Title
Population Ecology of the Desert Tortoise at Goffs, California, 1983-1986

Authors
Turner, Frederick B
Berry, Kristin H
Randall, David C
et al.

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by

Frederick B. Turner, Kristin H. Berry, David C. Randall and Gary C. White

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University of California
Laboratory of Biomedical and Environmental Sciences
900 Veteran Avenue
Los Angeles, California 90024

California Desert District Office
U.S. Bureau of Land Management
1695 Spruce Street
Riverside, California 92507

and

Department of Fishery and Wildlife Biology
Colorado State University
Fort Collins, Colorado 80523

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V. Executive Summary

In 1982 SCE announced changes in its energy policy, and the intention to promote development of solar, wind and geothermal energy sources. These land-intensive technologies raised issues associated with loss of habitats of various species of desert plants and animals. One of these species was the desert tortoise. Over the past 10 years this species has increased dramatically in social importance--not only in California, but also throughout its range in the western U.S. (including parts of Arizona, Nevada and Utah). State and federal agencies have supported studies of local distribution, abundance and habitats. These studies have shown that some habitats of the desert tortoise have been and are continuing to be seriously disturbed by human activities. Strong circumstantial evidence suggests that the abundance of the tortoise has declined in many parts of its range. Concern for the tortoise in southwestern Utah led to its listing as Threatened under the Endangered Species Act in 1980. In September 1984 the Defenders of Wildlife, Natural Resource Defense Council, and Environmental Defense Fund petitioned the U.S. Fish and Wildlife Service to list the tortoise as Endangered throughout its range in Arizona, California and Nevada. In December 1985 the Service determined that listng was warranted so the tortoise will remain a species of social and biological importance in California.

Causes of tortoise habitat disruption are manifold. One source of impacts--both past and present--is construction and operation of energy facilities. Development and transmission of energy involves building and maintenance of gas and water pipelines, transmission and distribution lines, roads, railroad spurs, wells and power plants. The desert tortoise played a conspicuous role in mitigation measures and research prescribed by the State

Energy Commission in its 1983 decision regarding certification of the Solar 100 facility in Johnson Valley.

The planning of long-term studies of the desert tortoise emphasized belief in the value of fundamental research relating to the population ecology of the species. While it was understood that basic research would not necessarily enable the prediction of effects of mitigating actions, it was believed that such investigations would provide an improved basis for planning specific mitigation-related experiments. The Goffs project, dealing with tortoise reproduction and survival, and the integration of these processes into a life-table, was developed in keepng with these convictions.

This report is the last in a series of four, and summarizes four years of work near Goffs, in eastern San Bernardino County, California. Rates of tortoise reproduction and survival were measured over this interval, and average rates of births and deaths used to construct a life-table. The table developed in this manner showed that the Goffs population is increasing at a rate of 2% per year. One result of simulation experiments with the life-table was the demonstration of how difficult it is to predict changes in the well-being of populations whose members may live for 80 years or more. Destructive effects may not be clearly discernible for many years. On the other hand, our findings suggest that short-term negative influences--if reversible--will not be dangerous to the long-term perpetuation of the species. Irreversible deterioration of environments will, however, eventually lead to local extinctions.

VI. Introduction

Woodbury and Hardy (1948) provided an extensive description of the natural history of the desert tortoise in southwestern Utah, but following their study no further research involving natural populations of this species occurred for almost 30 years. Congressional appropriation of money for the development of a management plan for the California Desert Conservation Area in 1976 stimulated new interest in conservation of the state's desert wildlife resources. The Desert District Office of the U.S. Bureau of Land Management sponsored various studies of the desert tortoise between 1976 and 1985, and these activities have been reviewed by Berry (1986).

The California Energy Commission was established in 1975, and the renewed interest in the desert tortoise stimulated concern in the Commission as to effects of power plant construction on tortoise populations. Some of the specific problems faced by the Southern California Edison Company in this respect have been reviewed by Pearson (1986). Utilities will have to consider likely effects of energy-related projects on the tortoise, and how such effects can be reduced or mitigated. For example, is it biologically defensible to relocate tortoises? If so, what are the most effective techniques and safeguards? Are there economically feasible ways in which tortoise habitat can be improved? Are there realistic procedures for protecting the quality of existing tortoise habitats? Attacking these questions requires, first, a sound understanding of the natural history of the tortoise and the dynamics of its populations and, second, the conduct of appropriately designed field experiments.

This study was directed towards the first of these two lines of endeavor, viz., the description and analysis of the dynamics of a natural population of desert tortoises. The study area selected was near Goffs, in eastern San Bernardino County, California (Fig. 1). This area supports a healthy population of tortoises on a site subjected to only slight human disturbance. The density of tortoises in this general region exceeds 400 per mi^2, which is high relative to estimated densities in other parts of the species' range. We measured rates of egg production over a period of four years, and were able to determine how reproductive rates were affected by female body size and year-to-year differences in rainfall and available plant food. We measured the incidence of destruction of eggs by predators, and the natural fertility rate of eggs escaping predation. At the same time we measured growth rates of tortoises and estimated size-specific death rates of tortoises of both sexes. These elements of population dynamics were combined in a life-table, in which our estimates of mean fecundity and survival were combined to illustrate the generalized function of the Goffs population. This model may have important bearing on future studies of tortoise-related mitigation measures.

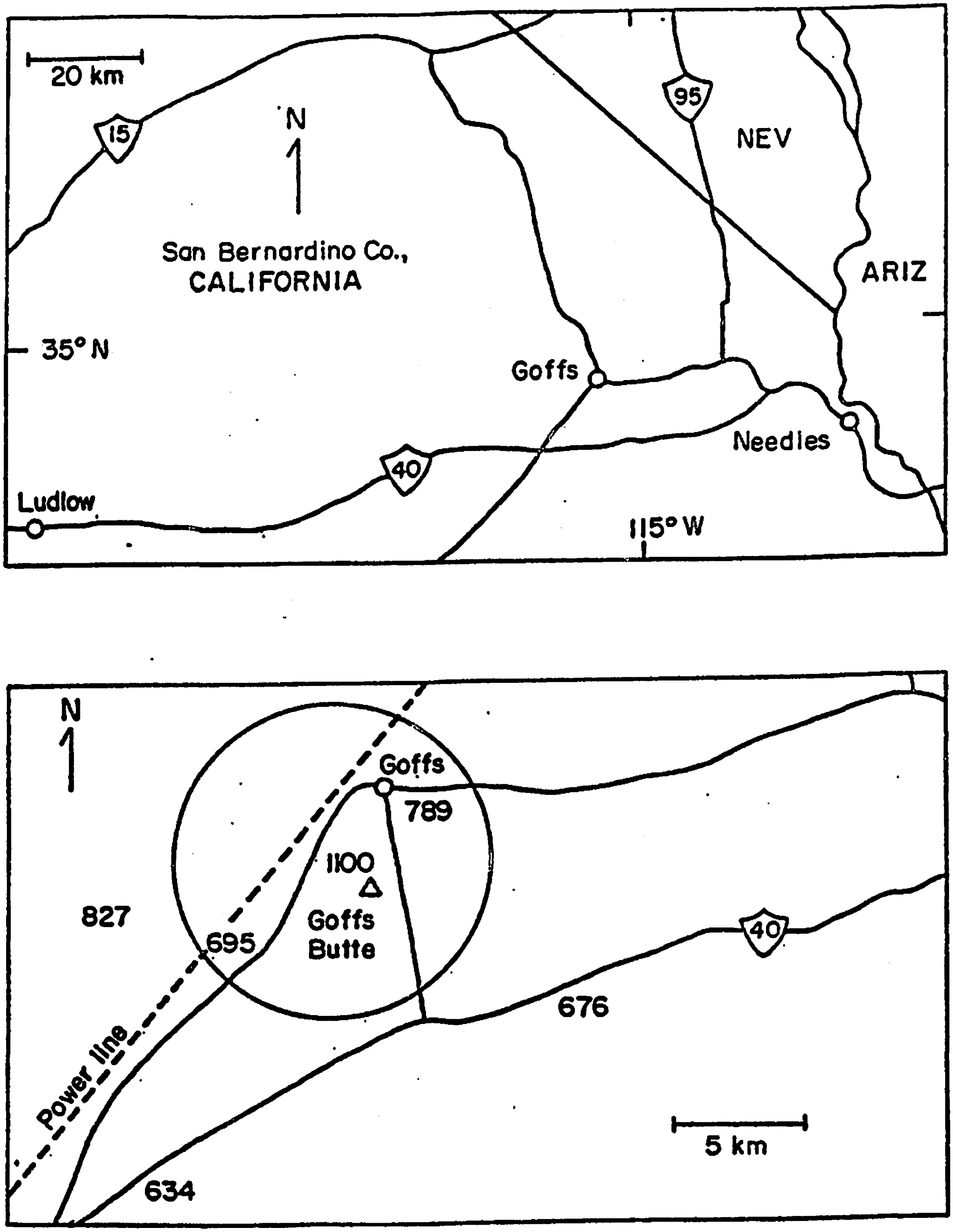

Fig. 1. General locale of study area (above) and expanded view of Goffs area (below). Figures in lower illustration give elevations (m).

VII. Methods and Results

A. Rainfall

Noy-Meir (1973) defined deserts as "...water-controlled ecosystems with infrequent, discrete, and largely unpredictable water inputs." Net primary production may be variable from one year to the next and the functioning of populations of desert animals are accordingly influenced by year-to-year changes in available food and energy (Turner and Chew, 1981). We began measurements of rainfall at Goffs during the spring of 1983 and continued these until the end of 1986 (Table 1).

The phenology of plants in the Mojave Desert is largely governed by winter rainfall (Beatley, 1974). The occurrence, or non-occurrence, of a heavy regional rain of at least 25 mm some time between late September and early December is the factor of greatest single importance in determining germination of annual plants and their subsequent growth. Because of this point we have supplemented the rainfall data in Table 1 with rainfall measurements made at Needles between 1 October and 31 December 1982 (43.3 mm) and 1 January and 31 March 1983 (75.2 mm). We recognize that mean annual rainfall at Needles exceeds that at Goffs.

Table 1. Rainfall (mm) at Goffs, 1983-1986

Years	Intervals	Plot 1	Plot 2
1983	April-June	5.0	4.0
	July	41.4	9.7
	August	110.4	136.4
	September	10.0	7.0
	October	61.0	45.0
	November	57.1	58.4
	December	16.5	16.5
1984	January-May	1.5	2.5
	June	29.7	5.6
	July	40.1	52.8
	August	22.9	18.4
	September	9.7	3.4
	October	0	0
	November	15.8	13.2
	December	39.0	43.5
1985	January	33.1	36.8
	February-March	3.1	2.0
	April-June	3.9	3.6
	July-August	3.1	4.7
	September	12.1	7.8
	October	7.5	4.7
	November-December	15.2	14.6
1986	January	7.9	9.3
	February-March	6.4	3.1
	April-July	1.3	2.5
	August	17.2	19.8
	September	2.8	4.6
	October	33.3	37.6
	November	6.9	8.1
	December	46.0	51.8

Table 2 summarizes rainfall data for the entire period of the study, drawing on our measurements (beginning in April 1983) and records from the Needles Airport (for October 1982 through March 1983).

Table 2. Summary of rainfall (mm) between October 1982 and December 1986. Hydrological years pertain to intervals between October (year *n*-1) through September (year *n*).

Year (*n*)	Calendar year		Hydrological year	
	Plot 1	Plot 2	Plot 1	Plot 2
1983	377	353	285	277
1984	159	139	239	203
1985	78	74	110	112
1986	122	137	58	59

$\bar{x}$ = 179.9 overall mean for 4 yrs, 2 plots, n=8

$\bar{x}$ = 167.9 so ~ 17 cm. ave rain over 4 yrs.

B. Abundance and Biomass of Annual Plants

Annual plants were sampled along two 100-m transects. Locations and orientations of these lines (I and II) were described by Burge (1980). Twenty-five sampling points were established at equal intervals along these transects and annual plants examined in quadrats at each point. Visual estimates of coverage by major species were made using 20 x 50 cm (0.1 m^2) quadrats. Data from 25 quadrats were then combined to estimate mean coverage (cm^2/m^2) by species. Procedures followed were similar to those used in sampling annuals along Transect I in 1980 (Burge, 1980).

We also estimated aboveground biomass of major species along each transect. Quadrats (I m^2) were established at 25 points along each line and plants growing in all (or portions) of these areas were collected, sorted, and placed in paper bags. Species of Pectocarya were not segregated. Areas collected within 1 m^2 quadrats varied from the entire area (for uncommon species) to subquadrats as small as 0.1 m^2 (for species like Pectocarya and Schismus). Plants collected were oven-dried at 70° C for 100 hours and then weighed. Estimated standing crops were computed by dividing total dry weights of species (or species groups) by the total area examined for each species.

Sampling during 1986 was carried out on 3-4 April. Winter rainfall preceding the 1986 growing season was scanty (Table 2) and few annuals germinated. We sampled early so as to measure what sparse growth occurred. No further growth was observed later in the season. Table 3 gives biomass estimates for 1986.

Table 3. Estimated aboveground dry matter biomass (g/m^2) of annual plants in Plot 1 in early April 1986.

Species	Transect I	Transect II
Mediterranean schismus (*Schismus barbatus*)	14.67	6.36
Pectocarya spp.	0.15	0.54
Peppergrass (*Lepidium lasiocarpum*)	0.11	0.01
Cryptantha spp.	0.01	0.12
Golden yarrow (*Eriophyllum* spp.)	-	0.10
Bird's foot trefoil (*Lotus tomentellus*)	0.06	-
Poppy (*Eschscholtzia minutiflora*)	0.06	-
Stylocline micropoides	-	0.07
Filaree (*Erodium cicutarium*)	0.01	-
Other species	0.01	0.01
Totals	15.1	7.2

Table 4 reviews estimates of mean net dry matter production by annual plants along the two transects in Plot 1 between 1983 and 1986, and also gives measurements (or best available estimates) of rainfall for a 6-month interval (October-March) preceding each growing season. The table distinguishes between net production by annual herbs and that by a grass--Mediterranean schismus (*Schismus barbatus*).

Table 4. Winter rainfall and net dry matter production by annual plants in Plot 1 at Goffs, 1983-1986.

Years	October-March rainfall (mm)	Mean dry matter net production (g/m^2)	
		Annual herbs and *Schismus*	Annual herbs only
1982-83	118[1]	42	14
1983-84	136[2]	4.3	0.3
1984-85	91	3.8	2.6
1985-86	37	11.1	0.6

[1] Needles Airport, no available data for Goffs

[2] only 1 mm after December 1983

There is no clear relationship between winter rainfall and plant production because of the apparently high winter rainfall value preceding the 1984 season. We commented on this in an earlier report (Turner and Berry, 1986: 42), emphasizing that the virtual absence of rain between 1 January and 31 May 1984 apparently inhibited vegetative development of plants germinated during the winter (see also Beatley; 1967, 1974). Turner and Berry (1984: 50) commented that during the spring of 1984, when both annual plants and *Schismus* were abundant, tortoises showed an overwhelming tendency to consume leguminous herbs and essentially ignored the grass. This observation implies a difference in the palatability (or possibly the nutritive quality) of the two kinds of plants, and is the reason for separating production estimates for herbs and grasses and for herbs only.

C. Structure of the Plot 1 Population

Table 5 gives the observed size distribution of the tortoises registered in Plot 1 in 1986. None of the sampling between 1983 and 1986 indicated anything other than a 1:1 sex ratio among adult tortoises. Table 6 summarizes the annual registries compiled between 1983 and 1986. A Chi-squared (X^2) test of these four distributions shows an extremely low probability that they could have all been drawn from the same population. The reason is that the 1983 sample differs from the other three in a relatively higher proportion of tortoises <100 mm long and a relatively lower proportion of tortoises >207 mm long. The 1984-1986

Table 5. Size distribution and sex ratio of desert tortoises registered in Plot 1 during the 1986 season.

Carapace length (mm)	Unsexed	Males	Females	Totals
<60	7			7
60-99	21			21
100-139	26			26
140-179	24			24
180-207		7	25	32
208-239		15	66	81
$\geq$240		58	2	60
Totals	78	80	93	251

Table 6. Observed size distributions at Goffs, 1983-1986.

Size (mm)	1983	%	1984	%	1985	%	1986	%
<60	24	5.4	13	4.7	10	3.6	7	2.8
60- 99	101	22.4	25	9.0	23	8.3	21	8.4
100-139	62	13.8	35	12.5	45	16.2	26	10.4
140-179	43	9.6	27	9.7	25	9.0	24	9.5
180-207	47	10.5	28	10.0	30	10.8	32	12.7
208-239	98	21.8	84	30.1	88	31.6	81	32.3
≥240	74	16.5	67	24.0	57	20.5	60	23.9
Totals	449		279		278		251	

samples do not differ significantly ($X^2 = 7.0$, $X^2_{0.05} = 21$).

We believe that the difference between the distributions in Table 6 is much more likely to reflect sampling biases rather than a real change in population structure. Note that far fewer tortoises were registered in 1984 than in 1983. Between 29 March and 8 May 1984 434 person-hours of searching yielded 153 tortoises (0.35/hr). The comparable figure for 1983 was 0.84/hr. These figures refer to tortoises of all sizes. Registrations of tortoises <140 mm long in 1984 and 1983 were, respectively, 0.04/hr and 0.30/hr. Following substantial rains during October-November 1983, only 18 mm of rain fell between December 1983 and the end of May 1984. Small tortoises were apparently more adversely affected by these conditions than larger ones.

Differences in sampling effort and focus may also influence population samples (Turner and Berry, 1986: 18). There is, then, no easy way to determine the true size distribution of a population of desert tortoises. Of the four distributions shown in Table 6, the best representation is that for 1983. Here we were fortunate to combine an intensive short-term sampling effort with favorable environmental conditions.

D. Egg Production by Tortoises

Measurements of egg production by tortoises were made between 1983 and 1986 in Plot 2 and during 1985 and 1986 in Plot 1. Subject female tortoises were fitted with batteries, radiotransmitters and antennae so that they could be located as required. Our general procedure was to locate a group of 4-6 females in the late afternoon. The following morning these were collected, X-rayed, and returned to the plot. These steps were repeated until all of the tortoises (or as many as could be found) were processed. We used a medium speed Cronex 4 X-ray film, metal cassettes with intensifier screens, and exposure times of 0.25 s. Further procedural details were given by Turner et al. (1986).

Tables 7 and 8 present information derived from radiographs in the two plots in 1986. Table 7 requires some additional explanation. Only the first 18 tortoises in the table were observed over the entire duration of the breeding season, and only these individuals provided estimates of clutch frequency. The records for tortoise number 623 show the presence of one oviductal egg in early April. This is the same small egg illustrated in Fig. 3D of an earlier report (Turner and Berry, 1986: 23), and was apparently retained in the tortoise between 30 June 1985 and 1 April 1986. Later in the 1986 season a normal clutch of four eggs developed and the 19 June X-ray showed that all of these eggs had been laid.

Table 7. Numbers of eggs in radiographs of desert tortoises in Plot 1 at Goffs in 1986. Underlining indicates the same clutch.

Tortoise number	Carapace length (mm)	Mar 30-Apr 1	Apr 9-11	Apr 23-24	May 8-10	May 22-24	June 4-8	June 18-22	Clutch frequency
8	222	0	0	0	5	5	0	0	1
18	220	0	0	0	0	0	4	0	1
20	224	0	0	0	5	5	0	0	1
45	250	0	0	0	7	7	0	0	1
48	229	0	0	0	6	6	0	0	1
52	203	0	0	0	0	3	0	0	1
67	211	0	0	0	4	4	0	0	1
188	194	0	0	0	2	2	2	0	1
234	211	0	0	5	5	0	0	0	1
253	213	0	0	0	0	0	0	3	1
414	228	0	0	3	3	3	3	0	1
430	216	0	0	0	4	4	0	0	1
432	196	0	0	5	5	5	0	0	1
455	227	0	0	0	0	5	5	0	1
590	217	0	0	4	4	0	0	0	1
592	229	0	0	4	4	6[1]	6	0	2
623	199	1	1	1	1	1	1	0	
						4	4	0	1
631	222	0	0	4[1]	5	0	0	0	1
4	230				3	3	0	0	
424	230				5	5	5	0	
676	210				3	3	3	0	
685	201					4	0	0	

---

[1] faint images

Table 8. Numbers of eggs in radiographs of desert tortoises in Plot 2 at Goffs in 1986. Underlining indicates different clutches.

Tortoise number	Carapace length (mm)	Apr 1-3	Apr 12-15	Apr 24-25	May 7-9	June 5-6	June 20-21	Aug 3-6	Clutch frequency
1007	196	0	0	4	4	0	0	0	1
1059	215	0	0	0	3	0	6	0	2
1061	213	0	3	3	0	4	0	0	2
1063	201	0	0	0	3	0	0	0	1
1064	192	0	3[1]	4	4	0	0	0	1
1067	191	0	0	3	3	2[1]	0	0	2
1072	195	0	0	3[1]	3	3	0	0	1
1074	202	0	0	3	3	3[1]	3	0	2
1077	218	0	0	3[1]	3	5	0	0	2
1078	189	0	0		4	0	0	0	1

[1] faint images

We examined the possibility of reproductive senescence among what we judged to be the oldest females in the Plot 2 population. Because female tortoises may stop growing anywhere between around 200 to 240 mm in length, body size alone is not a reliable basis for estimating the age of mature females. Berry and Woodman (1984) developed a classification of shell wear and believe that very worn shells with depressed areas of scute and bone (Class 7) are a sign of advanced age. Only two of the females with transmitters in Plot 1 (430 and 432) had shells judged as wear class 7, so we added four more (4, 424, 676 and 685) in late April 1986. Table 7 shows that all of these aged females laid eggs in 1986. We conclude that there is no justification for assuming a reduction, or cessation, of reproduction by very old female tortoises.

The information in Tables 7 and 8 show that the mean size of first clutches in Plots 1 and 2 were 4.33 and 3.30, respectively. The mean clutch size in Plot 1 was significantly greater than that observed in Plot 2 ($\underline{t} = 2.61$, $\underline{t}_{0.05} = 2.06$). This is probably a reflection of the fact that when clutch sizes measured in Plot 2 between 1983 and 1985 were analyzed we found that females laying but one clutch of eggs (as was generally true in Plot 1 in 1986) laid larger ones than females laying two clutches (Turner et al., 1986). A X^2 test shows that the mean clutch frequency in Plot 1 (1.06) was significantly less than that measured in Plot 2 (1.50). The X^2 value is 5.4 ($X^2_{0.05} = 3.8$).

Turner et al. (1986) commented that observations in 1984 and 1985 showed mean retention time of eggs (i.e., to the time of laying) to be 22.3 ± 0.58 days (range 19-25 days). Seven observations in Plot 1 in 1986 showed a mean retention time of 28.4 ± 2.33 days. This difference of about 6 days is highly statistically significant.

During the first three years of work at Goffs the smallest tortoise we X-rayed with eggs in Plot 2 was Number 1078, which was about 189 mm in length (Turner et al., 1986: 96-98). In 1985 we X-rayed a 182-mm female (Number 716) in Plot 1 between early May and the end of June. No eggs were observed (Turner and Berry, 1986: 22). In 1986 we had transmitters on five small females in Plot 1 and radiographs were obtained between early May and late June (Table 9).

Table 9. Results of radiographs taken of small female tortoises in Plot 1 in 1986. Underlining indicates the same clutch.

Tortoise number	Carapace length (mm)	May 8-10	May 22-24	June 4-8	June 18-22
190	186	0	0	0	0
314	185	0	0	0	0
404	178	0	0	3	3
665	186	0	0	0	0
716	182	0	0	0	0

While radiographs of four of these tortoises were consistently negative, the smallest female (178 mm) produced a clutch of three eggs. It is possible that some or all of the other four females might have had eggs earlier in the season but we judge this unlikely. Reproduction by a female only 178 mm long appears unusual, but we gave ourselves little opportunity to observe reproduction among such small females. Between 1983 and 1986 we had transmitters on 40 different tortoises in Plot 2 and only one of these was less than 190 mm in length. In 1985 and 1986 we made radiographs of 23 different tortoises ≥190 mm long, but only of five of lesser size. For purposes of making a life-table we will assume a size at sexual maturity of 185 mm, 4 mm less than what we estimated on the basis of earlier data.

The size of the 18 first clutches ($\underline{C}$) in Table 7 is positively correlated with female body size, $\underline{L}$ ($\underline{r}$ = 0.62):

$$C = 0.053\underline{L} - 7.202 \qquad (1)$$

In 1986 we registered 88 females $\geq$185 mm in length in Plot 1. We will assume that every one of these laid one clutch and that 1/18 of this group (5) laid a second clutch. Table 10 shows the size distribution of mature females in Plot 1 and a postulated schedule of reproduction consistent with Table 7. Second clutches are distributed among larger females in keeping with observations of Turner et al. (1986: Table 5).

Table 11 shows egg production estimates derived from Table 10 using Equation (1) to estimate the size of first clutches. We knew the size of only one second clutch (6). We used this value for two females >228 mm long, but smaller values (4 and 5) for three smaller females.

Because we have lowered our estimate of size of females at sexual maturity to 185 mm, we reviewed earlier analyses of egg production in Plot 1. We also examined more closely the records of females that were sometimes observed in Plot 1 and sometimes in adjoining sections. For example, some females were recorded outside of Plot 1 during the spring and within Plot 1 during August and September. We considered that these individuals did not lay eggs in Plot 1 during such a season. Only 81 females $\geq$189 mm long were recorded in Plot 1 in 1984. Because of the low sampling efficiency in that year we set the number of breeding females in 1984 equal to the number recorded in 1983, or 93 (Turner and Berry, 1985: 20-21). We did not make any such adjustment in 1985. When we reviewed the entire history of captures and recaptures of females between 1980 and 1986 we found that some females were captured in Plot 1 in 1983, 1984 and

Table 10. Observed size distribution of 88 female desert tortoises in Plot 1 in 1986 and a postulated schedule of clutch frequencies among members of the population.

Carapace length (mm)	Number of females	Postulated Number of clutches laid 1	2
184-187	2	2	
188-191	2	2	
192-195	5	5	
196-199	4	4	
200-203	4	3	1
204-207	5	5	
208-211	7	6	1
212-215	5	5	
216-219	7	7	
220-223	20	19	1
224-227	11	11	
228-231	9	8	1
232-235	2	2	
236-239	3	2	1
244-247	1	1	
248-251	1	1	
Totals	88	83	5

Table 11. Estimated numbers of eggs and nests produced by 88 mature desert tortoises in Plot 1 in 1986.

Midpoint of body size interval (mm)	Eggs in clutches		Number of nests
	1	2	
185.5	5.26		2
189.5	5.68		2
193.5	15.27		5
197.5	13.06		4
201.5	10.43	4	5
205.5	18.45		5
209.5	23.41	4	8
213.5	20.57		5
217.5	30.28		7
221.5	86.21	5	21
225.5	52.24		11
229.5	39.69	6	10
233.5	10.35		2
237.5	10.77	6	4
245.5	5.81		1
249.5	6.02		1
Totals	354	25	93

1986; or 1980, 1984, 1985 and 1986; or 1983, 1985 and 1986. In such instances we assumed that these females were part of the breeding population during the year not recorded.

Table 12 gives revised estimates of numbers of breeding females in Plot 1 (assuming sexual maturity at 185 mm in length) between 1983 and 1986, and new estimates of numbers of nests prepared during those four years.

Table 12. Revised estimates of numbers of breeding females in Plot 1 and numbers of nests prepared between 1983 and 1986.

Years	Estimated number of breeding females	Estimated number of nests prepared
1983	95	180
1984	90[1]	141
1985	92	174
1986	88	93

[1] 94 females were judged present in 1984, but this number was reduced by 3.85% because one mature female did not lay eggs

Turner et al. (1986) analyzed all of the clutches recorded at Goffs in Plot 2 between 1983 and 1985, and found an overall mean clutch size of 4.5. There was no statistical evidence of differences in the annual means. The mean size of the 15 clutches observed in Plot 2 in 1986 (3.53) was, however, significantly less than the overall mean between 1983-1985. Table 13 summarizes all available egg production data from Goffs in terms of mean values of clutch size and frequency.

Before we attempt to interpret the information in Table 13 it is worthwhile to review the initial procedures we adopted, the original assumptions underlying these methods, and what led us to change our approach after 1984. The BLM originally approved the use of Plot 1 for our study with the provision that disturbance and handling of tortoises occupying this Permanent Study Plot be minimized. In particular, the BLM did not wish for females in Plot 1 to be X-rayed. We established Plot 2, to the southwest of Plot 1, so that we could

Table 13. Mean clutch sizes (first and second clutches) and frequencies observed at Goffs, 1983-1986. Standard errors of means are also indicated.

Years	Variable	Plot 1	Plot 2
1983	Clutch size	-	4.17 ± 0.22
	Clutch frequency	-	1.89 ± 0.11
1984	Clutch size	-	4.28 ± 0.20
	Clutch frequency	-	1.57 ± 0.12
1985	Clutch size	5.15 ± 0.34	5.12 ± 0.21
	Clutch frequency	1.89 ± 0.11	1.75 ± 0.12
1986	Clutch size	4.42 ± 0.28	3.53 ± 0.26
	Clutch frequency	1.06 ± 0.06	1.50 ± 0.17

X-ray females in this area. The distance between the centers of the two plots was about 4.8 km. We believed that events observed in Plot 2 would be representative of what occurred in Plot 1. The basic plan, then, was to measure egg production in Plot 2, and to base other features of the study on measurements in Plot 1. These last included rainfall, estimates of dry matter production by herbs and grasses, and mortality rates of tortoises.

After a year we began to measure rainfall in both plots. Rainfall data showed that, whereas winter rainfall in the two plots was similar, summer and early fall rainfall (July-September) sometimes differed. Because we were in doubt as to possible effects of summer rain (and associated plant growth) on the energy budgets of female tortoises, we recommended to the BLM that tortoises in Plot 1 be X-rayed in 1985 and 1986. The agency concurred.

Our analysis of egg production data from Plots 1 and 2 in 1985 showed no statistically significant differences between the plots--either in terms of clutch sizes or clutch frequency (Turner and Berry, 1986: 24). The 1986 data, however, were not similar. We have shown (Table 4) that winter rainfall before the 1986 season was the lowest measured during the study, and it may be that the severe conditions during 1986 were somehow related to the plot differences. The estimates of net production by plants in Table 4 do not, however, support this idea.

We can group the clutch frequencies observed in Plot 2 between 1983 and 1986 as illustrated in Table 14, and ask whether there is evidence of year-to-year differences in clutch frequencies.

Table 14. Distributions of clutch frequencies among female tortoises in Plot 2 between 1983 and 1986. Expected values are given in parentheses.

Years	0-1 clutches	2-3 clutches
1983	3 (6.1)	16 (12.9)
1984	9 (7.3)	14 (15.7)
1985	6 (6.4)	14 (13.6)
1986	5 (3.2)	5 (6.8)

Total X^2 (with 3 d.f.) is about 4.4, and this is not a statistically significant value ($X^2_{0.05} = 7.8$). This result is the same as that obtained using data from 1983-1985 only (Turner et al., 1986: 98). These authors observed that when data from Ivanpah Valley (Turner et al., 1984) were combined with those from Goffs, the X^2-test of a possible difference between years was statistically significant. The very low mean clutch frequency measured in Plot 1 at Goffs in 1986 (1.06) supports this idea. Table 15 summarizes six estimates of mean clutch frequency among desert tortoise populations and includes associated estimates of net dry matter production by annual herbs. Data for 1980 and 1981 are those obtained in Ivanpah Valley.

Table 15. Estimates of clutch frequency in Plot 2 at Goffs and in Ivanpah Valley and related estimates of net dry matter production by annual herbs.

Locale	Years	Dry matter production by annual herbs (g/m^2)	Mean clutch frequency
Ivanpah Valley	1980	8.5	1.60
	1981	0.07	1.10
Goffs	1983	14	1.89
	1984	0.3	1.57
	1985	2.6	1.75
	1986	0.6	1.50

Figure 2 illustrates the information given in Table 15. When mean clutch frequencies are regressed on common logarithms of estimates of net dry matter production by annual herbs the positive correlation observed is statistically significant ($\underline{r} = 0.84$, $\underline{p} = <0.05$).

Taking into account these data and the two clutch frequency estimates for Plot 1 in 1985 and 1986, we believe that the frequency with which desert tortoises lay eggs in the California desert is affected by available spring

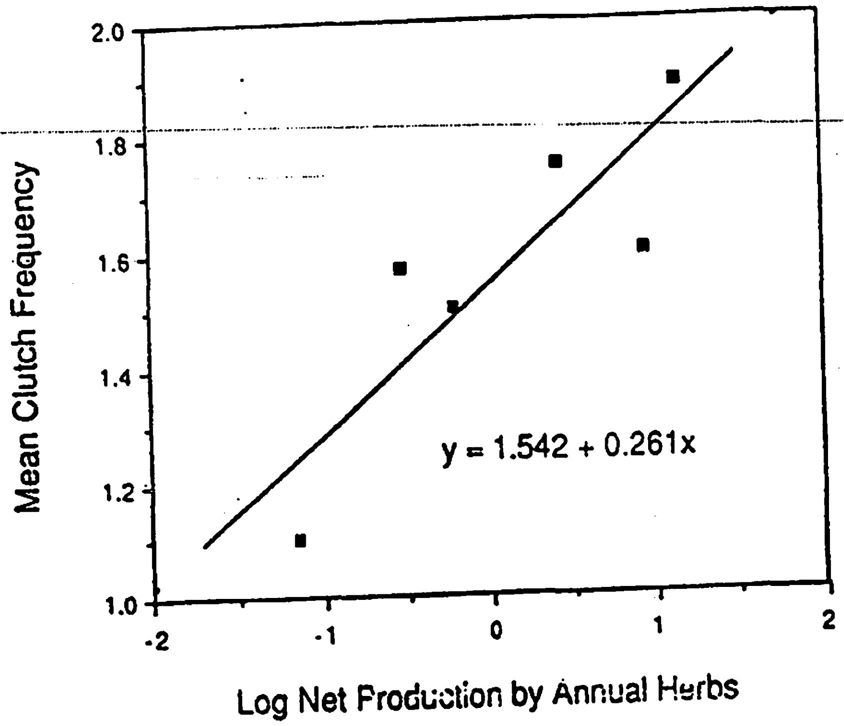

Fig. 2. Relationships between mean clutch frequency and net production by annual herbs (g/m^2)

forage (principally as represented by annual herbs) and that mean frequencies are higher in favorable years. The relationship is not a simple one and may be affected by small-scale local variations in available forage as well as by additional food resources stimulated by summer rainfall. This problem was reviewed in detail by Turner et al. (1986: 102-103).

When we construct a life-table for the tortoise we must reduce the available information concerning egg production to a set of age-specific fertility values. The table will not accommodate year-to-year variations, but can only reflect what might be judged the "average" experience of a population over a number of years. The principal determinant of female fertility is body size, which affects both clutch size and the probability that a female will lay two clutches. An analysis of all egg production data (Plots 1 and 2, 1983-1986) showed that the overall mean clutch size (based on 183 clutches), was 4.46, not significantly different than the mean of 4.50 based on 110 clutches laid in Plot 2 between 1983 and 1985 (Turner et al., 1986: 101). The 4-year analysis showed no significant difference between sizes of first and second clutches, but indicated that if a female laid a single clutch it was, on average, about 0.5 egg larger than the first clutch laid by a female laying two clutches. Clutches laid in 1985 were slightly larger, and those in 1986 slightly smaller, than those laid in 1983 and 1984. These points will be discussed more fully in our ensuing description of a life-table for the tortoise.

E. Mortality

Pre-natal mortality. Losses after eggs are laid may be owing to infertility, accidental breakage, and destruction by predators. Burge (1977) used a dissecting microscope to examine fragments of shells of 10 tortoise eggs which did not develop and 10 eggs which hatched normally. She reported that a "...visibly distinguishable characteristic was found to be...consistent for... undeveloped and hatched eggs." The inner surfaces of shells of undeveloped eggs are highly convoluted while those of developed eggs are eroded--with the relief of the convolutions reduced. Shells of undeveloped eggs are difficult to puncture without crushing, while fertile eggs (approaching the time of hatching) are easily broken by only slight pressures. In 1986 Burge examined shell fragments of 32 eggs found in nests excavated by predators in Plot 1. She concluded that shells of 28 eggs were clearly "eroded" or fertile and that one showed no evidence of erosion at all. Three others could not be unequivocally classified. These findings suggest a natural fertility rate of 97%. In 1985 field workers tracked the fate of nine nests given some protection from predators and 13 unprotected nests. A total of nine nests escaped predation and all 45 eggs in these nests were fertile. Turner et al. (1986) reported on the fates of 57 eggs in protected nests, of which 50 (88%) were fertile. In summary, of 131 eggs under observation during 1984-1986 only eight were judged infertile. We assume, then, a natural fertility rate of 93.9%. Observations in 1984 showed that 6.6% of eggs laid may be broken during oviposition or later (Turner and Berry, 1985: 28). Taking these factors into account, we estimate that 87.7% of eggs laid will be unbroken and fertile.

Estimating the extent of nest destruction by predators was a difficult procedure. Our general approach was to examine Plot 1 continually during May, June and August, and record the number of excavated nests. Presence of broken egg shells was taken as evidence of the destruction of a nest. The number of nests destroyed was then compared with the estimated number of nests prepared--based on numbers of reproductive females in Plot 1 and numbers of clutches laid during the season (Table 12). Another source of information was to observe the frequency of destruction among a group of marked nests, assuming that the fate of this group could be extrapolated to the entire array of nests in Plot 1. Table 16 summarizes information of both types and shows average nest destruction rates of 37% (above) and 63% (below).

We draw the following conclusions from the information in Table 16: (1) nest destruction rates were higher in 1985 and 1986 than in 1983 and 1984, (2) rates based on observations of small groups of marked nests tended to be higher than estimates based on total counts of nests, (3) it is possible to confer complete protection to eggs (1984), but this requires moving eggs from natural nests to cages, and (4) attempts to confer protection to undisturbed nests by means of screening (1985, 1986) ranged from moderately successful (1985) to virtually useless (1986). We do not know if the repeated inspections of marked nests tended to facilitate predation or not.

Table 16. Evidence of destruction of desert tortoise nests at Goffs, 1983-1986. All data from Plot 1 unless otherwise indicated.

Type of information	Years	Nests destroyed	Nests not destroyed	Nest destruction (%)
Total counts of excavated nests and estimates of total nests prepared	1983	49	131	27.2
	1984	34	107	24.1
	1985	77	97	44.3
	1986	49	44	52.7 $\bar{x}$ = 37%
Groups of nests under direct observation	1984[1]	0	14	0
	1984[2]	15	15	50.0
	1985	10	3	76.9
	1985[1]	3	6	33.3
	1986[1]	11	1	91.7

[1] protected

[2] Plot 2

Mortality of tortoises. In previous reports we discussed estimates of survival rates of tortoises in Plot 1 based on minimum rates of recapture from one year to the next and on numbers and sizes of carcasses found in the plot. As capture-recapture data pertaining to marked tortoises at Goffs increased, we decided it would be advantageous to use the annual registries (beginning with Burge's work in 1977) to make a more formal analysis of mortality. In this report we present an analysis of all available sampling data from Goffs, including results of the final season of work in 1986. The analysis considers survival of tortoises composing different sex and size groups between 1977 and 1985. It is this work that we later use as a basis for creating a life-table for the Goffs population.

A central assumption to our approach was that body size, and possibly sex, affect both the probability of capturing tortoises and their survival rates. We began, then, by establishing 11 groups of tortoises: (1) males >208 mm long, (2) females >208 mm, (3) males 180-208 mm, (4) females 180-208 mm, and (5) tortoises 155-179 mm, (6) 140-154 mm, (7) 120-139 mm, (8) 100-119 mm, (9) 80-99 mm, (10) 60-79 mm, and (11) <60 mm in carapace length. Because tortoises grew during the study, the analysis provided a mechanism allowing individuals to increase in size through time, and to change their group membership accordingly.

The modified Jolly-Seber model was used to estimate annual survival (ϕ) and probability of capture (P) for each of the 11 groups, using numerical procedures available in Program SURVIV (White, 1983). The following notation was used for survival and capture probability within a group: ϕ_1, ϕ_2, ϕ_3, ϕ_4, and ϕ_5 represented annual survival for the intervals 1977-1980, 1980-1983, 1983-1984, 1984-1985, and 1985-1986, respectively. These intervals extend from around mid-May of the first year to mid-May of the last year. The probabilities of capture in years 1980, 1983, 1984, 1985 and 1986 were represented by P_2, P_3, P_4, P_5 and P_6, respectively. To illustrate the use of such notation, the probability of next recapturing a tortoise in 1986 originally marked in 1984 is the product of the following four terms: ϕ_4, $(1-P_5)$, ϕ_5, and P_6. The notations apply to each of the 11 groups, but a different set of ϕ's and P's apply to each group because of the expected influence of body size on these parameters.

Because both survival and capture probability are assumed to be influenced by size, the logistic model was used to estimate capture probabilities and survival as a function of size across groups. For example, the estimated annual survival rate of tortoises in Group 6 can be expressed as:

$$\phi_1 = \frac{\beta_2}{1 + e^{(-\beta_o - 149\beta_1)}} \tag{2}$$

with β_0 the intercept, β_1 the slope and β_2 the asymptote of the logistic. The values of β_0, β_1 and β_2 are the same for all 11 groups of tortoises analyzed for any particular time interval. What varies in Equation (2) is the body size. The effect of body size is expressed by the multiplier of β_1. In Equation (2) the number 149 is the mean body length (mm) of the Group 6 tortoises whose survival is estimated by the equation.

Survival rates could be estimated for only the first four of the five intervals defined above: 1977-1980, 1980-1983, 1983-1984 and 1984-1985. An estimate of survival between 1985 and 1986 would require a sample taken in 1987. The first two of the foregoing intervals are three years, the last two one year. To maintain compatibility among parameters the functions for 1977-1980 and 1980-1983 were entered as ϕ_1^3 and ϕ_2^3. We thus assumed an invariant annual rate of survival for the two 3-year intervals. That is, if the overall 3-year survival rate was 70.5%, the annualized rate was $(70.5\%)^{1/3}$ or 89%.

The input for the survival analysis was composed of 11 sets of capture-recapture histories of tortoises at Goffs between 1977 and 1986. Each set pertained to one of the 11 size-sex groups defined previously. Table 17 illustrates three of the 11 sets: Group 1 (male tortoises greater than 208 mm in length), Group 4 (female tortoises 180-208 mm long), and Group 6 (tortoises 140-154 mm long). The table shows (for each group) the number of different individuals registered in each of the years 1977-1985 followed by numbers indicating years when first subsequent recaptures occurred. Average sizes of the tortoises in these groups were also part of the analysis, but we do not show these in Table 17.

Because of the complexity of the modeling procedure, a series of models was used to develop the final model. The first step was to use SURVIV to derive a model which assumed that probabilities of capture and survival rates of groups were constant throughout the course of the study (YEAR-SAME). Asymptotes for each logistic function were set at 1.0. This simple model had only six parameters and was a reasonable starting point for the modeling process. The next model (YEAR-DIFF) allowed for differences between years, but retained asymptotes of 1.0 for all groups. The most complex model (ASYMPTOTE) was like YEAR-DIFF, but permitted asymptotic values for logistic functions to vary. None of these three models provided an adequate fit to the observed data as determined by the X^2 goodness-of-fit test in Program SURVIV. Furthermore, the likelihood ratio test of the ASYMPTOTE model versus the simpler model YEAR-DIFF was not significant, indicating that allowing for variations in asymptote estimates did not improve model performance.

Table 17. Histories of annual registrations and first subsequent recaptures among three groups of desert tortoises at Goffs between 1977 and 1986.

Groups	Year of registration	n	Years first subsequently recaptured 1980	1983	1984	1985	1986
1	1977	40	31	3	0	0	0
	1980	93	-	72	1	0	0
	1983	108	-	-	75	8	2
	1984	84	-	-	-	62	9
	1985	75	-	-	-	-	55
4	1977	17	9	3	0	0	0
	1980	20	-	17	0	0	0
	1983	33	-	-	20	4	0
	1984	18	-	-	-	10	5
	1985	18	-	-	-	-	13
6	1977	6	3	1	1	0	0
	1980	15	-	12	0	0	0
	1983	16	-	-	6	3	1
	1984	11	-	-	-	3	3
	1985	12	-	-	-	-	7

Examination of the partitioned goodness-of-fit test in Program SURVIV revealed the basis for lack of fit: Group 2 females (>208 mm) contributed large X^2 values. The recorded numbers of captures usually exceeded expected numbers. This tendency was also evident among smaller females (180-208 mm). Conversely, adult males (Groups 1 and 3) generally exhibited fewer observed captures than expected.

We believe it possible that these disparities reflect real differences in the behavior of adult male and female tortoises. Female tortoises utilize somewhat smaller areas than males and have a higher fidelity to these areas. We believe there is more wandering in males, with a greater tendency to leave Plot 1 at certain times. More subtle social interactions between large dominating males and smaller males might also be at work. In any event, we experimented with effects of adding a parameter to the model allowing differential behavior of mature females. This parameter (β_3) pertains only to groups 2 and 4, and is incorporated into Equation (2) in the following manner:

$$\phi_1 = \frac{\hat{\alpha}}{1 + e^{[-\beta_o - \underline{L}^{t}{}_{1} - (\underline{L}-180)\beta_3]}} \qquad (3)$$

Here $\underline{L}$ is the average size of the females in the respective groups.

We ultimately experimented with seven different models of varying complexity and parameterization: (1) survival constant through time, (2) survival variable through time, (3) asymptotes variable (rather than fixed at 1.0), (4) survival constant among all size groups but variable over time, (5) probabilities of capture constant among all groups but variable over time, (6) asymptotes and female behavior variable, and (7) female behavior variable and survival variable through time. Some of these models are obviously unrealistic in a biological sense, and it was encouraging to find that most of these models failed to fit the observed data (Table 18):

Table 18. Results of goodness-of-fit tests of alternative models of desert tortoise survival at Goffs. Models are numbered as in the foregoing text.

Model Number	Log-likelihood	d.f.	Probability of larger X^2 value
1	-237.5	149	<0.001
2	-208.2	137	0.070
3	-205.4	128	0.030
4	-215.9	141	0.041
5	-263.3	141	<0.001
6	-192.8	125	0.259
7	-195.2	123	0.402

Here the smaller the value of $\underline{p}$ (right-hand column) the worse the fit. Only the last two alternatives performed well, and we judged that the most parsimonious model fitting the observed data is the one allowing for annual variations in survival and for differential female behavior (7). Table 19 gives estimates of the parameters used to compute annual survival rates of tortoises using this model.

Table 19. Values of β_o, β_1, β_2 and β_3 used to estimate annual rates of desert tortoise survival at Goffs, 1977-1986. Confidence intervals are given for estimates of β_o and β_1.

Model parameters	1977-1980	1980-1983	1983-1984	1984-1985
Intercept (β_0)	0.43	1.22	1.08	1.47
95% confidence interval (β_0)	-1.07 to 1.93	0.39 to 2.04	-0.10 to 2.27	01.23 to 4.17
Slope (β_1)	0.0088	0.0046	0.0011	0.0023
95% confidence interval (β_1)	0.0011 to 0.0165	0.00034 to 0.00896	-0.0046 to 0.00674	-0.0097 to 0.0142
Asymptote (β_2)	1.0	1.0	1.0	1.0
Adult female behavior (β_3)	0.0176	0.0176	0.0176	0.0176

Estimates of annual survival rates for all groups of tortoises are given in Table 20 and associated estimates of probabilities of capture are illustrated in Figure 3. The geometric mean annual survival rates (GMS) for different groups were computed so as to give triple weight to the estimates for 1977-1980 and 1980-1983, i.e., for the i_{th} group:

$$GMS_i = [(1977\text{-}1980)^3(1980\text{-}1983)^3(1983\text{-}1984)(1984\text{-}1985)]^{1/8} \quad (4)$$

For example, to estimate the geometric mean annual survival of tortoises 155-179 mm long, one would compute:

$$[(0.870^3)(0.880)^3(0.780)(0.864)]^{1/8} \quad (5)$$

Table 20. Estimated annual rates of desert tortoise survival at Goffs among 11 sex-size groups and weighted geometric means of estimates for four different intervals.

Tortoise groups (sizes in mm)	Size used in model (mm)	1977-1980	1980-1983	1983-1984	1984-1985	Geometric mean annual survival
Males >208	265	0.941	0.920	0.798	0.888	0.907
Females >208	225	0.961	0.955	0.893	0.941	0.944
Males 180-208	194	0.895	0.892	0.785	0.871	0.876
Females 180-208	194	0.916	0.914	0.823	0.896	0.901
155-179	167	0.870	0.880	0.780	0.864	0.861
140-154	147	0.849	0.870	0.776	0.858	0.848
120-139	130	0.829	0.860	0.773	0.853	0.836
100-119	110	0.802	0.849	0.769	0.848	0.821
80-99	90	0.773	0.837	0.765	0.842	0.804
60-79	80	0.757	0.830	0.763	0.839	0.795
<60	52	0.709	0.811	0.757	0.830	0.767

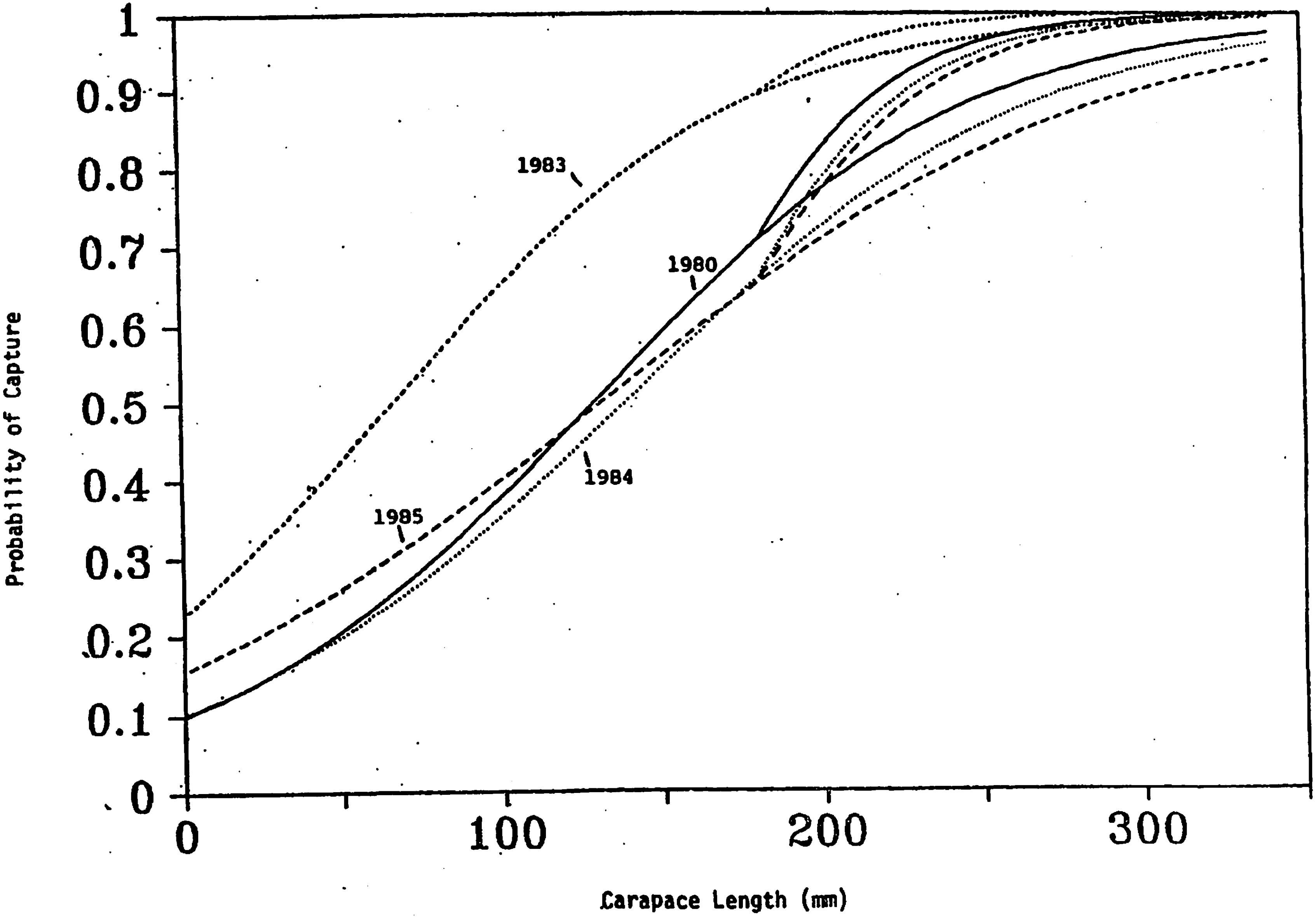

Fig. 3. Estimated probabilities of capture of desert tortoises at Goffs as a function of body size and sex, 1983-1986. The separation of lines at a size of 180 mm represents differences between females (upper) and male (lower) tortoises.

The process of deriving the definitive survival model, and comparisons of the ability of this model and various alternatives to fit observations, strongly support our assumptions of year-to-year differences in mortality as well as the effect of body size on this process. These points are eminently reasonable from a biological point of view. It is also a fact that allowing for differential behavior of females improved the fitting process greatly (see Table 18). Here we are less confident as to how, or whether, this can be interpreted in terms of the biology of tortoises. An earlier test of minimal survival of adult males and females between 1977 and 1980 showed no statistically significant difference between the sexes (Turner and Berry 1985: 32).

Turner and Berry (1986: 31) discussed the limitations of estimates of mortality based on remains of tortoises. One problem is that when one continues to work in an area (as we did between 1983 and 1986) one continues to find old remains, and each such discovery invalidates (to some degree) earlier estimates of survival. Counting carcasses does define a minimum number of deaths in the area of interest. Over and above this, however, one must decide on the time interval during which the deaths occurred and estimate the size of the population, or subpopulation, from which these remains derived.

Only two remains of tortoises were found in Plot 1 in 1986 and both of these were <140 mm in length. Inspections of Plot 1 between April 1983 and August 1986 yielded remains of 106 tortoises. Of these, 82 (77%) were <140 mm long. Of the 24 others (all ≥180 mm long) 20 were of discernible sex (7 females and 13 males). Forty-two of the 106 dead tortoises were judged to have died prior to 1983. Table 21 summarizes data pertaining to the 64 individuals that died in Plot 1 during the course of the study.

Table 21. Remains of desert tortoises found in Plot 1 and judged to have died during the course of the Goffs study, 1983-1986. Numbers in parentheses indicate numbers of marked tortoises.

Carapace length (mm) and sex	Estimated years of death			
	1983	1984	1985	1986
<140	37 (2)	11 (9)	5 (2)	2
Males 180-207		1 (1)		
Females 180-207	1 (1)			
Larger males		2 (2)	2 (2)	
Larger females			1 (1)	
Larger, unsexed	1	1		
Totals	39 (3)	15 (12)	8 (5)	2

Sixty-four deaths over 42 months in a population of at least 450 tortoises suggest a low rate of mortality. Turner and Berry (1985: 33) observed that survival estimates based on remains should be viewed as "maximal," and it is not surprising that the information in Table 21 and our earlier analyses of annual adult survival based on remains (ca. 97 to 98%) are higher than estimates in Table 20 (see Turner and Berry, 1984: 32; Turner and Berry, 1985: 31). In 1983 we registered 219 tortoises $\geq$180 mm long (Turner and Berry, 1985: 15). The sampling efficiencies for 1983 (see Fig. 3) suggest that there were about 228 tortoises of this size in Plot 1. If only nine of these died between April 1983 and August 1986 (Table 21), the annualized survival rate would be 98.8%. Estimates of annual survival between 1983-1984 and 1984-1985 for tortoises ≥180 mm (Table 20) are generally less than 90%.

F. Predators and their Prey

Mortality of desert tortoises varies from year to year, but the reasons for this are not known. Woodbury and Hardy (1948) commented: "The predator pressure on tortoise probably varies from time to time. Perhaps it is correlated with the rabbit cycle. Rabbits...were very abundant [in southwestern Utah] during the years 1941 and 1942, but the cycle reached a low from 1943 to 1946. During late 1945 and early 1946, tortoise fatalities obviously due to carnivores showed an increase when compared with the few such signs observed earlier. Perhaps the tortoise is subjected to a greater amount of...pressure from bobcats and coyotes when the usual food--rabbits--is scarce." Berry (1975) stated that the China Lake tortoise population experienced losses of 21 to 28% in the winter of 1972-73 because of canid predation (cf. an estimated annual loss rate of only 5% during the previous year). Turner et al. (1984) reported 4.4% annual mortality in Ivanpah Valley in 1980-81 and 18.7% mortality in 1981-82. None of these earlier studies presented data relating to the abundance of predators or rabbits.

At Goffs we made simple observations of the relative abundance of predators (including raptorial birds), rabbits and rodents, to see if such data could help to interpret observed death rates of tortoises. Observations of birds were made throughout Plot 1 whenever workers were in the area. Counts of rabbits and hares were also made in Plot 1. The degree of effort varied seasonally depending on numbers of workers and changes in duty assignments. All observations were converted to sightings per survey-hour.

Almost all potential predators observed in 1985 were birds, but--as in previous years--most dead tortoises found were apparently killed by canids. These mammals were rarely seen, so we recorded indirect signs of their presence, e.g., dens and numbers of scats. Observations of predatory birds and signs of mammals in 1986 are given in Table 22. Scat counts include data from predator sign concentrations, kit fox dens and other observations.

As in 1984, rodents were trapped along two parallel lines, each with 25 trapping stations and two traps per station. In 1986 we trapped on nights of 2 March, 11 May and 9 June. As pointed out previously (Turner and Berry, 1986:38), only data pertaining to kangaroo rats (Dipodomys merriami) were amenable to analysis. Table 23 compares trapping success between 1984-1986. Chi-squared tests of these data show that success in 1984 was better than in 1985 and 1986, while the latter two years did not differ.

We believe the apparent differences in bird observations may be more related to the efficiencies of different workers than to real events. Presence of kit foxes in Plot 1 was fairly stable throughout the study, but slightly reduced in 1986. The number of canid scats collected in 1985 was substantially lower than in the other three years. Measures of the presence of both lagomorphs and kangaroo rats in Plot 1 both indicated highest numbers in 1984.

Table 24 summarizes observations relating to predatory birds and canids, lagomorphs, and kangaroo rats in Plot 1 between April and August, 1983-1986. One problem with these data is that measures of the presence of preadators do not tell us what these animals are doing. The situation is analogous to that described by Turner et al. (1982a) in evaluating studies of "predation pressure"

Table 22. Indicators of predator activity in Plot 1 at Goffs in 1986.

Indicators	April	May	June	August
Observations of avian predators per survey-hour	0.073	0.812	0.108	0.051
Prairie Falcon		x	x	
Red-tailed Hawk	x	x		x
Other Hawks	x			
American Kestrel	x			
Greater Roadrunner			x	
Common Raven	x	x	x	x
Loggerhead Shrike	x	x	x	x
Number of occupied kit fox dens	0	1	3	4
Number of active or visited fox dens	18	no data	17	21
Number of fox dens observed by field workers	66	10	65	66
Predator scats for 1986				
Kit fox	337	8	103	155
Coyote	44	7	39	17
Badger (?)			1	
Raptor pellets	62	8	26	5

and broken tails among lizards. These authors observed that (1) counts of predators may not be consistently related to predator abundance, (2) numbers of coexisting predatory species are not necessarily simply related to predation

Table 23. Comparison of trapping success (*Dipodomys merriami*) in Plot 1, 1984-1986. Expected values (assuming equal success in all three years) are in parentheses.

Years	Traps with rats	Empty traps	Totals	Overall trapping success
1984	344 (303.6)	156 (196.4)	500	69%
1985	169 (182.2)	131 (117.8)	300	56%
1986	155 (182.2)	145 (117.8)	300	52%

Table 24. Observations of predators and their prey in Plot 1 between April and August, 1983-1986.

Indicators	1983	1984	1985	1986
Avian predators per survey-hour				
Range	0.05-0.12	0.04-0.22	0.02-0.33	0.07-0.81
Mean	0.09	0.10	0.15	0.26
Numbers of occupied kit fox dens	6	6	6	4
Total scats of coyotes and kit foxes	890	779	426	710
Numbers of hares and rabbits per survey-hour				
Range	0.02-0.26	0.25-0.32	0.14-0.33	0.14-0.25
Mean	0.13	0.28	0.24	0.20
Trapping success, kangaroo rats	no trapping	69%	56%	52%

pressure on prey species, and (3) allowances must be made for prey switching and the way in which predation is affected by changes in densities of participating species. We need direct measures of the actions of predators, not simply their presence. We obviously could not make such measurements within the limitations of our study. To make quantitative evaluations of year-to-year changes in food habits of predators, together with associated changes in numbers of predators and tortoises, was clearly beyond our resources.

We do have two measures of what predators did or did not do at Goffs: (1) analyses of 30 scats of kit foxes collected between April and June 1985 and (2) estimates of rates of tortoise nest destruction. Remains of heteromyid rodents occurred in 91% of fox scats collected in April-May and 68% of scats taken in June. Remains of lagomorphs were in 27% of April-May scats and 37% of those collected in June. There was no evidence of the presence of tortoises in scats. Two scats did contain leathery egg shells, quite possibly those of tortoise eggs. We have direct evidence of destruction of nests of tortoises and the consumption of all or most of the eggs therein. Table 25 summarizes estimates of nest destruction, presence of heteromyid rodents, and incidence of lagomorphs for the years 1983-1986. Here it may be observed that as measures of

Table 25. Proportions of desert tortoise nests destroyed in Plot 1 and estimates of the incidence of kangaroo rats and lagomorphs at Goffs, 1983-1986.

Indicators	1983	1984	1985	1986
Percent nests destroyed	27	24	44	53
Trapping success, kangaroo rats (%)	no data	69	56	52
Lagomorphs per survey-hour	0.13	0.28	0.24	0.20

the presence of rodents and lagomorphs declined (1984-1986), the apparent rate of destruction of nests increased. Our observations suggest that if the impact of canid predators is increased when mammalian prey is scarce, the effect is expressed as increased nest predation and not by direct attacks on tortoises themselves.

VIII. A life-table for the tortoise

General description

The general idea of a life-table is to evaluate the capacity of a cohort of females to replace itself during the lifetime of the cohort. Imagine a population of animals made up of 10 males and 10 females. One-year-old females are sexually immature and 4-year-olds are too old to reproduce. Only females of ages 2 and 3 years lay eggs. Each reproductive female lays two eggs and, on average, these two eggs will produce one male and one female offspring. All eggs are fertile and all hatch. The simple life-table expressing these relationships is illustrated in Table 26.

Table 26. An imaginary life-table showing survival and reproduction by initial cohort of 10 females.

Age, years	Number alive at beginning of interval (l_x)	Number of female eggs laid (m_x)	Total production of female offspring ($l_x m_x$)
0	10	0	0
1	8	0	0
2	6	1	6
3	4	1	4
4	2	0	0
5	0	0	0

The second column in this table is conventionally designated $\underline{l}_{\underline{x}}$ and represents age-specific survival. The third column is designated $\underline{m}_{\underline{x}}$ and shows age-specific fertility (in terms of female offspring). The final column is the product of the middle columns ($\underline{l}_{\underline{x}}\underline{m}_{\underline{x}}$) and shows the number of female offspring born to all females in the cohort during their lifetimes. In this example, the original cohort of 10 females replaces itself precisely, and (assuming normal survival by males) the population would be stable over time. Populations rarely achieve such balance, and schedules of survival and reproduction vary according to chance and conditions of the moment. If effects of bad and good years balance out over time the population will persist at about its original size and the age distribution will tend to be roughly stable. If, owing to a combination of poor survival and/or impaired reproduction, recruitment fails to replace numbers the population will decline. A population may also increase in size when good conditions persist over a long enough period of time. Constructing a life-table for a long-lived species like the tortoise will clearly be a difficult task. It should also be evident that any such table--representing invariant schedules of growth, reproduction and survival--can only be an abstraction of real events.

Size-age relationships among female tortoises

In all of our earlier reports we have discussed egg production and mortality in terms of size-classes of female tortoises. To construct a life-table we need to examine the relationship between size and age of female tortoises and to understand how they grow.

The Goffs data file (1977-1986) provided information relating to growth of female tortoises over a 9-year period (1977-1986). Samples were acquired in 1977, 1980, 1983, 1984, 1985 and 1986. We decided to look at growth over three 3-year intervals: 1977-1980, 1980-1983, and 1984-1986. Sex determinations were not made until tortoises reached a carapace length of 180 mm. Some tortoises were first marked at lesser sizes, became known as females later in life, and contributed information to our analyses. For example, one tortoise, marked in 1977 at a size of 104 mm, provided a continuing record of growth until the summer of 1986.

We first experimented with different rules for selecting pairs of measurements representative of growth over these intervals. The optimal data pair would be a measurement at the beginning of the first year (say, April 10) and another at the end of the third year (say, October 10). Obviously, records of most tortoises did not provide pairs of measurements of this nature. We tried other, more permissive, selection procedures which mobilized progressively more data. These tests showed that variations in growth of different tortoises had a much more pronounced effect on growth increments than subtleties involving the timing of pairs of measurements analyzed. Hence, we selected measurements so as to maximize the amount of available data.

All data were plotted as in Figure 4, in which the letter A represents a single datum, B two points, etc. We plotted the initial size of each tortoise along the horizontal axis and its size after three years of growth along the vertical axis. Clearly, most of the data pertained to tortoises ≥200 mm in length, whose 3-year increments were generally less than 5 mm. The lines in Fig. 4 show something about the variability of growth among females, and how the observations are distributed around the middle (or median) line. For example, half the tortoises with an initial size of 120 mm grew more than 33 mm in three

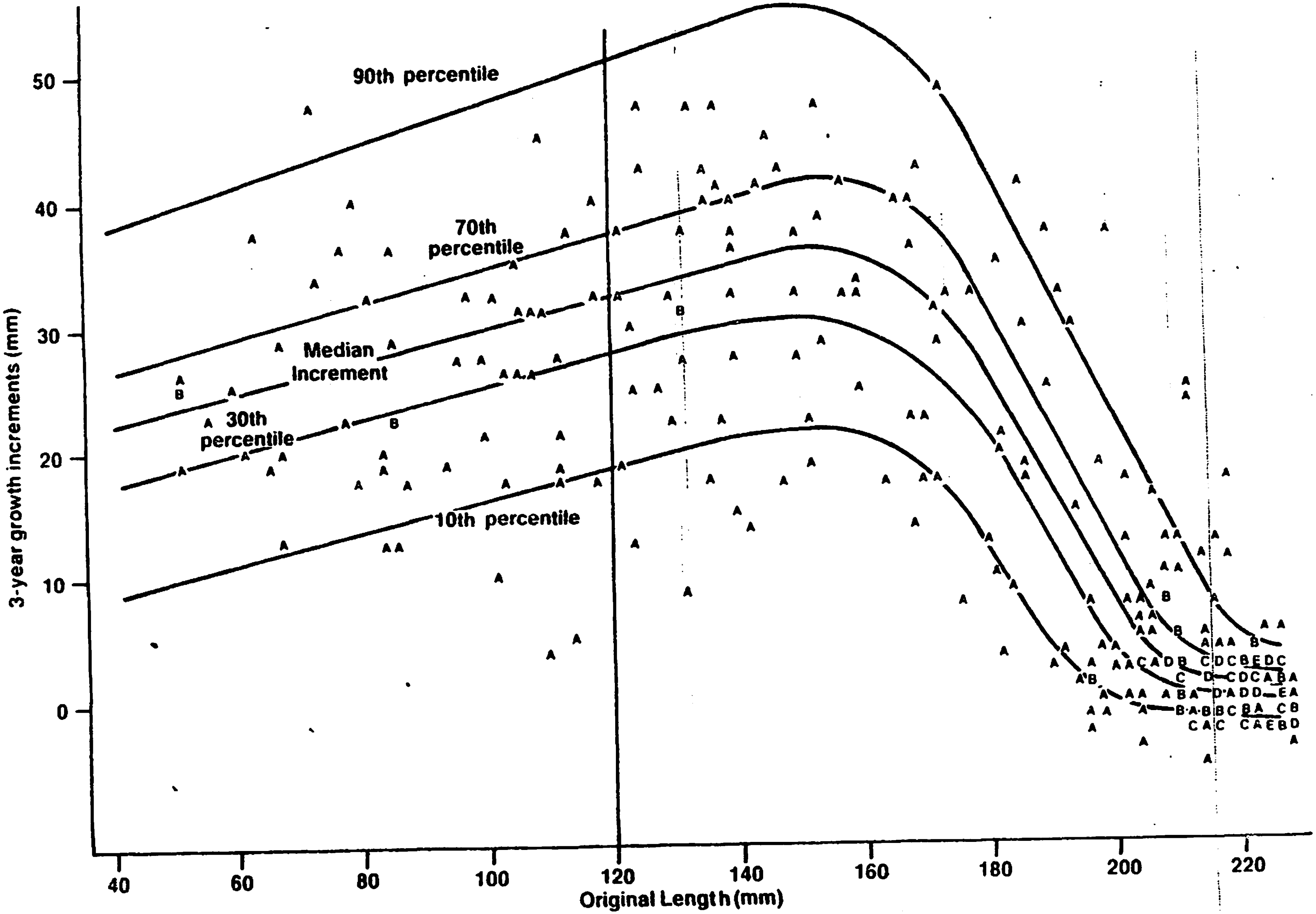

Figure 4. Three-year growth increments (ordinate) as a function of initial body length among female desert tortoises at Goffs, California.

years and half grew less. Three-year growth of 40% of the tortoises of this size ranged from 28 to 38 mm, and 80% of these tortoises grew anywhere from 19 to 52 mm in three years.

By integrating the curves in Fig. 4 we produced a set of growth curves from the time of hatching (age 0, size 45 mm) to around 36 years of age (Fig. 5). These curves show growth of five groups (quintiles) of females, each composing 20% of the female population. The first quintile is made up of the most slowly growing 20% of the population, the second quintile of more rapidly growing individuals, etc., so that the fifth quintile includes the fastest growing 20% of the female population. The lines were drawn assuming that members of each group continue to grow along the same curves throughout their lifetimes. By age 36 the most rapidly growing females reach a size of 248 mm, which is close to the largest female body size (250 mm) recorded in the Goffs population. Other, more slowly growing, individuals level off at lesser body sizes. The median curve (50th percentile) reaches 215 mm after 30 years. About 40% of the population of females attain maximal body sizes of between 209 and 225 mm.

Probably the most illuminating feature of this analysis is the variation in growth among individuals. This aspect of the growth data is so important that we decided to construct the life-table so as to allow for size differences among sexually mature females of the same age. That is, the table would not assume a cohort of females of the same body size (at a given age), but a group of females of varying sizes--and (most importantly) varying fecundity. Fig. 5 was created by assuming that individuals in each quintile would continue to grow at specified rates. That is, a slow-growing female tortoise remains such, while tortoises growing with unusual rapidity continue to outpace other members of the population. We examined this assumption by inspecting all growth records

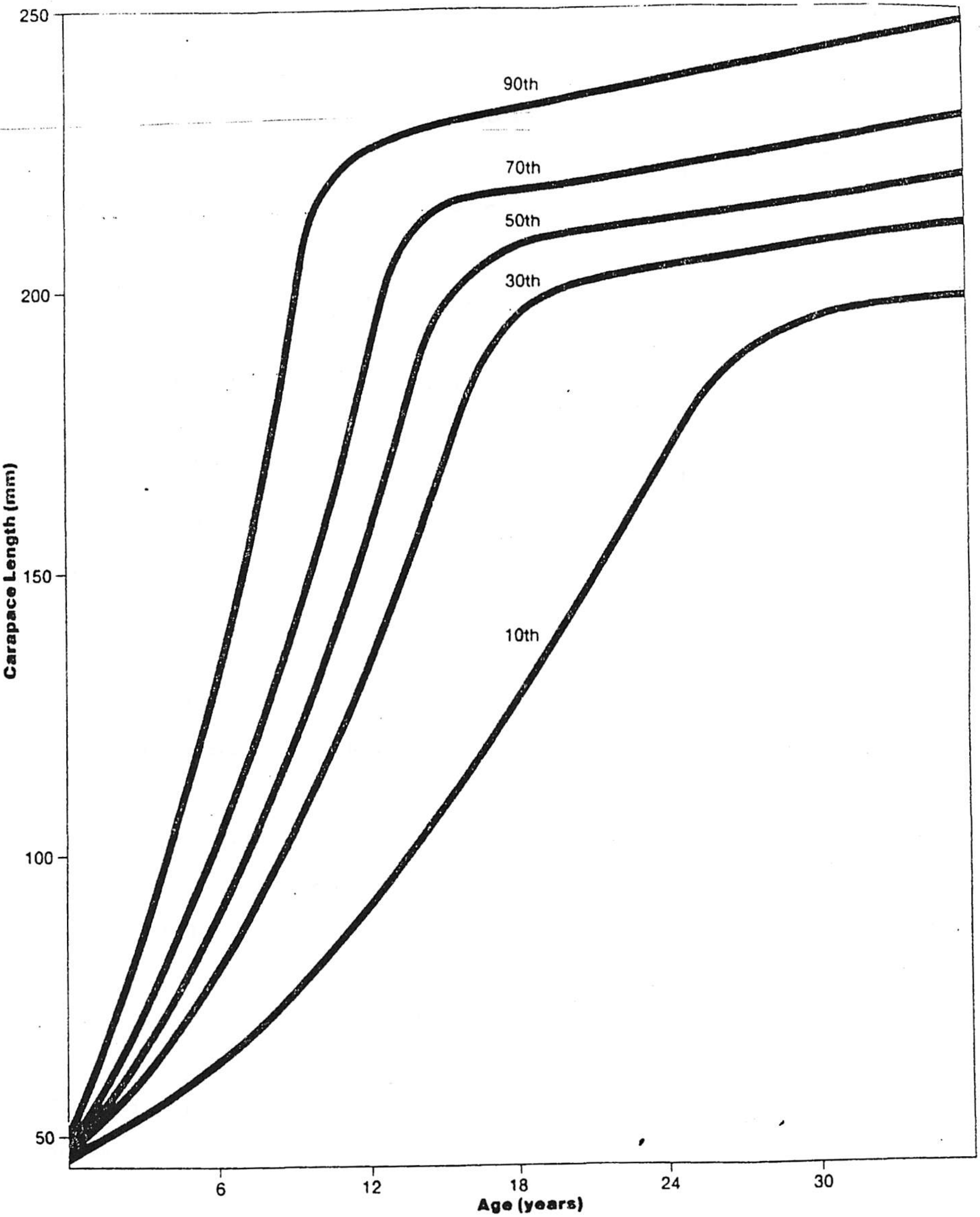

Fig. 5. Growth of female desert tortoises in quintiles composed of individuals with constant growth rates. Figures adjoining curves give midpoints of quintiles as percentiles.

pertaining to the same females during different 3-year growth intervals, e.g., mean growth rate between 1977-1980 contrasted with that between 1980-1983 or between 1983-1986. This analysis showed that once females attained lengths of 175 mm their relative growth rates did remain essentially constant--i.e, fast-growing females continued to grow rapidly, and slow-growing individuals slowly. Percentile scores of these larger tortoises during consecutive 3-year growth periods were highly and significantly correlated ($\underline{r}$ = 0.93). Conversely, consecutive percentile rankings of tortoises <175 mm long were only weakly correlated ($\underline{r}$ = 0.25). This means that smaller tortoises may grow slowly during one three-year period, but exhibit rapid rates of growth later (or the converse could be true).

A simple model was developed conforming with these observations. The first assumption was that females $\geq$175 mm in length would not shift from one quintile to another during their subsequent lifetime. A rate of growth was established and members of each quintile adhered to this pattern. The second step was to assign probabilities that smaller females would either (1) continue to grow at the same relative rate during two successive 3-year periods, or (2) exhibit changes in growth rates. If the latter, we assumed equal probabilities that a female in the $\underline{i}_{th}$ quintile during an initial 3-year period would switch to any of the other four quintiles in the ensuing triennium. We found that by assigning a probability of 0.40 to no change and probabilities of 0.15 for changes to any of four other quintiles produced a pattern of variation in growth consistent with the correlations described above. The new quintiles (Fig. 6) differ from Fig. 5 in that there is now a narrower range of variation, and the growth rate of the slowest quintile is appreciably more rapid than that shown in Fig. 5.

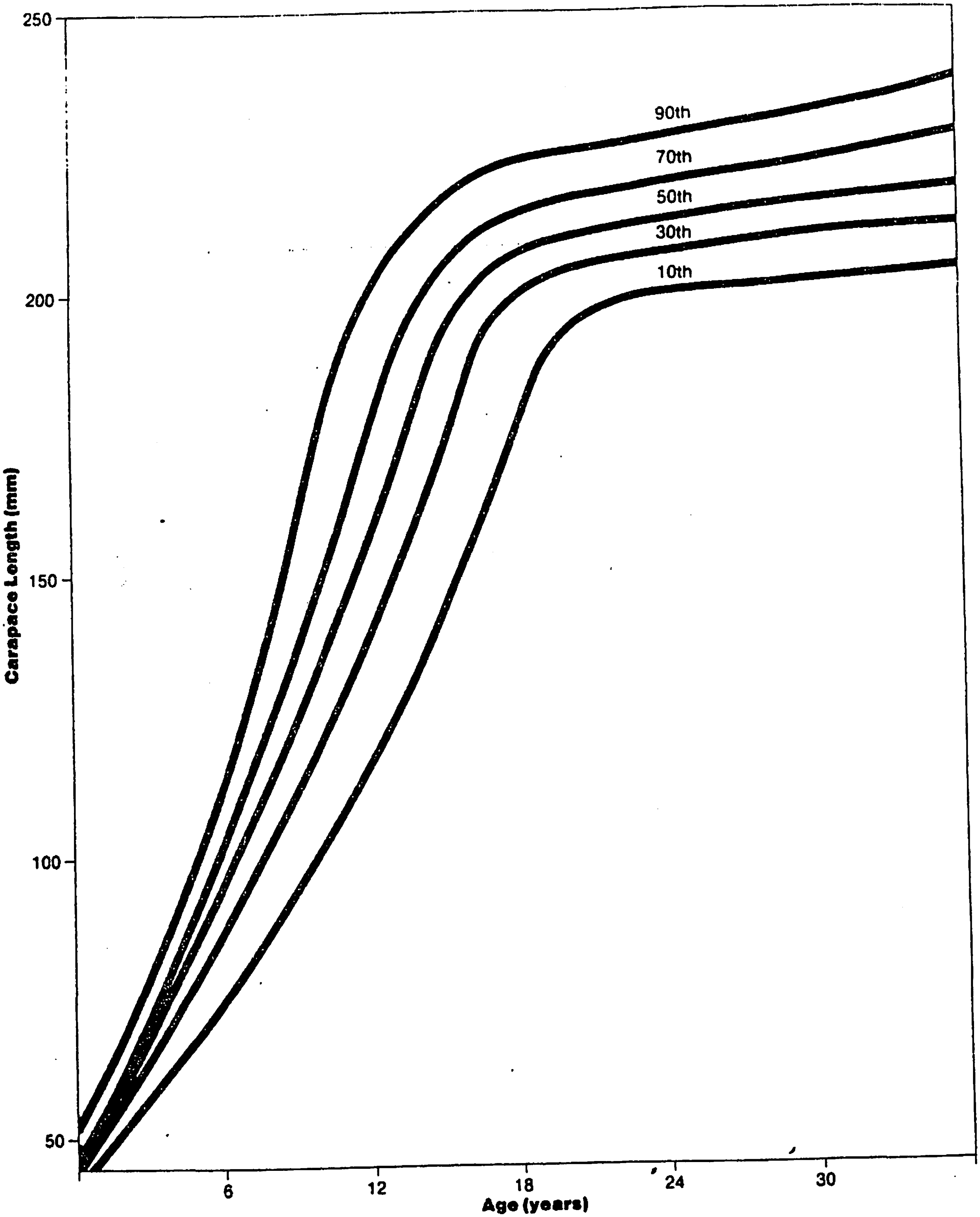

Fig. 6. Growth of female desert tortoises in quintiles composed of individuals with varying growth rates. Figures adjoining curves give midpoints of quintiles as percentiles.

The next step was to use this information in the life-table model--allowing for variation in individual growth rates while at the same time retaining tractability in the modeling process. A hypothetical cohort of female tortoises was analyzed by stepping through 81 years in successive 3-year intervals. Individuals were allowed to vacillate among different 3-year growth rate quintiles according to the above description. After each 3-year period the members of the cohort were sorted according to their size, and corresponding quintiles characterized. The set of quintiles emphasized as forcefully as possible the heterogeneity of the cohort in terms of mean growth rate at any time in the cohort's history. We assumed that mortality experienced by cohort members was independent of body size at a given age. The mean body lengths of individuals in each quintile versus age were taken as representative of the potential experience of a cohort rather than as representations of "typical" individuals.

The growth curves shown in Fig. 6 assumed a size of 45 mm at time zero (hatching). Minor adjustments in these curves to accommodate alternative hatching sizes (e.g., 40 to 50 mm) were built into the life-table program.

Implicit in the foregoing analysis is the assumption that females become mature at a particular body size, and not at any particular age. In the absence of evidence to the contrary we believe this a reasonable assumption. However, Gibbons et al. (1981) showed that female *Pseudemys scripta* in South Carolina become mature at a fixed *age*, while males mature at a fixed size.

Modeling Egg Production

Four years of measurement of egg production at Goffs were available for analysis, including data from two plots and clutch sizes among tortoises ranging from 189 to 250 mm in carapace length. Some tortoises laid a single clutch and some laid two (or, rarely, three). For purposes of modeling egg production we set the minimum body size at 185 mm (see p. 24) and allowed for the production of one or two clutches, but not more. We first considered what we will call a "full" model, which allowed for all main effects on clutch size (i.e., female body size, plots, years, sizes of first and second clutches, whether females laid one clutch or two), and various interactions. This model ($R^2 = 0.415$) had 33 terms and was far more complex than we deemed likely to be necessary.

We then experimented with effects of eliminating interactions. A single hypothesis test eliminated all but three first order interactions and led to a model with 10 variables ($R^2 = 0.314$). Then using backwards elimination and maximum R^2 techniques (SAS User's Guide, 1979) we further reduced the model to one with only four terms. This model included only main effects and had an R^2 of 0.287. All terms were significant at the 5% level. The four terms included an invariant slope coefficient (i.e., the effect of female body size on clutch size was constant), lacked any plot effects, and made no distinction between the size of first and second clutches nor between 1983 and 1984. The model distinguished between the size of an only clutch and that of the first of two clutches, and allowed for slight differences in clutch sizes in 1985 and 1986.

The above steps, then, reduced the original full model with 33 terms ($R^2 = 0.415$) to one with only four terms ($R^2 = 0.287$). We believe this reduction in R^2 (or the amount of observed variation explained by the model) is justified because of the much greater simplicity of the model and the likelihood that the 4-term model is apt to have more generality than the full model. Table 27 gives the terms of the 4-variable model as well as _F_-values and associated probabilities. The smaller the probability in Table 27 the greater the importance of the variable.

Table 27. Terms in a four-variable model predicting clutch sizes of desert tortoises at Goffs, 1983-1986.

Terms	*F*-values	Probabilities
Body size	38.6	0.0001
Lays one or two clutches	4.0	0.0478
1985	11.13	0.0010
1986	4.0	0.0469

Table 28 gives regression equations (derived from the four-variable model) for estimating clutch sizes in 1983 and 1984, 1985 and 1986 (taking into account the differences just described). The first three lines of the table show that if a tortoise lays only one clutch it is, on average, about 0.5 egg larger than the first clutch of a female of the same size laying two clutches. This point was also made following our earlier analysis of data from 1983-1985 (Turner et al. 1986). The models also show that 1985 clutches were, on average, about 0.7 egg larger and 1986 clutches about 0.6 egg smaller than those in 1983 and 1984.

We need to incorporate the foregoing information into what might be viewed as an "average" egg production model representing the overall experience observed between 1983 and 1986. Table 28 gives one pair of equations relating to 1983 and 1984 (two of the four years) as well as pairs of equations for the years 1985 and 1986. In combining these equations we need to give double weight to those pertaining to the two-year period (1983 and 1984). The last line of Table 28 gives average equations giving double weight to the 1983-1984 intercepts. It is these final two equations with which we computed age-specific fertility in our life-table model.

Table 28. Equations for estimating clutch sizes ($\underline{C}$) of female desert tortoises at Goffs. Female body size is $\underline{L}$.

Years	First and second clutches	One clutch
1983, 1984	$\underline{C} = 0.03935\underline{L} - 4.13$	$\underline{C} = 0.03935\underline{L} - 3.63$
1985	$\underline{\bar{C}} = 0.03935\underline{\bar{L}} - 3.41$	$\underline{\bar{C}} = 0.03935\underline{\bar{L}} - 2.91$
1986	$\underline{\bar{C}} = 0.03935\underline{\bar{L}} - 4.69$	$\underline{\bar{C}} = 0.03935\underline{\bar{L}} - 4.19$
Weighted mean	$\underline{\bar{C}} = 0.03935\underline{\bar{L}} - 4.088$	$\underline{\bar{C}} = 0.03935\underline{\bar{L}} - 3.588$

Table 29 shows how clutch sizes vary owing to differences in body size and clutch frequency.

Table 29. Estimated mean clutch sizes as a function of female body length and numbers of clutches laid.

Body length (mm)	Lays only one clutch	Lays two clutches
185	3.69	3.19
200	4.28	3.78
215	4.87	4.37
230	5.46	4.96
245	6.05	5.55

We next considered the problem of how to allocate clutch frequencies among the population of breeding females. Turner et al. (1986) analyzed 1983-1985 data from Plot 2 and showed that as females become larger the probability of laying two clutches increases. This effect was also apparent when we examined all available data (1983-1986) from Plots 1 and 2. We established the following probabilities of laying one clutch--depending on female body size: females 185-196 mm (0.696), females 197-215 mm (0.316) and females $\geq$216 mm (0.304). When we tested this system with observed female size distributions in 1985 and 1986 the predicted mean clutch frequencies were 1.68 and 1.65, respectively.

This result is consistent with overall experience at Goffs between 1983 and 1986 (see Table 13).

We have already discussed estimates of natural fertility of eggs (94%) and the fact that a few eggs (6.6%) may be accidentally broken during laying (see p. 36). We must also take into account that some eggs are destroyed by predators while the eggs are developing. We estimated nest predation rates in two ways: (1) by counting destroyed nests and comparing the total to the number of nests believed to have been constructed by breeding females in Plot 1, and (2) by counting nests destroyed among smaller numbers of nests under direct observation. The latter procedure generally produced higher estimates of nest predation. We have no way of resolving this apparent difference using existing data. For modeling purposes, we assumed an average nest predation rate of 37.1% based on total counts of destroyed nests in Plot 1 (see Table 16). We also assumed that the number of eggs in a nest has no influence on its vulnerability. Finally, only half the eggs laid are destined to produce female offspring. For female tortoises of any given age, the probablity that the total eggs laid ($\underline{E}$) will produce live female hatchlings is:

$$E(0.939)(0.934)(0.629)(0.5) \tag{6}$$

or 0.276, where 93.9% of eggs are fertile, 93.4% are unbroken, 62.9% are undestroyed, and 50% are females.

Age-specific mortality rates

Estimating survival of female tortoises involved two principal steps: (1) keeping track of numbers of females of different size-age relationships--as explained in the section on growth (pp. 54-61), and (2) using size-specific survivorship functions to compute annual survival of females of different ages from one year to the next.

Table 20 showed survival rates of female tortoises $\geq$180 mm in length and of various groups of tortoises of lesser size. These functions are continuous so we can estimate annual survival for tortoises of any size. We also wished to use estimates of the mean annual survival observed between 1977 and 1985 and not those values for the shorter intervals represented in Table 20. As explained earlier (p. 42), we could compute an average annual survival rate for tortoises of size x ($x \leq 179$ mm) by using x in Equation (2), then computing annual survival for the intervals 1977-1980, 1980-1983, 1983-1984, and 1985-1986, and finally computing the geometric mean of these values by giving triple weight to the three-year estimates. For example, to estimate the annual survival of a female tortoise 162 mm in length, one solves Equation (2) four times, using values for β_0, β_1, and β_2 as given for four intervals in Table 19. These estimates are, respectively: 0.865 (1977-1980), 0.877 (1980-1983), 0.779 (1983-1984), and 0.863 (1984-1985). The weighted mean survival is then:

$$[(0.865)^3(0.877)^3(0.779)(0.863)]^{1/8} \qquad (7)$$

or 0.858. For female tortoises $\geq$180 mm in length we used Equation (3) and followed the same procedure just described. For example, the four separate interval estimates for a female 200 mm long are 0.927, 0.924, 0.876 and 0.907, respectively. The weighted mean is 0.917.

Results

The final life-table, pertaining to the Plot 1 population, was created by integrating five subtables relating to quintiles of females growing at variable rates. The five subtables, each beginning with 2,000 female eggs, are given in Appendixes 1-5. The overall life-table is shown in Table 30. It begins with 10,000 female eggs, of which 5,517 hatch. The hatching success is the product of the following terms: 0.939 (fertility), 0.934 (unbroken) and 0.629 (undestroyed by predators). Some mortality (ca. 15%) is assumed to occur between the time eggs hatch (late summer and early fall) and the ensuing spring. By April of the year following hatching, at an age we designate year 1, 47% of females in the original roster of 10,000 eggs remain.

Tortoises in different quintiles grow at different rates, and the fastest growing survive better than the most slowly growing. The mean sizes of tortoises of the same age diverge and the rapidly-growing females make up progressively more of the surviving tortoises. Up to the size of 175 mm 60% of the females in any quintile switch randomly to some other quintile every three years. Hence, each quintile comes to be composed of females of different sizes, and the overall life-table reflects the weighted mean size of all of the females (in each of five quintiles) at any given age.

A consequence of the foregoing is that tortoises reach the assumed size of sexual maturity (185 mm) at different ages: 19-20 years, 16-17 years, 14-15 years, 13-14 years, and 11-12 years, depending on predicted growth rates. The summary life-table (Table 30) shows an estimated 429 tortoises 12 years old and the production of about 345 female eggs by this age group. The foregoing discussion makes it clear that only a fraction of the females alive at age 12 are reproducing. In fact, the only breeding females at this age are the 110 composing the fastest-growing quintile (Appendix 5). The $\underline{m_x}$ value shown in Appendix 5 (3.149) was computed on the basis of the mean size of the 12-year old females in this quintile (196.5 mm). At this size, 31.6% of females lay one

Table 30. A life-table for the desert tortoise at Goffs. The last three columns are defined as in Table 26.

Age, x (years)	Mean length (mm)	l_x	m_x	$l_x m_x$
Eggs		10000.0		
Hatch	45.0	5516.5	0.0	0.0
1	49.7	4698.4	0.0	0.0
2	56.2	3591.8	0.0	0.0
3	64.3	2769.7	0.0	0.0
4	73.0	2158.5	0.0	0.0
5	81.8	1700.4	0.0	0.0
6	91.3	1353.5	0.0	0.0
7	101.4	1088.8	0.0	0.0
8	111.8	885.3	0.0	0.0
9	122.8	727.2	0.0	0.0
10	134.4	603.6	0.0	0.0
11	146.4	506.0	0.0	0.0
12	159.0	429.0	0.804	345.087
13	171.0	369.7	0.932	344.713
14	181.	323.3	1.588	513.354
15	191.2	286.9	2.321	665.815
16	198.3	258.2	2.589	668.242
17	203.8	234.6	3.076	721.814
18	208.3	215.2	3.284	706.858
19	211.4	198.8	3.375	670.738
20	213.7	184.4	3.678	678.386
21	215.5	171.8	3.739	642.515
22	217.0	160.6	3.840	616.732
23	218.1	150.4	3.877	583.116
24	219.0	141.1	3.910	551.625
25	220.0	132.5	3.943	522.376
26	220.9	124.6	3.973	495.009
27	221.8	117.3	4.003	469.555
28	222.7	110.5	4.032	445.758
29	223.5	104.3	4.064	423.854
30	224.4	98.5	4.092	403.007
31	225.2	93.1	4.119	383.481
32	226.0	88.1	4.146	365.226
33	226.8	83.4	4.173	348.143
34	227.6	79.1	4.200	332.065
35	228.3	75.0	4.225	316.893
36	229.1	71.2	4.250	302.670
37	229.8	67.7	4.275	289.290
38	230.6	64.3	4.300	276.671
39	231.3	61.2	4.324	264.794
40	232.0	58.3	4.348	253.585
41	232.7	55.6	4.371	242.969
42	233.4	53.0	4.395	232.954
43	234.1	50.6	4.418	223.469
44	234.8	48.3	4.440	214.474
45	235.4	46.2	4.462	205.963
46	236.1	44.1	4.483	197.885
47	236.7	42.2	4.505	190.209

Table 30. (cont.)

Age, x (years)	Mean length (mm)	l_x	m_x	$l_x m_x$
48	237.3	40.4	4.526	182.935
49	237.9	38.7	4.546	176.028
50	238.5	37.1	4.566	169.433
51	239.1	35.6	4.586	163.174
52	239.7	34.1	4.606	157.212
53	240.3	32.8	4.624	151.516
54	240.8	31.5	4.643	146.092
55	241.4	30.2	4.661	140.917
56	241.9	29.1	4.680	135.999
57	242.5	27.9	4.699	131.308
58	243.0	26.9	4.716	126.800
59	243.5	25.9	4.734	122.529
60	244.0	24.9	4.751	118.411
61	244.5	24.0	4.768	114.480
62	245.0	23.1	4.784	110.687
63	245.5	22.3	4.799	107.061
64	245.9	21.5	4.815	103.584
65	246.4	20.8	4.830	100.261
66	246.8	20.0	4.845	97.073
67	247.2	19.3	4.859	93.988
68	247.7	18.7	4.874	91.061
69	248.2	18.0	4.890	88.251
70	248.6	17.4	4.903	85.528
71	249.0	16.9	4.917	82.915
72	249.4	16.3	4.930	80.406
73	249.8	15.8	4.944	77.992
74	250.1	15.3	4.955	75.648
75	250.5	14.8	4.967	73.395
Total				18413.867

clutch and the remainder lay two. Egg production by these females may be computed as follows:

$$0.316(129.7)[0.03935(196.5) - 3.588] = 169.85 \tag{8}$$

$$2\ 0.684(129.7)[0.03935(196.5) - 4.088] = 646.60 \tag{9}$$

Here the mean egg production equations from Table 28 are combined with the numbers of females alive and their respective body size. The 816 eggs are produced by 109.6 females. Half of the eggs are females so the mean female egg production by the 12-year-old cohort is 3.15(109.6) or about 345. Note that in the overall life-table (Table 30), the value of $\underline{m_x}$ (0.804) is computed in terms of all females alive (429) even though only 109.6 are actually reproducing.

By age 20 years, females in all quintiles are reproducing (Table 31) and the computation of total egg production is carried out along the same lines as indicated above. The mean body length of the 184.4 females alive is 213.7 mm, but the proportions of each quintile producing one or two clutches of eggs, and mean clutch sizes, are calculated according to the mean body sizes in each quintile. For example, the most slowly growing females (first quintile) are of a size at which about 70% lay one clutch of eggs, while the probability of fourth and fifth quintile females laying one clutch is only about 30%.

Table 31. Changes in mean carapace length and numbers of survivors among five quintiles of tortoises growing at variable rates. The first quintile reflects the slowest growth, the fifth the most rapid.

Age, years	Quintiles	Mean carapace length (mm)	Number of survivors
1	1	45.0	940
	2	46.6	940
	3	48.4	940
	4	51.5	940
	5	57.3	940
5	1	62.6	322
	2	74.6	333
	3	80.4	338
	4	87.3	346
	5	101.7	362
10	1	97.4	9
	2	117.5	112
	3	129.5	119
	4	144.6	128
	5	167.7	145
15	1	143.3	38
	2	170.6	47
	3	189.1*	53
	4	203.5*	64
	5	216.1*	85
20	1	189.9*	18
	2	203.8*	26
	3	209.5*	34
	4	216.4*	44
	5	224.8*	63

*sexually mature

The overall life-table was continued in this manner through the age of 75 years, by which time about 0.3% of the original cohort of hatched tortoises remained alive. The net reproductive rate (R_0) derived from Table 30 is 1.841, or the sum of the $l_x m_x$ column divided by the initial total of 10,000 female eggs. This value exceeds 1.0, and indicates that, were the assumptions in the table both correct and invariant, the Goffs population would be increasing in size.

We can compute the annual rate of increase by first calculating what Laughlin (1965) termed T_c, or cohort generation time. This parameter is estimated as:

$$T_c = \Sigma x l_x m_x / \Sigma l_x m_x \qquad (10)$$

The numerator of this expression, derived from Table 30, is 589,122, so the cohort generation time is about 32.0 years. One then computes r_c, or capacity for increase:

$$r_c = \ln(R_0)/T_c \qquad (11)$$

or 0.0191 per year. The factor by which the population would increase in a year is then $e^{0.0191}$, or 1.019, equivalent to an annual increase of about 1.9%.

The life-table constructed as we have described it predicts an increasing population, but the rate of increase is so slight that we have no way of confirming or rejecting the result on the basis of our sampling data. Turner and Berry (1984: 18 et seq.) reviewed various estimates of the Goffs tortoise population ranging from 243 to 502. An annual increase of from around 4 to 10 individuals--all recruited into the smallest size-class--would be undetectable by any feasible sampling program. In fact, because of the long cohort generation time (32 years) even very high (or low) values of R_0 predict annual rates of change that would be difficult to measure in the short term. For example, an R_0 value of 0.2 predicts an annual decrease of only 5%, and if R_0 is 50 the predicted rate of annual increase is about 13%. These observations emphasize how difficult it is to assess the status of a long-lived species, and how the impact of deleterious influences may be masked for many years. Our analysis also suggests that short-term negative influences, if reversible, will not be dangerous to the long-term well-being of the species. Irreversible degradation of environmental conditions, e.g., long-term decreases in rainfall and available forage, or continued anthropogenic disturbances to vegetation and/or soils could eventually lead to local extinctions. None of these conclusions is new, but the life-table emphasizes in a quantitative manner the special problems existing among long-lived species.

Of course, the Goffs life-table may be wrong in various ways, or may lack generality over much of the range of the species. These are not issues that can be resolved in this report. We did make two simple tests of effects of changing the life-table. One test involved extending the life-span beyond 75 years, and treating the survivorship curve as an infinite series. This had little effect, changing the estimate of R_0 to 2.08 and the estimated rate of annual increase to 2.3%. In another test we imposed more severe nest predation, assuming that 63% of nests are destroyed instead of 37.1%. This change reflected estimates based on groups of nests under direct observation (see Table 16). The new estimate of R_0 (1.145) did not change the cohort generation time and led to an estimated annual increase of 0.4%.

The life-table does not predict a stable age distribution, which would be true if R_0 were equal to 1.0. We computed an expected size distribution for the Goffs population assuming that all tortoises die at the age of 75 years and an annual rate of increase indicated by Table 30 (1.9%) over a period of

75 years. We did this by taking the size-categories used in our earlier reports (i.e., <60 mm, 60-99 mm, 100-139 mm, 140-179 mm, 180-207 mm, 208-239 mm and ≥240 mm) and grouping $\underline{l}_x$ values within these ranges for each of the quintiles shown in Appendixes 1-5 (not the same as using $\underline{l}_x$ values from Table 30). We compared this distribution with two kinds of distributions based on the size distribution observed at Goffs in the spring of 1983 (see Turner and Berry, 1986: 15). We adjusted the observed 1983 distribution by taking into account the estimated probabilities of capture of tortoises of different sizes in 1983 (see Fig. 3). From the uppermost curve in this figure we took values of $\underline{P}$ for tortoises with sizes of 50 mm (0.42), 80 mm (0.55), 120 mm (0.73), 160 mm (0.85), and for females 200 mm (0.95), and 225 mm (0.97), and divided numbers of female tortoises in the 1983 sample by sampling efficiencies appropriate to each size class. We assumed that half of the tortoises <180 mm long in the 1983 sample were females. We used the same sampling efficiency (0.97) for all female tortoises ≥208 mm long. Table 32 compares size distributions based on the life-table and on the 1983 sample for all size groups.

Table 32. Comparison of life-table size distribution and adjusted 1983 size distribution at Goffs.

Size (mm)	Number females observed in 1983	Adjusted 1983 sample n	Adjusted 1983 sample %	Life-table distribution (%)
<60	6[1]	14.3	5.2	39.7
60-99	51.5	93.6	34.0	32.0
100-139	31	42.5	15.4	10.7
140-179	21.5	25.3	9.2	4.5
180-207	33	34.7	12.7	4.1
208-239	62	63.9	23.2	7.8
240+	1	1.0	0.3	1.3

[1] based on 12 yearlings registered in spring

These two distributions are not in agreement, partly because of the deficiency of small tortoises in the observed distribution. This was an expected problem, and not one we can do much about. We have always believed that such tortoises are consistently underrepresented in samples (see Berry and Turner, 1986). The life-table distribution also predicts much lower proportions of larger females than observed, except in the very largest size category.

We can make a fairer test of the life-table values by limiting the comparison to tortoises ≥140 mm long, i.e., those size classes in the population that are presumably sampled with better than 80% efficiency. Table 33 makes this comparison. The accord is improved, and the only major incongruity is among the very largest females. The life-table size distribution in Tabl. 33 was modified in accordance with size-specific probabilities of capture to give a size distribution one might expect to observe in a sample of 117.5 desert

Table 33. Comparison of life-table size distribution and adjusted 1983 size distribution at Goffs, including only tortoises ≥140 mm long.

Size (mm)	Adjusted 1983 size distribution (%)	Life-table size distribution (%)
140-179	20.3	25.7
180-207	27.8	23.1
208-239	51.1	44.1
≥240	0.8	7.2

tortoises (the number of female tortoises $\geq$140 mm in length registered in 1983). When this distribution was compared with the 1983 distribution in Table 33, the total X^2 (3 d.f.) was 10.5 (p = 0.015). There is, then, a statistically significant difference between these two distributions owing to the higher predicted incidence of females $\geq$240 mm.

In the absence of further tests of the life-table model, we can only venture some intuitive comments. There is strong evidence that the life-table model is overestimating numbers of females attaining sizes of 240+ mm. Samples of tortoises from Plot 1 have shown that there are at least two females of this size in the area, though only one of these happened to be observed in 1983. Even allowing for this second individual, the relative abundance of such large females is apparently less than 2-3% in the Goffs female population. The overabundance of large females in the life-table may reflect any of several kinds of errors, or interactions thereof. Although there is certainly variability in growth rates of various females, we may have overestimated the force of this effect. An analysis of growth of 15 desert tortoises of known ages over a period of more than 20 years in southern Nevada suggests far less variability in size-age relationships (Turner et al., 1987). The predicted survival rates of older females may be too high, or the nature of the assumed size-survival rate function may change at advanced ages.

IX. Discussion

As with most models of the nature of our life-table, the results raise a new set of questions of increased complexity. The value of the life-table probably lies more in the development of its components and the definition of new questions than in the integration of the table itself. In spite of the problems we have reviewed, the overall product represents a substantial achievement in incorporating a large body of data into a quantitative expression of desert tortoise population function.

The literature contains only one other life-table for a chelonian--that developed for the painted turtle (Chrysemys picta) in Michigan (Wilbur, 1975; Tinkle et al., 1981). Table 34 contrasts some of the attributes of these tables.

Table 34. Attributes of life-tables for the painted turtle and desert tortoise

Attribute	Painted turtle Wilbur (1975)	Painted turtle Tinkle et at. (1981)	Desert tortoise
Sex ratio	1:1	1:1	1:1
Female age at maturity (yrs)	7	7	12-20
Annual survival rate after first year of life	0.76	0.76	0.76-0.97
Age-specific fecundity	6.6	2.8	3.7-5.0
R_0	1.0	1.5	1.8
Mean length of a generation (years)	11	-	32

The table devised by Wilbur was based on his research between 1968 and 1973 combined with older records of turtles collected from the same ponds between 1953 and 1957 (Sexton, 1959a, b; 1965). Tinkle et al. (1981) introduced two important changes in Wilbur's table: a substantial reduction in female fecundity and an increase in first-year survival from 18% (as estimated by Wilbur) to 67%. The net effect of these changes increased the value of R_0 by about 50%. The desert tortoise life-table is clearly more complex than these tables, incorporating age-specific variability into estimates of age at sexual maturity, egg production and survival. The tortoise table also differs from the painted turtle tables in that the former is based on survival rates increasing with age while the latter assume age-constant rates of mortality.

A life-table is limited in its predictive potential, assuming invariant schedules of reproduction and death and (unless R_0 is equal to precisely one) constant annual rates of increase or decrease in size. We know, however, that populations do not function in such ways. Wilbur (1975) actually constructed two life tables for the painted turtle--one for the period 1953-1957 and another for the period 1968-1972. These tables differed in their schedules of survivorship. According to Wilbur the 1972 table showed "...a higher survivorship from egg to hatchlings reaching the pond, but a reduced annual survivorship once turtles reached the pond." The mean generation time for the 1972 table was a little less than that for the 1957 table, indicating that the more recent population was "...turning over at a faster rate." If the Goffs population of desert tortoises were studied for another four years the life-table derived from that work would differ from the one described in this report.

A better instrument for management planning would be a simulation model driven by some abiotic variable (or variables) which could project fluctuations in the size and composition of a desert tortoise population over time. Two examples of such models for short-lived species are those for the Great Tit in England (Pennycuick, 1969) and the side-blotched uta in southern Nevada (Turner et al., 1982b). The ability to project hypothetical changes in population states becomes even more important when dealing with extremely long-lived animals like the tortoise. It is extremely difficult to infer the consequences of environmental change when the mean generation time of the subject species is more than 30 years. The Tit and uta models were based on many years of observations and/or experimentation, and incorporated an understanding of biological mechanism well beyond that existing for the desert tortoise.

While it would not be wise to attempt to devise a population model for the desert tortoise, we can nevertheless use information that has been derived from our study to estimate possible long-term effects of change on the Goffs population. A simple example is that provided by the use of two alternative values for nest destruction in the formulation of the life-table. When nest destruction was set at 37% the value of R_0 was 1.84; when nest destruction was set at 63% the value of R_0 was 1.14. Both assumptions imply populations with modest rates of annual increase (0.4 to 1.9%). Similar tests could be made of effects of changing the 1) rate of sexual maturation of females, 2) age-specific fecundity of females, and 3) rates of annual survival. Various combinations of changes could also be examined.

The most effective way to carry out these kinds of analyses is to prepare a computer program capable of 1) starting with a population of a particular size, sex ratio and age-distribution, 2) applying specified rates of fecundity and mortality predicting values of $R_0 \neq 1$, 3) computing new estimates of population attributes each year, and 4) tracking projected changes in the status of the population over intervals of 30 to 50 years. One might postulate, for example, some set of events--either natural or anthropogenic--reducing the production of food available to tortoises. This would then lead to reduced female fecundity--possibly to such a low level that the population would begin to decline. What would be the nature of the size distribution of such a population after 5, 15 or 20 years? Would such projections help us to interpret some of the size distributions reported for various California tortoise populations (Berry and Nicholson, 1984)? After a long period of decline in numbers, how long would it take for a population to "recover," given a return to normal conditions?

As shown in Table 20 our life-table assumes a difference in annual survival rates of male and female tortoises at body sizes exceeding 180 mm. On the other hand, we have emphasized (p. 18) that 1983-1986 samples of the Goffs population invariably indicated balanced sex ratios among adult tortoises. One would imagine that the postulated improved survival of older females would lead to populations with more adult females than males, which would be inconsistent with actual observations. By an extension of the procedures discussed above, we could examine long-term changes in the sex ratio of a population starting with a ratio of 1:1 but with differential adult survival rates. If disparities in the abundance of males and females occur, we would have to reexamine some of the assumptions underlying the survivorship models.

The development of the life-table has emphasized how difficult it is to estimate survival rates using capture-recapture data pertaining to marked tortoises. Table 19 shows that even the extensive body of information available for the Goffs population resulted in wide confidence ranges for parameters estimating intercepts and slopes of survival rate curves. This uncertainty may be contrasted with the modest standard errors of clutch size and frequency parameters (Table 13). These points are related to one of the purposes of this study, viz., the provision of improved bases for designing future mitigationoriented investigations of tortoise biology. Such studies may rely on attempts to measure various impacts on tortoises, possibly by comparing stressed and control populations. Our work shows that, in general, variables relating to reproduction will provide more reliable comparisons of field populations than variables relating to survival.

X. Summary

Research on the desert tortoise was conducted in two 2.59-km^2 (1-mi^2) plots near Goffs, California, beginning in the spring of 1983 and continuing through the early autumn of 1986. Production of eggs was measured by periodic radiography of females bearing radiotransmitters in Plot 2 in all four years and Plot 1 in 1985-1986. The composition of the Plot 1 population and survival of its members was evaluated by repeated censuses. We also made use of earlier samples from this population (1977, 1980) in analyses of growth and survival of tortoises. We estimated numbers of tortoises $\geq$140 mm in length in Plot 1 as about 215, but did not attempt to make estimates of numbers of smaller tortoises. We believe that at least 500-600 tortoises occupy Plot 1, but this estimate assumes the presence of far more small tortoises than we observed. The adult sex ratio is apparently 1:1.

Groups of from 10 to 26 females with transmitters were examined periodically during the breeding seasons of 1983 through 1986, and X-rays taken at about 2-week intervals between early April and late June. Numbers of clutches produced and the size of clutches were determined from radiographs. Females were reproductive at a body size of around 185 mm. Because growth rates of females vary, some individuals are mature at ages of 12 years while show-growing females may be as old as 20 years. With rare exceptions, females lay

1-2 clutches of eggs during May and June. The probability of a female >216 mm long laying two clutches (70%) is greater than that for females <197 mm in length (30%). Clutch frequency varies between years and is highest when production of herbaceous annuals, on which tortoises feed, is high. For example, in 1983--when herbaceous production was about 14 g/m^2--the average clutch frequency was 1.9. Conversely, when herbaceous production was 0.6 g/m^2 in 1986, females laid an average of 1.5 clutches. Observed clutch sizes ranged from one to ten eggs, and the overall mean during the study was 4.46. Clutch size is strongly and directly correlated with body size, and females 235 mm long lay clutches about 50% larger than do females 195 mm in length. If a female lays only one clutch, it is about 0.5 egg larger than the first clutch of a female laying two clutches. We measured small, but statistically significant, differences in mean clutch sizes in different years, but the main factor influencing annual changes in fecundity is clutch frequency.

About 12% of eggs laid are either infertile or broken during laying. Loss of eggs is principally owing to nest predation by foxes and coyotes. We estimated numbers of nests produced by the breeding females in Plot 1 and compared this number with numbers of destroyed nests counted in Plot 1 between June and September. Nest predation estimates ranged from around 25% in 1983 and 1984 to 44-53% in 1985 and 1986. We also estimated nest losses by counting nests destroyed among smaller groups of nests under direct observation. On average, over 60% of such nests were excavated by predators. The higher rate of nest predation (1985-1986) corresponded with apparent declines in abundance of kangaroo rats and lagomorphs (normal prey of foxes and coyotes) in Plot 1.

Annual survival rates of tortoises were estimated using capture-recapture data acquired between 1977 and 1986. Fitting the logistic model to observations led to conclusions that (1) survival rates were positively correlated with body size, (2) survival varied over time, and (3) mature females exhibited better survival than males of the same size. The poorest survival occurred between 1983-1984. Among tortoises $\geq$180 mm long the best survival ($\geq$90% per year) was during the periods 1977-1980 and 1980-1983. Estimated annual survival of small tortoises (50-100 mm) ranged from 70 to 80% between 1977 and 1985. All predictions had large confidence intervals, emphasizing the difficulty in deriving reliable estimates of survival even using an extensive body of oberations.

The foregoing information was combined in a life-table measuring the capacity of the Plot 1 population to replace itself over time. This table was based on average reproductive performance (as observed between 1983-1986) and survival (1977-1985), but allowed for variability in female growth rates. The female life span was set at 75 years. The rate of nest destruction by predators was taken as 37.1%. The net reproductive rate ($\underline{R}_0$) computed from the table was 1.84. This measure is <1 in a decreasing population, 1.0 in a stable population, and >1 in a growing population. If the measurements and assumptions built into the life-table remained invariant, the Plot 1 population would gradually increase in size. However, the cohort generation time (32.0 years) is so long that our model predicts an annual rate of increase of only about 2%.

The life-table provides only very general information as to management strategies for the desert tortoise. The tortoise depends on vegetation for food and cover, and its reproductive capacity is positively correlated with net production by annual plants. Destruction or alteration of native vegetation would obviously be deleterious. A reduction in the abundance of nest predators would increase recruitment, but this gain might be offset by unforeseeable mortality owing to other causes. Better management insights might be provided by using the life-table as a basis for computer simulations of long-term changes in tortoise populations resulting from environmentally or anthropogenically induced changes in rates of reproduction and survival.

XI. Conclusions

The following information about the Goffs desert tortoise population resulted from this study:

- Sampling between 1983 and 1986 failed to indicate changes in the size of the population. The number of tortoises $\geq$140 mm in length was about 215/mi^2. The sex ratio was 1:1.
- Female tortoises laid from one to two clutches during May and June. Larger females were more likely to lay two clutches than smaller ones. Mean clutch frequency varied from 1.1 to 1.9. Clutch frequency was positively and significantly correlated with aboveground production by annual herbaceous plants. There was no evidence that egg production declined among very old females.
- Clutches laid by tortoises ranged in size from one to ten eggs, and the 4-year mean clutch size was 4.5. Clutch size was positively correlated with body size.
- The heaviest toll on eggs was due to destruction of nests by kit foxes and coyotes.
- Growth of female tortoises was variable. A growth model including provision for this variation predicts that females become sexually mature at ages ranging from 12-20 years, with a median age of 14-15 years. Survival of tortoises was positively correlated with body size. Survival varied over time and mature females exhibited better survival than males of the same size.

- A life-table for the tortoise indicated that if conditions embodied in the table were invariant the Goffs population would increase at a rate of 2% per year.

The management implications of these findings are as follows:

- Many of the eggs laid by tortoises are destroyed by predators. If nests were protected by screening or cages, we could expect improved hatching success.
- Improved hatching success could also be achieved by the elimination of kit foxes and coyotes from portions of the tortoises' range.
- Because egg production is improved when there is more spring forage, any steps taken to improve germination and growth of herbaceous plants would tend to increase numbers of eggs laid. Artificial irrigation and/or elimination of grazing would be actions contributing to these ends.
- Not all of the above actions are economically feasible, and at least one (elimination of kit foxes) would be illegal. The tortoise has evolved in an environment with limited rainfall, and has long coexisted with natural preadators. The best management action is to take steps to prevent anthropogenic degradations of tortoise habitat or, when such steps are unavoidable, to make arrangements for appropriate habitat compensation.

XII. Recommendations

- Because of efforts sponsored by the U.S. Bureau of Land Management and because of the sustained investment by the Southern California Edison Company, the Goffs population of desert tortoises is a unique resource. SCE and the BLM should cooperate to insure that monthly records of rainfall in Plots 1 and 2 are sustained.
- The life-table described in this report can be improved. The model apparently overestimates the abundance of females attaining sizes exceeding 240 mm. The overabundance of very large females in the size-distribution predicted by the life-table may be owing to several types of errors. For example, we may have overestimated the growth rate of the most rapidly growing females. Another problem is that our analyses of capture-recapture data suggest that adult females have higher survival rates than males of the same age. On the other hand, the observed adult sex ratio is 1:1.
- Changes in one element of the dynamics of a population are often accompanied by compensatory changes in other processes. These kinds of interactions are difficult to measure and require complex and costly field experiments to test. The life-table model can be used to simulate the effects of postulated changes in birth rates and/or deaths rates, as well as changes in other elements of the table. For example, we could examine the effects of changing the 1) rate of sexual maturation of females, 2) age-specific fecundity of females, and 3) rates of annual survival. Various combinations of changes could also be examined.

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XIV. Appendixes

Appendix 1

Estimated schedule of survival and fecundity of female desert tortoises composing the 0-20th percentile (by length) of a cohort developing from 2,000 female eggs.

Age, x (years)	Mean length (mm)	l_x	m_x	$l_x m_x$
EGGS		2000.0		
HATCH	45.0	1103.3	0.0	0.0
1	45.0	939.7	0.0	0.0
2	46.5	713.6	0.0	0.0
3	51.7	543.1	0.0	0.0
4	57.1	416.3	0.0	0.0
5	62.6	321.5	0.0	0.0
6	68.8	250.0	0.0	0.0
7	75.3	196.0	0.0	0.0
8	81.8	154.9	0.0	0.0
9	89.4	123.3	0.0	0.0
10	97.4	99.1	0.0	0.0
11	105.7	80.3	0.0	0.0
12	114.5	65.6	0.0	0.0
13	123.5	54.1	0.0	0.0
14	133.4	45.0	0.0	0.0
15	143.3	37.7	0.0	0.0
16	152.7	31.9	0.0	0.0
17	163.4	27.2	0.0	0.0
18	174.2	23.3	0.0	0.0
19	182.9	20.2	0.0	0.0
20	189.9	17.7	2.382	42.120
21	195.2	15.8	2.516	39.684
22	197.7	14.2	3.187	45.381
23	198.7	12.9	3.219	41.609
24	199.4	11.8	3.243	38.112
25	199.9	10.7	3.261	34.901
26	200.3	9.8	3.272	31.930
27	200.7	8.9	3.287	29.265
28	201.2	8.1	3.302	26.841
29	201.5	7.4	3.314	24.617
30	201.9	6.8	3.325	22.590
31	202.2	6.2	3.335	20.734
32	202.5	5.7	3.345	19.041
33	202.8	5.2	3.355	17.496
34	203.0	4.8	3.363	16.077

Appendix 1 (cont.)

Age, x (years)	Mean length (mm)	l_x	m_x	l_xm_x
35	203.3	4.4	3.371	14.780
36	203.5	4.0	3.380	13.594
37	203.7	3.7	3.386	12.502
38	204.0	3.4	3.395	11.508
39	204.2	3.1	3.403	10.598
40	204.4	2.9	3.409	9.759
41	204.6	2.6	3.416	8.990
42	204.8	2.4	3.423	8.284
43	205.0	2.2	3.429	7.637
44	205.2	2.0	3.434	7.039
45	205.3	1.9	3.439	6.490
46	205.5	1.7	3.446	5.988
47	205.7	1.6	3.451	5.524
48	205.8	1.5	3.456	5.097
49	206.0	1.4	3.461	4.705
50	206.1	1.3	3.466	4.344
51	206.3	1.2	3.471	4.011
52	206.4	1.1	3.474	3.703
53	206.5	1.0	3.479	3.422
54	206.7	0.9	3.484	3.162
55	206.8	0.8	3.487	2.921
56	206.9	0.8	3.492	2.701
57	207.1	0.7	3.497	2.497
58	207.2	0.7	3.500	2.309
59	207.3	0.6	3.504	2.135
60	207.4	0.6	3.507	1.975
61	207.5	0.5	3.510	1.826
62	207.6	0.5	3.514	1.690
63	207.7	0.4	3.517	1.564
64	207.8	0.4	3.520	1.447
65	207.9	0.4	3.524	1.339
66	208.0	0.4	3.527	1.240
67	208.1	0.3	3.530	1.148
68	208.2	0.3	3.534	1.063
69	208.3	0.3	3.537	0.985
70	208.4	0.3	3.540	0.912
71	208.5	0.2	3.544	0.845
72	208.6	0.2	3.547	0.783
73	208.7	0.2	3.550	0.726
74	208.8	0.2	3.553	0.673
75	208.9	0.2	3.557	0.624
Total				632.934

Appendix 2

Estimated schedule of survival and fecundity of female desert tortoises composing the 21-40th percentile (by length) of a cohort developing from 2,000 female eggs.

Age, x (years)	Mean length (mm)	l_x	m_x	$l_x m_x$
EGGS		2000.0		
HATCH	45.0	1103.3	0.0	0.0
1	46.6	939.7	0.0	0.0
2	52.6	715.2	0.0	0.0
3	59.7	549.0	0.0	0.0
4	67.2	425.4	0.0	0.0
5	74.6	332.8	0.0	0.0
6	82.1	262.8	0.0	0.0
7	90.2	209.3	0.0	0.0
8	99.1	168.3	0.0	0.0
9	108.4	136.6	0.0	0.0
10	117.5	111.9	0.0	0.0
11	127.0	92.5	0.0	0.0
12	137.7	77.2	0.0	0.0
13	148.0	65.0	0.0	0.0
14	158.6	55.1	0.0	0.0
15	170.6	47.2	0.0	0.0
16	181.0	40.7	0.0	0.0
17	190.4	35.5	2.393	84.897
18	197.8	31.7	3.191	101.105
19	201.8	28.8	3.324	95.609
20	203.8	26.3	3.390	89.217
21	205.2	24.2	3.436	83.061
22	206.2	22.3	3.469	77.207
23	206.8	20.5	3.488	71.607
24	207.3	19.0	3.507	66.461
25	207.9	17.5	3.525	61.732
26	208.3	16.2	3.538	57.306
27	208.7	15.0	3.551	53.246
28	209.1	13.9	3.564	49.492
29	209.4	12.9	3.576	46.020
30	209.8	11.9	3.587	42.809
31	210.1	11.1	3.597	39.829
32	210.4	10.3	3.607	37.073
33	210.7	9.5	3.617	34.525
34	211.0	8.9	3.627	32.166

Appendix 2 (cont.)

Age, x (years)	Mean length (mm)	l_x	m_x	$l_x m_x$
35	211.2	8.2	3.635	29.967
36	211.5	7.7	3.644	27.932
37	211.8	7.1	3.654	26.056
38	212.0	6.6	3.662	24.304
39	212.3	6.2	3.670	22.682
40	212.5	5.8	3.678	21.173
41	212.8	5.4	3.687	19.774
42	213.0	5.0	3.695	18.472
43	213.2	4.7	3.701	17.256
44	213.4	4.3	3.708	16.124
45	213.6	4.1	3.715	15.071
46	213.8	3.8	3.721	14.091
47	214.0	3.5	3.728	13.179
48	214.2	3.3	3.734	12.329
49	214.4	3.1	3.741	11.537
50	214.6	2.9	3.748	10.800
51	214.8	2.7	3.754	10.112
52	215.0	2.5	3.761	9.471
53	215.2	2.4	3.766	8.868
54	215.3	2.2	3.771	8.307
55	215.5	2.1	3.778	7.786
56	215.7	1.9	3.782	7.295
57	215.8	1.8	3.787	6.839
58	216.0	1.7	3.792	6.411
59	216.1	1.6	3.821	6.049
60	216.3	1.5	3.826	5.673
61	216.4	1.4	3.829	5.319
62	216.5	1.3	3.834	4.991
63	216.7	1.2	3.839	4.683
64	216.8	1.1	3.842	4.394
65	216.9	1.1	3.848	4.125
66	217.1	1.0	3.852	3.873
67	217.2	0.9	3.856	3.635
68	217.3	0.9	3.861	3.415
69	217.5	0.8	3.866	3.208
70	217.6	0.8	3.869	3.013
71	217.7	0.7	3.872	2.830
72	217.8	0.7	3.876	2.659
73	217.9	0.6	3.879	2.498
74	218.0	0.6	3.882	2.347
75	218.1	0.6	3.886	2.206
Total				1554.108

Appendix 3

Estimated schedule of survival and fecundity of female desert tortoises composing the 41st-60th percentile (by length) of a cohort developing from 2,000 female eggs.

Age, x (years)	Mean length (mm)	l_x	m_x	$l_x m_x$
EGGS		2000.0		
HATCH	45.0	1103.3	0.0	0.0
1	48.4	939.7	0.0	0.0
2	55.2	717.1	0.0	0.0
3	63.3	552.3	0.0	0.0
4	71.9	430.0	0.0	0.0
5	80.4	338.4	0.0	0.0
6	89.6	269.0	0.0	0.0
7	99.2	216.1	0.0	0.0
8	108.8	175.5	0.0	0.0
9	118.9	143.9	0.0	0.0
10	129.5	119.1	0.0	0.0
11	140.4	99.5	0.0	0.0
12	152.3	84.0	0.0	0.0
13	164.5	71.5	0.0	0.0
14	177.1	61.5	0.0	0.0
15	189.1	53.3	2.359	125.730
16	197.4	47.4	3.177	150.717
17	202.5	43.0	3.345	143.932
18	205.8	39.4	3.455	136.187
19	207.9	36.3	3.526	128.111
20	209.5	33.6	3.578	120.235
21	210.7	31.2	3.618	112.746
22	211.7	29.0	3.652	105.766
23	212.6	26.9	3.682	99.240
24	213.2	25.1	3.702	92.988
25	213.8	23.4	3.722	87.203
26	214.5	21.9	3.745	81.922
27	215.1	20.4	3.764	76.936
28	215.5	19.1	3.779	72.245
29	216.0	17.9	3.819	68.332
30	216.5	16.8	3.835	64.277
31	217.0	15.7	3.852	60.505
32	217.5	14.7	3.867	56.968
33	217.9	13.8	3.882	53.669
34	218.4	13.0	3.897	50.592

Appendix 3 (cont.)

Age, x (years)	Mean length (mm)	l_x	m_x	$l_x m_x$
35	218.8	12.2	3.912	47.719
36	219.3	11.5	3.927	45.036
37	219.7	10.8	3.940	42.510
38	220.1	10.2	3.954	40.146
39	220.5	9.6	3.967	37.933
40	220.9	9.0	3.980	35.860
41	221.2	8.5	3.992	33.903
42	221.6	8.0	4.004	32.066
43	221.9	7.6	4.015	30.342
44	222.3	7.1	4.027	28.723
45	222.6	6.7	4.039	27.202
46	222.9	6.4	4.049	25.762
47	223.3	6.0	4.061	24.416
48	223.6	5.7	4.072	23.151
49	223.9	5.4	4.082	21.951
50	224.3	5.1	4.094	20.829
51	224.6	4.8	4.106	19.773
52	224.9	4.6	4.116	18.770
53	225.2	4.3	4.126	17.824
54	225.5	4.1	4.136	16.932
55	225.8	3.9	4.146	16.089
56	226.1	3.7	4.156	15.294
57	226.4	3.5	4.166	14.543
58	226.7	3.3	4.176	13.833
59	227.0	3.1	4.184	13.157
60	227.2	3.0	4.192	12.518
61	227.5	2.8	4.202	11.918
62	227.8	2.7	4.211	11.345
63	228.0	2.6	4.219	10.803
64	228.3	2.4	4.227	10.290
65	228.5	2.3	4.236	9.804
66	228.8	2.2	4.244	9.343
67	229.0	2.1	4.251	8.902
68	229.2	2.0	4.259	8.488
69	229.5	1.9	4.267	8.095
70	229.7	1.8	4.274	7.719
71	229.9	1.7	4.282	7.365
72	230.2	1.6	4.291	7.029
73	230.4	1.6	4.297	6.708
74	230.6	1.5	4.304	6.402
75	230.8	1.4	4.311	6.112
Total				2694.900

Appendix 4

Estimated schedule of survival and fecundity of female desert tortoises composing the 61st-80th percentile (by length) of a cohort developing from 2,000 female eggs.

Age, x (years)	Mean length (mm)	l_x	m_x	$l_x m_x$
EGGS		2000.0		
HATCH	45.0	1103.3	0.0	0.0
1	51.5	939.7	0.0	0.0
2	59.2	720.1	0.0	0.0
3	68.1	557.6	0.0	0.0
4	77.5	436.8	0.0	0.0
5	87.3	346.0	0.0	0.0
6	98.1	277.3	0.0	0.0
7	109.3	224.8	0.0	0.0
8	120.5	184.4	0.0	0.0
9	132.2	152.9	0.0	0.0
10	144.6	128.1	0.0	0.0
11	157.0	108.4	0.0	0.0
12	169.9	92.7	0.0	0.0
13	183.8	80.0	0.0	0.0
14	195.7	70.2	2.530	177.654
15	203.5	63.5	3.379	214.452
16	208.0	58.3	3.530	205.631
17	210.8	53.9	3.622	195.196
18	213.1	50.1	3.698	185.220
19	215.0	46.7	3.761	175.679
20	216.4	43.7	3.832	167.394
21	217.7	40.9	3.875	158.640
22	219.0	38.4	3.919	150.594
23	220.1	36.1	3.952	142.842
24	221.0	34.0	3.983	135.545
25	221.9	32.1	4.014	128.793
26	222.8	30.3	4.044	122.472
27	223.7	28.6	4.074	116.583
28	224.6	27.1	4.103	111.040
29	225.4	25.6	4.129	105.825
30	226.2	24.3	4.156	100.944
31	226.9	23.0	4.181	96.328
32	227.7	21.9	4.206	92.007
33	228.4	20.8	4.231	87.940
34	229.1	19.8	4.254	84.090

Appendix 4 (cont.)

Age, x (years)	Mean length (mm)	l_x	m_x	$l_x m_x$
35	229.7	18.8	4.276	80.430
36	230.4	17.9	4.298	76.989
37	231.0	17.1	4.319	73.735
38	231.7	16.3	4.341	70.672
39	232.3	15.5	4.362	67.771
40	232.9	14.8	4.382	65.009
41	233.5	14.2	4.402	62.395
42	234.1	13.5	4.422	59.919
43	234.7	13.0	4.441	57.549
44	235.2	12.4	4.459	55.307
45	235.8	11.9	4.477	53.173
46	236.3	11.4	4.494	51.130
47	236.8	10.9	4.511	49,187
48	237.3	10.5	4.527	47.339
49	237.8	10.0	4.544	45.580
50	238.2	9.6	4.559	43.887
51	238.7	9.2	4.574	42.277
52	239.1	8.9	4.589	40.738
53	239.6	8.5	4.604	39.274
54	240.0	8.2	4.619	37.872
55	240.4	7.9	4.632	36.523
56	240.9	7.6	4.647	35.248
57	241.3	7.3	4.662	34.026
58	241.7	7.0	4.676	32.848
59	242.1	6.8	4.689	31.721
60	242.5	6.5	4.702	30.643
61	242.9	6.3	4.716	29.610
62	243.3	6.1	4.727	28.609
63	243.6	5.8	4.739	27.653
64	244.0	5.6	4.750	26.733
65	244.3	5.4	4.762	25.853
66	244.7	5.2	4.774	25.006
67	245.0	5.1	4.784	24.185
68	245.3	4.9	4.796	23.407
69	245.7	4.7	4.807	22.657
70	246.0	4.6	4.817	21.930
71	246.3	4.4	4.827	21.231
72	246.6	4.3	4.837	20.558
73	246.9	4.1	4.847	19.912
74	247.1	4.0	4.855	19.282
75	247.4	3.8	4.864	18.677
Total				4631.375

Appendix 5

Estimated schedule of survival and fecundity of female desert tortoises composing the 81st-100th percentile (by length) of a cohort developing from 2,000 female eggs.

Age, x (years)	Mean length (mm)	l_x	m_x	$l_x m_x$
EGGS		2000.0		
HATCH	45.0	1103.3	0.0	0.0
1	57.3	939.7	0.0	0.0
2	67.0	725.8	0.0	0.0
3	78.1	567.7	0.0	0.0
4	90.0	450.1	0.0	0.0
5	101.7	361.7	0.0	0.0
6	113.8	294.4	0.0	0.0
7	126.8	242.6	0.0	0.0
8	139.8	202.3	0.0	0.0
9	153.5	170.5	0.0	0.0
10	167.7	145.4	0.0	0.0
11	182.6	125.2	0.0	0.0
12	196.5	109.6	3.149	345.087
13	206.4	99.2	3.474	344.713
14	212.2	91.5	3.667	335.700
15	216.1	85.3	3.819	325.633
16	218.7	79.9	3.906	311.894
17	220.5	75.1	3.968	297.790
18	222.1	70.7	4.021	284.345
19	223.4	66.8	4.064	271.339
20	224.8	63.1	4.109	259.421
21	226.1	59.8	4.154	248.384
22	227.3	56.7	4.193	237.783
23	228.4	53.9	4.229	227.819
24	229.5	51.2	4.266	218.519
25	230.5	48.8	4.301	209.747
26	231.5	46.5	4.333	201.379
27	232.4	44.3	4.365	193.524
28	233.4	42.3	4.396	186.141
29	234.2	40.5	4.425	179.061
30	235.1	38.7	4.453	172.387
31	235.9	37.1	4.481	166.086
32	236.8	35.5	4.510	160.137
33	237.6	34.0	4.538	154.513
34	238.4	32.7	4.565	149.140

Appendix 5 (cont.)

Age, x (years)	Mean length (mm)	l_x	m_x	l_xm_x
35	239.2	31.4	4.590	143.997
36	239.9	30.1	4.615	139.119
37	240.7	29.0	4.640	134.487
38	241.4	27.9	4.663	130.040
39	242.1	26.8	4.686	125.810
40	242.8	25.9	4.710	121.784
41	243.4	24.9	4.731	117.908
42	244.1	24.0	4.753	114.212
43	244.7	23.2	4.775	110.685
44	245.3	22.4	4.795	107.281
45	245.9	21.6	4.815	104.027
46	246.5	20.9	4.835	100.915
47	247.1	20.2	4.853	97.903
48	247.6	19.5	4.872	95.019
49	248.2	18.9	4.890	92.255
50	248.7	18.3	4.907	89.574
51	249.2	17.7	4.923	87.00[illegible]
52	249.7	17.1	4.940	84.530
53	250.1	16.6	4.955	82.129
54	250.6	16.1	4.970	79.820
55	251.0	15.6	4.985	77.598
56	251.5	15.1	5.000	75.461
57	251.9	14.6	5.015	73.403
58	252.3	14.2	5.028	71.399
59	252.7	13.8	5.042	69.466
60	253.1	13.4	5.055	67.603
61	253.5	13.0	5.068	65.806
62	253.9	12.6	5.080	64.052
63	254.2	12.2	5.092	62.358
64	254.6	11.9	5.103	60.721
65	254.9	11.6	5.115	59.140
66	255.3	11.2	5.127	57.612
67	255.6	10.9	5.137	56.117
68	255.9	10.6	5.149	54.689
69	256.3	10.3	5.160	53.307
70	256.6	10.0	5.170	51.954
71	256.9	9.8	5.180	50.645
72	257.2	9.5	5.190	49.377
73	257.5	9.3	5.200	48.148
74	257.7	9.0	5.209	46.944
75	258.0	8.8	5.217	45.776
Total				8900.527

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