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Development of Baseline Data and Procedures
for Monitoring Populations of the Flat-tailed
Horned Lizard, Phrynosoma mcallii 1/

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Final Report

Development of Baseline Data and Procedures
for Monitoring Populations of the Flat-tailed
Horned Lizard, Phrynosoma mcallii

Contract FG9268 AM. 2

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ABSTRACT

The results of a two-year study to develop baseline population data and procedures for monitoring populations of the flat-tailed horned lizard (FTHL), Phrynosoma mcallii, are presented herein. Capture-recapture methods and radio-telemetry were used in the field, and lab and field experiments were used to evaluate the use of scat for determining relative abundance among sites. Males and females did not differ in frequency of occurrence, body size, or growth rate. Two cohorts of hatchlings were produced each year. Hatchlings grew rapidly and reached adult size the following spring. The von Bertalanffy nonlinear growth model described the growth trajectory better than either logistic-by-length or logistic-by-weight models.

Reliable methods for attaching radio transmitters to FTHL were developed for long-term monitoring of individuals. Survival ranged from 55% in mid-summer to 100% in mid-winter. Known mortality (19) was attributed to four species of predators and motor vehicles. The active period extended from mid-February through mid-November. Winter dormancy, hibernation, was spent in shallow burrows that were excavated by the lizards. The foraging strategy of FTHL is intermediate to that of sit-and-wait predators and active foragers. The size of FTHL home ranges was much larger than that of other lizards of similar body size. The size of the home range of males and females did not differ. FTHL prefer sandy substrate, and two species of perennial shrubs were used preferentially.

Scat from adult FTHL contained primarily ants, and was larger in diameter than scat from sympatric species that contained primarily ants. FTHL produced about one scat per lizard per day. Some scat may remain intact for the duration of the standard survey season, but the amount of time that marked scat remained in situ varied greatly. Scat count estimates of relative abundance may not be reliable.

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INTRODUCTION

The flat-tailed horned lizard (FTHL), Phrynosoma mcallii, is one of the smaller species of the horned lizards and, like the others, it is characterized by enlarged head spines or horns, a dorsally flattened body shape, and cryptic coloration that matches the substrate. The FTHL is distinguishable from its congeners by the presence of a dark dorsal stripe, long slender horns, and a relatively long and dorsally flattened tail (Stebbins 1985). The lizard responds to potential predators by flattening its body on the ground and remaining immobile rather than fleeing. Their cryptic coloration and "freeze" response combine to make the lizard very difficult to find in the field.

The FTHL is found at lower elevations and in hotter regions than its congeners. It occurs in sparsely vegetated regions of southeastern California, southwestern Arizona, northeastern Baja California Norte, and northwestern Sonora, below about 180 m (591 ft) (Stebbins 1985). The FTHL is not distributed uniformly throughout its range, and its abundance relative to other sympatric lizards has been described as "the rarest" (Klauber 1939) to "the third most abundant" (Mayhew and Carlson 1986). The reasons for the discrepancy in apparent relative abundance are unknown.

In May, 1988, the California Fish and Game Commission accepted a petition to list the flat-tailed horned lizard as an Endangered Species. That action triggered the elevation of the species to the status of "Candidate Species" and initiated a yearlong process of review to determine if the

species warranted listing as an Endangered or Threatened Species pursuant to the California Endangered Species Act. In June, 1989, the Department of Fish and Game (CDFG) recommended that the Commission formally list the lizard as a Threatened Species, but the Commission declined to list the species on grounds that there was insufficient information to justify listing. However, in 1989 the U. S. Fish and Wildlife Service initiated a review of the status of the FTHL in an action complementing the recommendation of CDFG. Action on the federal listing proposal is pending at this time.

The state and federal interests in the status of the FTHL were aroused by studies that documented the loss of habitat and decline of populations throughout most of its range (Edwards 1979; Turner et al. 1980; Turner and Medica 1982; Johnson and Spicer 1985; Mayhew and Carlson 1986; Olech 1986).

The full extent of habitat loss is difficult to quantify. There are few data to quantify the loss of habitat to agriculture, urbanization, the formation of the Salton Sea and other human disturbance (Mayhew and Carlson 1986), and the species is not dispersed uniformly throughout its geographic range. However, the magnitude of the problem can be estimated from recent baseline data. Rado (1981) estimated that in 1981 there were 854 km² of optimal habitat of which 57% was subject to some kind of human disturbance and impact. A more recent analysis (Mayhew and Carlson 1986) indicates that 814 km² (95%) of the optimal habitat is subject to one or more detrimental human impacts.

Populations of flat-tailed horned lizards appear to be declining throughout most of their range. Recent surveys of five areas that were surveyed previously indicate a decrease in numbers in three areas, a low but stable population in one area and an increase in one area (Mayhew and Carlson 1986).

There is a general consensus among herpetologists that the FTHL is declining in abundance throughout its range. The results of recent surveys tend to reinforce this consensus. However, the survey results are derived from indices of relative abundance that are based primarily on the abundance of scat and the presumption that scat abundance and population size are correlated. The FTHL is cryptic and few are actually seen in the field. Thus, short term surveys have relied on indicators of abundance rather than actual counts and statistical estimation of population sizes.

The biology of the FTHL is poorly known and the relationship between scat abundance, scat production and decay rates, and population size has not been studied. These unknown relationships confound attempts to interpret the reliability of the relative abundance indices. For example, dried scat that are composed predominantly of ant exoskeletons are very brittle and disintegrate easily. These scat may disintegrate when blown by the wind or when abraded by windblown sand. Thus, the number of scat recovered on a survey may be a function of the preceding weather conditions rather than the abundance of FTHL in the area. A further confounding variable has been the recent discovery that during some times of the year the diet of the Coachella Valley

fringe-toed lizard, Uma inornata, consists of up to 50% ants (Durtsche 1987). During these times the scat produced by individual U. inornata may contain only ants. These scat are difficult to distinguish from those of FTHL which are sympatric in the Coachella Valley of Riverside County. Although U. inornata does not occur in Imperial County where most of the habitat for FTHL in California is located, its congener U. notata occurs in Imperial County and is widely sympatric with the FTHL. Detailed dietary studies of U. notata are lacking, but there is no a priori reason to suppose that their diet would differ greatly from U. inornata. Thus, the possibility exists that some of the scat counts from previous surveys may have included scat from Uma sp.

The objectives of this study were twofold: 1) to develop baseline data on population biology of the FTHL; and 2) to address some of the variables that influence the reliability of relative abundance surveys that are based on scat counts.

MATERIALS AND METHODS

Field Site

The field site was located on the U.S. Naval Air Facility (El Centro), Recovery Parachute Test Range, Range Target 2510, in the area of the Superstition Hills west of Brawley, Imperial County, California (T14S, R12E, Sec. 5, 8, 16, and 17, SBBM.) (Fig. 1).

The location for the field site was selected because the area was protected by the Navy from off-road vehicle trespass and vandalism. It was easily accessed via paved roads that

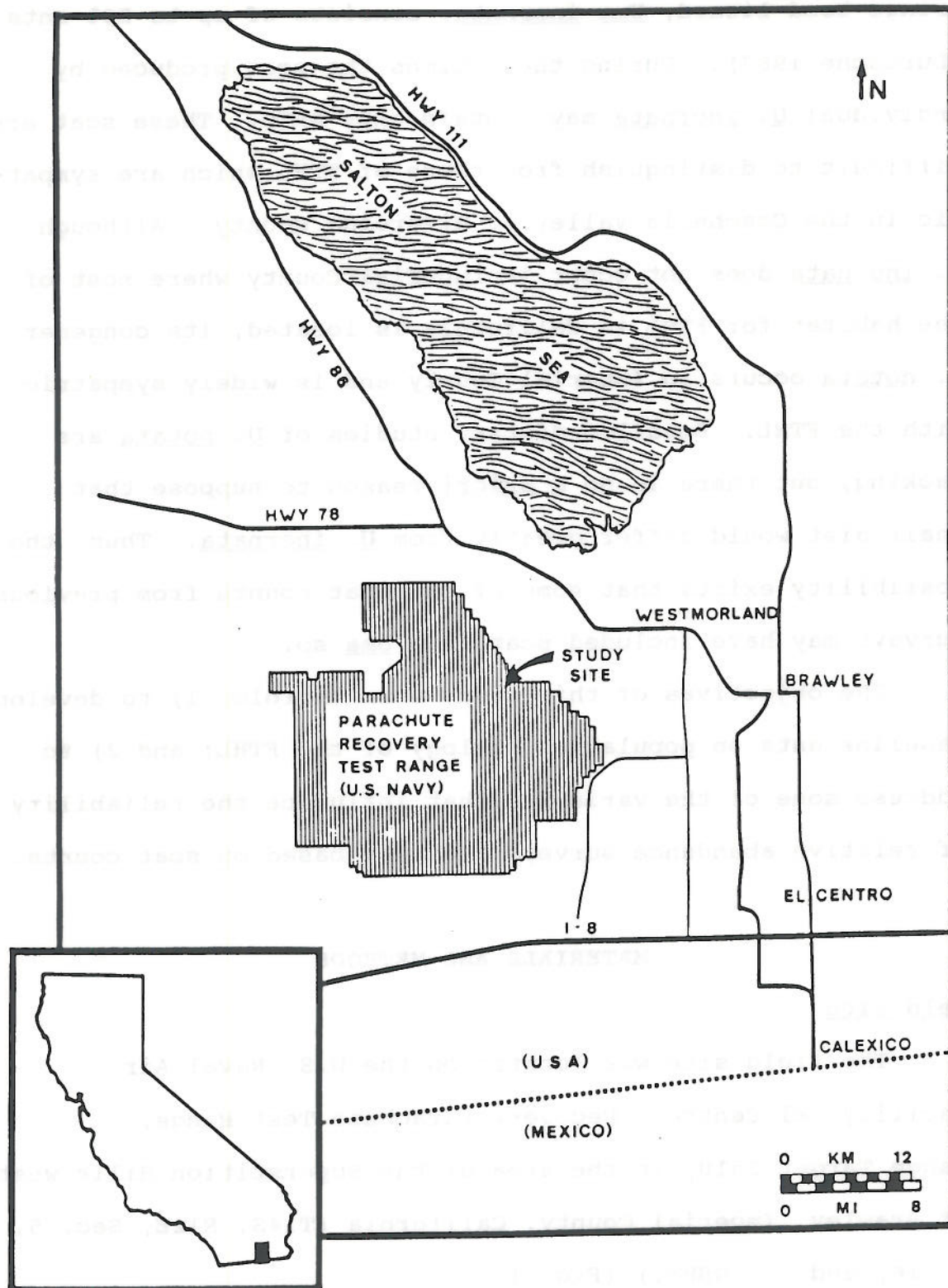


Fig. 1. Location map of the study site.

enabled us to find and capture large numbers of the otherwise cryptic FTHL. The area was known to have a relatively high population of FTHL in 1982 (M. Fisher, pers. obs.), and it was near a section that was designated as high relative density based on scat surveys (Olech 1986).

The study site contained a 3.0 km (1.8 mi) strip of paved road that was marked at 100 m (328 ft) intervals with wood stakes. The shape of the site was irregular and the area varied from time to time because the dimensions of the site were determined by the movements of the lizards that we were tracking. The study site was located in creosote bush scrub habitat that ranged in elevation from 38 to 53 m (125 to 174 ft).

Field Protocol And Data Collection

The site was surveyed from March 17, 1990 through July 23, 1992. Two to three days per week were spent on the site during the active period, and one day per week during the period of winter dormancy for a total of 164 field days.

FTHL were captured from the vehicle on or adjacent to the road. The road was surveyed repeatedly during the daily activity period(s) of FTHL. All FTHL found on the site were marked permanently with a unique identification number using colored beads (Fisher and Muth 1989), and the capture location (± 10 m, 33 ft), was recorded relative to the nearest road marker.

All individuals were measured and weighed when they were first captured. Snout-vent length (SVL) was measured with a clear plastic ruler (± 1 mm, 0.04 in) and a Pesola

Spring Scale (± 0.2 g (0.01 oz) if < 10 g (0.35 oz) and ± 0.5 g (0.02 oz) if > 10 g) was used to weigh the lizards. Their identification number, sex, and tail condition were recorded. Resighted individuals were remeasured if several weeks had passed since their last capture and measurement. Additional size and sex data were obtained from FTHL captured off-site on the Test Range.

Radio Tracking. Radio transmitters (AVM Instrument Co., Model SM1) were used to track some of the FTHL. The transmitters were carried on backpacks (3.0 g , [0.11 oz]) attached to lizards that weighed over 11.0 g (0.39 oz) (See Appendix A for details). The pulse rate of the transmitter was used as an indicator of decay of the transmitter battery.

Lizards with transmitters were located at various times of the day and night, and the location, surface temperature, substrate type, plant association, and the pulse rate of the transmitter were recorded. Individuals were recaptured at two to four month intervals for weighing, measurement, and to replace transmitters with low batteries.

Growth Models

Three models of growth rate in body size were fit to the recapture data: the von Bertalanffy model; the logistic-by-length model; and the logistic-by-weight model. The criterion of the lowest mean sum-of-squares was used to select the model that provided the best fit to the data (Schoener and Schoener 1978). All recapture data from each individual were used in the analysis.

The von Bertalanffy Model was used with Fabens' (1965)

method for fitting growth equations to data from animals of unknown ages (Frazer et al. 1990).

The general form of the von Bertalanffy equation is:

$$L_t = a(1 - be^{-kt}) \quad (1)$$

where L_t is the SVL at age t , a is the asymptotic length, b is related to size at birth, e is the base of natural logarithms, k is the intrinsic growth rate, and t is age.

Parameter b in equation (1) can be calculated after estimating parameters a and k . However, the average size at birth for this species is unknown, and it is necessary to solve for parameter b . We used the smallest SVL at which captures were made repeatedly to approximate the average size at day = 1. Thus at day $t = 1$, $kt = k$, and equation (1) reduces to:

$$b = e^k(1 - h/a) \quad (2)$$

where h is the SVL at day = 1.

Fabens' form of the von Bertalanffy equation is:

$$L_r = a - (a - L_c)e^{-kd} \quad (3)$$

where L_r is SVL at recapture, L_c is SVL at first capture, and d is the time interval between captures (days).

Least-squares nonlinear regression (Wilkinson 1988) was used to estimate a and k , the 95% confidence intervals (95% C.I.), and mean sum-of-squares.

The logistic-by-length model has the equation:

$$L_t = a/(1 + be^{-kt}) \quad (4)$$

The parameters are the same as in the preceding equations.

By substitution and rearrangement the interval equation:

$$L_r = aL_c/[L_c + (a - L_c)e^{-kd}] \quad (5)$$

can be used to estimate parameters a and k with least squares

nonlinear regression (Wilkinson 1988).

The logistic-by-weight model has the equation:

$$L_t = [a^3 / (1 + be^{-kt})]^{1/3} \quad (6)$$

The model assumes that weight is a function of the cube of the SVL. The parameters are the same as in the preceding equations. By substitution and rearrangement the interval equation:

$$L_r = \{a^3 L_c^3 / [L_c^3 + (a^3 - L_c^3)e^{-kd}]\}^{1/3} \quad (7)$$

can be used to estimate parameters a and k by least squares nonlinear regression (Wilkinson 1988).

Population Size

The number of animals that were actually on the site at any given time cannot be known with certainty. The population was not closed: immigration and emigration may have occurred; predation cannot be ignored in long-term studies; and additions to the population occurred in late summer and fall when hatchlings emerged. However, an estimate of the minimum number of animals on the site was derived from capture-recapture data for each month. The sum of the number of animals marked during a one-month period and those that were marked prior to that month and were subsequently recaptured during or after that month is an estimate of the minimum population size during the month. Unmarked animals were found on the site during each month that the animals were active. Thus, the minimum population size underestimated the "true" population size.

The minimum population size was used to estimate the

true population size (N) using Bailey's binomial form of the Lincoln-Petersen method (Begon 1979):

$$N = r(n+1)/(m+1) \quad (8)$$

where r is the minimum population size during a month, n is the number of individuals actually captured during that month, and m is the number of individuals captured that were marked previously. We used Bailey's formula for computing the standard error (SE) of the estimate:

$$SE_N = [r^2(n+1)(n-m)/(m+1)^2(m+2)]^{1/2} \quad (9)$$

We also estimated the monthly population size using the method of Minta and Mangel (1989). The Minta-Mangel model is a Monte Carlo simulation that uses the frequency distribution of sightings of marked individuals to estimate the number of individuals represented by sightings of unmarked animals. We used the distribution of sightings of individuals known to be alive during a one month period but initially captured before that period (= marked) to estimate the number of individuals represented by the number of sightings of animals that were captured initially during that period (= unmarked). The sum of the number known to be alive and the estimated number of unmarked animals is the population estimate for that period. The software provided by Minta and Mangel (1989) also calculated asymmetrical 95% likelihood intervals (95% L.I.). We used only those animals, both previously marked and new, that were sighted on or immediately beside the road for the Minta-Mangel estimate. Young-of-the year were omitted from the computations.

POPULATION DENSITY

The true size of the population on the study site was unknown. Hence, we estimated the density of the population by using the minimum population size and calculated the area of the site from the length of the road and the average size of a home range. We assumed that: 1) the road bisected the home range of individuals that were known to be alive during a given period; 2) the average home range is approximately circular in shape; and 3) the width of the site was equal to the diameter of the home range. Thus, the area of the plot was equal to the length of the road multiplied by the diameter of the home range.

The population density was calculated for the minimum population size and for both the area of the average home range size, and the average home range size for individuals with equal to or greater than the median number of sightings (see Home Range). Population densities were also calculated for the Minta-Mangel population size estimates for each year.

Survival

Survival estimates were calculated using a procedure that was developed for animals tagged with radio transmitters (Trent and Rongstad 1974). The weighted mean daily survival rate, S_d , is given by:

$$S_d = (x - y)/x \quad (10)$$

where x is the number of radio-lizard days, and y is the number of mortalities. A radio-lizard day is one radio-tagged lizard in the field for one day. Survival over time n , S_n , can be calculated as:

$$S_n = [(x - y)/x]^n \quad (11)$$

where S_n equals S_d^n .

The Trent and Rongstad (1974) method assumes that: "... (1) each [lizard] day was an independent trial, (2) there was a constant probability of survival or death for each trial over a time period of n days. Each [lizard] day can have only one of two possible results; either the animal is alive or dead. Each [lizard] day is a binomial event and over a given time period of n days the distribution of deaths should follow a binomial distribution. Since the sample ... was quite large compared to the number of mortalities, we can assume a Poisson distribution as a special case of the binomial...." The 95% confidence intervals for the daily survival, S_d , were calculated using the method of Fisher and Yates (1957) for a Poisson distribution.

Survival rate was calculated using pooled data from the two years of this study. Survival rates were calculated for bimonthly periods, an entire year (365 d), and for the active and inactive seasons. Survival was calculated from the number of lizard days of individuals whose fate was known at the end of the study. Adjusted survival rates were calculated also. Adjusted survival rate included the lizard days of individuals that survived through a given period and then disappeared or lost a transmitter after that period. For individuals first captured within a given period, the adjusted survival also included the number of lizard days between the first date of that period and the date the lizard was captured, provided that--based on growth data--it hatched

prior to the start of that period. The number of lizard days of small individuals that may not have hatched prior to the start of a given period was tallied from the date of first capture.

Predation

The causes of mortality for radio-tagged FTHL were determined from physical evidence. However, several of the individuals that "disappeared" may have been carried off the site by predators. It was impossible to determine which of these disappearances were the result of predation and which were the result of transmitter failure.

Temporal Activity

Seasonal Activity. The onset and duration of the inactive period during fall and winter (dormancy) was determined from radio-tagged individuals. The onset was the first day an individual was located inside of its dormancy burrow. The duration was the time (days) between the onset and the day the individual was first seen out of its burrow. The active period, in turn, began on the first day that the individual was observed out of the burrow and ended the first day of the following dormancy period. The mean onset and ending dates for the hibernation period were determined by transforming the calendar date into the Julian date.

Lizards were excavated during hibernation to replace transmitters with low batteries. The depth and the temperature ($^{\circ}\text{C}$) of the floor of the burrow beneath the lizard were recorded. A new transmitter was attached, and the lizard was returned to the burrow.

Time/Activity Budget. Daily activity was assessed by observing six individuals throughout their active period (i.e. from the first movement in the morning to the last movement at night) in May, 1992. Activity was divided into four basic categories: movement, motionless, feeding, and digging burrows. Movement consisted of short running spurts interrupted by rest periods of less than a minute, and excluded feeding except for an occasional ant encountered while moving from one point to another. Motionless encompassed any period of immobility after the first movement in the morning and prior to the last movement at night, or to the last movement before an individual went down a hole. The time spent in each of these activities was summed for all individuals to calculate an activity budget expressed as a percentage of the total daily activity time.

Home Range Size

Home range size was calculated from locations of radio-tagged FTHL. The location of each recapture (sighting) was recorded as a pair of distances and directional coordinates relative to permanent location markers that were placed near the site of the initial capture. The location markers were placed 50 m (164 ft) apart, and approximated a North-South or East-West course, perpendicular to the road. The distances were measured (± 1 m) (3.3 ft) with an optical rangefinder (Leitz Model 8026-15). The distances and coordinates were plotted on graph paper and converted to x-y coordinates. A minimum convex polygon (Southwood 1966) was drawn for each individual for each year. The area of the polygons was cal-

culated using "The Digital Paintbrush" (Jandel Corp.) computer graphics and digitizing software. Cumulative activity area was plotted as a function of the number of sightings of an individual and performance curves (Brower and Zar 1977) were fit to the data using SigmaPlot (Jandel Corp.) graphics software. The asymptote of the performance curve defines the number of sightings required to obtain 100% of the home range of an individual. Activity polygons underestimate the area of a home range if an individual's performance curve does not reach an asymptote.

As a guide to future researchers, we performed an a posteriori estimation of the number of recaptures that would be needed to determine the "true" home range size of an individual. We used the logistic growth model (eqn. 5) as an analogue model to estimate the asymptote (home range size, m^2) and number of captures needed to describe 100% of the home range size. Inputs to the model were the size of the home range at three captures (L_C) and the size of the home range at the last capture (L_T) for each individual.

Vegetation and Substrate Characteristics

Vegetation and substrate characteristics of the site were determined from 20 line-intercept transects (Brower and Zar 1977). The transects were 100 m in length and were perpendicular to the road, starting 4 m (13 ft) from the edge of the road. The start point and side of the road to begin the transect were chosen from a random number table.

Substrate Preference. The substrate type was recorded for each lizard sighting that was made off of the road. Four

classes of substrate were found on the site: 1) hardpan, concreted silt that was impenetrable to FTHL; 2) sand, both windblown and in washes; 3) hardpan/sand, a patchy combination of hardpan and sand with neither constituent larger in area than the body size of an adult FTHL; and 4) rock, sandstone rocks with a larger surface area than the body size of an adult FTHL. A Chi-square test was used to compare the frequency of sightings on each class of substrate to the expected frequency based on the results of the line-intercept transects (Brower and Zar 1977). The null hypothesis for the Chi-square test was that the frequency of sightings on each substrate type did not differ from the frequency of each substrate type on the site.

Plant Preference. Plant species preference was determined using sightings that were associated with perennial plants. A Chi-square test was used to compare the frequency of sightings associated with each perennial species to the expected frequency based on the results of the line-intercept transects (Brower and Zar 1977). The null hypothesis for the Chi-square test was that the frequency of sightings associated with each perennial species did not differ from the frequency of each perennial species on the site.

Soil Temperature. Soil temperatures were recorded continuously with three-point soil thermographs (WEATHERtronics Model 4030) for the duration of the study. The soil temperatures were measured in one location. The temperature probes were positioned to bracket the range of soil temperatures that a lizard might experience while on the surface or in a

burrow. Temperature was measured ($\pm 1.0^{\circ}\text{C}$, $\pm 1.8^{\circ}\text{F}$) at three depths, 0, 5, and 10 cm, (0, 2, and 4 in) in the full sun and in the shade. These data provide a general indication of the thermal milieu of soil accessible to FTHL on the site.

Scat Analysis

Scat from FTHL and six other species of lizards that were common on the study site were collected during the period in which scat surveys are conducted: May through July. The lizards were collected on site or on an adjacent road that traversed an area of sand dunes. The species, sex, SVL, mass, tail condition, and capture location were recorded. The lizards were kept in paper bags for one to two days to recover scat, and then they were released at the original point of capture. Thus, all scat used in the analysis were from individuals of known size and species. The length and diameter of each scat was measured with a vernier caliper (Cenco; ± 0.01 cm, 0.004 in). The surface was recorded as either regular or irregular, and the ends as acute, obtuse, or rounded. Contents were described as primarily ants, some ants plus other invertebrates, other invertebrates without obvious ants, invertebrates plus plant material, and solely plant material. However, for the analysis described herein, the data were combined into two categories, primarily ants and few ants.

The rate of scat production was estimated from captive animals and observations of radio-tagged individuals.

An analysis of the amount of time that scat could

remain on the surface was conducted in the lab and in the field. In the lab, scat of known origin were placed in a drying oven at a constant 45 °C (113 °F), and their condition was checked periodically. In the field, the site of scat deposited by radio-tagged individuals was marked with wire flags and the status of the scat was checked periodically. "Scat corrals" were also used to monitor the life span of scat on the surface. Two FTHL scat were placed in each of two scat corrals: a 1.0 m and a 1.5 m diameter pen of aluminum flashing with walls that extend 10.0 cm (4 in) above the surface. The 1.0 m corral contained only sandy substrate, and the 1.5 m corral contained a small shrub (Ambrosia dumosa) and sandy substrate. The location and condition of each scat were recorded weekly.

Statistical Procedures

All statistical procedures were implemented with "SYSTAT 4.0" (Systat Inc.) except where otherwise noted. A Lilliefors test for normality was used to determine if parametric (Student t test) or nonparametric (Mann-Whitney U test) statistics were appropriate for analysis of data. Two standard errors of the mean are given in parentheses after each mean reported herein, and a $P = 0.05$ level of significance was used throughout.

RESULTS

Capture Data

A total of 363 FTHL were captured, and there were 1,683 sightings. On-site 284 individuals were marked, and an additional 79 individuals were marked off-site. A total of 42

individuals were tagged with transmitters for a total of 7,944 lizard-days.

Sex Ratio. The sex-ratio did not differ significantly from 1:1 for all individuals captured, for all adults, for all immatures, and for all individuals captured during any month (Table 1).

Body Size. SVL ranged from 3.0 to 8.4 cm (1.2 to 3.3 in). Adult males (SVL \geq 6.5 cm, 2.6 in) had a mean SVL of 7.3 cm (2.9 in). The largest male had a SVL of 8.1 cm (3.2 in). Adult females (SVL \geq 6.5 cm) had a mean SVL of 7.4 cm (2.9 in). The largest female had a SVL of 8.4 cm (3.3 in). The mean SVL of adult males and females did not differ significantly ($U = 2401.5$, $p = 0.254$). Hatchlings had a minimum SVL of 3.0 cm. The smallest SVL recorded for several individuals ($N = 5$) was 3.3 cm (1.3 in).

Two cohorts of hatchlings were produced each year. The first cohort emerged in late July, the second in September (Fig. 2). The hatchling cohorts had a dramatic effect on the size class structure of the population (Fig. 3). In late spring (May), most of the population (88%) was composed of adults, but by early fall (September) most of the population (79%) was composed of juveniles.

Growth

Growth Rate. The mean SVL of the first hatchling cohort increased from 3.6 cm (1.4 in) (± 0.2 cm) in July to 6.0 cm (2.4 in) (± 0.4 cm) in October. The mean growth rate was 0.8 cm/mo (0.3 in/mo). The growth rate of marked hatchlings from the first cohort ranged from 0.03 to 0.05 cm/d (0.01 to 0.02

TABLE 1. Sex Ratio of The Superstition Population of FTHL. Sex ratios are given for individuals encountered on-site and off-site, combined totals for all individuals, and the sex ratio for all individuals captured in a given month. N.R. indicates data not recorded in the field (given to match totals in other tables). N.R. numbers were not used to calculate Chi-square values or sex ratio. The sex ratio was not significantly different from 1:1 (Chi-square critical value = 3.841, with 1 DF).

	M	F	SEX N.R.	TOTAL	X ²	SEX RATIO
<u>ON SITE</u>						
Adult	94	79	1	174	1.13	1:0.84
Immature	50	56	1	107	0.24	1:1.12
SVL N.R.			3	3		
TOTAL	144	135	5	284	0.23	1:0.94
<u>OFF SITE</u>						
Adult	19	19	0	38	0.03	1:1.00
Immature	20	18	0	38	0.03	1:0.90
SVL N.R.	2	1	0	3		
TOTAL	41	38	0	79	0.05	1:0.93
<u>COMBINED</u>						
Adult	113	98	1	211	0.93	1:0.87
Immature	70	74	1	144	0.06	1:1.06
SVL N.R.	2	1	3	6		
TOTAL	185	173	5	363	0.34	1:0.94
<u>BY MONTH:</u>						
January	0	0		0		
February	4	10		14	1.79	1:2.50
March	11	8		19	0.21	1:0.73
April	28	16		44	2.75	1:0.57
May	39	38		77	0.00	1:0.97
June	21	24		45	0.09	1:1.14
July	34	24	1	59	1.40	1:0.71
August	10	9	1	20	0.00	1:0.90
September	19	27	2	48	1.07	1:1.42
October	16	14	1	31	0.03	1:0.88
November	2	3		5	0.00	1:1.50
December	1	0		1	0.00	1:0.00

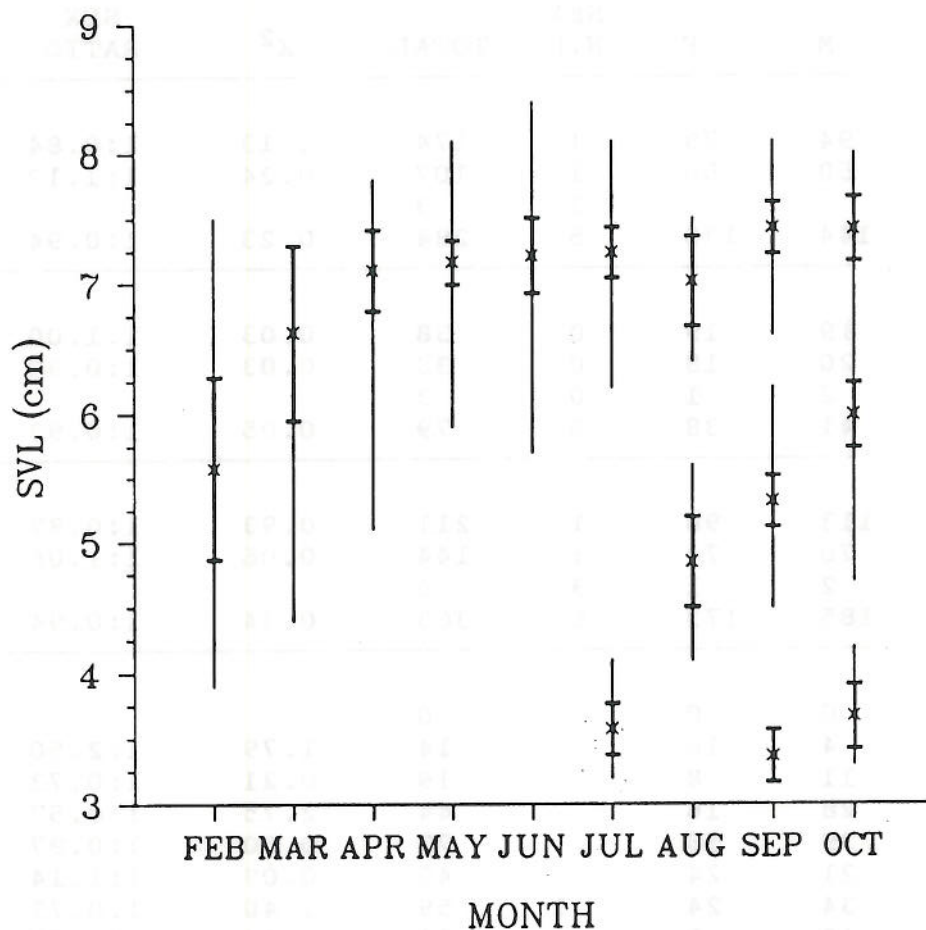


Fig. 2. The mean SVL (± 2 SE and range) of all FTHL captured during the active season, February through October. Note the presence of two distinct size classes in July and August, and three distinct size classes in September and October.

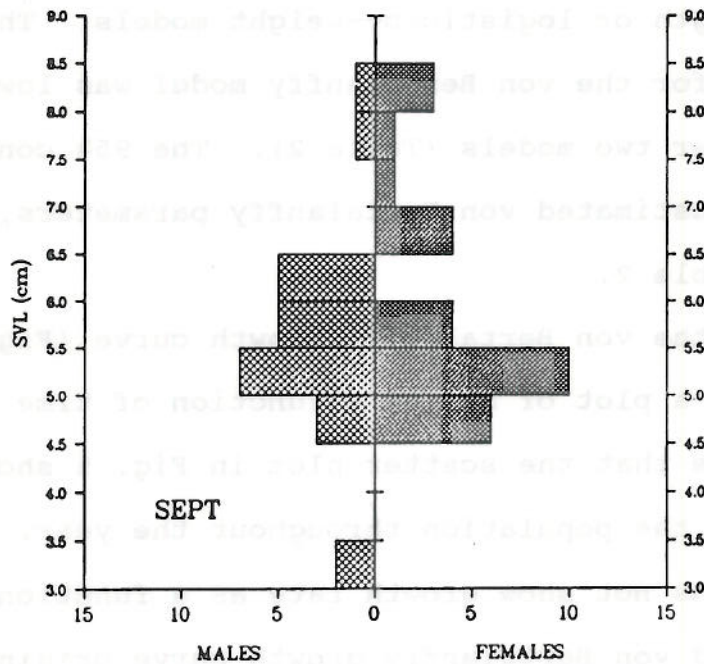
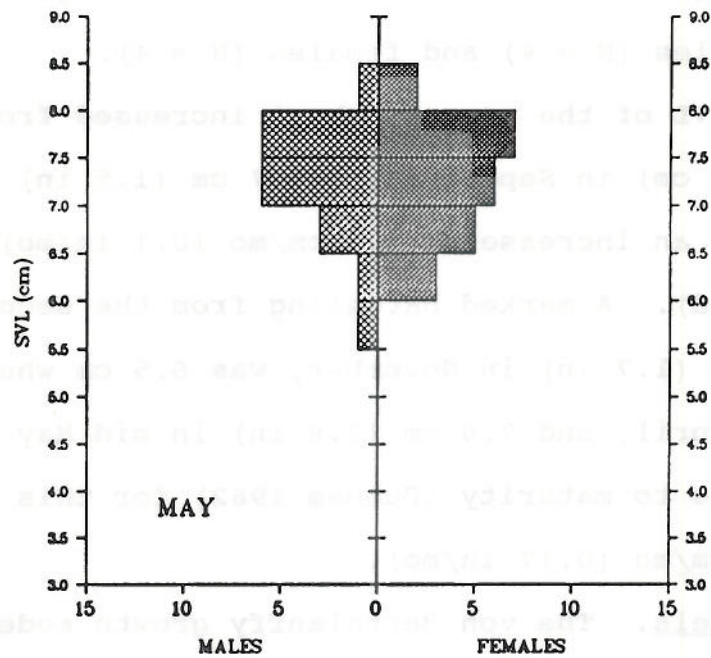


Fig. 3. Size structure of the population for May and September, 1991 and 1992 combined.

in/d), the mean growth rate ($N = 8$) was 0.04 cm/d (± 0.02). There was no significant difference between the growth rates of hatchling males ($N = 4$) and females ($N = 4$).

The mean SVL of the second cohort increased from 3.4 cm (1.3 in) (± 0.1 cm) in September to 3.7 cm (1.5 in) (± 0.2 cm) in October, an increase of 0.3 cm/mo (0.1 in/mo), or 0.01 cm/d (0.004 in/d). A marked hatchling from the second cohort measured 4.3 cm (1.7 in) in November, was 6.5 cm when recaptured in late April, and 7.0 cm (2.8 in) in mid May. The mean growth rate to maturity (Dunham 1982) for this individual was 0.44 cm/mo (0.17 in/mo).

Growth Models. The von Bertalanffy growth model described the growth trajectory of FTHL better than either logistic-by-length or logistic-by-weight models. The mean sum-of-squares for the von Bertalanffy model was lower than that of the other two models (Table 2). The 95% confidence limits for the estimated von Bertalanffy parameters, a and K , are given in Table 2.

A plot of the von Bertalanffy growth curve (Fig. 4) superimposed on a plot of SVL as a function of time is given in Fig. 5. Note that the scatter plot in Fig. 5 shows the range of SVL in the population throughout the year. The scatter plot does not show growth rate as a function of time. The superimposed von Bertalanffy growth curve originates on July 15, about the time of emergence of the first cohort. There is good correspondence between the calculated growth trajectory and the size distribution of the first cohort. The model indicates that most of the first cohort hatchlings

TABLE 2. Parameters for Three Growth Models, and the 95% Confidence Limits (95% C.L.) for the von Bertalanffy Model. N is the sample size, a is the asymptotic body size, and K is the intrinsic growth rate. The mean sum-of-squares (SS/N) and r^2 values for the nonlinear regressions are given.

Logistic-By-Length

SEX	N	a	K	SS/N	r^2
M	24	7.5	0.021	0.091	0.998
F	23	7.6	0.022	0.175	0.997

Logistic-By-Weight

SEX	N	a	K	SS/N	r^2
M	24	7.5	0.031	0.118	0.998
F	23	7.6	0.032	0.193	0.997

von Bertalanffy

SEX	N	a	95% C.L.	K	95% C.L.	SS/N	R^2
M	24	7.5	7.4-7.7	0.013	0.008-0.017	0.064	0.999
F	23	7.7	7.4-8.0	0.015	0.007-0.023	0.155	0.997
MF	47	7.6	7.4-7.8	0.013	0.009-0.017	0.107	0.998

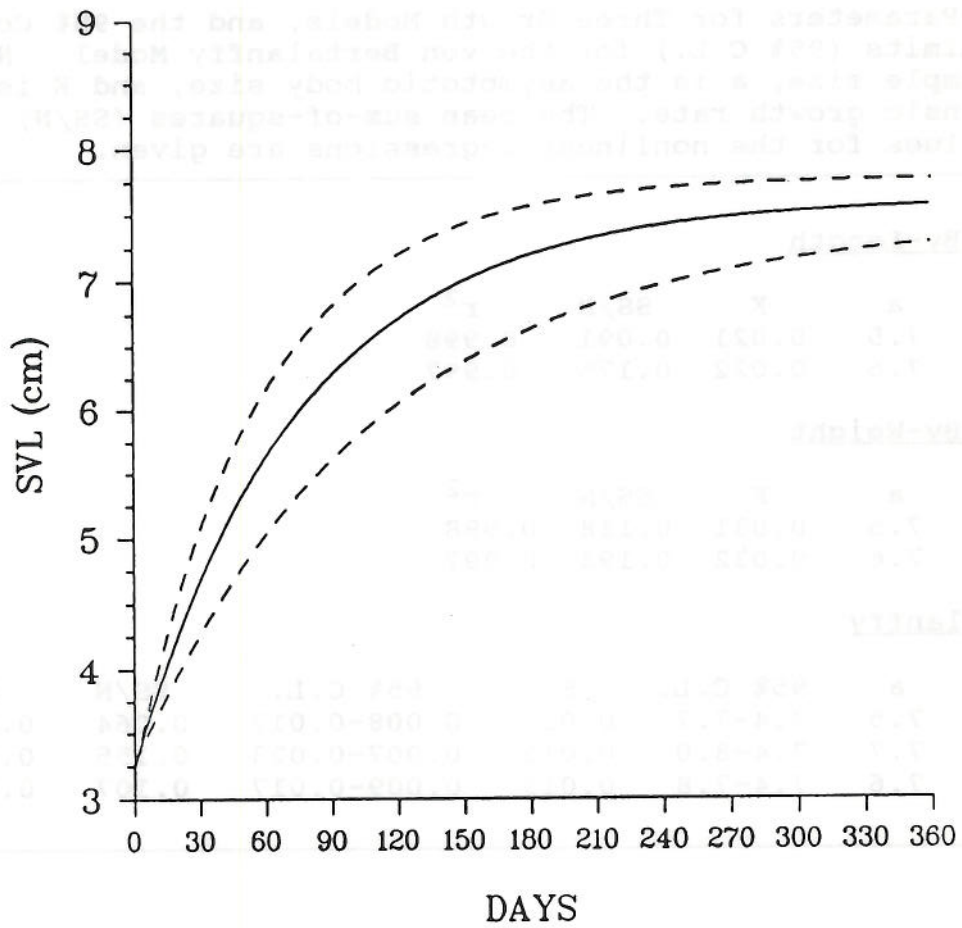


Fig. 4. The von Bertalanffy growth model ($\pm 95\%$ CI) for the Superstition population of FTHL.

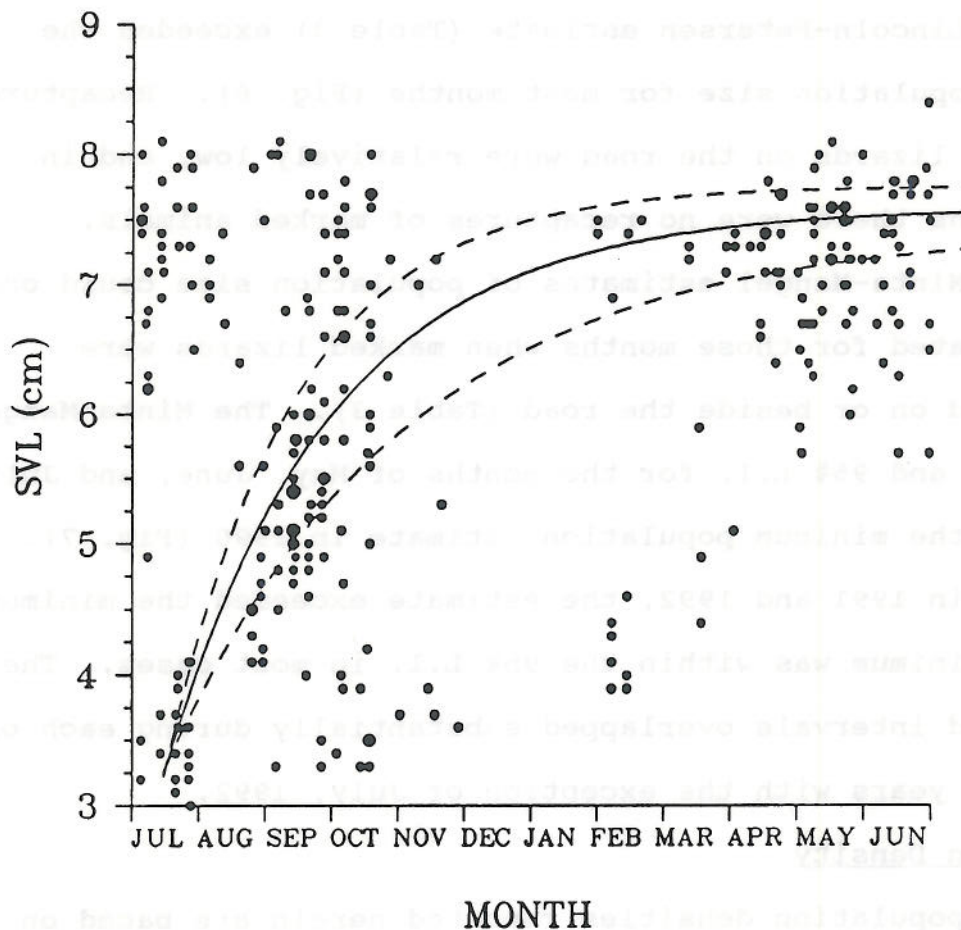


Fig. 5. Scatter plot of SVL as a function of month of the year. The von Bertalanffy growth curve ($\pm 95\%$ CI) with its origin on July 15 is superimposed on data from the first cohort.

should reach adult size prior to dormancy in November which is in accord with the field data.

Population Size

The minimum population size per month (Table 3) was lowest during the cool months and increased during the April through October period. Comparisons between years suggested that 1991 and 1992 had larger population sizes than did 1990.

The Lincoln-Petersen estimate (Table 3) exceeded the minimum population size for most months (Fig. 6). Recapture rates for lizards on the road were relatively low, and in some months there were no recaptures of marked animals.

The Minta-Mangel estimates of population size could only be calculated for those months when marked lizards were recaptured on or beside the road (Table 3). The Minta-Mangel estimates and 95% L.I. for the months of May, June, and July exceeded the minimum population estimate in 1990 (Fig. 7). However, in 1991 and 1992, the estimate exceeded the minimum but the minimum was within the 95% L.I. in most cases. The likelihood intervals overlapped substantially during each of the three years with the exception of July, 1992.

Population Density

The population densities reported herein are based on minimum population sizes. Hence, the calculated densities underestimate the actual densities and, for that reason, we report only the estimated maximum population densities for each year (Table 4). The greatest density estimates occurred in 1992: 1.30 FTHL/ha (0.53 FTHL/ac) based on the known minimum population size; and 1.39 FTHL/ha (0.56 FTHL/ac) based on

TABLE 3. Minimum Population Size(MPS), Lincoln-Petersen and Minta-Mangel Estimates of Population Size of Flat-tailed Horned Lizards on the Superstition site, 1990-1992. Numbers in parenthesis are 2SE for the Lincoln-Petersen estimate, and the upper and lower bounds of the 95% likelihood interval for the Minta-Mangel estimate.

MONTH	MPS			LINCOLN-PETERSEN					
	YEAR			YEAR					
	90	91	92	90	91	92	90	91	92
Jan	--	12	20	--	--	12	---	20	--
Feb	--	16	25	--	--	21	(6.0)	42	(16.6)
Mar	1	14	23	--	--	16	(3.4)	31	(9.6)
Apr	6	19	39	--	--	32	(12.4)	76	(39.6)
May	9	38	61	18	(9.6)	85	(29.8)	168	(58.4)
Jun	14	33	56	34	(18.6)	46	(10.0)	108	(29.2)
Jul	17	42	44	34	(17.0)	84	(25.4)	79	(20.6)
Aug	20	24	--	32	(10.6)	39	(12.8)	--	--
Sep	15	59	--	17	(3.4)	236	(105.6)	--	--
Oct	16	39	--	21	(6.0)	105	(44.4)	--	--
Nov	14	24	--	15	(2.2)	33	(9.8)	--	--
Dec	12	20	--	12	---	20	---	--	--

MINTA-MANGEL ESTIMATE

Month	YEAR			YEAR			YEAR		
	90			91			92		
May	9	(-- - --)		56	(41 - 85)		62	(48 - 82)	
Jun	33	(17 - 72)		43	(31 - 62)		65	(54 - 77)	
Jul	40	(25 - 67)		41	(30 - 56)		33	(29 - 38)	

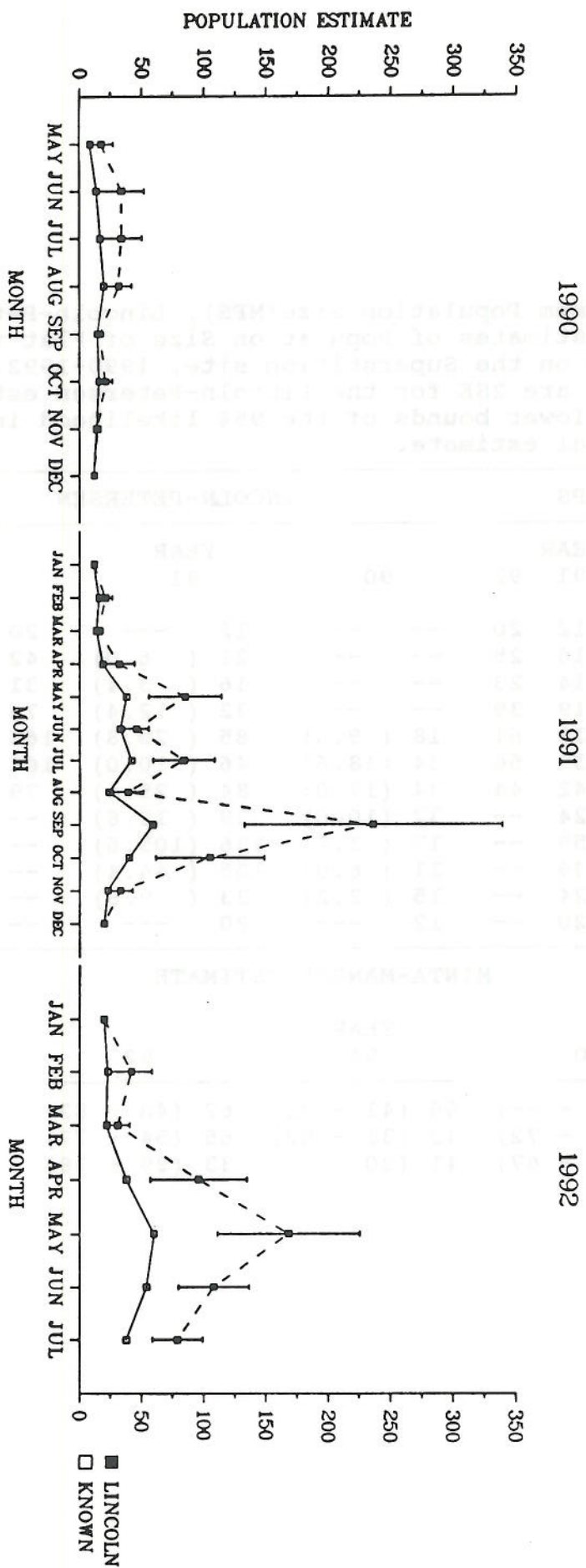


Fig. 6. The minimum population size and Lincoln-Petersen estimates of population size ($\pm 95\%$ C.I.) for 1990-1992.

Fig. 7. The minimum population size and Minta-Mangel population estimates of population size ($\pm 95\%$ L.I.) for 1990-1992.

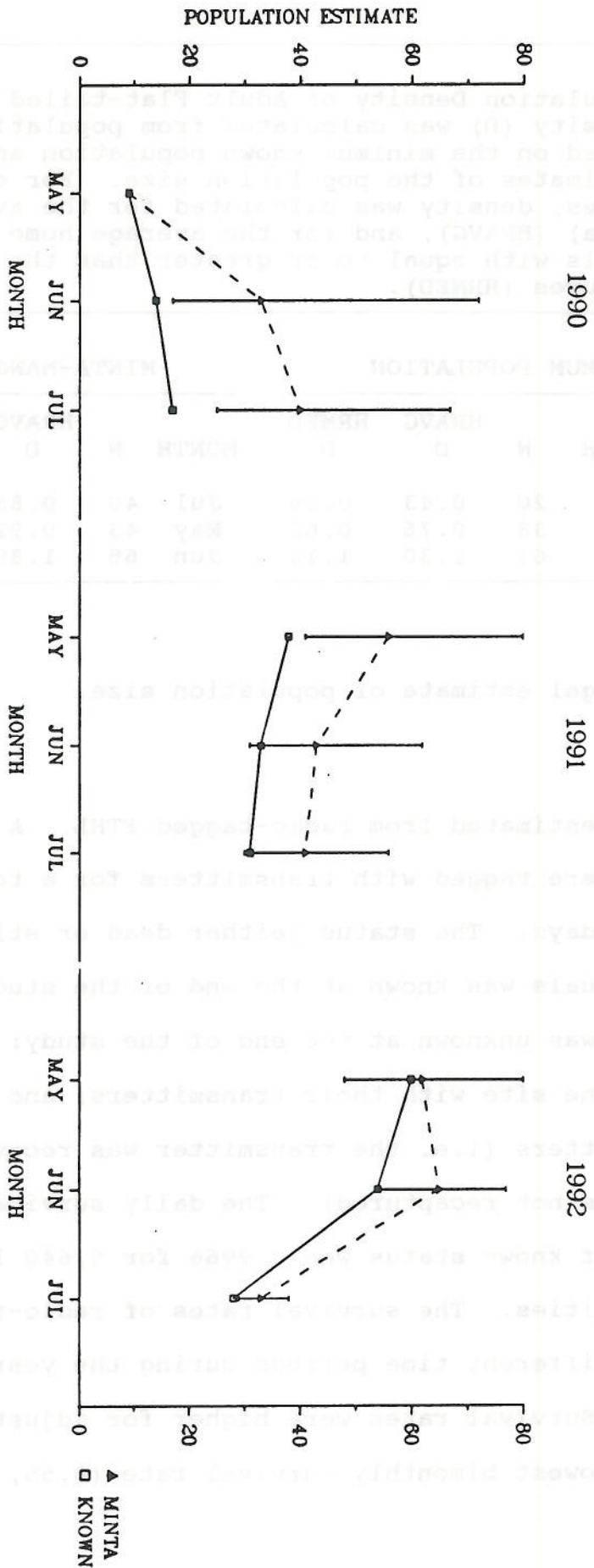


TABLE 4. Population Density of Adult Flat-tailed Horned Lizards. Density (D) was calculated from population estimates (N) based on the minimum known population and for Minta-Mangel estimates of the population size. For each of these estimates, density was calculated for the average home range size (ha) (HRAVG), and for the average home range size for individuals with equal to or greater than the median number of recaptures (HRMED).

MINIMUM POPULATION					MINTA-MANGEL			
YEAR	MONTH	N	HRAVG D	HRMED D	MONTH	N	HRAVG D	HRMED D
1990	Aug	20	0.43	0.36	Jul	40	0.85	0.72
1991	May	38	0.76	0.68	May	43	0.92	0.77
1992	May	61	1.30	1.10	Jun	65	1.39	1.17

the Minta-Mangel estimate of population size.

Survival

Survival was estimated from radio-tagged FTHL. A total of 42 individuals were tagged with transmitters for a total of 7,944 lizard-days. The status (either dead or still alive) of 27 individuals was known at the end of the study. The status of 15 was unknown at the end of the study: 10 disappeared from the site with their transmitters; and five lost their transmitters (i.e. the transmitter was recovered, but the lizard was not recaptured). The daily survival (Sd) for the lizards of known status was 0.9966 for 5,640 lizard-days and 19 mortalities. The survival rates of radio-tagged lizards for different time periods during the year are given in Table 5. Survival rates were higher for adjusted estimates. The lowest bimonthly survival rate (0.55, 0.70

TABLE 5. Survival Rate (S_n) of Radio-tagged FTHL for Bimonthly, Seasonal, and Yearly Periods. The 95% confidence intervals (95% CI) are given for periods of n days Duration. LD is the cumulative number of lizard-days that radio-tagged lizards were alive during the period. M is the number of deaths. Adjusted LD and S_n values allow the use of more lizard-days (see text for details).

PERIOD	LD	n	M	S_n	95% CI	ADJUSTED		
						LD	S_n	95% CI
Jan-Feb	944	59	0	1.00	-----	1121	1.00	-----
Mar-Apr	807	61	0	1.00	-----	1375	1.00	-----
May-Jun	1028	61	7	0.66	0.42-0.89	1629	0.77	0.58-0.93
Jul-Aug	943	62	9	0.55	0.32-0.76	1583	0.70	0.51-0.96
Sep-Oct	972	61	1	0.94	0.70-1.00	1384	0.96	0.78-1.00
Nov-Dec	1037	61	2	0.89	0.65-0.99	1281	0.91	0.71-0.99
Active	3888	276	17	0.30	0.14-0.50	8338	0.57	0.40-0.72
Winter	1459	89	2	0.89	0.25-0.99	1815	0.91	0.70-0.99
1990	1473	365	6	0.23	0.04-0.58	5705	0.68	0.40-0.84
1991	3551	365	13	0.26	0.10-0.49	5237	0.40	0.21-0.62
YEARLY	5024	365	19	0.25	0.11-0.44	10942	0.53	0.37-0.69

adjusted) occurred in the July-August period, and the highest survival rates (1.00) occurred in the winter and early spring periods.

Predation

The predators were identified for 19 deaths of radio-tagged lizards. The Round-tailed Ground Squirrel, Spermophilus tereticaudus was responsible for eight deaths, four were attributed to snakes (one definite, three possible), three were attributed to the Loggerhead Shrike, Lanius ludovicianus, three were attributed to motor vehicles (two ORV, one on pavement), and one to a canid, either a coyote, Canis latrans, or a kit fox, Vulpes macrotis.

Temporal Activity

Seasonal and daily activity was analyzed for radio-tagged FTHL.

Seasonal Activity. Seasonal activity consisted of two periods: the active period during the warm months; and an inactive period, winter dormancy, during the cold months. The mean onset of winter dormancy was 13 November (N=19), (± 9 d) and the range was from 5 October to 12 December. The mean duration of winter dormancy was 89 days, (± 13 d), and the range was 14 to 138 days. The mean end of dormancy was 11 February, (± 10 d), and the range was 12 December to 17 March.

Adults dug the burrows that they occupied during the dormancy period. The burrow floor where dormant lizards were located had a mean depth of 5.6 cm (2.2 in), (± 2.1 cm), with a range of 2.5 to 10.0 cm (1.0 to 4.0 in, N = 6). Burrow

temperature was less than 1.0 °C (1.8 °F) different from the thermograph temperature measured at a depth of 5 cm (2 in) in the sun.

The active period extended from the end of winter dormancy to the onset of the next dormancy period; on average 277 days. All individuals were active daily when weather permitted. There was no indication of a period of inactivity, estivation, during the late summer.

Time/Activity Budget. Six individuals were observed throughout their daily activity period in May. Activity began between 0730 and 1145 (mean 0945, ± 74 min), and terminated between 1120 and 1816 (mean 1434, ± 132 min). The mean duration of activity was 290 min (range 125-411 min). FTHL spent 32% of the active period moving (excluding feeding and digging), 46% of the time was spent motionless, 11% was spent feeding, and 11% was spent digging burrows.

Home Range Size

Radio-tagged individuals with three or more captures ($N = 43$) were used to determine home range size. The mean home range size was 19,200 m² (209,280 ft²) ($\pm 7,736$ m²), range 891 - 131,300 m² (9,712 - 1,431,170 ft²). All but one of the estimates failed to reach an asymptote when the cumulative home range size was plotted as a function of the number of captures. The median number of captures was 18.5. The mean home range size for individuals with more captures than the median was 26,975 m² (294,028 ft²), ($\pm 12,210$ m², $N = 22$).

The a posteriori estimation model indicated that about

70 recaptures would be needed to estimate the size of a home range which was predicted to be about 81,512 m² (20.1 ac) (Fig. 8).

The mean home range size for all males (N = 22), 17,894 m² (\pm 6,823 m²) (195,045 ft²), and all females (N = 23), 19,703 m² (\pm 13,773 m²) (214,762 ft²), did not differ significantly (data log transformed, $t = 0.544$, $p = 0.589$).

Both radio-tagged and non-tagged individuals were recaptured periodically on the road. There was no significant difference in the distance travelled between subsequent sightings of 12 tagged and 30 non-tagged individuals (data log transformed, $t = 0.648$, $p = 0.107$).

Vegetation and Substrate Characteristics

Substrate Preference. The substrate coverage was characterized as 82% hardpan, 17% sand, 1% hardpan/sand, and 0.05% rock.

Substrate preference was tested for bimonthly periods and for all months combined. For all periods analyzed FTHL showed a preference for sandy substrate (Table 6).

Plant Preference. A total of 6% of the surface is covered by plants: 3% of the cover is from "live" plants; and 3% is from dead/dormant plants. A list of the perennial plant species, and the relative frequency of each species in percent by number and percent by coverage are given in Table 7.

The make up of perennial plant species was expressed as the percentage of each species in the following categories: 1) the total number of living plants; 2) the total number of plants, both alive and dead or dormant; 3) the total coverage

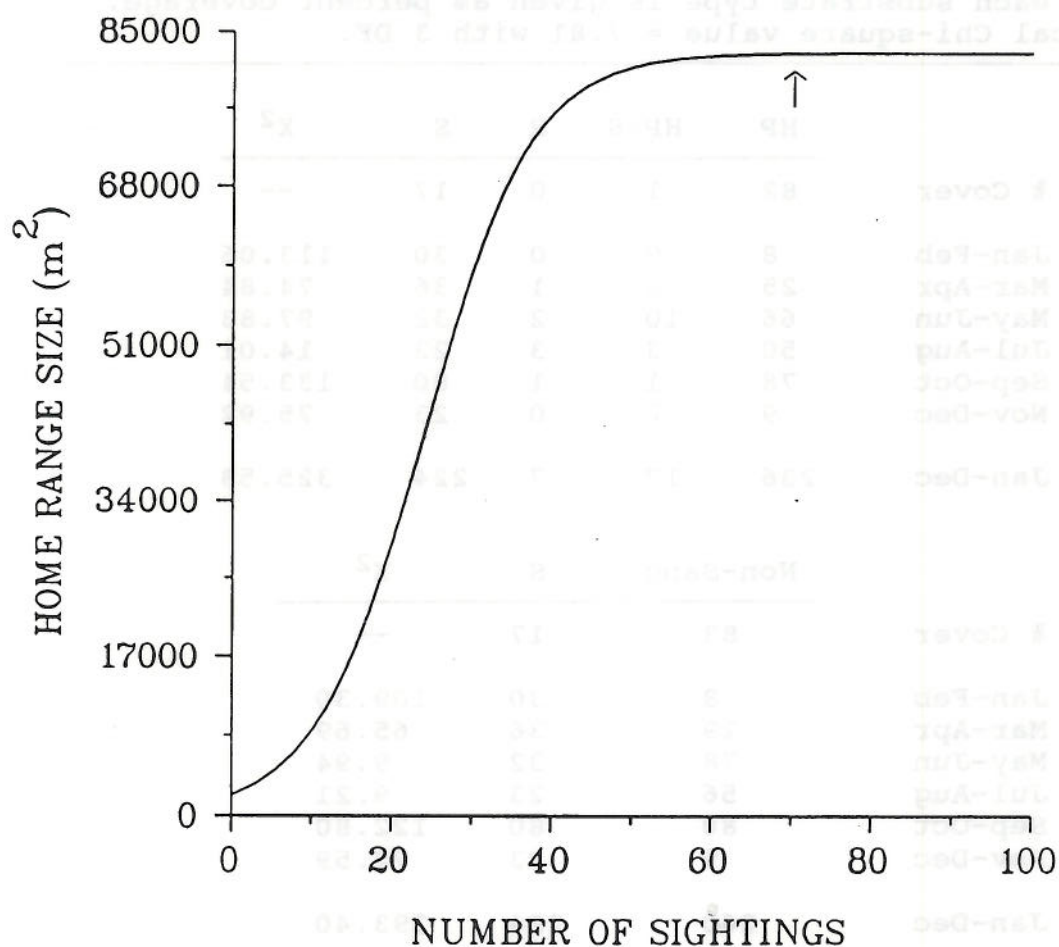


Fig. 8. Home range size as a function of the number of recaptures estimated by an analogue logistic-by-length growth model. Home range size reaches an asymptote at about 70 recaptures.

TABLE 6. The Number of FTHL Sightings on Each Substrate Type for Bimonthly Periods and All Months Combined. HP is Hardpan, HP/S is Patchy Hardpan and Sand, R is Rock, S is Sand, and NON-SAND is HP, HP/S, and R combined. The relative frequency of each substrate type is given as percent coverage. The critical Chi-square value = 7.81 with 3 DF.

	HP	HP/S	R	S	χ^2
% Cover	82	1	0	17	--
Jan-Feb	8	0	0	30	113.06
Mar-Apr	25	3	1	36	74.84
May-Jun	66	10	2	32	97.83
Jul-Aug	50	3	3	23	14.01
Sep-Oct	78	1	1	80	133.54
Nov-Dec	9	0	0	23	75.92
Jan-Dec	236	17	7	224	325.58

	Non-Sand	S	χ^2
% Cover	83	17	--
Jan-Feb	8	30	109.30
Mar-Apr	29	36	65.69
May-Jun	78	32	9.94
Jul-Aug	56	23	9.21
Sep-Oct	80	80	122.80
Nov-Dec	9	23	72.59
Jan-Dec	260	224	293.40

TABLE 7. Line-intercept Transect Estimates of Perennial Plant Composition. The relative frequency of each species is given as a percentage of: 1) the total number of plants; 2) the total number of living plants; 3) the total coverage of plants; and 4) the coverage of living plants. Total number includes both living and dead/dormant plants. In "% Total" columns, the percentage of the total number of plants on the transects that was comprised of living plants of a given species is followed by the percentage comprised of dead/dormant plants of a given species.

Species	% TOTAL NO.	% NO. ALIVE	% TOTAL COVER	% COVER ALIVE
<u>Ambrosia dumosa</u>	3 (17)	8	3 (16)	7
<u>Asclepias subulata</u> *	0 (0)	0	0 (0)	0
<u>Croton californicus</u>	0 (0)	1	0 (0)	1
<u>Ephedra trifurcata</u>	1 (1)	3	4 (1)	8
<u>Eriogonum deserticola</u>	0 (0)	0	0 (0)	0
<u>Haplopappus acradenius</u>	0 (2)	1	0 (5)	0
<u>Hilaria rigida</u>	5 (0)	11	10 (0)	20
<u>Larrea tridentata</u>	6 (1)	14	18 (2)	36
<u>Palafoxia linearis</u>	5 (1)	11	3 (0)	5
<u>Psoralea emoryi</u>	3 (4)	7	3 (3)	6
<u>Psoralea schottii</u> *	0 (0)	0	0 (0)	0
<u>Tequilia palmeri</u>	18 (32)	43	8 (23)	16
<u>Tequilia plicata</u>	1 (0)	2	0 (0)	1
Total surface coverage:			6	3

*Species occur on site, but at densities too low to be measured by line-intercept method.

of living plants; 4) the total coverage of plants, both alive and dead or dormant; 5) the total number of dead or dormant plants; and 6) the total coverage of dead or dormant plants. Chi-square contingency tables were used to test the null hypothesis that the frequency of sightings was not associated with perennial plant species. The expected frequencies were based on the results of the line-intercept transects. The null hypothesis was rejected for all six of the above cases. Sightings are not distributed independent of plant species. The resultant χ^2 values were 62.05, 84.96, 59.17, 103.04, 44.22, and 36.81, respectively; the critical value at 11 DF is 19.68 (Rohlf and Sokal 1969).

For the total number of living plants, category 1 above, Ambrosia dumosa and Psoralea emoryi have a much higher frequency of association with FTHL sightings than expected, and Tequilium palmeri has a much lower frequency of association than expected. Excluding these three species from the analysis of the total number of living plants results in a χ^2 value of 15.09; the critical value at 8 DF is 15.51 (Rohlf and Sokal 1969). Thus, for the remaining plant species, the null hypothesis is accepted and the frequency of sightings is distributed independent of species. Likewise, for category 3 above, based on percent coverage by live plants, the frequency of association with A. dumosa and P. emoryi are again much higher than expected, and the observed frequency of association with Larrea tridentata is much lower than expected. Excluding these three species resulted in a χ^2 of 2.60 with 8 DF. Excluding A. dumosa, P. emoryi, and

T. palmeri from category 2, and A. dumosa, P. emoryi, and L. tridentata from category 4 failed to significantly alter the results. Thus, the null hypothesis was rejected for each of these cases ($X^2 = 22.47, 16.40$, respectively, at 11 DF).

Summarizing the above: FTHL preferred Ambrosia dumosa and Psoralea emoryi, and avoided Tequilia plicata which was the most abundant plant on the site. The plant with the greatest total coverage, Larrea tridentata, was also avoided. For all other plants on the site, the frequency of sightings associated with each plant species did not differ from the frequencies of occurrence of the plant species on the site.

Soil Temperature. The average monthly high soil temperature in sun and shade is plotted in Fig. 9. The voluntary minimum (29.3 °C, 85 °F) and maximum (41.0 °C, 106 °F) body temperatures (Brattstrom 1965) are superimposed on the graph. The voluntary activity range of body temperatures is bracketed by these body temperatures. The daily high soil temperature at 5 cm in the sun first reached the voluntary minimum body temperature during the week of February 4-6 in 1991 and February 26-28 in 1992. The daily high soil temperature at 5 cm is correlated with the minimum voluntary body temperature and the end of winter dormancy in mid-February.

Scat Analysis

All FTHL scat contained primarily ants during May through July. Although the other species' scat also contained some ants, only Uma notata and Callisaurus draconoides produced some scat (4/50 and 6/13 respectively) that contained primarily ants.

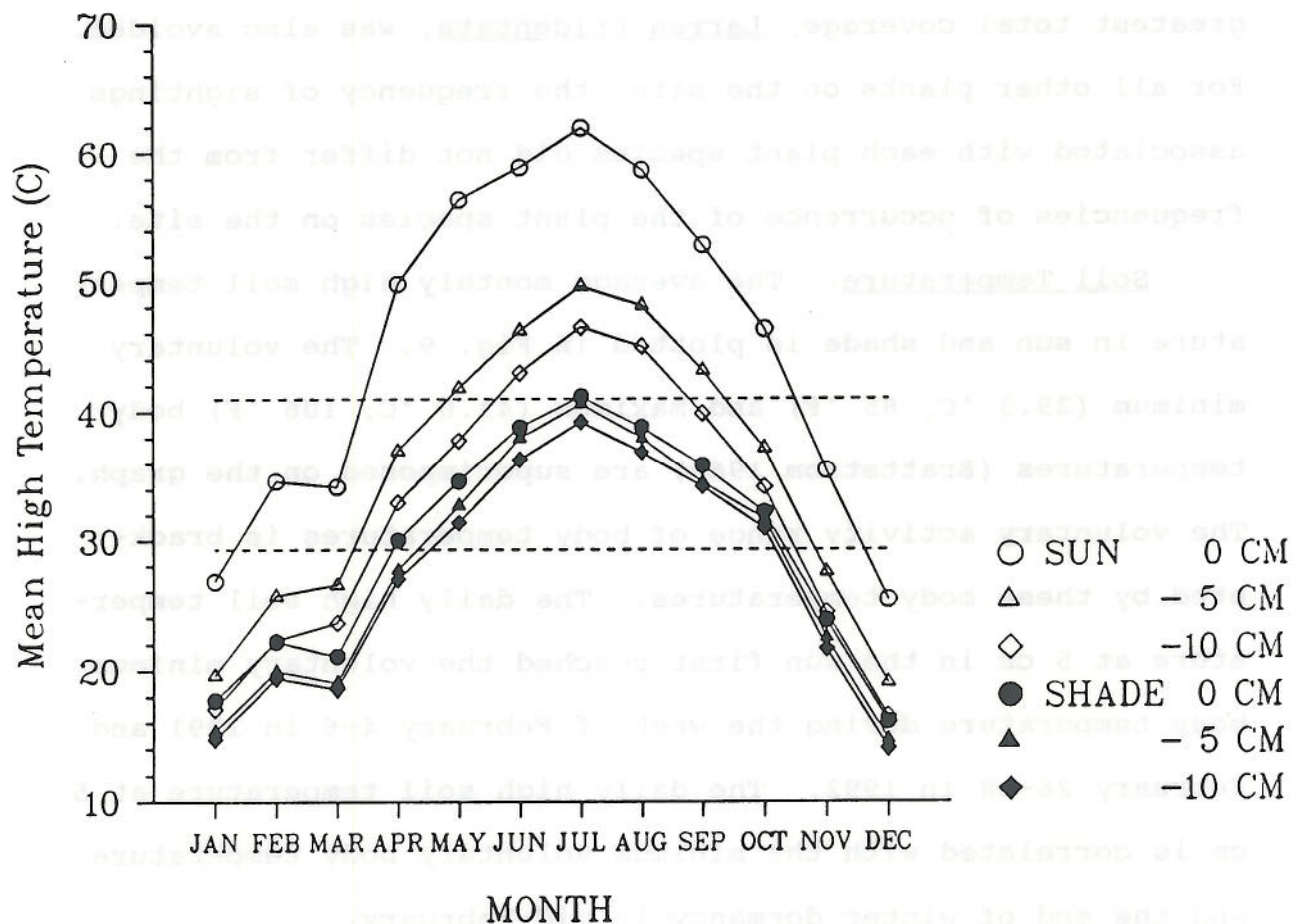


Fig. 9. The monthly mean high soil temperature in the sun and shade at three depths. The dashed lines are the minimum and maximum voluntary body temperature of the FTHL.

Scat morphology tends to differ among species. FTHL scat are elliptical in outline with a smooth, regular surface and have obtuse to rounded ends. Scat from other lizard species are more irregular in outline and surface, and usually have acute ends. However, scat from U. notata and C. draconoides that contain primarily ants resemble that of P. macalli in shape more so than scat with few to no ants. The surface is smooth and regular and the ends are obtuse as in FTHL scat.

The length and diameter of FTHL scat are, on average, longer and of greater diameter than that of other species (Table 8). Scat diameter overlapped less among species than did scat length, but there was still considerable overlap among species.

The overlap of scat diameter can be reduced by excluding hatchlings and considering only species whose scat contain primarily ants: FTHL; U. notata; and C. draconoides. Of the non-FTHL scat that contained primarily ants, 90% was smaller than 5.5 mm (0.22 in) or less in diameter, whereas all FTHL scat from adult animals was larger than 5.5 mm (Fig. 10).

A comparison of scat length among the three species indicated that there was about 50% overlap in the length of scat. The length of scat containing primarily ants can not be used to differentiate adult FTHL from other species.

The production rate of scat from captive and radio-tagged FTHL was about one scat per day. Captive FTHL (N = 33) produced 1.05 scat/lizard/d. Radio-tagged lizards that

TABLE 8. The Dimensions of Scat for FTHL and Five Species of Sympatric Lizards. Presence or absence of scat containing primarily ants is indicated in the "ANTS" column.

SPECIES	SCAT LENGTH (cm)					SCAT DIAMETER (cm)					ANTS
	N	MIN	MAX	MEAN	2SE	N	MIN	MAX	MEAN	2SE	
<u>P. mcallii</u>	52	0.71	2.71	1.74	0.13	53	0.32	0.90	0.64	0.03	YES
<u>C. draconoides</u>	13	0.68	1.37	1.01	0.12	13	0.25	0.48	0.37	0.04	YES
<u>C. variegatus</u>	12	0.52	1.30	0.92	0.14	12	0.29	0.46	0.35	0.03	NO
<u>G. wislizenii</u>	7	0.32	1.40	0.98	0.27	7	0.18	0.63	0.42	0.13	NO
<u>U. notata</u>	50	0.57	2.11	1.38	0.09	50	0.21	0.70	0.52	0.03	YES
<u>U. stansburiana</u>	5	0.60	0.90	0.79	0.10	5	0.31	0.39	0.36	0.03	NO

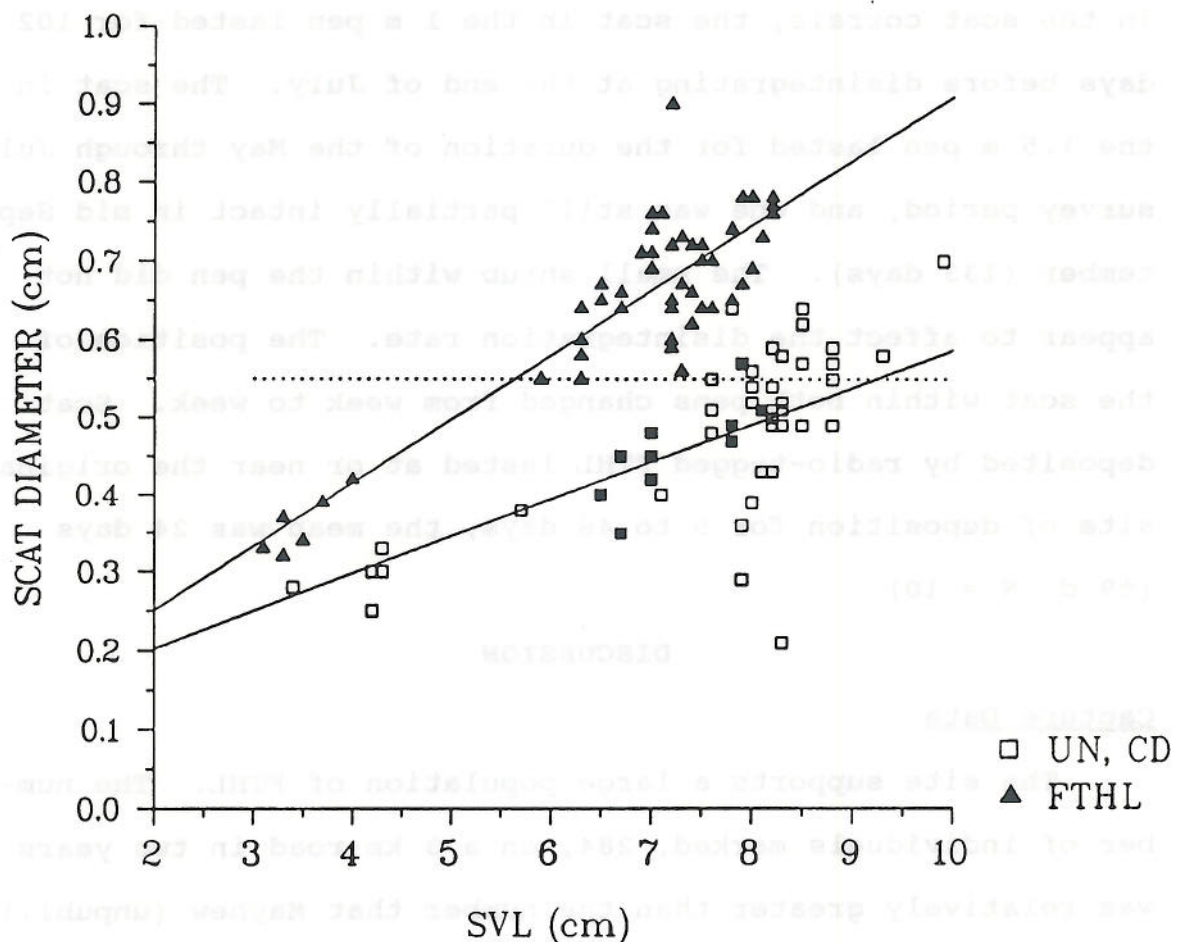


Fig. 10. Scat Diameter as a Function of Snout-vent Length for the flat-tailed horned lizard (FTHL), Uma notata (UN) and Callisaurus draconoides (CD). Solid symbols indicate scat containing primarily ants. Solid lines are least squares regression lines for FTHL ($Y = 0.083X + 0.085$, $r^2 = 0.79$), and UN and CD combined ($Y = 0.048X + 0.103$, $r^2 = 0.58$). All adult FTHL produced scat > 5.5 mm in diameter (dotted line).

were followed throughout their daily activity period were observed defecating only in the morning, between 0723 and 1145 (N = 7), and produced one scat each.

The persistence of scat on the surface was tested in lab and field experiments. In the laboratory, eight scat placed in a drying oven at 45 °C (113 °F) remained intact through the entire survey period without any visible deterioration. In the scat corrals, the scat in the 1 m pen lasted for 102 days before disintegrating at the end of July. The scat in the 1.5 m pen lasted for the duration of the May through July survey period, and one was still partially intact in mid September (133 days). The small shrub within the pen did not appear to affect the disintegration rate. The position of the scat within both pens changed from week to week. Scat deposited by radio-tagged FTHL lasted at or near the original site of deposition for 5 to 46 days, the mean was 24 days (± 9 d, N = 10).

DISCUSSION

Capture Data

The site supports a large population of FTHL. The number of individuals marked, 284, on a 3 km road in two years was relatively greater than the number that Mayhew (unpubl.) collected, 381, in 3½ years on an 11.3 km (7.0 mi) road on East Mesa, Imperial County, California. We found 47.5 lizards/km/year compared to Mayhew's 9.6 lizards/km/year.

Sex Ratio. Sex ratio in the Superstition Hills population is in agreement with results from East Mesa (Mayhew, unpubl.), and the Yuha Basin (Turner and Medica 1982). The

sex ratio did not differ significantly from 1:1 for collections made in all months of this study. This result indicates that males and females are equally catchable throughout the year which is an important assumption of statistical based models for population estimation.

Body Size. Males and females did not differ significantly in mean body size (SVL) or growth rate. In this study we adopted 6.5 cm SVL as the minimum adult body size for both males and females. Howard (1974) found that males of SVL \geq 6.5 cm were reproductively active, but the smallest size that females were reproductively active was 6.6 cm (2.6 in). The von Bertalanffy growth curve indicates that a 6.5 cm female would reach 6.6 cm within eight or nine days. The distinction between these body sizes is probably of little consequence for management considerations for the FTHL.

The pooled size data indicate two periods for the emergence of hatchlings, in concurrence with reproductive data from Howard (1974). It should be noted, however, that this may not occur in all years. In 1990 no individuals from the first cohort were collected, but the second cohort was represented. In 1991 both cohorts were evident. Reproduction is probably correlated with environmental conditions and it is conceivable that neither cohort may be produced in bad years.

The SVL data clearly indicate that two cohorts of hatchlings can be produced in some years. The distinct cohorts could have been the result of: 1) the production of one or two clutches by some females that were mature by the early

spring (including females from the first clutch of the previous fall); 2) single clutches, including the delayed production of a first clutch by late maturing females from the second cohort of the previous fall; or 3) some combination of the two preceding scenarios. The methods used in this study do not enable us to distinguish among these alternatives.

Growth

Hatchlings from the first cohort can grow to adult size by the following spring, and hatchlings from the second cohort can grow to adult size by mid-summer of the following year. The former result is not in agreement with Turner and Medica's (1982) estimate of 20 months to maturity for all hatchlings, and the latter result is not in agreement with Howard's (1974) estimate of maturity after two growth seasons for hatchlings produced in late summer. We suggest that because they did not have the benefit of large sample sizes with multiple recaptures, they probably were unable to resolve the existence of two cohorts. By September there are three nonoverlapping size classes that, without recapture data, might be interpreted as being from three separate years. But in fact, the largest size class contains lizards \geq one year old, and the middle and smaller size classes represent the first and second cohorts of the current year.

Growth Models. The von Bertalanffy growth model is in good agreement with the size data for the first cohort. The curve indicates that adult size, 6.5 cm, should be reached by late October. This exceeds slightly the mean size of the first cohort, 6.0 cm SVL, in late October. The von Berta-

lanffy curve reached an asymptote at 7.6 cm (3.0 in). Although many individuals were larger than 7.6 cm, the mean size of the adult population was 7.3 cm which is in accord with the test proposed by Frazer et al. (1990) whereby "... the average adult size should lie just below the estimated asymptotic value for the population."

The von Bertalanffy growth model described the growth trajectory of FTHL better than either logistic-by-length or logistic-by-weight models. This is contrary to the results of Schoener and Schoener (1978) for several species of anoline lizards. They found that for most cases the logistic-by-weight model fit their data better than the von Bertalanffy model.

Population Size

The entire population was not marked, and the minimum population size underestimated the true size. However, the minimum population size should reflect trends in the true population size. Nearly all of the lizards were captured on or beside the road, with the exception of those that were radio-tagged. The trends seen in minimum population size reflect trends in activity near and on the road. Road use can vary with time of year. In the winter and early spring very few animals are found on the road, even when they are known to be active. However, during the warmer months the animals are more active and have a better likelihood of being encountered on the road. Hence, we feel that the minimum population size is a good relative measure of the true population size during the May through October period.

In an idealized annual population cycle, the population should peak following emergence of the young-of-the-year and then gradually decrease as animals die or emigrate from the population. However, the minimum population size shows an apparent increase between May and August in 1990 (Table 3), but no hatchlings were found until October of that year. The apparent increase is an artifact of having marked only a small part of the population at the start of that field season. After a peak in August the 1990 minimum population size declined as expected. The 1991 minimum population size peaked in July and again in September. These peaks coincide with the emergence of two clutches of hatchlings. The decline following the September peak may reflect both losses to the population and the decrease in lizard activity with the onset of cooler weather in mid October. The 1992 data indicate a decrease in the population size in July when an increase would be expected with the emergence of the first hatchling cohort of the year. The decrease probably reflects the termination of the study rather than an actual decline in the population. Individuals that were marked prior to July, but were not seen during July could not be verified as alive by a resighting sometime after July.

The Lincoln-Petersen estimates follow the trends in the minimum population size. The estimates are also greater than the minimum population size as would be expected. However, two assumptions of the Lincoln-Petersen model are not met: the population was not closed; and all individuals were not equally catchable. Radio-tagged individuals were

obviously resighted more frequently than others, and all animals without radios were not equally likely to be sighted on the road during a census. During 1991, for example, 147 known individuals were alive. Nearly all of these were sighted initially on the road. Subsequent resightings on the road occurred with the following frequencies: one was seen six times; one was seen four times; one was seen three times; eight were seen two times; 18 were seen one time; and 118 were never resighted on the road. Equal catchability and closed populations are rigid assumptions of the Lincoln-Petersen method and all of its descendent models. Hence, we are skeptical of the estimates derived by the Lincoln-Petersen method.

The Minta-Mangel method does not assume equal catchability, but it does assume a closed population. With regard to catchability the model assumes that sightings of unmarked individuals on the road occurred with the same array of frequencies with which marked individuals were resighted on the road. We dealt with the closed population assumption by omitting young of the year, and by adjusting the procedure to effectively close the population. Only those animals that were known to be alive during each monthly sample period were included in the computations, thus, death and emigration would not be a factor. Immigration would not be a factor because we used the frequencies of sightings of animals that were marked prior to the survey period and so were known to be on site during the period.

The Minta-Mangel estimates follow the trends shown by the

minimum population size. The estimates are higher than the minimum as would be expected. The 95% likelihood intervals for these estimates overlapped considerably between months and within months between years. This indicates that the true population sizes may have been stable and did not differ significantly between years. However, this interpretation should be considered cautiously and be weighted by the following observations. Recruitment was low in 1990, but two large cohorts were produced in 1991. Within 1992, the July estimate did not overlap with the May or June estimates. The low estimate for July, 1992, may be an artifact of termination of the study as discussed previously. We gave population size estimation a higher priority in 1992 and more time and effort were allotted to censusing the road than in the other years. Thus more lizards were captured on or beside the road, and a higher proportion of the population was marked. This may explain the smaller range of the likelihood intervals in 1992 than in the other years. Future applications of this technique should strive to mark a sufficient portion of the population to minimize the range of the likelihood intervals.

Population Density

The difficulties encountered in estimating both the population size and the home range size affected the estimation of density. The calculated densities should only be considered to be rough approximations at best. The usual procedure of systematically searching for individuals on a study plot of known size yields better estimates of density. However, this

is not a practical or appropriate procedure to use for cryptic species with large home ranges and low population density.

Turner et al. (1978) surveyed nine plots in Imperial and Riverside County to determine the presence and relative abundance of FTHL. They were able to estimate the population size and density for one plot, but few recaptures or no observations of FTHL precluded estimation of the population size and density on the other plots. The greatest densities that we calculated, 1.30 FTHL/ha for the minimum population size and 1.39 FTHL/ha for the Minta-Mangel estimate, were considerably lower than the estimate of 6.1 FTHL/ha that Turner and Medica (1982) calculated for plot 15 in the Yuha Basin. Turner and Medica used the Schumacher and Eschmeyer (1943) procedure to estimate the population size on their 4.41 ha site. This procedure assumes that: the population is a constant size; there are no births or deaths; no animals leave the area or enter the area during the experiment; and all marked and unmarked animals are equally catchable (Caughley 1977). Our data on activity and home range size indicate that it is likely that lizards wandered into and away from their study site during the experiment. This would have violated two assumptions of the estimation procedure, and may have resulted in either an over- or underestimation of the size of the population.

We calculated the 95% confidence limits (DeLury 1958) of the population estimate (≈ 27) from data in Table 3 of Turner and Medica 1982. The 95% confidence limits of the

population estimate ranged from 21.3 to 39.9 which translates to densities of 4.8 - 8.4 FTHL/ha. The lower bound of their density estimate is still more than three and a half times greater than the density on the Superstition site. We do not know if the apparent high density is real or an artifact of the procedures used to estimate the density. However, the site merits reexamination to determine if the high density is real, and if so, how the habitat differs from other sites that support lower densities of lizards.

Survival

The survival of FTHL was estimated for radio-tagged adults. The results for the bimonthly periods and for the inactive period indicate that survival is high during winter dormancy. Survival of dormant FTHL is actually higher than it appears to be based on the calculations. Two mortalities occurred in November after the mean date for the onset of dormancy for individuals that had not initiated dormancy. There were no deaths for dormant FTHL. Survival was lowest during the late spring and summer when the lizards were active and exposed potentially to more encounters with predators.

Predation

When temperatures are appropriate the FTHL is active before sunrise and after sunset and often spends the night in the open. Thus, they are accessible to both nocturnal and diurnal predators.

The Round-tailed Ground Squirrel, Spermophilus tereticaudus, was responsible for nearly half of the known mortality.

ties. No predation was observed, but for deaths attributed to the squirrel, the transmitters were found in squirrel burrows along with the partially eaten carcasses. Squirrel feces in the burrows often contained lizard scales. In all cases of predation the carcass and transmitter were inside of the burrow where they could not have been found without the transmitters. Predation on FTHL by squirrels and other burrowing animals may occur frequently, but is difficult to document without the use of radio telemetry.

Rodents are known predators of horned lizards. The grasshopper mouse, Onychomys torridus, is known to take P. modestum (Munger 1986), and it occurs in the area of the study site (Hall 1981). Although O. torridus may be responsible for some FTHL predation, we do not believe that any of the deaths that we documented were caused by the mouse rather than the squirrel.

The four mortalities attributed to snakes included one that was swallowed partially then regurgitated. The others were found dead with no obvious cause of mortality other than a slight discoloration where they may have been bitten by a sidewinder, Crotalus cerastes. All appeared to be healthy and the stomachs and intestines contained ants, indicating recent feeding. One was still alive at the entrance to a burrow, and displayed the same sluggish, unresponsive behavior observed in envenomated Uma inornata and Dipsosaurus dorsalis (MF and AM pers. observ.). It died a short time later. Funk (1965) observed C. cerastes predation on FTHL. Other known lizard-eating snakes (Stebbins 1985) that were

seen on the site included the diurnal coachwhip, Masticophis flagellum, patch-nosed snake, Salvadora hexalepis, the nocturnal glossy snake, Arizona elegans, and leaf-nosed snake, Phyllorhynchus decurtatus. It is probable that these snakes take FTHL but, for at least the smaller species, predation may be restricted to juvenile FTHL.

Three of the dead FTHL were found impaled on plants in the characteristic fashion of the loggerhead shrike, Lanius ludovicianus. Shrikes were seen commonly on the site during the active season of the lizard and are known to take FTHL (M. Jorgensen, Chief Naturalist, Anza Borego Desert State Park, unpubl., in Turner and Medica 1982).

Only one mortality which was characterized by round puncture wounds was attributed to a canid. Both coyotes, Canis latrans, and kit foxes, Vulpes macrotis, were seen often on the site. In one case a FTHL burrow containing a radio-tagged lizard was excavated overnight by a V. macrotis (footprints were found at the excavation site). However, the lizard was found nearby in the morning. Canids probably take FTHL and could have carried an ingested transmitter far off-site where we would not have been able to locate it. This probably accounts for some of the cases (10) where lizards with good transmitters just simply disappeared from the site.

Motor vehicles accounted for three mortalities. In spite of warning signs, no trespass signs and fences, off-road vehicles (ORVs) occasionally trespassed on the Range and violated the study site. Two of the radio-tagged FTHL

were crushed by ORVs. It is interesting to note that although the paved road on the site was driven daily by security personnel, only one radio-tagged FTHL was found crushed on the road. The sample size is small, but these observations support the notion held by many biologists that although it is difficult to demonstrate, ORVs probably have a substantial negative impact on populations of small vertebrates.

Other species that were seen on the site and are known or suspected of taking FTHL include badgers (Taxidea taxus), leopard lizards (Gambelia wislizenii), American Kestrels (Falco sparverius), Red-tailed Hawks (Buteo jamaicensis), and Great-horned Owls (Bubo virginianus).

Temporal Activity

Seasonal Activity. Winter dormancy began in mid-November, on average, and most but not all radio-tagged FTHL remained in the dormancy burrow until mid-February. One individual was active periodically throughout the winter and changed locations frequently. Also, juveniles were seen occasionally throughout the dormancy period on days the surface temperature in the sun exceeded the minimum voluntary body temperature. Some individuals, especially juveniles, remained active in the winter. Laboratory experiments (Mayhew 1965a) indicate that FTHL are obligate hibernators (brumators). Dormancy and metabolic adjustments to hibernation are controlled separately and are induced by reduced photoperiod and reduced temperature, respectively. However, the active juveniles that we observed during the winter were clearly not

obligate brumators. The apparent conflict between the results of the laboratory studies and our field observations may be more apparent than real. Mayhew (pers. commun.) did not use juveniles in his laboratory experiments. The biological clocks of juvenile and adult FTHL may not respond to the same environmental cues; juveniles may be refractive to changes in day length that induce dormancy in adults. It is not immediately obvious why it would be advantageous for adults of a non-territorial species to be active during a period of presumably marginal environmental conditions and resources. Juveniles, on the other hand, may have good reason to be active when ever possible. They simply may not have enough fat reserves to get through the winter without supplementation. Alternatively, there may be a selective advantage to reach reproductive size at the earliest possible age. Juveniles that are active may be able to sequester enough energy to grow during the winter and reach reproductive size at an earlier age in the spring.

FTHL spent the dormant period in burrows that they dug. All of the dormant lizards that were excavated were found at depths of 10 cm or less. Cowles (1941) found two lizards at 30 cm (11.8 in) and two between 3 and 25 cm (1 and 9.8 in). The duration of dormancy is believed to be under endogenous control. Hence, the time of emergence from hibernation is thought to be independent of temperature (Mayhew 1965a). We found that most lizards emerged when the temperature at a depth of 5 cm reached the voluntary minimum body temperature. The correlation between minimum voluntary body temperature

and emergence from dormancy is compatible with Mayhew's (1965a) results. Under natural conditions there should be synchronization, on average, between endogenously controlled periodicities and the physical environment. However, the correlation that we found need not be interpreted as causation.

The active period began with the cessation of dormancy in mid-February. Data from radio-tagged individuals indicate that they were active daily throughout the active period (weather permitting).

Time/Activity Budget. Observations of the daily activity of radio-tagged individuals indicated that the species was relatively active: 54% of the day was spent in some sort of movement. The foraging strategy of the FTHL appears to be intermediate to that of a sit and wait predator and an active forager (Schoener 1971). Comparative examples include less than 5% movement for the sit and wait predator Uma inornata (Durtsche 1987), 1.5% movement for the sit and wait predator Callisaurus draconoides, and 91% movement for the active forager Cnemidophorus tigris (Anderson and Karasov 1981).

Home Range Size

The highly active nature of FTHL is reflected in the large size of the home range. Members of the genus Phrynosoma are not sedentary as proposed by Pianka and Parker (1975), but instead have a propensity for travelling great distances (Tanner and Krogh 1973). Turner et al. (1969) found that the home range size of lizards is correlated with body size. All of the species that they reviewed with body

sizes less than 20 g (0.70 oz) had estimated home range sizes of less than 10,000 m² (2.5 ac). The FTHL is an exception to this generalization. The average size of radio-tagged FTHL in this study was 15.5 g (0.55 oz), and the average home range size was 19,200 m² (4.7 ac). The FTHL also have larger home ranges than much larger lizards that are sympatric over broad areas of their range: adult male Uma inornata (SVL ≥ 80 mm, Mayhew 1965b), 1,040 m² (0.26 ac) (Muth and Fisher 1991); and adult male Dipsosaurus dorsalis (SVL ≥ 110 mm, Mayhew 1971), 611 m² (0.15 ac) (Krekorian 1976).

In our estimation of home range size we used all individuals with three or more captures. However, in only one case did the performance curve of cumulative area as a function of the number of recaptures reach an asymptote. Thus, the home range size of all but one individual was underestimated. The addition of more recaptures should result in a larger home range until that point (the asymptote) where the entire home range has been encompassed by the convex polygon describing the home range. Any subsequent recaptures will not add significantly to the home range size. Thus, the actual home range size for FTHL is probably much larger than that reported herein. The mean home range size for all individuals with more than 18 recaptures (the median number of recaptures) is 26,975 m² (± 26,975 m²) (6.7 ac), a 70% greater area than the mean for all animals. Even the one performance curve that did reach an asymptote may also represent an underestimate of home range size because on two occasions we were unable to locate the lizard within or near its known

home range, but it returned within the following three weeks with its transmitter operating.

Although our data underestimate home range size, the estimates are still an order of magnitude larger than the estimate of Turner and Medica (1982). They note that their estimates, $1,287 \text{ m}^2$ (0.32 ac) for males and 509 m^2 (0.05) for females, underestimate the true mean because of few sightings per individual (the maximum was six).

The reliability of our estimates of home range size was limited by the number of recaptures. Our a posteriori estimation indicated that about 70 recaptures would be needed to estimate the size of a home range which was predicted to be about $81,512 \text{ m}^2$ (20.1 ac).

Is the unexpectedly large size of the calculated and predicted home range an artifact of radio-tagging? Did carrying the telemetry backpack cause the lizards to move around more than unencumbered lizards? To address these questions we compared the distances travelled between sightings of tagged and non-tagged individuals on the road. There was no significant difference in the distance between sightings which supports our belief that radio-tagging did not artificially inflate the size of home ranges.

The mean home range size of males and females did not differ significantly. This result is unusual for iguanid lizards, most of which are sexually dimorphic in body size, and are territorial (Stamps 1977) with males usually having a home range that is twice that of females (Rose 1982). In contrast to most other iguanids, there is no sexual dimorph-

ism in body size of FTHL and they are probably not territorial. Thus, although the size of the home range is unexpectedly large, the lack of sexual dimorphism in home range size is consistent with the factors that are thought to influence the size of home ranges in other iguanids.

Vegetation and Substrate Preferences

Plant Preferences. The vegetation on the site was sparse, but resembled that described by other researchers as good quality habitat (Stebbins 1985, Turner et al. 1980). Only six percent of the total surface was covered with plant material, and half of the plants were either dead or dormant. Many of the perennials in the creosote bush scrub plant community are drought deciduous, but would be expected to revive following a winter of normal rainfall, such as when the line-intercept transects were taken. Most of the plants that were listed as dead or dormant were probably dead.

A small, short-lived perennial, Tequilia palmeri was the most abundant species on the site in terms of number of individuals, but the much larger creosote bush, Larrea tridentata, was most abundant in terms of percent coverage by living plants. Creosote bush and burr weed, Ambrosia dumosa, are expected to be the dominant species in the creosote bush scrub plant community (Munz 1974).

A variety of substrate types and perennial plant species were accessible to individuals within their home range. FTHL prefer sandy substrates which are associated with the growth form and shading characteristics of some plant species. Plant species that form multiple stems arising from the crown

at ground level are able to catch windblown sand. Sand does not accumulate beneath those with a central stem that branches above the surface (Burk 1977). Both Ambrosia dumosa and Psoralea emoryi were preferred by FTHL when comparing the number of sightings with both the percent of total living plants and the percent coverage of living plants. Both species are low growing, densely branched shrubs with multiple branching at the crown and they accumulate more sand at the base than do single stem species on the site. Thus, a species that has a preference for sand would be associated more often with these plants than with others that did not trap blowsand. A concomitant feature of the densely branched growth habit is that it provides denser shade than an open growth form.

Creosote bush, Larrea tridentata, had the greatest percent coverage of living plants on the site, but it was avoided by FTHL. It has multiple branches at the base and traps blowsand but, is more loosely branched and the branches are higher than both A. dumosa and P. emoryi. The quality of shade that it provides is less than that of A. dumosa and P. emoryi.

Tequilia palmeri was the most common plant, 43% of the total number of living plants, but it was avoided by FTHL. It is a small plant that accounted for only 16% of the total coverage of living plants. All but the largest plants were unusable for shade or shelter, and the plant accumulated little or no blowsand.

Soil Preferences. Hardpan (concreted silt) was the most

abundant (80%) type of substrate on the site. Only 17% of the site was covered by sand which was confined to small accretion dunes on the lee side of shrubs or was in small washes. The substrate composition is similar to that described by Turner et al. (1980) as the best FTHL habitat.

Stebbins (1985) stated that the FTHL is "... restricted to fine windblown sand.... sharing the habitat with fringe-toed lizards." Although none of the habitat on the site contained exclusively sand, there were small numbers of fringe-toed lizards, Uma notata, even in areas with no obvious blow-sand. Both species may occur in a broader range of habitats than previously expected. This aspect of the biology of both species merits further attention.

Soil Temperatures. Soil temperatures on the site exceeded the maximum voluntary body temperature in the sun at all measured depths during the summer. The mean high temperature in the shade for all measured depths approached the maximum voluntary body temperature (the daily high temperature exceeded it on many days) in June through August.

The critical thermal maximum body temperature (CTM) is not known for the FTHL, but it is known for two other species of horned lizards: P. coronatum, 46.7 °C (116.1 °F); and P. platyrhinos, 45.5 °C (113.9 °F) (Brattstrom 1965). If the CTM for the FTHL is in the 45 - 46 °C range, than the daily high burrow temperatures at 5 and 10 cm in the shade from June through August may fall within the thermal tolerances of the FTHL. However, there would be little margin for error. Few burrows were constructed in shaded substrate. These data

indicate that the availability of burrows deeper than 10 cm are necessary components of the habitat for FTHL in this part of their range.

The mean high temperature on the surface in the sun fell below the minimum voluntary body temperature only in December and January. The mean high temperature at 5 and 10 cm in the sun and at all depths in the shade were below the minimum voluntary body temperature from November through March. However, the daily high soil temperature at 5 cm in the sun first exceeded the minimum voluntary body temperature in mid-February. The daily high soil temperature at 5 cm is correlated with the minimum voluntary body temperature and the end of winter dormancy in mid-February.

Scat Analysis

The relative abundance of FTHL and habitat quality is usually assessed by a survey method developed by Turner et al. (1980) and modified by Olech (1984). The method relies on counts of FTHL scat on transects during the months of May through July. FTHL are myrmecophageous (Pianka and Parker 1975; Turner et al. 1978), and the differentiation of FTHL scat from that of other species was based on contents: scat was presumed to be from FTHL if it contained almost exclusively ants. All FTHL scat that we analyzed during May through July contained primarily ants.

The survey method relies on the high degree of myrmecophagy characteristic of FTHL, and tacitly assumes that sympatric species of lizards are not myrmecophagous. The latter assumption is incorrect. All of the lizard species on

the site ate ants. Some Callisaurus draconoides (46%) and Uma notata (8%) ate primarily ants and produced scat that was almost indistinguishable from FTHL scat in both contents and shape. Although 16% of the scat from those two genera contained primarily ants, the percentage of the population that eats primarily ants may vary from year to year and from site to site. The error that these scat induce in the survey will be related to the relative abundances of the different species on the survey sites.

Scat from adult FTHL were larger in diameter than 90% of the scat from other species, but the diameter of scat from juvenile FTHL overlaps considerably with that of other species. The first clutch of FTHL hatches in mid to late July. Thus, there are juvenile FTHL in the population during the scat survey period. The scat survey method can be modified to minimize the problem of overlap in scat diameter and enhance the reliability of the surveys: Include only scat that has a diameter greater than 5.5 mm (0.22 in) to eliminate most of the non-FTHL scat. The resulting relative abundance estimates would also exclude young FTHL from the estimate, removing the influence caused by the sudden appearance of hatchlings at sites surveyed in July.

The FTHL produced about one scat per lizard per day. This occurred in the morning, and was near the location that an individual spent the night. Scat may not be deposited evenly throughout an individual's home range, but may be more abundant in those areas that are preferred as overnight locations. The home ranges of FTHL are large and cover a broad

spectrum of microhabitats, but scat may have a clumped distribution within the home range. This possibility has not been recognized previously, and the importance of microhabitat diversity within the home range of FTHL has not been considered. Thus, in heterogeneous habitats, scat counts may be a better indicator of overnight locations than of habitat utilization and quality per se.

The amount of time that scat persists in situ varies greatly. The lab and scat corral experiments indicate that heat and movement by the wind do not cause disintegration of scat for at least the duration of the survey period. However, wild scat persisted for a shorter duration. These results indicate that the wild scat was probably not destroyed, but was moved from the original location. We suspect that wind may be an important agent in moving scat. Penned scat was frequently moved by the wind and was usually found on the lee side of an object within the pen. Wild scat is probably moved a variable distance from the original location by the wind until it comes to rest on the lee side of a plant where it may be covered by the canopy or windblown sand. The variation in persistence in situ may be attributable to differences in wind regimes at the deposition sites. Additional factors that may be involved in the destruction or removal of scat include destruction by insects, rain, and flooding.

RECOMMENDATIONS

The data presented herein are based on two field seasons of research. All aspects of this study would benefit from larger sample sizes and long-term continuation through several more seasons. The results of this study are a "snapshot in time" without long-term context. Do the results of this study represent "normal" reproduction and growth conditions for the population or an exceptional response to two good years of rainfall? We do not know the answer to this question, but we do know that it could be a grave error to base management decisions on short-term studies.

1) We recommend that the results of this study be used as an interim guide for management considerations pending further research based on long-term studies.

The Superstition population was studied for two years. The results of the study indicate large gaps in our knowledge of several crucial aspects of the life history of the FTHL.

2) Future research should focus on population size, reproduction, brumation, social structure, home range size and the determinants of home range size, and population viability analysis.

The reliability of the scat count method of estimating relative abundance of FTHL is compromised by two unknown factors: the origin of the scat; and the age of the scat.

3) We recommend the following changes to the scat count survey protocol: a) clear scat from the survey route and allow one to two days to pass before initiating the scat count sur-

vey; b) count only scat greater than 5.5 mm diameter.

Scat may have a clumped distribution within the home range of FTHL, and may not be an indicator of habitat utilization or quality.

4) The scat count method should only be used to determine relative abundance. Habitat quality should not be inferred from scat counts.

The Navy conducts training operations, target bombing and strafing at the facility day and night. In spite of this, the test range supports a large population of FTHL. The actual bombing and strafing impact area consists of a small ($\approx 7.7 \text{ km}^2$, 3 mi^2) target area surrounded by a significant buffer area that is relatively undisturbed. Incidental take of lizards in the impact area must occur, but in our opinion, the take is compensated by the protection afforded by the buffer area that shields the habitat from development and most offroad vehicle abuse.

5) We recommend that the Navy continue to restrict offroad activities to normal target maintenance and operations as currently practiced.

If the past is prologue to the future, there may come a time when geopolitics dictate the need for expansion of the facilities to include more impact areas. The FTHL may be listed by CDFG and/or USFWS. If the lizard is listed, then expansion of facilities may result in the take of FTHL.

6) Mitigation for future expansion should include a commit-

ment to secure the facility from unauthorized offroad vehicle trespass by constructing additional fencing, and patrols especially on the south side of Superstition Mountain.

7) If the FTHL is listed and future budget constraints result in closure of the facility, CDFG or USFWS should acquire the facility for an Ecological Reserve or a unit of the National Wildlife Refuge system.

SUMMARY

The results of a two-year study to develop baseline population data and procedures for monitoring populations of the flat-tailed horned lizard (FTHL), Phrynosoma mcallii, are presented herein. Capture-recapture methods and radio-telemetry were used in the field, and lab and field experiments were used to evaluate the scat count method for determining relative abundance among sites.

A total of 363 individual FTHL were captured, and there were 1,683 sightings. On-site 284 individuals were marked, and an additional 79 individuals were captured off-site. A total of 42 individuals were tagged with transmitters for a total of 7,944 lizard-days. Size ranged from 3.0 - 8.4 cm SVL. Males and females did not differ in frequency of occurrence, size, or growth rate. There were two cohorts of hatchlings per year that grew to adult size by May of the following year. The von Bertalanffy growth model described the growth trajectory of FTHL better than logistic-by-length or logistic-by-weight models.

Radio transmitters are invaluable for field studies of

small cryptic lizards. A total of 42 individuals were fitted with radio transmitters. The mean annual survival was 53% and survival over bimonthly periods ranged from 55% in mid-summer to 100% during dormancy. Deaths (19) were attributed to round-tailed ground squirrels, snakes, Logger-head Shrikes, canids, and off-road vehicles.

Seasonal activity was divided into two periods: winter dormancy and the active period. Dormancy, mid-November to mid-February, is spent in shallow burrows that are dug by the lizard. Juvenile FTHL are not obligate brumators as are the adults. The end of the dormant period is correlated with the soil temperature at 5 cm depth. During the active period, the lizards are active daily and, contrary to Howard's (1974) suggestion, there is no estivation during the summer. The foraging strategy is intermediate to that of sit-and-wait predators and active foragers.

The size of the home range is large relative to the SVL of the lizard and there is no significant difference between the size of home ranges for males and females. The large size of the home range encompassed a broad spectrum of perennial plant species and substrate types. The FTHL preferentially associated with sandy substrate and two species of perennial shrubs. Shaded substrate and/or the ability to dig burrows at least 10 cm deep appear to be important components of the habitat.

We were able to differentiate scat from adult FTHL from that of other species. FTHL scat contained primarily ants during the survey period, and was larger than most of the

scat from other species that also contained primarily ants. However, we were unable to distinguish scat from juvenile FTHL from that of other myrmecophagous species.

FTHL produced about one scat per lizard per day, and scat had the potential to remain intact throughout the entire survey period. Scat that are counted on surveys are of unknown age. The scat count method should only be used to determine relative abundance of FTHL. Given our current understanding of the biology of the FTHL, the scat count method can not be used to estimate population size.

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LITERATURE CITED

- Anderson, R. A. and W. H. Karasov. 1981. Contrasts in energy intake and expenditure in sit-and-wait and widely foraging lizards. *Oecologia* 49:67-72.
- Begon, M., 1979. Investigating Animal Abundance. University Park Press, Baltimore, 97 p.
- Brattstrom, B. H. 1965. Body temperatures of reptiles. *Am. Midl. Nat.* 73(2):376-422.
- Brower, J. E. and J. H. Zar. 1977. Field and laboratory methods for general ecology. Wm. C. Brown Co., Dubuque, IA. 194 p.
- Burk, J. H. 1977. Pages 869-889 in M. G. Barbour and J. Major, eds. Terrestrial vegetation of California. J. Wiley and Sons, New York. 1002 p.
- Caughley, G. 1977. Analysis of Vertebrate Populations. John Wiley & Sons, New York, 234pp.
- Cowles, R. B. 1941. Observations on the winter activities of desert reptiles. *Ecology* 22(2):125-140.
- DeLury, D. B. 1958. The estimation of population size by a marking and recapture procedure. *J. Fish. Res. Bd. Canada* 15(1):19-25.
- Dunham, A. E. 1982. Demographic and life-history variation among populations of the iguanid lizard Urosaurus ornatus: implications for the study of life-history phenomena in lizards. *Herpetologica* 38(1):208-221.
- Durtsche, R. D. 1987. Foraging and food of the fringe-toed lizard Uma inornata, an endangered species from the Coachella Valley, California. Ms. Thesis, California State

- University, Fullerton. 148 p.
- Edwards, C. 1979. A report on the distribution, abundance, population trends, and habitat requirements for the flat-tailed horned lizard on the lower Colorado River. Unpubl. Report, Arizona Game and Fish Department.
- Fabens, A. J. 1965. Properties and fitting of the von Bertalanffy growth curve. *Growth* 29:265-289.
- Fisher, M. and A. Muth. 1989. A technique for permanently marking lizards. *Herp. Review* 20(2):45-46.
- Fisher, R. A. and F. Yates. 1957. Statistical tables for biological, agricultural and medical research. Oliver and Boyd Ltd. London. 138 p.
- Frazer, N. B., J. W. Gibbons and J. L. Greene. 1990. Exploring Fabens' growth interval model with data on a long-lived vertebrate, Trachemys scripta (Reptilia: Testudinata). *Copeia* 1990(1):112-118.
- Funk, R. S. 1965. Food of Crotalus cerastes laterorepens in Yuma County, Arizona. *Herpetologica* 21(1):15-17.
- Hall, E. R. 1981. The mammals of North America. J. Wiley and Sons, New York. 1181 p.
- Howard, C. Wayne. 1974. Comparative ecology of horned lizards (Genus Phrynosoma) in southwestern United States and northern Mexico. *Jour. Ariz. Acad. Sci.* 9(3):108-116.
- Johnson, T. B. and R. B. Spicer. 1985. Status Report; Phrynosoma mcallii (Hallowell 1852). Unpubl. Report. Contract # 14-16-002-81-224, USDI, FWS, Albuquerque, New Mexico.

- Klauber, L. M. 1939. Studies of reptile life in the arid southwest. Bull. Zool. Soc. San Diego 14:1-100.
- Krekorian, C. O. 1976. Home range size and overlap and their relationship to food abundance in the desert iguana, Dipsosaurus dorsalis. Herpetologica 32:405-412.
- Mayhew, W. W. 1965a. Hibernation in the horned lizard, Phrynosoma m'calli. Comp. Biochem. Physiol. 16:103-119.
- _____. 1965b. Reproduction in the sand-dwelling lizard Uma inornata. Herpetologica 21(1):39-55.
- _____. 1971. Reproduction in the desert iguana, Dipsosaurus dorsalis. Herpetologica 27(1):57-77.
- _____. and B. W. Carlson. 1986. Draft status of the flat-tailed horned lizard (Phrynosoma mcallii) in California. Unpubl. Report, Contract # C-1355 85/86, California Department of Fish and Game.
- Minta, S. and M. Mangel. 1989. A simple estimate based on simulation for capture-recapture and capture-resight data. Ecology 70(6):1738-1751.
- Munger, J. C. 1986. Rate of death due to predation for two species of horned lizard, Phrynosoma cornutum and P. modestum. Copeia 1986(3):820-824.
- Munz, P. A. 1974. A flora of Southern California. University of California Press, Ltd., Berkeley. 1086 p.
- Muth, A. and M. Fisher. 1991. Population biology of the Coachella Valley fringe-toed lizard, Uma inornata: development of procedures and baseline data for long-term monitoring of population dynamics. Final Report, California Department of Fish and Game Contract

- # C-1330 85/86.
- Olech, L. A. 1984. Monitoring report for Yuha Basin Area of Critical Environmental Concern and Yuha Desert Wildlife Habitat Area. Unpubl. Report, USDI, Bureau of Land Management, El Centro, California.
- _____. 1986. Status of the flat-tailed horned lizard (Phrynosoma mcallii) on Bureau of Land Management administered land in California. Unpubl. Report, USDI, Bureau of Land Management, El Centro, California.
- Pianka, E. R. and W. S. Parker. 1975. Ecology of horned lizards: a review with special reference to Phrynosoma platyrhinos. Copeia 1975(1):141-162.
- Rado, T. 1981. Analysis of actual and potential loss of flat-tailed horned lizard (Phrynosoma mcallii) habitat. Unpub. Draft Rept. USDI, Bureau of Land Management, Sacramento, California. 20 pp.
- Rohlf, F. J. and R. R. Sokal. 1969. Statistical tables. W. H. Freeman and Company, San Francisco. 253 p.
- Rose, B. 1982. Lizard home ranges: methodology and functions. J. Herp. 16(3):253-269.
- Schoener, T. W. 1971. Theory of feeding strategies. Ann. Rev. Ecol. Syst. 2:369-404.
- _____. and A. Schoener. 1978. Estimating and interpreting body-size growth in some Anolis lizards. Copeia 1978(3):390-405.
- Schumacher, F. X. and R. W. Eschmeyer. 1943. The estimation of fish populations in lakes and ponds. J. Tenn. Acad. Sci. 18:228-249.

- Southwood, T. R. E. 1966. Ecological methods. Methuen and Company, Ltd., London.
- Stamps, J. A. 1977. Social behavior and spacing patterns in lizards. Pages 265-334 in C. Gans and D. Tinkle, (eds). Biology of the Reptilia, Volume 7, Ecology and Behaviour A, Academic Press, New York. 720 p.
- Stebbins, R. C. 1985. A field guide to western reptiles and amphibians. Houghton Mifflin Company, Boston. 334 p.
- Tanner, W. W. and J. E. Krogh. 1973. Ecology of Phrynosoma platyrhinos at the Nevada Test Site, Nye County, Nevada. Herpetologica 29:327-342.
- Turner, F. B., R. I. Jennrich and J. D. Weintraub. 1969. Home ranges and body sizes of lizards. Ecology 50:1076-1081.
- _____, P. A. Medica and H. O. Hill. 1978. The status of the flat-tailed horned lizard (Phrynosoma mcallii) at nine sites in Imperial and Riverside counties, California. Report Contract # YA-512-CT8-58, USDI, Bureau of Land Management, Riverside, California.
- _____, J. C. Rorabaugh, E. C. Nelson and M. C. Jorgensen. 1980. A survey of the occurrence and abundance of the flat-tailed horned lizard (Phrynosoma mcallii) in California. Report Contract # YA-512-CT8-58, USDI, Bureau of Land Management, Riverside, California.
- _____ and P. A. Medica. 1982. The distribution and abundance of the flat-tailed horned lizard (Phrynosoma mcallii). Copeia 1982(4):815-823.
- Trent, T. T. and O. J. Rongstad. 1974. Home range and sur-

- vival of cottontail rabbits in southwestern Wisconsin. *Southwest. Wildl. Manage.* 38(3):459-472.
- Wilkinson, L. 1988. SYSTAT: The system for statistics. SYSTAT, Inc., Evanston, Illinois.
- Stamps, J. 1983. *Lizards*. Pages 365-385. *Biology of the Reptiles, Volume 7. Ecology and Behavior*. Academic Press, New York. 720 p.
- Stamps, J. 1983. A field guide to western reptiles and amphibians. Houghton Mifflin Company, Boston. 334 p.
- Tanner, W. W. and J. E. Knapp. 1977. *Ecology of Phrynosoma platyrhina at the Nevada Test Site, Nye County, Nevada*. *Herpetologica* 33:327-342.
- Turner, P. A., R. T. Jennings and J. D. Weinbaum. 1983. Home ranges and body sizes of lizards. *Ecology* 64:1076-1081.
- _____, P. A. Medina and H. G. Miller. 1978. The status of the flat-tailed horned lizard (*Phrynosoma mcallii*) at pine sites in Imperial and Riverside counties, California. Report Contract 4 YA-515-CT8-58, USDI, Bureau of Land Management, Riverside, California.
- _____, J. C. Rotenberry, E. G. Nelson and H. G. Thompson. 1980. A survey of the occurrence and abundance of the flat-tailed horned lizard (*Phrynosoma mcallii*) in California. Report Contract 4 YA-515-CT8-58, USDI, Bureau of Land Management, Riverside, California.
- _____, and P. A. Medina. 1987. The distribution and abundance of the flat-tailed horned lizard (*Phrynosoma mcallii*) in California. *Copeia* 1987(4):819-821.
- Trent, T. T. and G. J. Rongstad. 1974. Home range and sur-

Relatively little is known of the population biology of the flat-tailed horned lizard (UTM), *Phrynosoma muniti*. This is not an unusual situation for a small lizard, and the usual approach to the problem is to initiate a program of capture-recapture studies to determine basic information such as home range size, activity patterns, growth rates etc. However, capture-recapture methods obviously depend on the ability of researchers to relocate individual animals which is not always possible with less than fully cooperative or highly cryptic animals such as the UTM. To circumvent this problem, we developed a radio transmitter backpack and harness that enabled us to relocate individuals and use capture-recapture methods in our field studies of this cryptic species.

APPENDIX A TRANSMITTERS AND BACKPACKS

The transmitter is a modified configuration of an SM1 transmitter (AVM Instrument Company). The battery (LI 803) and electronics were potted in dental acrylic, and a 1 cm whip antenna extended posteriorly from the middle of the transmitter. The mass of the transmitter was less than 5.0 g and was essentially balanced on either side of the midline of the backpack. A backpack and harness was used to secure the transmitter to the lizard using materials that are readily available in fabric stores: polypropylene pleating tape; and clear polypropylene elastic.

The backpack is made from pleating tape that consists of a 5 cm wide polypropylene mesh that is reinforced by two parallel strips of tightly woven polypropylene running lengthwise through the tape. The backpack is shaped like an

Relatively little is known of the population biology of the flat-tailed horned lizard (FTHL), Phrynosoma mcallii. This is not an unusual situation for a small lizard, and the usual approach to the problem is to initiate a program of capture-recapture studies to determine basic information such as home range size, activity patterns, growth rates etc. However, capture-recapture methods obviously depend on the ability of researchers to relocate individual animals which is not always possible with low density populations of highly cryptic animals such as the FTHL. To circumvent this problem, we developed a radio transmitter backpack and harness that enabled us to relocate individuals and use capture-recapture methods in our field studies of this cryptic species.

The transmitter is a modified configuration of an SM1 transmitter (AVM Instrument Company). The battery (Li 803) and electronics were potted in dental acrylic, and a 4 cm whip antenna extended posteriorly from the middle of the transmitter. The mass of the transmitter was less than 4.0 g and was essentially balanced on either side of the midline of the backpack. A backpack and harness was used to secure the transmitter to the lizard using materials that are readily available in fabric stores: polypropylene pleating tape; and clear polypropylene elastic.

The backpack is made from pleating tape that consists of a 5 cm wide polypropylene mesh that is trisected by two parallel strips of tightly woven polypropylene running lengthwise through the tape. The backpack is shaped like an

inverted "T" which is cut from the pleating tape (Fig. 1A). The vertical leg of the "T" (≈ 2 cm) is fashioned from a woven strip of the pleating tape, and the horizontal bar (2 cm long by 1 cm wide) is fashioned from the surrounding mesh material (Fig. 1B). Both ends of the woven strip and the perimeter of the mesh material should be melted with a soldering iron to fit the shape of the transmitter package and to prevent unravelling.

The harness straps (0.5 cm wide) are made from a 10 cm strip of clear polypropylene elastic. This material is thin and light weight, and in exposure tests it maintained its elasticity much longer than woven elastic materials. The straps are positioned at about 45° and are fastened to the vertical leg of the "T" with superglue and a stitch of thread (Fig. 1B and sample enclosed). The backpack and transmitter are then joined together with dental acrylic.

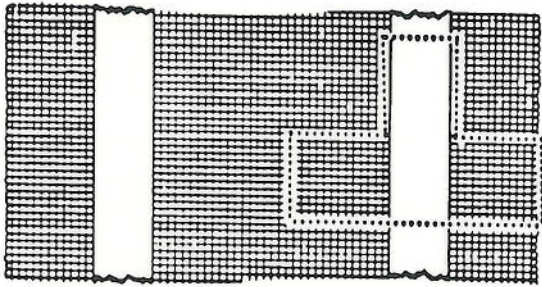
The backpack is attached to the back of the lizard by positioning the package with the straps on the lizard's neck and the antenna pointing posteriorly (Fig. 1C). A strap is pulled over the shoulder of one leg, across the chest, through the axilla of the other leg, and is fastened to the top of the transmitter with a drop of cyanoacrylic glue (superglue). The second strap is fastened in the same way, and a drop of superglue is applied between the straps where they cross on the ventral side (Fig. 1D) to keep the package from shifting. Thus the package sits firmly on the back of the lizard and does not restrict movement of the head or legs.

Captive lizards have been observed feeding immediately after attachment of a transmitter. The harness does not noticeably alter the normal activity of released lizards which have been observed to eat, breed, and construct burrows with no apparent interference caused by the transmitter.

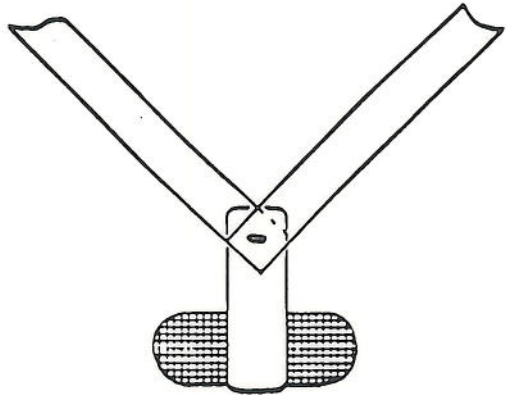
The total mass of the telemetry package (< 4 g) was about 25% of the body mass of a lizard (mean 15.8 g, range 11.0 - 25.0 g) that was fitted with a backpack. As a matter of perspective, the mass of the backpack was about that of a clutch of eggs, 27% of the total body mass of the female (Pianka and Parker 1975).

The signal from the transmitter was received on an AVM LA12-DS Receiver using a three element AVM HHC Yagi antenna. The reception range varied with the position of the lizard above or below ground, but was usually about 100 m.

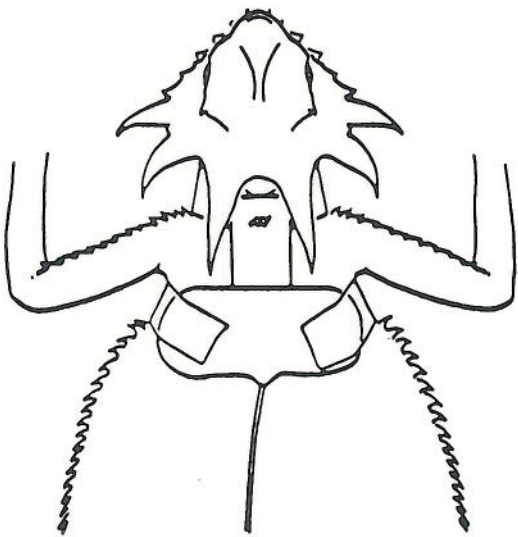
The backpack method of attaching transmitters has been used on 42 FTHL since April, 1990. A few lizards shed the harness, but most carried the package for at least the duration of the battery life (3 - 6 months).



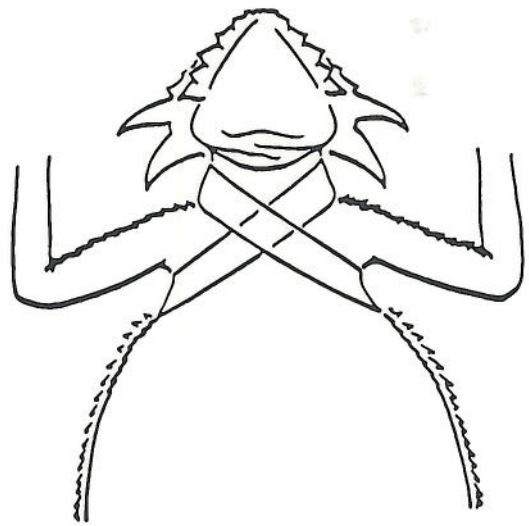
A.



B.



C.



D.

Fig. A1. Backpack construction and attachment to the lizard.

