26	7/11	—	3	33	0.3	42	0.7	—	—
604	225	1	5/24	7/04	—	6	36	0.4	43	0.9	—	—
638	231	1	5/09	5/08	5/24	2	40	0.7	48	1.1	—	—
		2	5/24	6/08	6/22	5	38	0.4	47	0.3	9/09	5
641	229	1	5/11	5/11	5/23	2	36	1.4	44	1.1	—	—
649	262	1	5/25	5/25	6/08	5	36	0.3	45	0.4	9/09	4
873	219	1	4/21	4/21	5/09	5	36	0.2	50	1.0	8/21	4
		2	5/24	5/24	6/08	3	35	0.7	46	1.4	9/09	3
896	203	1	5/10	6/07	6/22	5	36	0.2	45	0.7	8/28	3
904	224	1	5/10	5/23	6/07	5	35	0.3	45	0.6	9/12	4
914	226	1	4/20	5/08	5/23	6	37	0.2	41	1.4	8/21	4
1000	272	1	4/28	4/28	5/10	8	41	0.3	44	0.7	8/22	8
		2	5/23	6/07	6/21	10	40	0.4	44	0.3	9/07	9

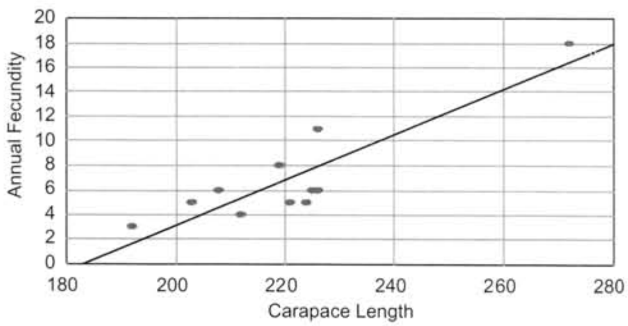

Figure 1. Relationship between annual fecundity and carapace length of reproductive desert tortoises on the Beaver Dam Slope, Washington County, Utah, 1989 ($y = -32.97 + 0.18 * CL$; $r^2 = 0.77$; $p = 0.0002$; $n = 12$).

not egg length ($F_{1,12} = 0.54$, $p = 0.47$, $r^2 = 0.04$). Mean clutch size was significantly correlated with egg width ($F_{1,12} = 4.98$, $p = 0.04$, $r^2 = 0.29$) but not egg length ($F_{1,12} = 0.50$, $p = 0.49$, $r^2 = 0.04$).

Hatchling Success. — Fifty-two of 71 eggs (73%) that were monitored, hatched (Table 2). There were no signs of predation on the 13 nests observed in this study. The earliest observation of hatching was on 21 August, the latest was on 12 September. Time from egg deposition to hatching was estimated at 89.7 ± 3.25 days ($n = 12$, range = 67–104). Mean hatchling CL was 45.0 ± 0.33 mm ($n = 51$, range = 39-49; Table 3). Carapace length of emerging hatchlings was significantly correlated with CL of adults ($F_{1,8} = 7.07$, $p = 0.03$, $r^2 = 0.47$). Hatchling size was not correlated with egg width ($F_{1,8} = 0.65$, $p = 0.44$, $r^2 = 0.07$) or egg length ($F_{1,8} = 1.95$, $p = 0.20$, $r^2 = 0.20$).

Home Range. — Female desert tortoises in the Beaver Dam Slope study area had a mean MCP of 25.6 ± 10.29 ha during the nesting season (range = 4.3–186.0, $n = 18$; Table 4). Reproductive tortoises had a smaller home range (mean = 13.48 ± 4.40 ha, range = 4.3–16.4, $n = 12$) than non-reproducing tortoises in the study (mean = 49.97 ± 28.58 ha, range = 5.6–186.0, $n = 6$). However, this difference was not significant ($t = -1.26$, 16 df, $p = 0.26$).

Table 3. Number of hatchlings per clutch, mean hatchling midline carapace length (CL), and standard error (SE) for reproductive desert tortoises on the Beaver Dam Slope Study Area, Washington County, Utah, 1989.

Tortoise Number	CL (mm)	Clutch	Hatchling Descriptive Statistics: No. Hatchlings	Mean CL (mm)	SE
508	208	1	3	43.0	0.00
559	212	1	2	39.5	0.50
578	221	1	2	43.5	1.50
638	231	2	5	44.8	0.37
649	262	1	4	46.2	0.63
873	219	1	4	48.0	0.41
		2	3	44.7	0.88
896	203	1	3	42.0	0.58
904	224	1	4	44.2	0.48
914	226	1	4	43.5	0.87
1000	272	1	8	46.4	0.71
		2	9	46.3	0.60

DISCUSSION

Baseline desert tortoise reproductive data was collected on the Beaver Dam Slope, Washington County, Utah, in 1989. Although this study was completed at the northeastern edge of the desert tortoises' geographic range, many results are similar to other Mojave tortoise reproductive studies, including number of clutches per season, clutch size, annual fecundity, nesting season, and hatchling emergence. The number of clutches per season on the Beaver Dam Slope is

Table 4. Carapace length (CL), clutch size, home range estimate, number of locations, and number of observations, for female desert tortoises ($n = 18$) on the Beaver Dam Slope, Washington County, Utah, 1989.

Tortoise #	CL	Clutch 1 Size	Clutch 2 Size	Home Range Estimate (ha)	No. of Locations	No. of Observations
Reproductive Females						
508	208	6	0	16.4	59	159
548	226	7	4	9.9	91	190
559	212	4	0	7.2	68	180
578	221	5	0	9.4	90	200
584	191	3	0	61.0	89	165
604	226	6	0	11.6	90	142
638	231	2	5	7.0	74	165
873	219	5	3	8.2	72	190
896	203	5	0	8.8	84	173
904	224	5	0	4.3	80	165
914	226	6	0	9.0	79	170
1000	272	8	10	9.0	79	140
Mean ± SE				13.48 ± 4.40		
Non-Reproductive Females						
414	202	0	0	5.6	52	136
560	192	0	0	60.0	49	135
564	198	0	0	34.0	58	189
566	204	0	0	7.7	43	189
582	188	0	0	186.0	39	189
905	234	0	0	6.5	56	188
Mean ± SE				49.97 ± 28.58		

similar to other known populations in the Mojave desert with female tortoises typically laying between zero to two clutches (Mueller et al., 1998; Wallis et al., 1999), although some females are capable of producing up to three clutches in a season (Turner et al., 1986; Karl, 1998). Clutch size and annual fecundity on the Beaver Dam Slope were similar to the rest of the Mojave Desert with average clutch sizes of 4 to 5 eggs and total egg production of 7 to 8 eggs annually (Turner et al., 1986; Karl, 1998; Mueller et al., 1998; Wallis et al., 1999). The results of this study indicate that the nesting season and hatchling emergence on the Beaver Dam Slope is similar to other Mojave tortoise populations with oviposition beginning in mid-May and extending to early or mid-July (Turner et al., 1984, 1986; Karl, 1998; Mueller et al., 1998; Wallis et al., 1999). Rostal et al. (1994) suggested that nesting in the northern Mojave Desert is timed so that hatchling emergence will coincide with potential summer rains and forage. Few desert tortoise studies report nonsynchronous egg development (Turner et al., 1986) and splitting of clutches as observed on the Beaver Dam Slope. Exclosures constructed around nest sites probably explains why the hatchling success rate on the Beaver Dam Slope was higher than reported in other studies (Burge, 1977; Turner et al., 1986). Variation in hatching success results noted in the literature are largely due to study methods ranging from natural unprotected nests (Burge, 1977), artificial protected nests (Turner et al., 1986), and captive nests (Lee, 1963).

In this study, as well as in other studies, body size was significantly correlated with clutch size (Turner et al., 1986; Karl, 1998; Mueller et al., 1998; Wallis et al., 1999), clutch frequency (Turner et al., 1986; Wallis et al., 1999), annual egg production (Karl, 1998; Mueller et al., 1998; Wallis et al., 1999), and egg dimensions (Wallis et al., 1999). Larger females may be able to store more nutrients (i.e., water, protein, and calcium) for egg laying than smaller females (Wallis et al., 1999). Smaller females may have less body nutrient reserves and greater dependence on winter annuals in the spring, relative to larger females (Henen, 1997; Wallis et al., 1999). Consistent with other studies (Congdon and Gibbons, 1990a; Spotila et al., 1994), hatchling size was correlated with egg size on the Beaver Dam Slope. Several selective advantages of greater egg width and hatchling size have been proposed to increase hatchling survival and include: providing an increased yolk reserve for hatchlings, reduction of water loss due to lower surface-to-volume ratio, decreased predation due to larger size, as well as increased ability to process highly fibrous plants (Congdon and Gibbons, 1990b; Morafka, 1994).

Factors that may affect an individual's annual egg production include environmental condition, available resources, and home range quality (Henen, 1997; Wallis et al., 1999). In this study, mean home range size of reproductive females was smaller than that of non-reproductive females, although the difference was not statistically significant. This lack of significance may be due to low sample size, high resource variability within the study area, as well as limitations of the estimation technique (Jennrich and Turner, 1969; White and Garrott, 1990; O'Connor et al., 1994). The time reproductive animals spend foraging (Meienberger et al., 1993), defending burrows (Barrett and Humphey, 1986; Henen, 2000), and maintaining or laying eggs (McLuckie, 1995) may contribute to smaller home ranges.

Geographic variation in rainfall may explain some of the variation in egg dimensions and minimum size at reproduction throughout the range of the desert tortoise (Mueller et al., 1998; Wallis et al., 1999). A longitudinal moisture gradient exists within the range of the desert tortoise with rainfall increasing as one moves south (Germano et al., 1994). To a lesser extent, a latitudinal and elevational gradient has been identified, with the Western Mojave Desert receiving less rainfall than the Eastern Mojave Desert (Wallis et al., 1999). Mean egg dimensions on the Beaver Dam Slope are consistent with results from the Western Mojave (Wallis et al., 1999) and the Sonoran Desert (Murray et al., 1996), but larger than those reported in the Eastern Mojave (Wallis et al., 1999). The smaller egg dimensions recorded by Wallis et al. (1999) may be related to increased summer rain and an associated increase in available food for emerging hatchlings in the Eastern Mojave Desert (Wallis et al., 1999). The minimum size of reproductive animals in this study is similar to several reproductive studies in the Mojave Desert (Turner et al., 1986; Wallis et al., 1999). However, in the Western Mojave Desert, Germano (1994) documented reproductively mature females as small as 176 mm CL while the smallest female to reproduce at Yucca Mountain, Nevada, was 209 mm (Mueller et al., 1998).

Clutch frequency, as well as the percent of females that reproduced on the Beaver Dam Slope, was lower than that reported in other Mojave studies (Turner et al., 1986; Mueller et al., 1998; Wallis et al., 1999). Seven of 21 mature female tortoises (33%) failed to reproduce on the Beaver Dam Slope and only four of 18 tortoises (22%) monitored throughout the season produced a second clutch. In other reproductive studies in the Mojave and Sonoran Deserts, 75 to 100% of females were reproductive during the study (Murray et al., 1996; Karl, 1998; Mueller et al., 1998; Wallis et al., 1999). Turner et al. (1986) reported that all but one female tortoise ($n = 62$) laid at least one clutch of eggs during their three year study and 64–84% of females laid more than one clutch. Turner et al. (1986) demonstrated that clutch frequency was correlated with winter rainfall and influenced by net production of annual forbs and grasses. The Beaver Dam Slope received above average rainfall in 1987 (253.49 mm) and below average rainfall in 1988 (177.29 mm) and 1989 (183.39 mm) when compared with the 30 year mean (NOAA, 1971–00). Since the amount of precipitation during the study (October 1988 to March 1989 = 100.84 mm) exceeded the minimum required for winter germination and growth of annuals (Turner and Randall, 1989), additional environmental and physiological factors likely contributed to the low clutch frequency and percent of reproducing mature females observed on the Beaver Dam Slope (Wallis et al., 1999).

The tortoise population on the Beaver Dam Slope has experienced population declines (Woodbury and Hardy, 1948; USFWS, 1980). Declines rangewide have been attributed to habitat degradation and disease, as well as a host of other factors (USFWS, 1994). The severity of these factors could negatively affect the reproductive output of a desert tortoise population, resulting in lower clutch frequency and fecundity (Henen, 1994, 1997). The number of eggs that a female can produce in a season is dependent on a variety of factors, including environment, habitat, and physiological condition of the animal (Henen, 1997). Mueller et al. (1998) suggested that body condition during July to October may determine the number of eggs a tortoise can produce the following spring. Therefore, egg production in a given year is dependent on body condition and availability of forage and drinking water during periods of growth and maintenance (Henen, 1997). In addition, under relatively poor conditions with little herbaceous growth, tortoises that delayed reproduction were limited to a single clutch because they could not maintain follicles for a second clutch (Mueller et al., 1998). Therefore, low clutch frequency and fecundity may indicate the overall condition of the population.

Knowledge of a species' reproductive characteristics is important in assessing the status of a population. Since the early 1980s, the Beaver Dam Slope has experienced population declines due primarily to disease and habitat degradation and alteration (USFWS, 1980, 1994). Life history characteristics of desert tortoises (i.e., delayed sexual maturity, low fecundity, low juvenile recruitment) make populations highly sensitive to population declines. Understanding demographics related to reproduction is necessary to manage the population by assessing threats and implementing regulatory mechanisms for the tortoises' recovery.

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