AUTECOLOGY OF <u>CROTAPHYTUS</u> <u>COLLARIS</u>

By

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TABLE OF CONTENTS

Chapter Page

LIST OF TABLES

Table Page

LIST OF FIGURES

CHAPTER I

INTRODUCTION

The study of relations between organisms and the totality of physical and biological factors affecting them or influenced by them is termed ecology (Pianka, 1978). Autecology concerns the ecology of a particular species. This is an autecological study of the collared lizard, Crotaphytus collaris, in northeastern Oklahoma.

Two study sites were chosen to compare site-specific autecologies in relation to environmental differences. In reference to published descriptions of habitat preferred by collared lizards, one site could be considered inferior (few rocks and abundant vegetation) while the other could be designated superior (many rocks and sparse vegetation). Structural associations, lizard postures, and spatial distributions reflect habitat characteristics. The disappearance of lizards into winter hibernacula, the earliest recorded activity in the spring, and the appearance of hatchlings indicate the seasonal progression of the collared lizard's life cycle. The times lizards were observed and the associated weather data suggest necessary conditions for lizard activity. Community sex ratios and productivity are noted. Differences in lizard sizes, growth rates and molting frequencies are documented. The observation frequency of individual lizards, the total number of sightings per lizard, the population density, and home range sizes are reported. Adult-juvenile and adult male-female groups are compared within and between sites for all variables to detect patterns of natural history associated with age/sex groups and geographical sites.

The selection of C. collaris, the state reptile of Oklahoma, for use in this study is partly due to its ready availability in close proximity to Oklahoma State University. Also, collared lizards are hardy creatures, fairly sedentary, large in size, and diurnal: all characteristics which allow relative ease in field observations. Furthermore, little research on collared lizard ecology has been documented since the study done on the University of Kansas Natural History Reservation, in Douglas County, Kansas (Fitch, 1956). This present study might serve as the basis for future studies on C. collaris involving specific relationships between ecology and home range, territory quality, fitness, aggression, and social status.

CHAPTER II

LITERATURE REVIEW

The collared lizard, *Crotaphytus collaris*, belongs to the saurian family Iguanidae. This saxicolous lizard is also commonly called the mountain boomer. It is perhaps the most pugnacious of the larger lizards seen in the United States. The geographic range of this brightly colored species is fairly extensive. The public is, therefore, better acquainted with this lizard than with most native reptiles. The collared lizard is sometimes dissected as an example of a typical reptile in comparative anatomy courses (Fitch, 1956). Otherwise, economic importance seems nonexistant. Relatively little field or laboratory research on *C. collaris* is documented in the literature. The basic background material in this chapter has been provided by Fitch (1956).

Morphology and Sexual Dimorphism

The collared lizard bears two sooty black "collar" markings around its neck. The anterior one is typically more fragmented. Sexual dimorphism is obvious in the color patterns of adults. Males are more territorial than females, and as a consequence, are larger in size. The fine, granular, epidermal scales are arranged in a more distinctive pattern than those of females. At the height of the breeding season, males have a brighter coloration (Burt, 1928). The color pattern of females and subadult males is a blurry rendition of the juvenile pattern. Dull colored scales (grays, browns, yellows) predominate. Rich green to turquoise scales accented by orange throat scales characterize an older male (Woodbury, 1952). This coloration advertises sex and territorial claims. The bright colors dull with progressing seasons. Even so, males remain more colorful than females throughout life.

Adult males possess a wide tail base due to the presence of copulatory organs, the hemipenes. Femoral pores, on the underside of the thigh, are often enlarged in males (Cole, 1966). These pores in males are sometimes filled with easily discernable secretion plugs. Both sexes have approximately the same number of femoral pores. Male collared lizards show a transverse row of enlarged scales behind the vent (postanals). Use of coloration, tail base width, femoral pores, and postanal plates should allow relative certainty in determining the sex of any specimen. Males also possess wider heads due to the presence of enlarged temporal muscles.

Habitat and Range

All collectors of C. collaris unanimously agree on one habitat preference of these lizards: rock. Rocks of all sizes may be used as combination lookout posts and basking spots. Sheltering crevices for escape and use during inactivity are also necessities. Other requirements include an abundance of hot, clear summer days and a food supply of large, diurnal, terrestrial insects.

The discontinuity of rocky habitats, the complete or partial isolation from other mountain boomer populations, and the eons of time spent basking in open areas have contributed to the evolution of many different camouflage variations. Natural selection for the brown to green coloration is promoted by the various habitats used by collared lizards. Climatic conditions range from semi-mesic to temperate xeric (Montanucci, 1974; Smith and Tanner, 1974). Rainfall, which causes rank growths of vegetation, is a limiting factor to collared lizard populations; habitats featuring sparse vegetation are preferred. Collared lizards run swiftly over rock or barren soil but cannot travel quickly through thick vegetational growth. Sparse vegetation does not obscure the collared lizard's view from its rocky perches. Pleistocene fossils of _C_. _collaris_ are generally found in formerly sandy, xerophytic, open terrestrial situations (Holman, 1964).

Although recorded in both Louisiana and Crawford County, Indiana, the collared lizard's geographic range more typically extends over Mexico and the west-southwestern United States: Arizona, Arkansas, California, Colorado, Idaho, Kansas, Missouri, Nevada, New Mexico, Oklahoma, Oregon, Texas, and Utah. Collared lizards inhabit many diverse habitats in these arid and semi-arid parts of North America. They live in the Chihuahuan and Sonoran desert scrub, pinyon-juniper woods, tall or short grass prairies, and open glades of deciduous forests (Montanucci, Axtell and Dessauer, 1975). Elevations from 742 to 2286 m are typical. Valleys and broad sedimentary basins are effective barriers to mountain boomer dispersal (Axtell, 1972; Smith and Tanner, 1974).

Seasonal Activity

During cold weather, collared lizards hibernate under rocks. A typical hibernaculum consists of a tunnel leading to a chamber. The chamber is just large enough to house the lizard. The tunnel begins at an unburied rock edge and is partially filled with dirt. Legler and Fitch (1957) found that the total depth of cover over a hibernaculum is greater for adults than juveniles. They postulated that adults spend more time excavating the hibernacula. Adults become inactive in early autumn when ground temperatures are much lower than air temperatures. Juveniles become inactive later when much colder temperatures inhibit all activity. Collared lizards hibernate in a characteristic posture: head depressed, eyes closed, torso bent laterally, limbs close to body, and tail curved alongside.

Fitch (1956) found that _C_. _collaris_ has higher temperature thresholds for various activities than other Kansas reptiles. Below $10^{\circ}C$, this species is completely helpless. The growing season for mountain boomers is definitely shortened by this temperature restriction. The earliest collared lizard activity in Kansas occurred in April or May for the years 1949 to 1954. The population emerging from hibernation consists of adults and the previous summer's hatchlings which show great size variation. The stage of development reached by the time of a lizard's first hibernation is influenced by early autumn weather (Davis, 1967).

Several weeks after emergence from hibernacula, the breeding season begins. By late May (and throughout the breeding season), adults may be observed in male-female pairs. These pairs bask side-by-side or even in actual contact. Several days after insemination, scarlet spots appear along the sides and back of a female (Shaw, 1952; Vinegar, 1972). Due to the physiological changes associated with gravidity, these spots persist for several weeks after oviposition.

Cooper and Ferguson (1973) induced development of these spots with either progesterone or testosterone injections. Greater color intensities were achieved with progesterone. Pretreatment with estrogen accelerated spot appearance in response to progesterone. Faintly visible spots developed maximum color intensity in less than twelve hours (Ferguson, 1976).

No adaptive function for these spots has yet been ascertained. Carpenter (1967) suggested that they partially inhibit male sexual advances. Fitch (1956) pointed out the similar color patterns of juveniles and gravid females. He hypothesized that the spots partially inhibit adult male predation on juveniles. Complete inhibition of these behaviors has not evolved. Males occasionally eat scarlet-spotted juveniles and court scarlet-spotted females. Partial inhibition, however, might be sufficient for maintenance of these colored spots. On the other hand, gravid females probably prevent copulation primarily through behavioral postures (Medica, Turner and Smith, 1973). Yedlin and Ferguson (1973) suggested that the signal value of these scarlet spots may be related to increased female-female aggression. The increased aggression is explained by the hypothesis of nest site defense. Nesting females may accidently dig up another female's previously deposited clutch. A female's aggression may prevent this. Thus, her clutch has a greater probability of hatching.

Male spermiation occurs in early May through late June. At the end of the breeding season in late June, the testes enter a regressed, quiescent phase. The next testicular cycle is initiated by recrudescence of the testes in late July and August (Parker, 1973; Trauth, 1979). Gravid females may be observed in June and early July.

Oviposition occurs toward the end of July. The reproductive cycles of both sexes are synchronized even though seminal receptacles are present in the oviducts (Montanucci, 1971). Thus, reproductive efficiency is maximized. This allows more time and energy per individual for nonreproductive activities.

Once oviposition has occurred, adult lizards become less conspicuous. Spring territorial perches are deserted in favor of shadier shelters. Activities taper off as more time is spent underground. Old adults are rarely seen after early August. The individuals most in evidence from late July through August are the previous summer's hatchlings. These lizards are reaching average adult size at approximately one year of age. Hatchlings appear from August through October. In these months, adults and yearlings are seldom observed because of relative inactivity. The new juveniles remain active until late September or October. When hibernation begins, they are nearly half-grown. Juvenile desert side-blotched lizards (Uta stansburiana) approach maturity after the adults disappear in the fall. Home range establishment can then be achieved without competition from adults (Tinkle, McGregor and Dana, 1962). This is feasible for collared lizards also.

Temperature

Moderate to severe winter climates prevail throughout the geographic range of C. collaris. Air temperatures often drop below -18°C. Insulation is necessary for winter survival. Mountain boomers are rather inefficient burrowers so life among rocks may force them to depend on natural crevices. Their low temperature tolerance limit is unknown. But below 6°C, a torpid collared lizard cannot be roused. When stimulated at 12°C, _C. collaris_ is barely capable of locomotion. Similar results occur at 2°C for the five-lined skink, _Eumeces fasciatus_. This indicates the dependence of mountain boomer activity on higher temperatures (Fitch, 1956).

Body temperatures of active lizards range widely (20°-43°C). The optimum, however, approximates 37.5°-38.7°C (Soulé, 1963). Fairly constant, near-optimum body temperatures are maintained by restriction of activities and thermoregulatory behavior. Activity of collared lizards has been recorded over a wide range of air temperatures (13°C -36°C). Most activity occurs at air temperatures lower than optimum body temperatures (between 23°-34°C).

High summer temperatures are common over the collared lizard's geographic range. The surface temperature of soil in direct sunlight is always higher than the air temperature. The air temperature may approximate optimum lizard body temperature. Such conditions rigidly confine collared lizards to shady or underground seclusions. Arboreal behavior may provide an escape from high temperatures on the ground. This behavior is exhibited by mountain boomers (Clark, 1974).

Hunsaker and Johnson (1959) examined the possible functions of internal pigmentation in reptiles and amphibians. Collared lizards have black peritoneum. Some species of North American lizards lack peritoneal melanin. They represent only five genera: _Eumeces_, _Cnemidophorus_, _Coleonyx_, _Xantusia_, and _Anniella_. The distribution of _Eumeces_ centers in forests of the southeastern United States. Distributions of other North American lizard genera center in the southwestern United States or Mexico. _E. fasciatus_ emerges early in the spring when night temperatures are still below freezing. Lizards of the genus *Cnemidophorus* never remain long in direct sunlight. Short hunting forays are conducted in the sunshine. But these lizards quickly return to cooler environmental conditions. This behavior indicates that body temperatures are close to the critical level. The prairie racerunner, *C. sexlineatus*, maintains a body temperature of 39°-40°C. Most species of *Coleonyx* and *Xantusia*, the nocturnal lizards, lack internal pigmentation. Thus, among the more diurnal, heliothermic lizards, internal pigmentation has a probable function in temperature regulation.

Dawson and Templeton (1963) studied physiological responses to temperature in collared lizards and compared them with other lizards. Respiratory rate varies directly with temperature (Templeton and Dawson, 1960). Panting begins at temperatures of 42.5°-43°C (Templeton and Dawson, 1963). At these high body temperatures, panting aids in heat dissipation (Templeton, 1967). Panting in the desert iguana, *Dipsosaurus dorsalis*, involves a marked compression of the lizard's sides. The partially extended, blood-engorged tongue is exposed to a rapid flow of ambient air.

Dawson and Templeton (1963) also estimated evaporative water cooling of *C. collaris* based on evaporative water loss data. Heat production was estimated on the basis of oxygen consumption. At temperatures between 32°-40°C, one-fourth of a mountain boomer's heat production is alleviated by evaporative cooling. Due to respiratory changes (including the onset of panting) between 40°-44°C, evaporative water loss accelerates. Evaporative cooling then dissipates about 1.3 times the calories which result from metabolism. At high body temperatures, therefore, all heat produced by C. collaris in water metabolism can be dissipated. A small amount of heat gained from the environment can also be dissipated. This well-developed evaporative cooling may allow collared lizards to remain out longer in the heat of the day.

The ratio of evaporative water loss per metabolic unit (measured in mg H_2 lost/cc O_2 consumed) was calculated for several organisms (Dawson and Templeton, 1963). For a collared lizard, this ratio is relatively high. Between 32°-40°C, it loses 2.2 mg H_2O per cc O_2 consumed; at 44°C, 11.8 mg H_2O/cc O_2. For small desert rodents at 25°C, 0.5-0.9 mg H_2O are lost for every cc O_2 consumed. In arid regions, preformed water must be obtained through the collared lizard's carnivorous habits. Metabolic water production simply cannot sustain water balance.

When standardized by body weight, evaporative water losses of the collared lizard are unexpectedly similar to those of small desert rodents. Dawson and Templeton (1963) compared organisms of 25-35 g in weight. Water loss of resting mountain boomers was determined at 40°C (mammalian body temperature). In one hour, 0.73 mg H_2O was lost per gram of body weight. Water loss was determined for resting mammals in the absence of thermal stress (air temperature of 25°C). In one hour, the pocket mouse (Perognathus sp.) lost 0.9 mg H_2O per gram of body weight. The Merriam kangaroo rat (Dipodomys merriami) lost 1.2-1.8 mg H_2O per gram of body weight in one hour.

Reproduction

Typical iguanid reproductive behavior is modified by male mountain boomers. Their approach to a female is termed the "interrupted strut". The gait is peculiar: loose-jointed, relaxed slithering interspersed with rapid vibratory nods of the lowered head. This typical bobbing also advertises territorial claims and intimidates intruders. Extension of the relatively incomplete throat fan allows a full view of the orange throat (Burt, 1931). The final dash toward the female is "interrupted" by the nodding. This dash, instead of a "strut" is probably an adaptation to the speed characteristic of this desert species (Greenberg, 1945).

Courtship is usually initiated by the male. A female, however, may attract a male's attention with a nudge of her snout. Males frequently nip or lick the female during courtship. The female often reciprocates similarly. Fitch (1956) suggested that these gestures represent olfactory "social releasers" even though iguanids are not particularly keen-scented. But, tongue extrusions pick up environmental molecules which subsequently stimulate the paired Jacobson's organs (Gravelle and Simon, 1980). The frequency of tongue extrusions in Sceloporus jarrovi was significantly greater in response to a novel cage than to a familiar home cage; and significantly greater in response to a conspecific's cage than to a washed cage (DeFazio et. al., 1977).

For most iguanids with femoral pores, each pore is located in the center of a scale on the underside of the thigh. The femoral pores of collared lizards, however, are found between scales. A femoral gland is associated with each pore. These glands are rudimentary in the female. The male's glands enlarge during the breeding season. A comb-like series of waxy exudations may protrude from the male's pores. These exudations probably produce some tactile stimulation of the female as the male glides over her.

Occasionally, a male and female crawl over and around each other. This circling behavior has been interpreted as courtship. It was included in one description of the rejection behavior exhibited by other female iguanids. Yedlin and Ferguson (1973) observed circling both during and after the time span for oviposition. They also distinguished this behavior from typical "female avoidance of male approach" interactions. Circling, therefore, seems more characteristic of the postparturition period while courtship characterizes the time period before copulation. Their suggestion was to classify circling not as courtship, but as pair-bonding behavior.

An unreceptive female rejects male advances with a distinctive posture. Standing high off the ground, her body is dorsoventrally compressed. Her throat is extended and her tail raised. Her wide open mouth completes this threat. But the male may refuse to acknowledge this rejection. The female may then avoid the male's neck or shoulder grip by shaking her head, rolling onto her back, kicking and clawing, hopping to reverse position, moving behind the male, or stalking away on stiff, extended legs.

A receptive female eventually allows the male to grasp her loose neck or shoulder skin with his mouth. He then places his hindquarters into position for intromission. Resting on the female's right side, the male clasps her tail-base with his left hind leg and inserts the left hemipenis; or vice versa. Copulation lasts several seconds to a few minutes.

Hatchlings may mature sexually after their first hibernation. Minimum mature snout-vent length averages 92 mm (Tinkle, Wilbur and

Tilley, 1970). This early maturity at smaller body sizes plus being multiple-brooded designates the collared lizard as relatively r-selected (Parker and Pianka, 1976). Thus, C. collaris has a greater reproductive potential than most lizards of North America.

An average clutch of 6.1 eggs is laid sixteen to nineteen days after copulation (Vitt, 1977). A second clutch may be laid two to three weeks later. Whether this results from a second mating or a retention of sperm from the first mating is unknown. Larger clutches are typically produced by larger, older females. Two to twenty-four eggs per clutch are reported in the literature. But the extreme of twenty-four is probably due to mistaken field observations or data collected from enclosures containing several females.

Robison and Tanner (1962) compared ovarian counts of tiny eggs with the actual number laid. High counts of small ovarian eggs in collared lizards and western skinks (E. skiltonianus) did not correspond with the number laid. In the western skink, these little eggs atrophy. In C. collaris, however, tiny eggs are still present when others are ready to be laid. These smaller eggs may remain for later use while others enlarge for immediate use.

Female collared lizards deposit their eggs below large, flat rocks. A short, shallow tunnel is dug. At the end of this tunnel, the eggs are laid in loose earth or sand. After oviposition, the tunnel entrance is plugged with tightly packed dirt. A female carrying mature eggs appears plump and distended. A thin, wrinkly female has just recently laid her eggs. After completion of the nest site, the female devotes no more attention to either eggs or young. Average egg size is 20.2 mm by 12.8 mm (Clark, 1946). These cylindrical eggs are immaculately white to pinkish in color. The shells are flexible. Egg incubation periods range from 51 to 94 days (Parker and Pianka, 1976). Eggs are incubated by the surrounding warm soil. Low soil temperatures increase incubation times. A poor nest site, low air temperatures, heavy rains, and persistant cloud cover decrease soil temperatures.

Growth

Remarkably rapid growth characterizes the mountain boomer (Tables 1, 2); most lizards require more time to attain sexual maturity. In collared lizards, snout-vent length may increase more than 1 mm daily during the first weeks of life. The voracious feeding of hatchlings is supplemented by the egg yolk retained in the body cavity. At a snout-vent length of 90 to 95 mm, growth of females slows abruptly. Breeding for the first time generally occurs. Males now average several millimeters longer than females. During ontogeny, body proportions of the sexes as well as length change significantly (Ingram and Tanner, 1971). This sexual dimorphism in size is shown in Table 3.

A two-tone pattern of yellow and dark brown characterizes hatchlings. Rounded, dark brown spots on a pale background are separated by five, narrow, transverse, yellowish bands. These spots are large and distinct along the middorsal line. Outlines of the smaller, lateral spots are blurred. These spots fade into the immaculately white venter. Irregular dark brown markings dot the side of the face plus the dorsal surface of legs and tail. The black collar marks are well-developed. Other bright adult colors (scarlet, orange, yellow,

Table 1. Growth rates in young collared lizards of different size groups from Fitch, 1956. Measurements are in millimeters and sample sizes are shown in parentheses.

Mean snout-vent length	Mean increment in snout-vent length per day
?-42	1
43-53	0.71 (8)
60-70	0.52 (45)
75-80	0.30 (15)
82-85	0.20 (7)

Table 2. Comparison of growth rates in males and females of similar sizes from Fitch, 1956. Measurements are in millimeters and sample sizes are shown in parentheses.

Males		Females	
Mean snout-vent length	Mean increment in snout-vent length per day	Mean snout-vent length	Mean increment in snout-vent length per day
64.0	0.53 (21)	62.1	0.43 (19)
88.1	0.28 (9)	86.2	0.23 (8)

Table 3. Sexual dimorphism in collared lizard size from Burt, 1928; Fitch, 1956. Measurements are in millimeters and sample sizes appear in parentheses.

Characters	Males	Females
Snout-vent length	87.7 (659)	82.1 (597)
Tail length	171.8 (595)	154.8 (554)
Total length	257.3 (595)	236.9 (554)
Tail length as percentage of total length	66.3% (595)	65.3% (554)
Tail length as percentage of snout-vent length*	178.6% (8)	171.3% (6)

*For ten hatchlings, tail length averaged 145.2% of snout-vent length.

green, blue) are lacking. Without adult coloration, the sex of these young lizards cannot be distinguished with certainty.

As growth continues, the original bands are lost. Enlarging dark spots leave only faint remnants of these markings. The original pattern obscures faster in males. Bright scarlet spots, similar to the spots of a gravid female, dot the sides and dorsal surface of juveniles. These spots disappear at a snout-vent length of about 80 mm. In males, the characteristic green tint replaces these scarlet marks. Females retain the duller tones of the hatchlings; the obscured crossbands reflect the major difference. Dorsal surfaces of adults are dotted with white. Individual color varies widely. Dull, dark patterns typically depict a cold, sluggish lizard. Pale, sharper markings are apparent in warm, fully active lizards (Fitch and Tanner, 1951). Other than age and temperature, factors which affect color patterns include season, light, background color, sex, state of excitation, and the general condition of the lizard. Color patterns are definitely associated with geographic location and possibly with different diets.

Tail Regeneration

Tail autotomy, characteristic of many lizard species, is lacking in _C_. _collaris_ (Montanucci, 1969). Capture of mountain boomers by the tail-base without breakage is typical. Accidental loss of tail tips may result in partial regeneration (Weiner and Smith, 1965).

Molt

Like most reptiles, _C_. _collaris_ periodically sheds the epidermis. Little water loss occurs in this molting process. Daily routines and lizard dispositions seem unaffected. Several major splits appear in the translucent epidermis. Then it rapidly peels off.

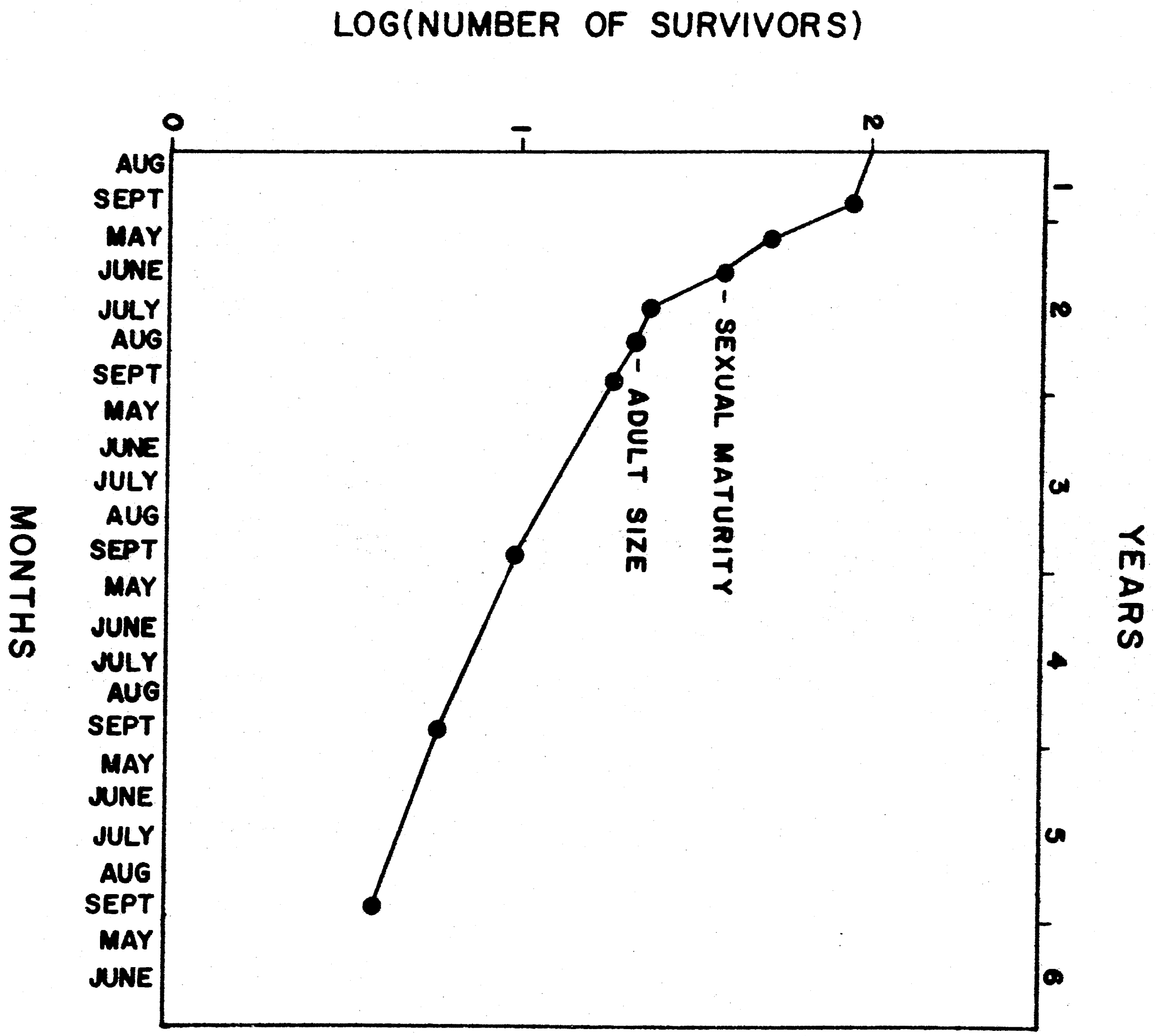
Little is known about molting frequency in nature. A postnatal molt is observed for many lizards and snakes. It has yet to be discovered for the collared lizard. The most rapid growth occurs between hatching and the first hibernation. Frequent molts are involved in this period: four in seven to eight weeks. As the first full growing season ends (just before the second hibernation), adult size is nearly attained. Four or five molts, one every 23 days on the average, occur in that summer. After two or more hibernations, a mature adult molts every 25.4 days, approximately. Thus, the typical adult growing season involves five molts.

Numbers and Mortality

Remarkably little information pertaining to the population density of mountain boomers can be found in the literature. In Douglas County, Kansas, on the University of Kansas Natural History Reservation, a collared lizard community inhabited less than one acre. Fitch (1956) reported that five to nine collared lizards seem to represent the carrying capacity of that environment.

Survival of August hatchlings to September is quite probable (Figure 1). Through hibernation and other activities between September and the next May, more than one third of these juveniles are eliminated. Between the months of May and June, another one-third are lost. As sexual maturity approaches, territorial pressures increase. Approximately half of the June survivors are irradicated during July. Once through this critical period, survival chances are again more

Figure 1. Survivorship in the population of collared lizards studied on the University of Kansas Natural History Reservation, Douglas County, Kansas from Fitch, 1956. Mortality is high at first; after adult size is obtained, the lizards live in relative security (Type III survivorship curve).


LOG(NUMBER OF SURVIVORS)
0
1
2
AUG
SEPT
MAY
JUNE
JULY
AUG
SEPT
MAY
JUNE
JULY
AUG
SEPT
MAY
JUNE
JULY
AUG
SEPT
MAY
JUNE
JULY
AUG
SEPT
MAY
JUNE
MONTHS
1
2
3
4
5
6
YEARS
- SEXUAL MATURITY
- ADULT SIZE

secure through September.

Especially susceptible to death are the recent hatchlings, the half-grown young just reaching sexual maturity, and the subordinant adult males (Fitch, 1958). The egg-laden females are also vulnerable. The responsibilities of nest-digging and egg-laying lead them farther from their accustomed refuges. Mean life expectancy for mountain boomers is 1.2 years (Tinkle, 1969). The bright hue and more conspicuous territorial perches explain the more frequent observations of males. Fitch (1956) postulated that females possess a slightly longer life expectancy due to fewer territorial pressures and probably outnumber the males.

Home Range

Few species wander completely at random. Home range is, therefore, an important consideration in the ecology of animal populations. Area estimations of this parameter are commonly included in natural history studies of terrestrial vertebrates. The intensity of use varies from section to section within a home range. Population structure may be substantially influenced by these different use intensities (Jorgensen and Tanner, 1963). The value, function, and comparative size of lightly-used habitat within home ranges need elucidation. These considerations also need to be applied to buffer areas between home ranges. Knowledge of focal points of concentrated activity in terms of type, frequency, and duration would lend more significance to home range biology.

These differences in use intensity sometimes result from competition in heavily-used sections of the home range. The availability of resources such as food, shelter, and basking spots also affect intensity of use. Some animals may rely on a regular home base for shelter and escape. In this case, the tendency is to stay within easy reach of this refuge. Activities in outlying portions of the home range become increasingly diffuse (Fitch, 1958). Other home ranges may be more randomly used. Capture frequency at a particular spot has been thought to indicate intensity of use (Hayne, 1949). The assumption is that an organism can be captured over all "ecologically significant" areas of its home range; and where not caught, not often present.

Structural restrictions on body size ultimately limit the extent of daily wanderings. Body weight influences energy requirements and the rate of energy expenditure. Inter-specifically, lizard home range size appears directly proportional to body weight (Turner, Jennrich and Weintraub, 1969). This also seems true intra-specifically: smaller (and more sedentary) female mountain boomers possess smaller home ranges and territories than those of males (Yedlin and Ferguson, 1973). Large predators have large energy requirements. They usually feed on large-sized prey species. These large energy packets are mandatory unless a superabundant food supply of small packets exists. An extra-efficient method of collecting small prey would also negate the necessity of large prey (for example: whales). But large home ranges are typical of large predators. Only a large home range can support a sufficiently numerous large-size prey population. Restrictions on home range size may force a predator to exploit diverse food sources. A diversified diet partially alleviates the need for a large home range.

Home range sizes are related to population density. Yearly home range changes of female Uta stansburiana are inversely correlated with annual density differences (Turner, Jennrich and Weintraub, 1969). Densely populated areas are characteristic of species with small area requirements. Species that require large home ranges cannot maintain locally dense populations. Highly mobile hunters are the only exception. The requirement of large home ranges indicates that energy resources in a given area are limited.

Accuracy in home range size determinations is important biologically but quite difficult in practice. Home range boundaries, in contrast to those of a territory, are poorly defined. Many different methods have been used to estimate home range size. All include biases related to the time period, the observation techniques, and the mathematics of area calculations. Direct comparison of these methods is difficult due to the different assumptions and algorithms. Interpretation of the results must be tempered by the specific limitations of the method used. Species and individual differences, social behavior, population density, age and sex structure, food sources, habitat heterogeneity, observer-caused disturbances, and small sample sizes are only some factors which should be considered in the interpretation of home range data.

Area calculations for any geometric figure depend on shape. The recognition of true home range shape is, therefore, a basic requirement in calculations of the actual area. Observations for one individual may not provide enough data to determine home range shape. Mohr and Stumpf (1966) used composite ranges of several individuals to define an average home range shape for a species. Construction of these composite ranges involves superimposing the mean centers and axes of individual ranges. Use of median centers and axes (the median-composite method) seems appropriate in some home range shape determinations. The result is a very compact, stable core with an increasingly wider scatter of exterior points. Although affected by habitat, the core appears to be a species-specific characteristic.

Home range statistics involve manipulations of locational data over a time unit (Koeppl, Slade and Hoffmann, 1975). Various methods have been derived.

Polygon Method

One of the simplest techniques of home range size calculations is the polygon method. Both graphical and algebraic evaluations are simple. Connection of the peripheral recapture points outlines the minimum convex polygon. With only four captures per individual, this method accurately estimated home range sizes of *U. stansburiana* (Tinkle, McGregor and Dana, 1962). With only three captures per individual of this same species, this method approximated 50 to 60% of the actual home range sizes (Jorgensen and Tanner, 1963). Consistant results are obtained with this historically prominent method. There is, however, a sample size bias. As the number of captures per individual increases, the home range size often increases. The rate of increase is reduced with each locational data point until it becomes insignificantly small.

The minimum polygon is obtained by dropping the convex requirement. All capture points per individual should be connected counterclockwise around the geometric center. This rigorous definition is necessary. Otherwise, the shape of the polygon, and consequently the area, depend on the order in which the capture points are connected (Hatfield, 1978). This minimum polygon encloses only the area where the animal was definitely present. It is a conservative estimate; the home range is at least a certain size. An increasing number of locational data points cause unwieldy graphical evaluations, but the algebraic evaluations remain simple.

A boundary zone may be added to the home range area calculated by either of these polygon variations. The true home range is assumed to extend beyond the capture points (Hayne, 1949). The possibility that the animal never used this boundary zone is a definite disadvantage to this practice. Another disadvantage is the inconsistancies created between investigators.

Circular Method

Home ranges for some organisms can be visualized as nearly circular. Fitch (1958) pointed out the major advantage to this assumption: small amounts of data suffice. Only two recapture loci (locational data points) per organism are necessary. He considered these two data points randomly situated with respect to one another. Distances between successive locations (usually more than two) for each individual were then calculated. These distances were averaged in totality for a species or according to season, sex, or age group. Each average represented a home range radius by which random recapture loci were separated. Two errors are inevitable: 1) most home ranges deviate significantly from a circular shape and 2) certain parts of a home range may be used more intensely than others.

The geometric center of all recapture loci per individual has been called the center of activity. Separate averages of abscissas and ordinates are calculated for all recapture loci per organism. The average abscissa and ordinate then pinpoint the coordinates of the center of activity (Hayne, 1949). Concentric circles, based on the normal probability distribution, are drawn at various distances (recapture radii) from the activity center. The mean recapture radius plus several standard deviations (depending on the confidence level desired) constitutes the radius of the circular home range. Ninety-five percent of an animal's activity should be contained in a circle of mean recapture radius plus two standard deviations; 99% by a circle of mean recapture radius plus three standard deviations.

The probability of capturing an animal is inversely proportional to the length of the recapture radius: the further from the center of activity, the smaller the probability of capture. An animal may be captured farther from the activity center of its home range than in past recaptures. Statistics can then determine if this departure might be expected by chance. It may represent a spatial change in activity or even a home site change. Comparisons of two sets of capture points for an individual can determine whether the activity centers are actually estimates of the same point. Also, certain behaviors may be predicted to occur at a given distance from the activity center.

Recapture radii show the various distances of observed travel from the activity center. Tinkle and Woodward (1967) measured the relative movements of *U. stansburiana* using recapture radii. Fairly constant results were obtained even with 1) different numbers of captures (>5) per individual, 2) different numbers of individuals (>10), 3) different years in the same study area, 4) different periods of time (mean number of days between the first and last captures of an individual), and 5) different study areas within the same general habitat. The mean recapture radius is sensitive to changes in density with which it varies inversely.

Three major disadvantages are inherent in the circular method. One is that a circle typically overestimates home range size. Area is included where the animal might not have been. Jorgensen and Tanner (1963) calculated circular home range areas of _U. stansburiana_ in Nevada. Tinkle, McGregor and Dana (1962) calculated home range sizes of the same species at the same site via the polygon method. Home range sizes were larger when calculated by the circular method.

Despite this overestimation bias, Jorgensen and Tanner (1963) argue that results obtained from the density probability function agree more closely with field observations than those of the minimum polygon method. They recorded individual distances moved in one direction in an hour. The maximum distance traveled by an organism during an observation period has been used to represent the diameter of a circular home range or the major axis of an elliptical home range. Areas based on such diameters were larger than the mean home range size calculated by the minimum polygon method. Such comparisons are complicated by the basically different approaches of these two Nevada studies. Besides different home range definitions, Tinkle and Woodward (1967) point out different capture techniques, different time periods of observations, and different definitions of sexual maturity.

A second disadvantage of the circular method involves the temptation to identify the center of activity as the home range site. This point becomes fairly stationary after five to six captures but ordinarily has no unique biosignificance. It is simply an average of all capture points per individual. It shows little sensitivity to small changes in home range size. In cases where several individual ranges overlap, the center of activity can be effective in the separation process.

The third disadvantage is that this method fails to respond properly to home range shape. Lack of circular symmetry gives biased results. Although insufficient for most studies, the idea of a basically circular home range is still useful in certain theoretical applications.

Elliptical Method

Most home ranges are distinctly longer than wide, more elliptical than circular. Concentric ellipses can be drawn for a scatter of recapture loci. These ellipses are based on the bivariate normal probability distribution. The intensity of use for each point of an organism's habitat is expressed by this distribution. These confidence ellipses reveal the probability of finding an individual at any given location.

Three variations of the elliptical method are commonly discussed. Jennrich and Turner (1969) based elliptical home range area calculations on the determinant of the capture point covariance matrix. This sample covariance matrix, as defined mathematically, is based on a divisor of n-1. Used thus, home range size is consistantly under-estimated (Hatfield, 1978). Without explanation, Jennrich and Turner (1969) substituted a divisor of n-2 into home range area calculations. This substitution compensated for the sample size bias. Home range was defined as the area of the smallest ellipse which includes a specified proportion (usually 95%) of an individual's total utilization. Calculated axes of natural location data are seldom perfectly aligned with the arbitrarily determined axes of a grid. This causes the major bias of this method.

For results similar to those of Jennrich and Turner, trigonometric transformations have been used (Hatfield, 1978). Through these transformations, standard deviations of the X-coordinates and the Y-coordinates can be calculated for each individual. These standard deviations are proportional to the lengths of ellipse axes. Elliptical areas can be calculated using the standard deviations. The orientation and shape of the ellipse may affect the standard deviations. Thus, the major bias of the determinant method also affects this method.

Basic measures of dispersion about the activity center are variance, standard deviation, and covariance. From these statistics, Koeppl, Slade and Hoffmann (1975) calculated two other statistics termed eigenvalues. These eigenvalues are also called characteristic roots of the sample covariance matrix. The smallest eigenvalue describes variability along the minor axis of the home range; the largest, along the principal axis (Hatfield, 1978. These axes are weighted according to the frequency of the individual's occurrence at particular locations. They are orthogonal (perpendicular and independent) axes and they intersect at the activity center. Using the eigenvalues, the standard deviations of the X-coordinates and the Y-coordinates can be corrected for orientation of the ellipse. Trigonometric transformations can also be corrected for this bias and used in this method. Thus, the bias associated with misalignments of home range axes and arbitrary grid axes is eliminated by this method (Hatfield, 1978).

Koeppl, Slade and Hoffmann (1975) defined the standard home range as the 95% confidence ellipse. Sample size affects the variances and covariances used to calculate the standard ellipse; home range size is usually overestimated. Incorporation of the appropriate F-statistic, however, compensates for this sample size bias.

Territoriality

Defended areas within a home range constitute the territory (Simon, 1975). Common elements of defensive displays in iguanids include lateral compression of the body, an extended dewlap, stiff bobs, and a display of accessory pigments. The combat display is an attempt to intimidate a male's adversary. This defensive display occurs before actual combat or even as a substitute. Male iguanids are typically larger and more colorful than females. The stereotypic display renders a male even more conspicuous.

Territorial defense is well developed in male C. collaris. Within ten minutes after hatching, juveniles can demonstrate aggressive posturing without nods or bobs (Cooper, 1971). Typical aggressive patterns vary with individuals, time of year, and where in the home range intrusion occurred. Intensity of aggression increases during the breeding season. With an arched back, puffy orange throat, and laterally flattened body, the male flexes and extends his forelimbs. With each stiff, deliberate bob, the male jerkily rises higher. Through these posturing displays, territorial claims are established and maintained without physical combat. Displays eventually lead to open warfare if a rival is not sufficiently intimidated.

Avoiding attack is best achieved by remaining in one's own relatively small, familiar area. Boundaries are ordinarily respected by neighboring lizards. Another way to curb an attack involves submissive postures. Such postures are more frequently used by females than by males. Stalking away stiff-legged with a puffy throat, arched tail, and dorsoventrally flattened body excuses the subordinate from a fight. A psychological advantage favors an individual in his home range; an intruder usually fares poorly, even against a smaller, weaker opponent.

A change of location may warrant an assertion display--a keep-your-distance warning. Directed to all lizards in the immediate vicinity, this display consists simply of two or three bobs. Normally, all male displays occur on prominent rocks. Other suitable substrates, however, may be used during confrontations (Sanborn and Loomis, 1979).

Observations indicate that a male mountain boomer may associate with several females at different times during the same day. Yedlin and Ferguson (1973) reported that a male's home range core area coincided with the overlap of several female home ranges. The female home ranges did not overlap outside the male's core area. Since the majority of male aggressive responses occurred in this core area, they suggested that males defend females from other males. They also found that June was the peak month of male-male aggression. This coincided with oviposition and peak female-female aggression. Increased female aggression after egg-laying seems consistant with the hypothesis of nest site defense.

Simon (1975) studied territoriality in Sceloporus jarrovi. The females, just as C. collaris females, defend smaller territories than males. Food abundance was inversely correlated with territory size. Food supplements caused a relocation of territorial boundaries. The center of the new, smaller territory was located near the extra food. An easily accessible food supply is defended through the territorial behavior of S. jarrovi.

Greenberg (1945) studied the social behavior of collared lizards under laboratory conditions. A dominance hierarchy was established. During three months, one male was dominant. Aggression of the other males was inhibited in his presence. Removal of this male simply allowed another to ursup his place. When the group was divided, a dominant male emerged in each subdivision. Sex recognition by males was apparent: females were courted and other males, fought. Distinctive color patterns seemed essential to this phenomenon. Male fighting responses were partially elicited by another male's orange throat. If the orange color was not visible, the subordinate was not molested.

Females were reported to be completely passive (Greenberg, 1945). Female-female pursuit and attack has been observed, however. Yedlin and Ferguson (1973) described typical female aggressive displays as weaker and less elaborate than those of males. The legs are extended to raise the arched and laterally flattened body high. Throat inflation is also involved but females do not employ the bobbing movements. They tolerate a closer approach by an intruder before resorting to displays or attack.

Objects of territorial hostility are never members of the opposite sex. Small, sexually mature males are even tolerated by older adult males. This tolerance continues as long as the older male's dominance is not challenged. Stereotypic hostility to hatchlings or juveniles has not been observed. Although the young are wary of larger individuals, adults usually ignore them. Occasionally, however, adults prey upon the hatchlings (Fitch, 1956).

Hatchling tolerance of other hatchlings remains after their surroundings become familiar. Even after favorite basking and lookout posts are chosen, hatchlings may stay within a meter of each other. Intolerance appears at several weeks of age and territorial conflicts begin in earnest (Fitch, 1956).

Food Habits

Mountain boomers, as sit-and-wait predators, survey their surroundings from rocky perches. Prey in motion attracts the attention of these diurnal lizards. The vibratory head nodding of courtship and aggression also appears in stalking prey (Montanucci, 1971). With a sudden rush, an insect is captured. Massive jaw muscles and fine, sharp teeth cooperate to crush the prey. The insect is then gulped down whole (inertial feeding).

The collared lizard is a generalist carnivore, even capable of jumping to catch flying insects. The main dietary items are grasshoppers and beetles (Pack, 1923; Knowlton, 1934; Knowlton and Thomas, 1936; Little and Keller, 1937). Grasshoppers predominate in the diet. This is probably due to their ready availability in collared lizard habitat (Blair and Blair, 1941). Occasionally, smaller lizards may be consumed, but the mountain boomer is seldom fortunate enough to capture such vertebrates (Weiner and Smith, 1965). Stomach contents sometimes include vegetable matter (Banta, 1960). Fleshy red berries of the solanaceous desert shrub, *Lycium andersonii*, have been found in stomach contents of Nevada collared lizards (Turner et al., 1969).

C. collaris, as a predator, is most active between the hours 0800 and 1200; and again between 1700 and 1900 (Tanner and Krogh, 1975). Peak activity occurs from 1100 to 1200 in June, 0800 to 0900 in July, 1000 to 1100 in August, and 1300 to 1400 in September (Parker and Pianka, 1976).

The collared lizard is extremely sensitive to noise and movement. Hearing ranges from 300 to 4000 Hz. Greatest sensitivity occurs between 400 and 2500 Hz except for a notch at 700 Hz (Davidson and Richardson, 1970). The middle ear is highly adapted for the reception of aerial sounds up to 35 db. Maximum transform efficiency of the middle ear is similar to that of acutely hearing mammals (Wever and Werner, 1970).

Walls (1931) reported that lizard retinal cones contain brightly colored oil droplets. These yellow (and perhaps red or green) oil droplets probably reduce chromatic aberration and thus, improve visual acuity.

Characteristic scats accumulate around mountain boomer perches. They are one to two inches long and approximately 1/4-inch in diameter. The frequency of various prey items in the diet can be estimated from these scats. Diets are influenced by the season, weather, stage of plant succession, and individual lizard preferences.

Predation

The chief enemies of _C. collaris_ include raptors (especially hawks) and snakes (especially racers). These predators hunt by sight in open areas. They also are swift enough to catch running lizards.

Wariness varies from population to population of collared lizards and between individuals. Escape mechanisms of juveniles and adults differ. Young lizards are still relatively unaccustomed to their environment. A hurriedly chosen retreat may offer only partial concealment. Older, more experienced lizards utilize several basic escape mechanisms. Basking lizards rely on cryptic coloration as a predator defense. In the cooler air at sunset, a slow approach followed by a quick grab was effective in collecting collared lizards (Fitch, 1956). Once flushed though, their exceedingly rapid movements allowed escape. A fully-warmed, foraging lizard relies on its fleetness as a predator defense. Reflexes of a fully-warmed, active lizard are quicker than those of a person. The slow, stealthy approach followed by the quick grab was seldom successful (Fitch, 1956). Mountain boomers occasionally dive into water when alarmed (probably unintentionally). Typical refuges include rock crevices, burrows, or the base of thickly clumped bushes.

Collared lizards are fairly sedentary. Considerable time is spent perched on rocks. A quadrupedal gait is typically used in walking, unhurried runs, and short dashes. But, like a mini-dinosaur, _C. collaris_ is capable of speedy locomotion on its large, strong hind legs. Fairly extensive individual home ranges are therefore feasible (Lewis, 1950). Bipedal locomotion can begin directly from a resting position, but elevation of the forebody usually requires gaining speed

(Snyder, 1949). Off the ground, the tiny partially-flexed forelimbs are relatively unimportant in these powerful locomotory efforts (Weiner and Smith, 1965). Bipedalism is more efficient for rapid locomotion. The bipedal stride of an adult lizard is roughly 30 cm or three times the snout-vent length (Snyder, 1952; Fitch, 1956). During leaping and running, some balance is provided by the extra-long, cylindrical tail.

Stress patterns include the ballooning of thoracic-abdominal regions, a threatening mouth gape, and hissing (Davidson and Richardson, 1970). This hissing may not be deliberate vocalization but simply the sudden expiration of air in the alarm reaction (Wever, Hepp-Reymond and Vernon, 1966).

Parasites

Fitch (1956) studied the chigger infestations common among Kansas collared lizards. The smaller body surface of juveniles allowed fewer chiggers. During June, adults averaged more than 200 chiggers per individual. Hot, humid weather encouraged the heaviest infestations; lighter infestations prevailed in later summer. Chiggers were concentrated in epidermal regions protected from dry air and direct sunlight: eyelids, groin, and edges of the gular fold. The mountain boomer habit of basking provided some protection from chiggers. Molting also rid the lizards of these parasites. Dead, dried-out chiggers were observed on patches of sloughed skin.

Habitat Influences on Behavior

Few studies directly reflect habitat influences on behavior. In one which does, Barash (1974) compared the social systems of three *Marmota* species. The woodchuck, *M. monax*, is found east of the Mississippi. It inhabits fields and forests at low elevations. A long growing season is possible: more than 150 days in southern Pennsylvania. Woodchucks are aggressive, solitary mammals. Association between adult sexes is limited to copulation; females bear young annually. The mother-offspring relationship is the only lasting social tie and it terminates at weaning when the young disperse. Woodchuck dispersal occurs during the year of birth. One-third of the eventual adult weight has been achieved. Yearlings average 80% of their eventual adult weight and often are sexually mature.

The Olympic marmot, *M. olympus*, is found in Olympic National Park, Washington. Alpine meadows at or above timberline are inhabited exclusively. The growing season is short: 40 to 70 days. This marmot is highly social, very tolerant, and playful. Social groups of three to six individuals feed together. Distinctly organized colonies usually consist of the young of the year, yearlings, two-year-olds, and several adults (generally one male and two females). All parts of the colony are equally shared by all colony members. There are no territories and no distinct individual home ranges. Indistinct dominance relationships exist but are nonpunitive. "Greeting" behaviors are apparently associated with individual recognition. Active greetings are frequent; the average is one greeting per animal per hour. Seasonal and diel cycles of greeting frequencies are predictable. High frequencies occur in spring seasons and in the early morning hours each day. Females produce litters in alternate years only. Less than 25% of eventual adult weight is gained during the year of birth. Yearlings average 30% eventual adult weight. As two-year-olds, Olympic marmots average 70% adult weight and disperse. Sexual maturity occurs at three years of age.

The yellow-bellied marmot, _M. flaviventris_, is found at elevations intermediate to those of the woodchucks and Olympic marmots. Typical environments range from sea-level to mountain meadows. This study was conducted in Yellowstone National Park, Wyoming, where the growing season averages 70 to 100 days. An intermediate social system is correlated with this intermediate environment. Yellow-bellied marmots are less solitary than the woodchuck and less socialized than the Olympic marmot. Adults congregate in colonies but also maintain distinct individual home ranges. Plenty of physical space remains between marmots. The infrequent social interactions are fairly aggressive. Greetings average one-tenth that of Olympic marmots. Females may bear young annually or they may skip a year. During the year of their birth, yellow-bellied marmots gain less than 25% of their eventual adult weight. The weight of yearlings has increased to 60% adult weight when they disperse. Sexual maturity occurs at two years of age.

In this study, the length of the growing season is correlated with a specific social system. Shorter growing seasons are associated with increased social organization. Growth rate, age at dispersal, and sexual maturation are also correlated with growing season length and elevation. Body weight must be sufficient for the demanding processes of dispersal and reproduction. Adult aggression has been implicated as an initiator in the dispersal of yearling yellow-bellied marmots. Aggression may play the same role in the other two species. Selection seems to favor that degree of aggression which results in an optimum dispersal age for each environment. The nutrient availability of each environment influences the marmot reproductive cycles.

Barash (1974) also compared the social biology of two colonies of yellow-bellied marmots. Both were located in Rocky Mountain National Park, Colorado. One colony was found at medium elevation where the growing season is of intermediate length. Social behavior resembles that of the yellow-bellied marmots studied in Wyoming. The second colony inhabits an area of higher elevation. Social behavior reveals characteristics similar to those of Olympic marmots.

Two studies showed habitat influences on U. stansburiana autecology. Tinkle (1967) studied two populations of these lizards: one in west Texas and the other in western Colorado. Differences in climate are shown in Table 4. Sage, yucca, and mesquite characterize the sandy, wind-blown Texas site. Both sexes are highly aggressive. The push-up sequence is short: only four component movements. Home ranges overlap little and territoriality is well-developed. Sexual dimorphism in color patterns is striking. Average adult biomass was 50 g/acre.

Texas females of snout-vent length 40 mm are usually mature. The male courtship display is elaborate: considerable bobbing, circling, and shuddering are performed. The female rejection mechanism is retreat. The male is not easily discouraged so courtship may be attempted several times. If receptive, the female allows the male to

Table 4. A comparison of some climatic differences between study sites in west Texas and western Colorado from Tinkle, 1967.

Item	Texas	Colorado
Isotherm	16°C	10°C
General climatic classification	hot summer mild winter	short, mild summer cold winter
Normal precipitation	ca. 381 mm	ca. 305 mm
Normal annual snowfall	ca. 152 mm	ca. 1270 mm
Date of 75% probability of frost in fall	after December 15	November 1-10
Normal % October nights below freezing	1%	40%
Normal number of nights below freezing	ca. 90	ca. 130
Normal number of days with temperatures continuously below freezing	ca. 4	ca. 20
Normal number of days with temperatures of -18°C or lower	0.5	7
Normal number of days with snow cover	ca. 3	ca. 40
Duration of season with little or no plant growth	30	150
Normal January daily minimum temperature	4°C	-7°C
Normal January daily maximum temperature	10°C	2°C
Date when normal daily temperature rises above 10°C	late February	early April
Date of 75% probability of no frost in spring	mid-February	mid-March
Normal length of frost-free season	215 days	175 days

mount. Three to six copulatory thrusts occur in less than ten seconds. The pair rarely remains *in copulo* after thrusting stops. During the breeding season, adult females lay at least four clutches which average four eggs each. A female produces an average of fifteen young in one breeding season. Adults presumably die in late summer; the yearly adult turnover is about 90%.

An emigrant lizard was defined as first marked in the study area and last recorded outside the study area. Lizards that moved distances of greater than one-half the diameter of the study site were termed distant emigrants. Fewer than ten of 3500 Texas individuals were distant emigrants.

The Colorado study site includes rocky arroyos and hillsides. Lizards are seldom found on the sagebrush flats of the area. Colorado lizards are less wary and less aggressive than Texas lizards. Many social interactions are prevented by the landscape; lizards often pass in close proximity but never see each other. Assertive push-up displays and fighting were observed less frequently. The push-up display is longer and involves five component movements. The bob is more shallow than that used by Texas lizards. A non-resident that displays the submissive posture is tolerated. Challenges may never be returned; retreat occurs first. Such behavior was never observed in Texas and suggests a dominance hierarchy. There is also great overlap of home ranges. Sexual dimorphism is minimal. Tail bands are practically the only dorsal markings. Thus, better camouflage is obtained for this saxicolous population. Density was less than that in Texas: average adult biomass was 40 g/acre.

Colorado females of 37 mm snout-vent length are usually sexually mature. The breeding season is at least one month shorter than that in Texas. Male courtship is faster and more direct. Quicker licking and nipping of the female characterize the Colorado courtship display. If unreceptive, the female quickly discourages the male with a shudder bob, similar to the male courtship bob. If receptive, the female allows the male to mount. Ten or more copulatory thrusts occur in twenty seconds. The pair remains _in copulo_ for more than one minute. During the breeding season, a mature female may lay three clutches, each averaging three eggs. A female produces an average of seven young in one breeding season. The incubation period for the eggs is nearly a month longer than in Texas. One-third of the adults live to reproduce a second season; many females reproduce three seasons. A submissive lizard has a longer life expectancy in Colorado. It, therefore, has a greater chance to reproduce in another season. Nearly ten percent of all Colorado lizards marked were distant emigrants; all were young adults in their first breeding season. This study shows how habitat can influence aggression, courtship, reproduction, emigration, and life expectancies.

Fox (1978) studied _U. stansburiana_ on Tinkle's site in west Texas. Marked lizards were followed through time in large, enclosed field plots. Thus, lizard disappearance indicated death. Conditions for activity of survivors and nonsurvivors were compared. Clearer skies and warmer temperatures characterized survivor activity. Survivors were active later in the morning and earlier in the evening. They were seen less frequently than nonsurvivors. Home range quality of survivors and nonsurvivors was also compared. Survivors were associated with vegetation furnishing more shade (yucca). More shelter holes were also present on their home ranges. Diversity of home range elements was greater for survivors than for nonsurvivors.

Home range quality probably influences behavior. Fox (1978) categorized survivor behavior as more specialized. Survivors seemed to maximize the density of certain vegetation on their home ranges. By enlarging a defensible area, the survivor acquires all vegetation which increases home range diversity. But, activity is specialized around the prime elements. Survivor-nonsurvivor differences may be related to microhabitat differences in food quality (indirectly reflected by the features measured in this study). Survivors seem to forage quickly and efficiently under optimal ecological conditions. Subsequent retirement to safe seclusions minimizes predation risk.

Holmes (1967) studied the habitat influences on two dunlin (Calidris alpina) populations in Alaska: one at Barrow and the other at Kolomak River. At Barrow, the flat arctic tundra is covered by grasses and sedges. Occasional rivers and streams cross this plain; fresh water lakes and ponds are numerous. Patches of well-drained tundra rise above the surrounding marshes. From early September to late May, snow covers the tundra. In the spring, it takes two or three weeks for the snow to melt. From late June through August, the tundra is snow-free. Drainage causes the ponds to shrink in size but cold rains in late July and early August resaturate the tundra. Rain or snow may occur any time during the summer. Midsummer temperatures average 2^{o}-5^{o}C. Only a few types of food suitable for dunlin are present; adverse weather conditions may annihilate the only alternative food supply.

Dunlin arrive at Barrow during the snow-melt period and are restricted to breeding territories until the eggs hatch. Courtship, pair-bonding behavior, nesting, and feeding occur within territorial boundaries. Territory size averaged 6.5 ha; density was six pairs of dunlin per 40 ha.

The study site at Kolomak River is an extensive marsh; more than 50% of the tundra is underwater. Tidal fluctuation affects rivers and channels many kilometers inland. Severe storms in September and October cause the brackish water in channels to overflow and flood many tundra ponds and lakes. Pond water levels remain fairly constant throughout the summer. Sedges, grasses, and a few forbs grow in this marsh. The snow-free season extends from late May or early June to September. Summer temperatures average 7°-15°C and rains are frequent. Freezing temperatures or snow is rare between 1 June and 1 September. Insect prey is more abundant and less affected by rains than at Barrow.

Dunlin arrive at Kolomak River during the snow-melt period and confine activity to territories until the eggs hatch. Late in the incubation period, however, some dunlin move to favorite feeding ponds. As more trespassing occurs, the frequency of active displays increases at the territories. But at the feeding ponds, formerly aggressive neighbors feed passively side by side. Territory size averaged 1.3 ha; density was 30 pairs of dunlin per 40 ha.

The density of breeding dunlin is closely related to the abundance, availability, and dependability of their food supply. At Barrow, where insect prey is less abundant, territory size is larger. Food abundance is, thus, directly related to territorial behavior.

Brown and Orians (1970) reviewed spacing patterns in mobile animals. Habitat was shown to influence these patterns of dispersion.

Herring gulls (*Larus argentatus*) are normally colonial; but where lakes are very unproductive in gull food, they are solitary and highly territorial. Jaegers (*Stercorarius*) are territorial where they exploit lemmings as prey. In coastal regions, however, prey is stolen from sea birds to feed the young. Since this resource is indefensible, colonies are formed. Stenger (1958) showed that territory size of ovenbirds (*Seiurus aurocapillus*) varies inversely with the amount of food available.

Habitat also influences reproduction. Brown and Orians (1970) recorded that great reed-warblers (*Acrocephalus arundinaceus*) prefer territories in beds of *Phragmites*. If males establish territories in beds of *Typha* and *Scripus*, they are unsuccessful in breeding. Females simply cannot build suitable nests from such coarse vegetation. Best (1977) showed a positive correlation between certain plants and the mating frequency of field sparrows (*Spizella pusilla*). The size of field sparrow territories is also significantly related to certain plants.

The intrinsic quality of the environment may be modified by the presence of other individuals (Brown and Orians, 1970). Crews (1975) studied reproduction in the American chameleon, *Anolis carolinensis*. Temperature and photoperiod are known to trigger different phases of the annual testis cycle in this lizard. Male courtship facilitates environmental induction of ovarian activity. Experiments were conducted to test the relative effectiveness of various components of male courtship. The ability to extend the dewlap (and not the dewlap color) is a critical factor. Courtship insures normal gonadotropin secretion. In the absence of male courtship, gonadotropin secretion is subnormal; the eggs laid are unshelled. Male-male aggression, on the other hand, inhibits environmentally induced ovarian recrudescence.

Among seasonally breeding, temperate vertebrates, males emerge first from winter hibernacula or arrive first at the breeding grounds. Territorial boundaries are established in the absence of females. Male-male aggression then subsides. Females arrive and male territorial behavior shifts to courtship. Along with environmental stimuli, courtship acts to facilitate ovarian recrudescence in *A. carolinensis* (Crews, 1975) and perhaps in other vertebrates. It is adaptive for females to remain dormant while territories are being established and male-male aggression is high. Once females are active, male-male aggression declines, allowing females to reach breeding condition rapidly. Furthermore, females are not unnecessarily exposed to predation while the males establish territories.

Different microhabitats affect escape behaviors. Schoener (1968) studied four *Anolis* species on the island of South Bimini. *A. sagrei* uses the lowest perches available and escapes by jumping to the ground. *A. distichus* frequents the trunks of large trees. In an escape attempt, these lizards run rapidly around to the other side of the trunk and up. *A. angusticeps* was generally observed high in the crown on tiny branches. To avoid threats, stealth and deception are used; cryptic coloration completely hides these lizards from view on the back of a twig. *A. carolinensis* uses perches at heights between those of *A. distichus* and *A. angusticeps*. Juvenile *A. carolinensis* escape into twisted tangles of vines. Adults climb higher into the leafy portion of the canopy or plunge into the dark central cores of the crown.

Schall and Pianka (1980) studied escape behaviors in Cnemidophorus species. Escape behavior diversity varies among different sites and is negatively correlated with plant species diversity.

Methods of Lizard Collection

Many different methods have been devised to catch lizards. The noose is one of the most frequently used techniques. An efficient noose consists of two components. A short piece of fine wire, or monofilament or nylon fishing line is attached to the smallest end of a cane fishing pole. For ease of transportation, a cane pole in three extensions is best. A slip knot connects the fishing line circularly. This loop of fishing line is placed around the lizard's neck. Then with a jerk of the cane pole, the lizard is captured.

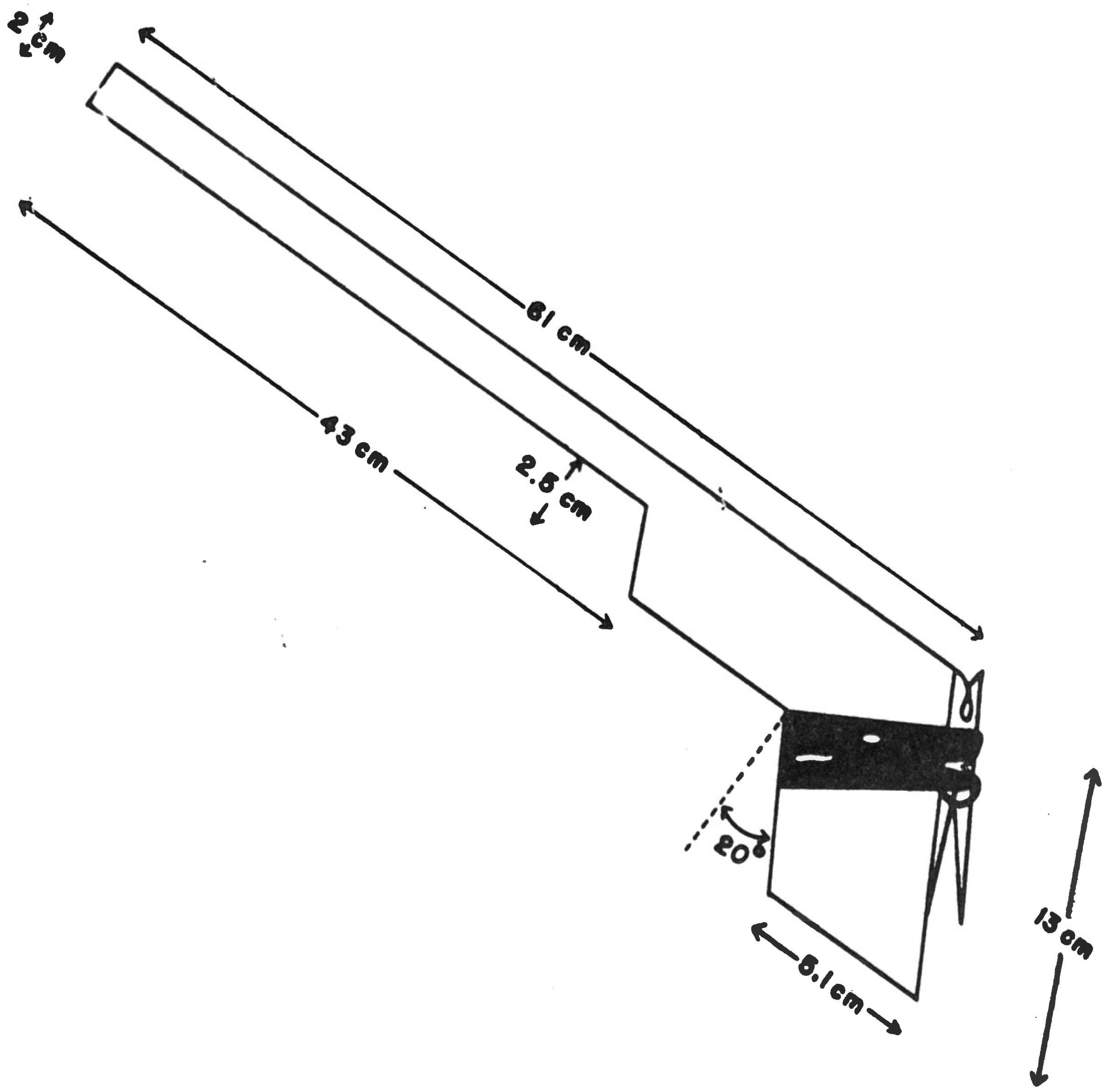
Engelhardt (1917) used a beanshooter to capture lizards. A stout forked handle, two 13 cm by 1.5 cm rubber bands plus a shallow, soft leather pocket are tied together with a shoestring. Pebbles or number four or eight shot are used in this beanshooter. Lizards can be stunned from a distance of 3 to 5 m. The flipper is loaded according to the lizard's size: 30 to 40 number eight shot or 20 to 30 number four shot. Aimed at the lizard's head, the ammunition may cause a slight flow of blood or a rare mutilation. Often, the lizard revives before it can be captured. A shotgun or small bore pistol may be more reliable but causes greater mutilation.

Brown (1946) manually discharged rubber band chains to stun or kill lizards. The result depends on the tension used. Three 1 cm wide bands are cut from a bicycle inner tube and knotted together in a chain. One end of this chain is looped over the vertically-held index finger of the collector's extended right hand. Tension is obtained by drawing the other end of the chain with the left hand toward the body at eye level. This missile, aimed at the lizard's head, should be released perpendicularly to the surface on which the target lizard rests. Lizards are not exceptionally alarmed if a rubber band strikes close to them, so two attempts are possible. A disadvantage of this method is the considerable strain on both hands. Of the specimans shot at, an expert can secure about 90%.

Dundee (1950) reported another version of the rubber band method. A 61 cm wooden gun can be kept loaded with automobile inner tube bands, ready for immediate use (Figure 2). A heavy inner tube binds a tacked-on clothespin to the gun handle to provide trigger tension. To load the gun, the clothespin jaws are opened. One end of the 2 cm wide rubber band is placed between the jaws. The rubber band, knotted in the middle, is held in place by the closed jaws. With the gun handle between the collector's knees, the free end of the rubber band can be stretched out over the gun muzzle. A squeeze of the clothespin releases the missle. For best results, it should be shot perpendicularly toward the surface on which the lizard rests. The use of 600 x 16 tube bands stuns <u>Crotaphytus</u> at distances up to 3 m. More elastic rubber bands of less width have less striking power. These are perfect for smaller organisms.

Tinkle and Lawrence (1956) reported the use of blowguns in lizard collecting. These blowguns are constructed from 1.2-1.8 m of Reynolds aluminum tubing. The bore is 1.5 cm and the outside diameter, 2 cm. Used with darts, these blowguns allow 50% survival of potential lizard specimans. The dart base is a cork, shaved for a

Figure 2. Rubber band gun from Dundee, 1950.


2 cm
61 cm
43 cm
2.5 cm
20°
5.1 cm
13 cm

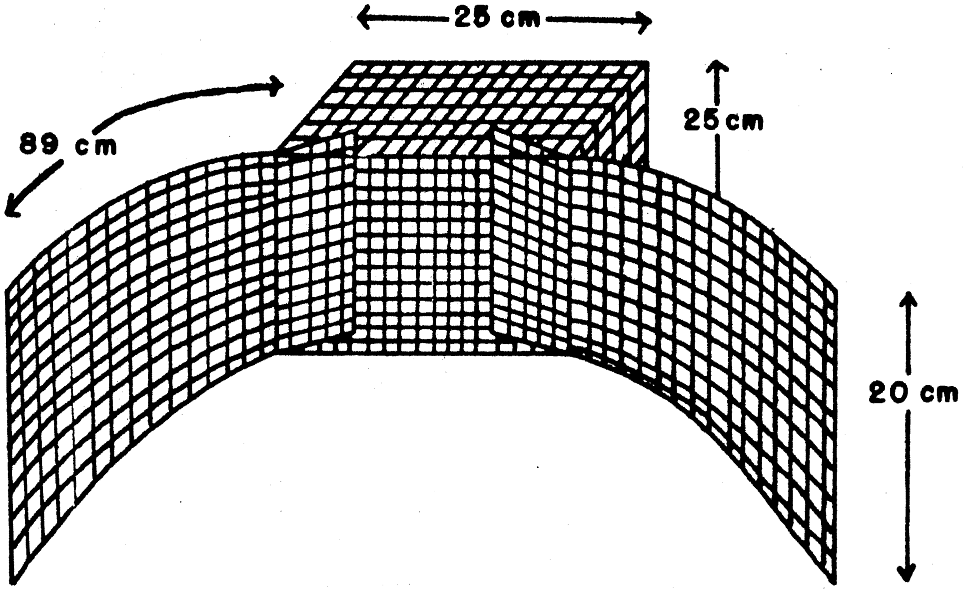
snug fit inside the tube. Long carpet needles or stainless steel wires are fitted into the shaved corks. Inserted in the oral end of the tube, the darts are expelled with a puff of air. Dart trajectory causes considerable inaccuracy at distances greater than 4 m. With experience, 80 to 90% accuracy may be achieved. Large samples for reproductive information or statistical studies are easily gained. Blowguns are more powerful, accurate, and quicker in shooting than rubber band guns. They are just as effective as the shot pistol commonly used for lizard collections but are cheaper to obtain and operate. Another advantage is that most property owners prohibiting firearms do not object to blowguns.

Lizards often seek shelter under suitable rocks. In this situation, the most frequently used technique is to grab the lizard by hand. This method may be used in other situations when more "sophisticated" techniques fail.

One trapping method involves a winged box constructed from hardware cloth of 0.3 cm mesh (Figure 3). This trap is set beside a rock or vegetation where a lizard took refuge. On the other side of this refuge, the collector tries to shoo the lizard into the box section of the trap. This technique has been used successfully with _U. stansburiana_ (Fox, 1973).

Pitfall traps involve burying jars or tin cans in the ground. Entomologists use this method to collect surface-crawling insects; herpetologists have expanded it for use with small reptiles (Banta, 1957). Containers are buried so that their mouths are flush with the ground surface. Boards or rocks camouflage the container, inviting small animals to seek shelter there. Banta (1957) found five quart

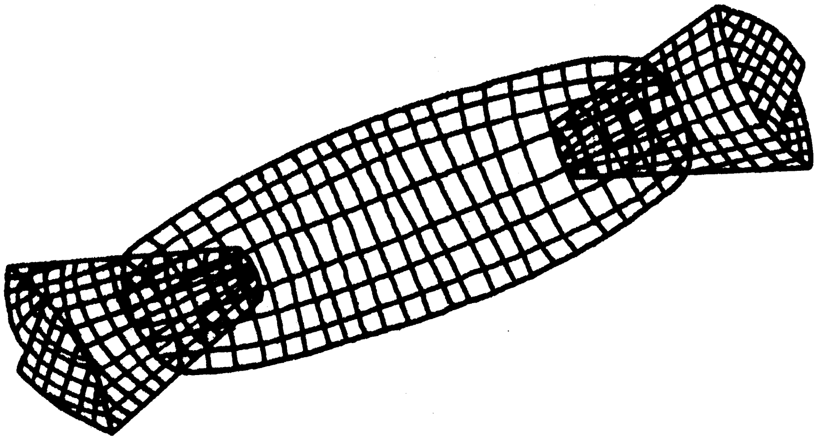
Figure 3. Winged box trap from Fox, 1973.


25 cm
89 cm
25 cm
20 cm

tin cans most successful; one and five gallon metal containers had insufficient depth to prevent escape of larger organisms. Metal containers camouflaged by rocks sometimes become too hot for reptiles. Disassembled corrugated cardboard boxes with better insulative properties solved this dilemma. Pitfall trapping has two major disadvantages: plenty of space is needed for the equipment (cans or jars) and backbreaking work is required to dig the holes.

Fitch (1951) reported that funnel traps were employed in "pest control" of bullsnakes and prairie rattlers. Hardware cloth (0.3-0.6 cm mesh) is rolled into a cylinder (Figure 4). The edges are turned back and pounded together to hold the shape. Approximately 1 cm at each end of the cylinder is then turned perpendicularly inward. These skirtings hold two entrance funnels in place; shingle nails reinforce contacts between the funnels and cylinder. Valve-type doors of transparent cellulose acetate pivot on a perforated upper edge threaded with fine wire. Traps are placed so that natural objects (logs, walls, rock outcrops) serve to guide reptiles into the funnel mouth. Different sized traps can be made for large or small organisms.

Figure 4. Side view of wire funnel trap from Fitch, 1951.



CHAPTER III

DESCRIPTION OF STUDY AREAS

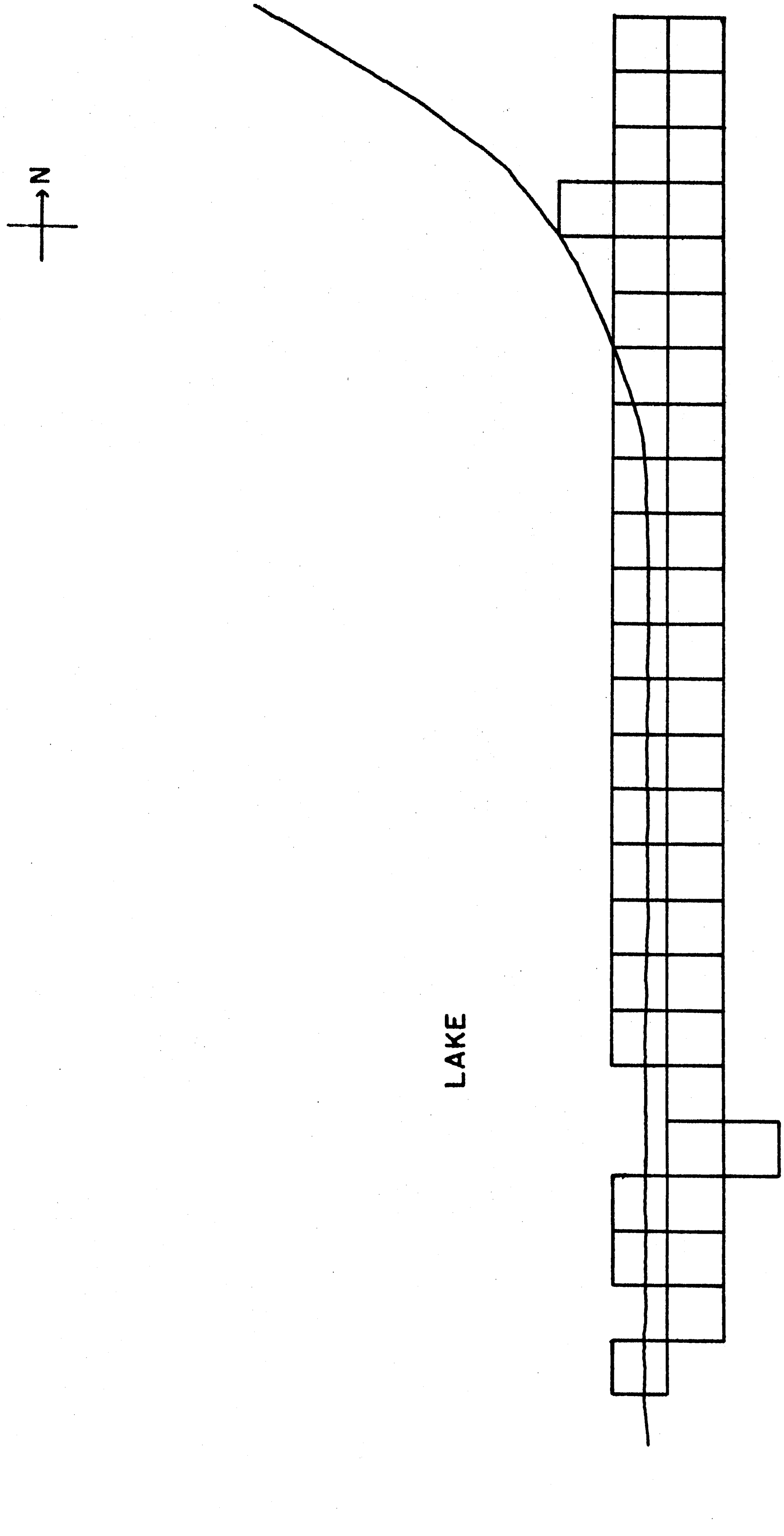
Collared lizards mostly restrict themselves to rocky, hilly environments. Two such habitats, near Stillwater, in Payne County, Oklahoma, were designated as study sites. The elevation of this area is 270 meters. A preliminary study was conducted during the summer of 1978. Most data were collected from April through November of 1979. Annual rainfall for 1979 was 830 millimeters. The summer of 1979 was slightly cooler than usual for the Stillwater area. There were fewer days when the temperature surpassed 37.78°C. Table 5 shows the maximum, minimum, and overall mean temperatures for each month in 1979.

The larger study site is the northwestern slope of the Lake Carl Blackwell (LCB) dam, 11 km west of Stillwater (Figure 5). Approximately 10,800 m^2 in area, this site is extremely rocky. Common herbaceous plants include Bermuda grass (*Cynodon dactylon*), Johnson grass (*Sorghum halapense*), American germander (*Teucrium canadense*), Carolina horse nettle (*Solanum carolinense*), Virginia wild rye (*Elymus virginicus*), wax goldenweed (*Haplopappus ciliatus*), and Louisiana sagewort (*Artemisia ludoviciana*). The common shrubs are grape (*Vitis* spp.), smooth sumac (*Rhus glabra*), buckbrush (*Symphoricarpos orbiculatus*), and buttonbush (*Cephalanthus occidentalis*). Common trees of the area are cottonwood (*Populus deltoides*), black willow (*Salix nigra*), western hackberry (*Celtis reticulata*), and rough-leaved hackberry (*C. occidentalis*).

Table 5. Mean 1979 temperatures (^{o}C) for the vicinity of Stillwater, Oklahoma from Oklahoma State University Department of Agronomy Weather Station.

Month	Mean maximum	Mean minimum	Mean overall
January	-0.3	-10.4	-5.3
February	4.7	-8.3	-1.8
March	16.3	3.6	9.9
April	20.7	8.1	14.4
May	24.7	12.7	18.7
June	30.6	18.5	24.6
July	32.9	21.7	27.3
August	32.9	20.1	26.5
September	29.6	14.2	21.9
October	26.1	8.9	17.5
November	14.2	1.1	7.6
December	12.1	-1.7	5.2

Figure 5. Lake Carl Blackwell study site.


N
LAKE

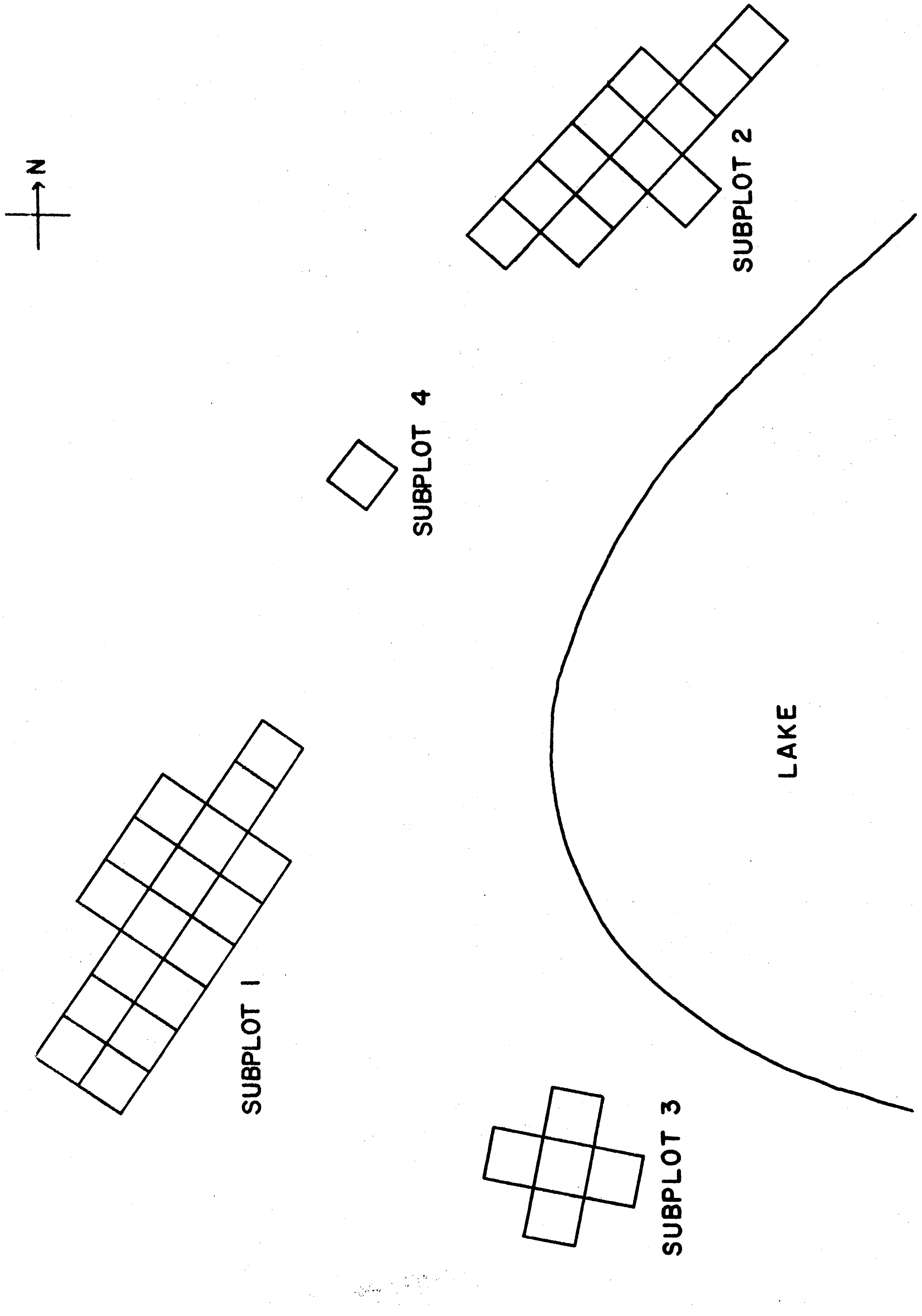
The smaller study site is located near Sanborn Lake (SL) on the northwest edge of Stillwater. Approximately 7875 m^2 in area, this site is composed of four subplots (Figure 6). Although not as rocky as the LCB site, this region also provides numerous hiding places for collared lizards.

The primary subplot, located southwest of the lake is approximately 3825 m^2 in area. A large flat area of white sandy soil dominates this subplot. Gulches of eroded red clay descend steeply to a stream bed boundary. Common plants of this area include white sweet clover (*Melilotus alba*), scurf pea (*Psoralea tenuiflora*), bastard indigo (*Amorpha fruticosa*), tickseed (*Desmodium sessilifolium*), annual sunflower (*Helianthus annuus*), soft sunflower (*H. mollis*), ragweed (*Ambrosia psilostachya*), fleabane (*Erigeron tenuis*), switchgrass (*Panicum virgatum*), white dalea (*Dalea candida*), goldenrod (*Solidago* spp.), smooth sumac, and *Gaillardia pulchella*. Common trees are cottonwood, American elm (*Ulmus americana*), and salt cedar (*Tamarix gallica*).

The second subplot, approximately 2700 m^2 in area, extends along the stream bed northwest of the lake. Common to this subplot are white sweet clover, goldenrod, bastard indigo, prairie acacia (*Acacia angustissima*), woolly dalea (*Dalea lanata*), bush clover (*Lespedeza stuevei*), cattails (*Typha latifolia*), and *Sporobolus asper*. Trees common to this section include cottonwood, red elm (*U. rubra*), American elm, and black willow.

The third subplot, an area of approximately 1125 m^2, is located south of the lake. This region includes a flat bare patch of clay and a slight incline up to an aggregation of rocks. A scattering of

Figure 6. Sanborn Lake study site.


N
SUBPLOT 2
SUBPLOT 4
SUBPLOT 1
LAKE
SUBPLOT 3

rocks is also found among such common plants as Bermuda grass, Johnson grass, white sweet clover, bastard indigo, partridge pea (*Cassia fasciculata*), Japanese rose (*Rosa multiflora*), Japanese brome (*Bromus japonicus*), Louisiana sagewort, and bush clover. The common shrub is smooth sumac and the common tree, black willow.

The fourth and smallest subplot lies between the two major subplots. This large accumulation of rocks is across the stream bed, west of the lake. On this hillside area of approximately 225 m^2, the few plants include cottonwood, post oak (*Quercus stellata*), tree of heaven (*Ailanthus altissimus*), dogwood (*Cornus drummondii*), snow-on-the-mountain (*Euphorbia marginata*), and goldenrod.

CHAPTER IV

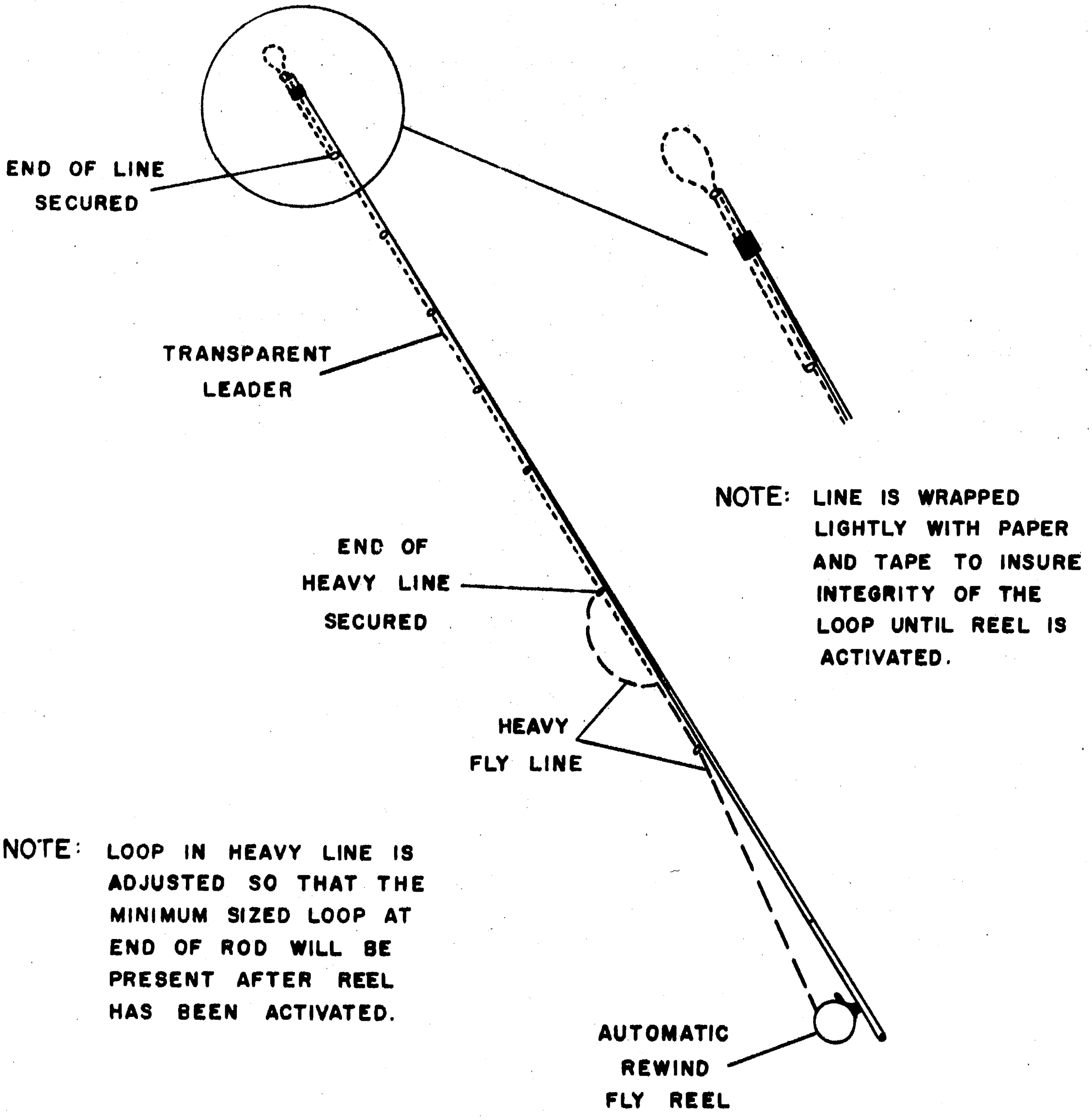
MATERIALS AND METHODS

The usual method of collared lizard capture in this study was by noose. As seasonal temperatures increased, the lizards seemed to grow more wary through quickened reflexes. Therefore, a more elite version of the noose, composed of a fly rod and reel, was devised (Figure 7). With a touch of the reel's small button, the loop was quickly drawn taut about a lizard's neck. Hand captures (especially when overturning rocks) were also used in this study.

Lizards caught for the first time were marked by toeclips. Each toe is numbered (Figure 8), so a unique combination of two clipped toes per lizard (one toeclip per foot) created a permanent identification system. To avoid regeneration but to minimize possible handicap, toes were clipped slightly basal to the first knuckle. Toes 15 and 20, in slight opposition to the other digits on their respective feet, were not clipped.

A different color combination of four paint spots per lizard provided a secondary method of identification. Airplane enamel was squirted onto the dorsal surface of each lizard with disposable syringes. Easy, accurate identification was then possible through binoculars. It was necessary to restore these color codes periodically due to epidermal molts. Even so, these tactics decreased the number of disturbances to the lizards. Excessive captures were avoided to

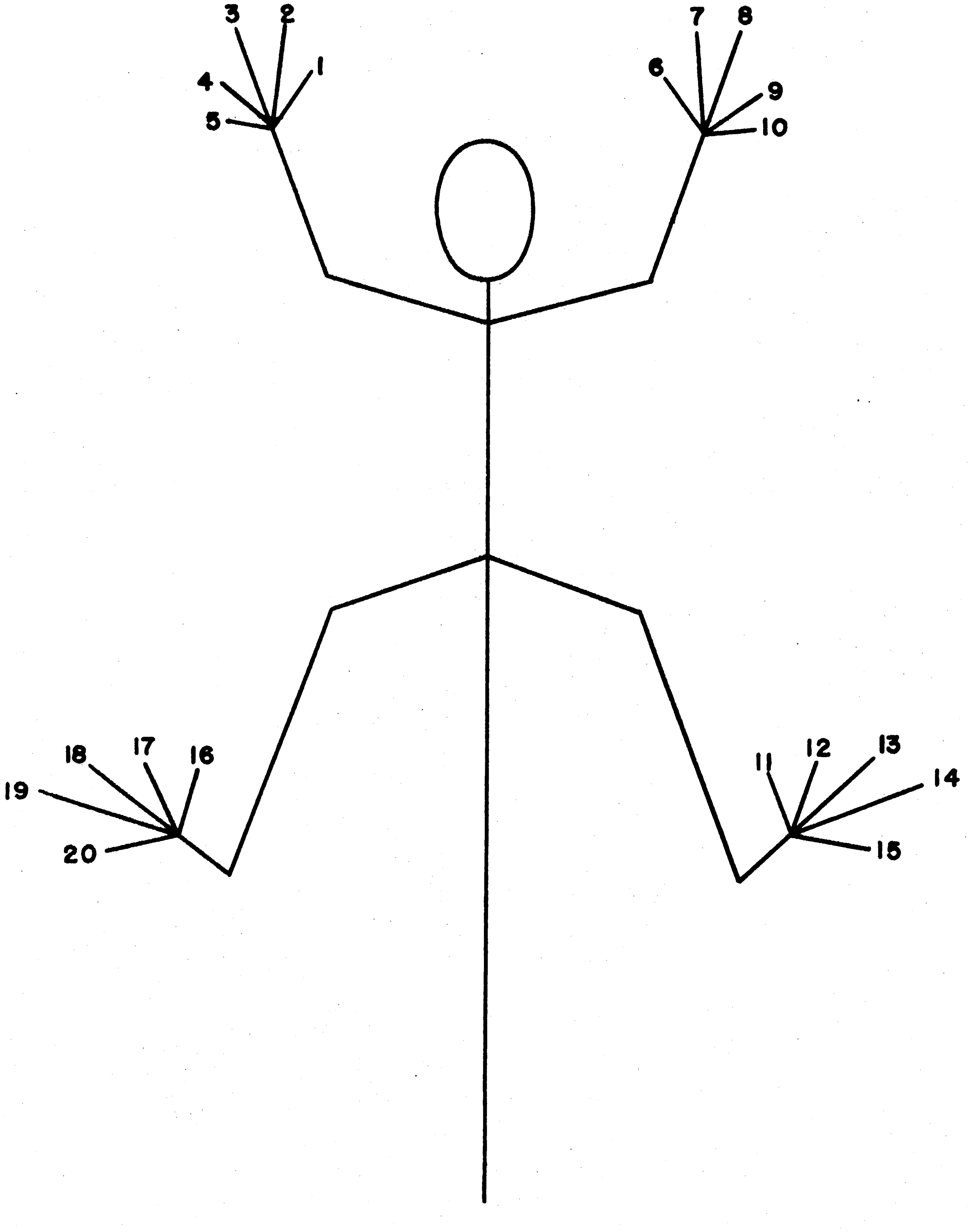
Figure 7. Elite version of lizard noose.



NOTE: LINE IS WRAPPED LIGHTLY WITH PAPER AND TAPE TO INSURE INTEGRITY OF THE LOOP UNTIL REEL IS ACTIVATED.

NOTE: LOOP IN HEAVY LINE IS ADJUSTED SO THAT THE MINIMUM SIZED LOOP AT END OF ROD WILL BE PRESENT AFTER REEL HAS BEEN ACTIVATED.

Figure 8. Numbering system used for toe-clipping lizards (dorsal view).


3
2
1
4
5
7
8
6
9
10
18
17
16
19
20
11
12
13
14
15

reduce the chance of behavioral alteration in the lizards.

At each study site, a grid was constructed to obtain location data. Each grid cell was 15 m square; corners were designated by numbered stakes. At LCB, there were 48 such cells; at SL, 35. An effort was made to census the sites randomly throughout the field season in terms of direction and time of day. Lizard locations were determined by triangulation from two adjacent stakes. In the case of captures, location was recorded as the spot where the lizard was first seen, not where it was eventually caught. Specific data were collected at each observation: date, time of day, location, structural association[1], posture[2], and (if captured) molt condition, and measurements of size (total length or TL, snout-vent length or SVL, and mouth gape or MG). Sex determination of each lizard was attempted at first capture and subsequently reaffirmed as sexual dimorphism became more distinctive with age.

Although most weather parameters were collected by the Oklahoma State University Department of Agronomy weather station (on the west edge of Stillwater), sky conditions were recorded at each study site. Classifications were: (1) clear--no clouds in the region of the sun, (2) partly cloudy, (3) cloudy--sun's position observable through clouds, (4) overcast--sun's position undiscernable, and (5) rain.

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[1] Three structural associations were defined for this study: (1) under a rock, (2) in the shade, or (3) in direct sunlight.

[2] Posture was defined as: (1) curled-under a rock with tail curved alongside body, (2) adpressed basking-length of body pressed flat against substrate, (3) lookout-seated on haunches with front legs extended, or (4) stilting - of the arched body, only toes are in contact with the substrate.

After the field data were transferred onto computer cards, analyses proceeded via the Statistical Analysis System, otherwise known as SAS (Helwig and Council, 1979). Although normal distributions were not characteristic of the data, no non-parametric tests analogous to the two-way analysis of variance exist. So, even though some assumptions may be violated, two-way Model I analysis of variance was used to separate the observed variation within each variable between the factors age (juvenile or adult) and study site, or adult sex and study site.

After triangular measurements were converted to cartesian coordinates, home range areas were calculated by the convex hull or polygon method (Hatfield, 1978). The relative dependence of home range area on the number of sightings and its log transform was checked using regression analyses. Differences in regression slopes for selected groups were tested using covariance analyses.

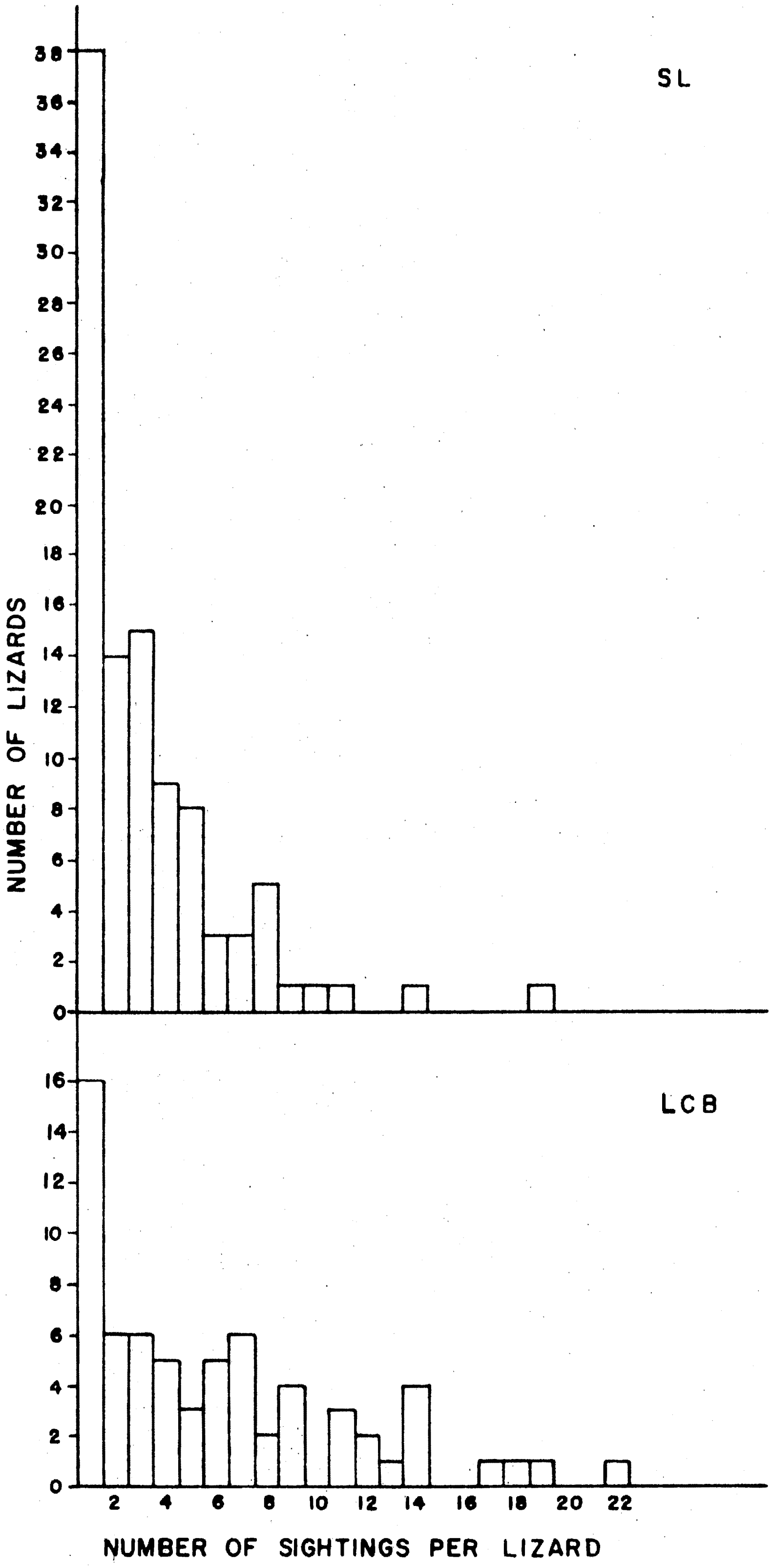
CHAPTER V

RESULTS

Fifty Lake Carl Blackwell (LCB) censuses and 62 Sanborn Lake (SL) censuses were conducted. Census frequency, as indicated by the number of days between censuses at each plot, was not significantly different (Mann-Whitney U-test: $t = 0.97$, $p>0.05$). The time span recorded for each census began with the first lizard sighted and ended with the last one sighted. No record of time spent in the field before or after these two points was kept. The amount of time needed to complete each census at LCB, the larger study site, was not significantly different (Mann-Whitney U-test: $t = 1.24$, $p>0.05$) from that needed at SL. Although this indicates similar efforts at both sites, the time of day for censuses conducted at LCB was significantly different from that of SL censuses (Mann-Whitney U-test: $t = 2.37$, $p<0.05$); midpoints of LCB censuses (median = 14.1 h, $n = 41$) were later than those at SL (median = 12.6 h, $n = 42$).

At the close of the 1979 field season, 167 collared lizards had been captured and marked. Sixty-seven lizards were caught at LCB: 12 adult males, 13 adult females, and 42 juveniles. Sixteen (23.9%) of these lizards were seen only once (Figure 9). At SL, 100 lizards were caught: 11 adult males, 15 adult females, 1 adult of undetermined sex, and 73 juveniles. Thirty-eight percent of these lizards were seen only once (Figure 9). A G-test shows these site distributions to be

Figure 9. The number of sightings per lizard vs. the number of lizards at SL (upper graph) and at LCB (lower graph).


SL
LCB
NUMBER OF LIZARDS
NUMBER OF SIGHTINGS PER LIZARD
0
2
4
6
8
10
12
14
16
18
20
22
24
26
28
30
32
34
36
38
0
2
4
6
8
10
12
14
16
2
4
6
8
10
12
14
16
18
20
22

significantly heterogeneous ($G_H = 19.38$, df = 6, $p<0.01$). Although not tested statistically, such graphs for separate age classes showed similar site distributions.

The mean number of days between observations (MDBO) for a lizard inversely reflects how frequently it was seen. The MDBO for a LCB lizard was typically less than that for a SL lizard; LCB lizards (adults and juveniles) were, therefore, observed significantly more often than SL lizards (Table 6). Adults were observed less often than the juveniles (Table 6). Of the adult sexes, males were observed less frequently than the females (Table 7). MDBO for adult females and juveniles were not significantly different (Mann-Whitney U-test: $t = 0.82$, $p>0.05$), whereas adult male MDBO (median = 9.5, n = 15) was significantly larger (Mann-Whitney U-test: $t = 3.11$, $p<0.01$) than that of juveniles (median = 4.67, n = 57). Adult males were, thus, observed less frequently than either adult females or juveniles, with more time between observations.

The number of potential sightings for each lizard was designated as the number of site censuses between the first and last records of the lizard. The actual number of sightings per lizard was then divided by its potential number of sightings. No significant differences in actual/potential sightings were found for adults, either between the sexes or between study sites (Table 7). Juvenile actual/potential sightings were, however, significantly larger than those of adults (Table 6). Actual sightings per juvenile lizard were fewer than for adults, but juveniles were seen over a shorter time span, so the mean number of potential sightings was also smaller than for adults.

Table 6. Two-way Model I analysis of variance tables for the variables MDBO and actual/potential sightings. The two factors are age (juvenile or adult) and study site.

Variable	Source	DF	Mean square	F
MDBO	Age	1	451.708	15.25***
	Study site	1	164.748	5.56*
	Interaction	1	1.960	0.07
	Within cells	89	29.616	
Actual/potential sightings	Age	1	0.592	6.23*
	Study site	1	0.112	1.18
	Interaction	1	0.0001	0.00
	Within cells	163	0.095	

*$p<0.05$
**$p<0.01$
***$p<0.001$

Table 7. Two-way Model I analysis of variance tables for the variables MDBO and actual/potential sightings. The two factors are adult sexes and study site.

Variable	Source	DF	Mean square	F
MDBO	Sex	1	447.885	7.98**
	Study site	1	58.513	1.04
	Interaction	1	10.762	0.19
	Within cells	32	56.102	
Actual/potential sightings	Sex	1	0.031	0.32
	Study site	1	0.094	0.99
	Interaction	1	0.295	3.11
	Within cells	47	0.095	

*p<0.05
**p<0.01
***p<0.001

Capture Statistics

For the 167 lizards marked, the total number of records was 736. Of these sightings or observations, 287 (39%) included capture of the lizard; 449 (61%) were simple observations. At LCB, records totaled 407: 133 (33%) captures and 274 (67%) simple sightings. SL lizards were recorded 329 times: 154 (47%) captures and 175 (53%) observations.

Collared lizards can be difficult to capture because of their speed. During the last part of the field season, a record was kept of all lizards seen but missed. Some of these were marked but disappeared so quickly, color codes could not be deciphered. The number of missed lizards per total seen and caught in one day was not significantly different between plots (Mann-Whitney U-test: $t = 1.18$, $p>0.05$).

Habitat

Habitat characteristics are reflected by the structural associations and postures of collared lizards. Open areas receiving plenty of sunshine or vegetation-crowded areas are denoted by these two parameters; the sizes and distribution of rocks, indications of the feasibility of rock-turning, are also suggested. Structural association was ranked along an exposure continuum from (1) under a rock, to (2) shaded, or (3) sunny positions. All sightings were used in the analyses without averaging per individual. Controlling for age differences, LCB lizards were observed in sunnier positions than SL lizards (Table 8). As study site variations were controlled, adults were associated with sunnier places than juveniles (Table 8). The significant interaction between age and study site shows that the age

Table 8. Two-way Model I analysis of variance tables for the variables structural association, posture, and hibernation date. The two factors are age (juvenile or adult) and study site.

Variable	Source	DF	Mean square	F
Structural association	Age	1	52.330	225.83***
	Study site	1	165.277	713.24***
	Interaction	1	58.124	250.83***
	Within cells	676	0.232	
Posture	Age	1	4.221	8.70**
	Study site	1	112.891	232.71***
	Interaction	1	10.727	22.11***
	Within cells	498	0.485	
Hibernation date	Age	1	93324.046	379.89***
	Study site	1	1.920	0.01
	Interaction	1	1222.458	4.98*
	Within cells	107	245.658	

*$p<0.05$
**$p<0.01$
***$p<0.001$

classes at LCB and SL were found in different structural associations (Table 8). SL lizards were observed in sunnier positions as they grew older but LCB lizards were seen in even sunnier associations than SL adults. No significant difference was seen between adult sexes (Table 9). LCB adults (both sexes) were sighted in sunnier associations than SL adults (Table 9).

Posture was ranked along an exposure continuum as (1) curled, (2) adpressed basking, (3) lookout, or (4) stilting. All sightings were again used for analyses without averaging per individual. Controlling for study site variations, adults utilized the more exposed postures (lookout and stilting) with a greater frequency than juveniles (Table 8). As age differences were controlled, LCB lizards used significantly more exposed, alert postures than SL lizards (Table 8). The significant interaction between age and study site reveals that the age classes at SL and LCB utilized different postures (Table 8). Differences between the age classes were greater at SL where lizards were more often observed in the adpressed basking posture as they grew older; the curled posture was typical of SL juveniles. LCB adults and juveniles were characterized by the lookout posture. LCB adults were sighted in significantly more exposed, alert postures than SL adults (Table 9). No significant difference was shown between the adult sexes (Table 9).

Seasonal Activity

The last observation date of each lizard could represent death, emigration, or the approximate date hibernation began. Except for known deaths, the last observation dates were analyzed as beginning

Table 9. Two-way Model I analysis of variance tables for the variables structural association, posture, and hibernation date. The two factors are adult sexes and study site.

Variable	Source	DF	Mean square	F
Structural association	Sex	1	0.199	1.04
	Study site	1	10.508	54.87***
	Interaction	1	0.007	0.04
	Within cells	286	0.192	
Posture	Sex	1	0.220	0.42
	Study site	1	16.695	31.70***
	Interaction	1	0.536	1.02
	Within cells	140	0.527	
Hibernation date	Sex	1	124.621	0.74
	Study site	1	276.318	1.63
	Interaction	1	1836.453	10.84**
	Within cells	35	169.486	

*$p<0.05$
**$p<0.01$
***$p<0.001$

hibernation dates. Adult hibernation typically began between 28 July and 11 August. The majority of juveniles presumably entered hibernacula between 22 September and 6 October. Controlling for site variations, this difference between the age classes is significant (Table 8). No significant difference is shown between study sites (Table 8). The significant interaction between age and study site reveals that the age classes at LCB and SL differed in respect to beginning hibernation dates (Table 8). LCB adults began hibernation later than SL adults. In contrast, LCB juveniles entered hibernacula earlier than those at SL. The interaction between adult sexes and study sites was also significant although neither main effect was (Table 9). LCB and SL adult lizards showed different trends in beginning hibernation dates depending upon their sex. Hibernation dates of adult males were more similar between plots than those of females; LCB females entered hibernacula later than females at SL.

Recorded activity for collared lizards of this study first occurred in April. Hatchlings (SVL < 50 mm) were first discovered at LCB on 2 August and at SL, on 27 August but no significant difference was found for dates of hatchling appearance between the two sites (Mann-Whitney U-test: $t = 0.14$, $p>0.05$). The bulk of hatchlings appeared between 25 August and 8 September at both sites.

Weather Parameters

Activity of collared lizards is related to weather conditions. In this study, conditions for activity in terms of temperature, relative humidity, precipitation, wind speed, sky conditions, and solar radiation were analyzed. As for the parameters structural association and posture, data were not averaged per lizard so individual lizards may be represented in these analyses more than once. Lizards with large numbers of sightings may bias results, but reducing the data to an individual basis would devaluate statistical analyses by the smaller sample sizes of site, age, and sex categories. Probably, few lizards were seen so frequently (Figure 9) as to greatly bias results.

Temperature

For each lizard observation, maximum and minimum temperatures for the specific date were recorded for analyses. The temperature for the specific time of observation (hourly temperature) was also recorded and analyzed.

Maximum daily temperatures were significantly higher for adult sightings in comparison to juvenile sightings as study site variations were controlled (Table 10). The increase in temperature with age was complicated by a significant interaction with the different study sites (Table 10). SL juveniles were sighted more often during days with higher maximum temperatures than LCB juveniles. Adult sightings showed the opposite trend between plots. At each site, adult females were sighted more frequently at higher maximum daily temperatures than were adult males (Table 11).

Minimum daily temperatures of adult sightings were significantly higher than those of juveniles (Table 10). No significant differences were found between study sites or between adult sexes (Tables 10 and 11).

Hourly temperatures of lizard sightings at LCB were significantly higher than those at SL for both adult sexes (Table 11) and for adults and juveniles (Table 10). Adult sightings occurred at significantly

Table 10. Two-way Model I analysis of variance tables for three temperature variables. The two factors are age (juvenile or adult) and study site.

Variable	Source	DF	Mean square	F
Maximum temperature	Age	1	6034.600	168.73***
	Study site	1	3.270	0.09
	Interaction	1	219.740	6.14*
	Within cells	714	35.765	
Minimum temperature	Age	1	31078.534	481.91***
	Study site	1	97.175	1.51
	Interaction	1	49.759	0.77
	Within cells	714	64.490	
Hourly temperature	Age	1	5976.666	166.91***
	Study site	1	2655.592	74.16***
	Interaction	1	3.049	0.09
	Within cells	583	35.808	

*$p<0.05$
**$p<0.01$
***$p<0.001$

Table 11. Two-way Model I analysis of variance tables for three temperature variables. The two factors are adult sexes and study site.

Variable	Source	DF	Mean square	F
Maximum temperature	Sex	1	169.046	5.45*
	Study site	1	58.693	1.89
	Interaction	1	16.680	0.54
	Within cells	313	30.995	
Minimum temperature	Sex	1	75.431	2.43
	Study site	1	19.767	0.64
	Interaction	1	4.213	0.14
	Within cells	313	31.003	
Hourly temperature	Sex	1	38.910	1.57
	Study site	1	838.322	33.82***
	Interaction	1	26.932	1.09
	Within cells	194	24.790	

*$p<0.05$
**$p<0.01$
***$p<0.001$

hotter hourly temperatures than juvenile sightings (Table 10).

Relative Humidity

Lizard observations at SL occurred under consistantly more humid conditions than at LCB (Tables 12 and 13). Adults were active under more humid conditions than juveniles (Table 12). No significant difference in relative humidity was shown for the sightings of adult males and females (Table 13).

Precipitation

Field work was seldom conducted in the rain. It is not surprising, therefore, that no significant differences were found in either of the precipitation analyses (Tables 12 and 13).

Wind Conditions

Two wind speed parameters were recorded for each lizard observation: average wind speed for the specific date and actual wind speed at the specific time of observation. No significant differences appeared between study sites, age groups, or adult sexes (Tables 14 and 15).

Sky Conditions

Sky conditions were ranked along a continuum as (1) clear, (2) partly cloudy, (3) cloudy, (4) overcast, or (5) rainy. When site variations were controlled, juveniles were sighted under significantly clearer skies than adults (Table 16). Controlling for age, SL lizards were observed under cloudier skies than LCB lizards (Table 16). Dif-

Table 12. Two-way Model I analysis of variance tables for the variables relative humidity and precipitation. The two factors are age (juvenile or adult) and study site.

Variable	Source	DF	Mean square	F
Relative humidity	Age	1	24339.077	121.43***
	Study site	1	29484.784	147.10***
	Interaction	1	109.880	0.55
	Within cells	583	200.434	
Precipitation	Age	1	10006.188	2.12
	Study site	1	1563.783	0.33
	Interaction	1	3214.080	0.68
	Within cells	25	4731.058	

*p<0.05
**p<0.01
***p<0.001

Table 13. Two-way Model I analysis of variance tables for the variables relative humidity and precipitation. The two factors are adult sexes and study site.

Variable	Source	DF	Mean square	F
Relative humidity	Sex	1	196.880	1.19
	Study site	1	7871.356	47.40***
	Interaction	1	202.128	1.22
	Within cells	194	166.076	
Precipitation	Sex	1	426.894	0.07
	Study site	1	8064.389	1.25
	Interaction	1	592.012	0.09
	Within cells	18	6447.150	

*$p<0.05$
**$p<0.01$
***$p<0.001$

Table 14. Two-way Model I analysis of variance tables for two wind speed variables. The two factors are age (juvenile or adult) and study site.

Variable	Source	DF	Mean square	F
Average wind speed	Age	1	136.405	0.31
	Study site	1	55.920	0.13
	Interaction	1	0.269	0.00
	Within cells	666	445.085	
Actual wind speed	Age	1	6283.471	2.67
	Study site	1	72.642	0.03
	Interaction	1	8842.298	3.76
	Within cells	580	2350.361	

Table 15. Two-way Model I analysis of variance tables for two wind speed variables. The two factors are adult sexes and study site.

Variable	Source	DF	Mean square	F
Average wind speed	Sex	1	0.095	0.00
	Study site	1	16.489	0.09
	Interaction	1	184.238	1.01
	Within cells	267	183.300	
Actual wind speed	Sex	1	191.469	0.17
	Study site	1	3517.488	3.13
	Interaction	1	2945.961	2.63
	Within cells	191	1122.077	

Table 16. Two-way Model I analysis of variance tables for the variables sky conditions and solar radiation. The two factors are age (juvenile or adult) and study site.

Variable	Source	DF	Mean square	F
Sky conditions	Age	1	30.687	40.58***
	Study site	1	16.803	22.22***
	Interaction	1	13.288	17.57***
	Within cells	659	0.756	
Solar radiation	Age	1	3177.767	0.63
	Study site	1	599528.987	118.47***
	Interaction	1	9501.165	1.88
	Within cells	583	5060.639	

*$p<0.05$
**$p<0.01$
***$p<0.001$

ferent age trends with respect to sky conditions are apparent in LCB and SL lizard sightings (Table 16). Clearer skies were associated with LCB juveniles in contrast to LCB adults. At SL, both juveniles and adults were associated with partly cloudy skies. Adult females were associated with significantly clearer skies than adult males, regardless of study site (Table 17).

Solar Radiation

Solar radiation was significantly higher at LCB in comparison to SL (Tables 16 and 17). No significant differences in solar radiation were found between age groups (Table 16) or between adult sexes (Table 17).

Reproduction

Higher productivity was associated with the SL site. For the 1979 season, the population consisted of 72% juveniles and 28% adults (12% males, 15% females, 1% individuals of undetermined sex). An average of five juveniles per female was produced at SL. In contrast, the LCB population consisted of 63% juveniles and 37% adults (18% males, 19% females) and average productivity was three juveniles per female. Thus, it seems that SL females laid larger and/or multiple clutches.

Size

Average size measurements per lizard were calculated for a month of relatively high density: July for adults and October for juveniles. Four size parameters were included in these analyses: total length (TL), snout-vent length (SVL), tail length (TAIL), and mouth gape (MG). Tail length was defined as the difference between total length and snout-vent

Table 17. Two-way Model I analysis of variance tables for the variables sky conditions and solar radiation. The two factors are adult sexes and study site.

Variable	Source	DF	Mean square	F
Sky conditions	Sex	1	3.826	4.00*
	Study site	1	0.031	0.03
	Interaction	1	1.095	1.14
	Within cells	263	0.957	
Solar radiation	Sex	1	1483.817	0.27
	Study site	1	141604.670	26.13***
	Interaction	1	12470.490	2.30
	Within cells	194	5419.644	

*p<0.05
**p<0.01
***p<0.001

length; this parameter was also analyzed as a percentage of total length (TAILTL). No significant differences were found between study sites for any of these parameters (Tables 18 and 19). Adult males were significantly larger than adult females in all parameters (Table 19). Adults were significantly larger than juveniles in all parameters but the proportion, TAILTL (Table 18).

Growth

For each lizard, mean growth rates of SVL and MG over a month were calculated. In the age-study site analyses of variance, adult growth rates in June were compared to those of juveniles in September since little temporal overlap exists between age groups. There were no significant differences associated with SVL (Tables 20 and 21). The June growth rate of adult MG was significantly less than juvenile MG growth rate in September (Table 20). The interaction between study sites and adult sexes was significant for the June MG growth rate although neither main effect was (Table 21). LCB females had a greater MG growth rate than the LCB males but SL females had a slower MG growth rate than the SL males.

Molt

If molting is not observed at successive captures of an individual lizard, it may be assumed that this process occurred between captures. An equal probability exists at each capture that molting has just been completed or is soon to begin. Thus, molting frequency may be inversely approximated by the average number of days between successive captures of an individual. No significant differences in molting frequency were

Table 18. Two-way Model I analysis of variance tables for the size variables SVL, TL, MG, TAIL, and TAILTL (adults in July, juveniles in October). The two factors are age and study site.

Variable	Source	DF	Mean square	F
SVL	Age	1	22592.237	323.82***
	Study site	1	81.910	1.17
	Interaction	1	18.697	0.27
	Within cells	75	69.769	
TL	Age	1	189339.255	230.08***
	Study site	1	218.363	0.27
	Interaction	1	451.733	0.55
	Within cells	75	822.941	
MG	Age	1	1313.855	160.28***
	Study site	1	22.396	2.73
	Interaction	1	2.194	0.27
	Within cells	74	8.197	
TAIL	Age	1	81124.805	168.46***
	Study site	1	32.795	0.07
	Interaction	1	286.625	0.60
	Within cells	75	481.576	
TAILTL	Age	1	10.511	1.50
	Study site	1	3.491	0.50
	Interaction	1	3.185	0.45
	Within cells	75	7.031	

*$p<0.05$
**$p<0.01$
***$p<0.001$

Table 19. Two-way Model I analysis of variance tables for the size variables SVL, TL, MG, TAIL, and TAILTL (in July). The two factors are adult sexes and study site.

Variable	Source	DF	Mean square	F
SVL	Sex	1	770.941	15.29***
	Study site	1	3.419	0.07
	Interaction	1	160.902	3.19
	Within cells	36	50.435	
TL	Sex	1	18857.902	37.00***
	Study site	1	475.620	0.93
	Interaction	1	277.022	0.54
	Within cells	36	509.657	
MG	Sex	1	150.502	17.03***
	Study site	1	5.151	0.58
	Interaction	1	28.700	3.25
	Within cells	36	8.837	
TAIL	Sex	1	12003.011	34.53***
	Study site	1	398.386	1.15
	Interaction	1	15.676	0.05
	Within cells	36	347.585	
TAILTL	Sex	1	77.147	7.50**
	Study site	1	8.316	0.81
	Interaction	1	11.293	1.10
	Within cells	36	10.287	

*$p<0.05$
**$p<0.01$
***$p<0.001$

Table 20. Two-way Model I analysis of variance tables for the growth variables SVL and MG (adults in June, juveniles in September). The two factors are age and study site.

Variable	Source	DF	Mean square	F
SVL	Age	1	0.351	2.47
	Study site	1	0.071	0.50
	Interaction	1	0.126	0.89
	Within cells	41	0.142	
MG	Age	1	0.022	5.16*
	Study site	1	0.002	0.57
	Interaction	1	0.001	0.25
	Within cells	41	0.004	

*p<0.05
**p<0.01
***p<0.001

Table 21. Two-way Model I analysis of variance tables for the growth variables SVL and MG (in June). The two factors are adult sexes and study site.

Variable	Source	DF	Mean square	F
SVL	Sex	1	1.175	3.50
	Study site	1	0.101	0.30
	Interaction	1	0.110	0.33
	Within cells	11	0.336	
MG	Sex	1	0.011	4.64
	Study site	1	0.004	1.56
	Interaction	1	0.012	5.06*
	Within cells	11	0.002	

*p<0.05
**p<0.01
***p<0.001

found between the study sites (Tables 22 and 23). Adults molted less frequently than juveniles (Table 22) and adult males molted less often than adult females (Table 23).

Density

Density analyses were based on the assumption that individual lizards were present on the sites between the times each was actually observed. At LCB, adult males were observed from 21 April through 11 August (Figure 10). Peak density occurred between 16 and 30 June. LCB females were seen from 5 May through 6 October. The peak female density occurred between 14 July and 11 August. From 28 July through 17 November, juveniles were observed at LCB. Maximum juvenile density occurred from 8 to 22 September.

SL males ranged the study site between 21 April and 8 September (Figure 10). Peak density occurred from 30 June through 14 July. Females at SL were present from 21 April through 11 August. Maximum female density occurred between 14 and 28 July. From 14 July through 17 November, juveniles were observed at SL. The peak in juvenile density was between 22 September and 6 October.

At each study site, adult male peak density preceded that of females (Figure 10). Peak juvenile density followed. In general, density differences over time for the separate age/sex groups were similar at both sites.

The LCB study site consists of 48 grid cells (each 15 m square). No sightings occurred in two cells. Thus, of 10,800 m^2, the total utilized area was 10,350 m^2. Of the 35 grid cells (each 15 m square) at SL, no sightings occurred in three cells. The total utilized area

Table 22. Two-way Model I analysis of variance tables for the variable molt. The two factors are age (juvenile or adult) and study site.

Variable	Source	DF	Mean square	F
Molt	Age	1	2890.176	11.70**
	Study site	1	725.723	2.94
	Interaction	1	177.895	0.72
	Within cells	70	247.118	

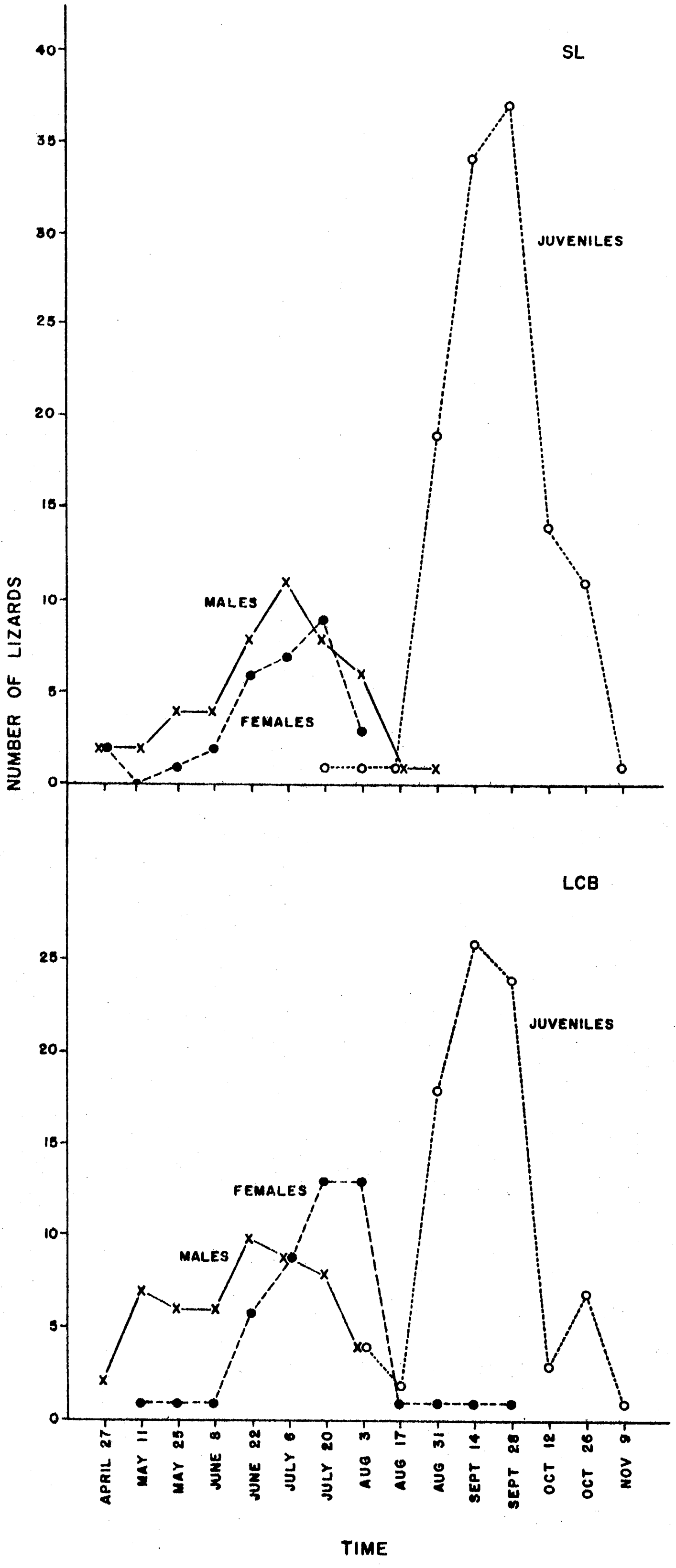
*p<0.05
**p<0.01
***p<0.001

Table 23. Two-way Model I analysis of variance tables for the variable molt. The two factors are adult sexes and study site.

Variable	Source	DF	Mean square	F
Molt	Sex	1	3925.861	9.83**
	Study site	1	447.409	1.12
	Interaction	1	295.869	0.74
	Within cells	30	399.507	

*p<0.05
**p<0.01
***p<0.001

Figure 10. Density through time for SL lizards (upper graph) and LCB lizards (lower graph). Each point represents the midpoint of a two-week interval.


SL
LCB
NUMBER OF LIZARDS
TIME
MALES
FEMALES
JUVENILES
0
5
10
15
20
25
30
35
40
APRIL 27
MAY 11
MAY 25
JUNE 8
JUNE 22
JULY 6
JULY 20
AUG 3
AUG 17
AUG 31
SEPT 14
SEPT 28
OCT 12
OCT 26
NOV 9

was, thus, only 7,200 m^2 of a possible 7,875 m^2. Using these reduced areas, cumulative densities (defined as the number of lizards caught during this study divided by the area) were calculated for adult males, adult females, and juveniles at each site. All group densities were higher at SL (Table 24).

Not all lizards were active at the same time so a time-related or temporal density was calculated. Areas under each density curve (Figure 10) are the products of the number of lizards and the different seasonal intervals of activity for individuals. Converted to the convenient units of lizard-days and divided by the site area produces this average measure of instantaneous density (Table 25). Juveniles and adult males had greater temporal densities at SL. Adult female temporal density was greater at LCB.

Spatial Distribution

The spatial distribution of lizard activity was not uniform across either habitat, as shown by the number of sightings per cell over the season (Figures 11 and 12). At both sites, the greatest number of sightings occurred in cells with the most and/or the largest rocks. At LCB, these largest and flattest rocks were located near the top of the dam; in the morning, the sun's warmth reached these rocks first. Many hiding places were also available among these rocks. At SL, more rocks, more sand, and the least amount of vegetation characterized the cells with the most sightings.

Table 24. Cumulative density (lizards/m^2) at each study site, corrected for area reductions due to cells with no lizard observations.

	LCB	SL
Adult males	0.0012	0.0015
Adult females	0.0013	0.0021
Juveniles	0.0041	0.0101
Total	0.0065	0.0139

Table 25. Temporal density (lizard-days/m^2) at each study site, corrected for area reductions due to cells with no lizard observations.

	LCB	SL
Adult males	0.067	0.091
Adult females	0.065	0.054
Juveniles	0.113	0.234

Figure 11. Hotspots of lizard activity at LCB.

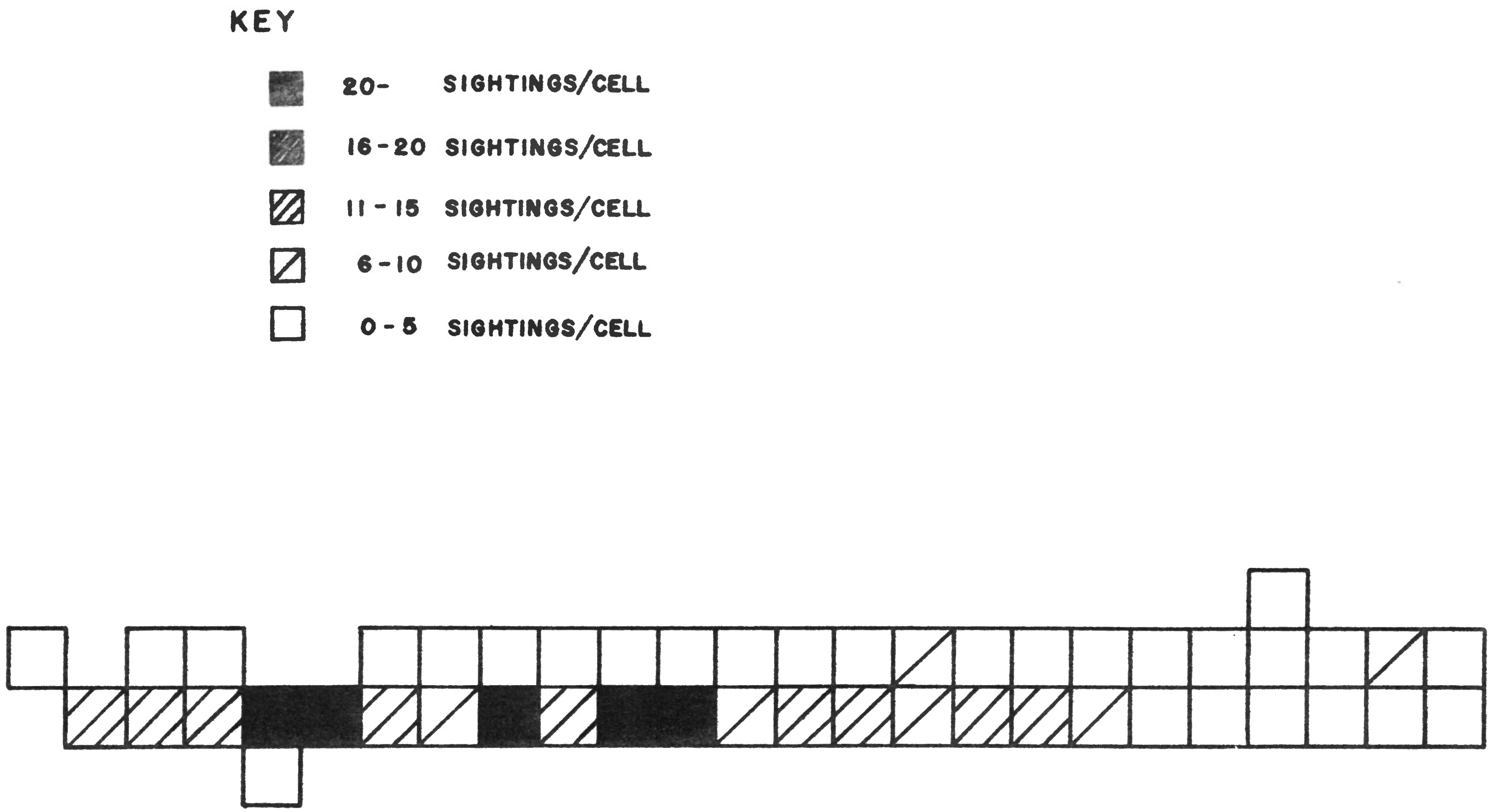
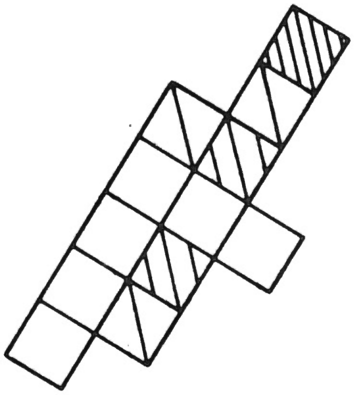
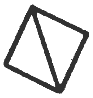
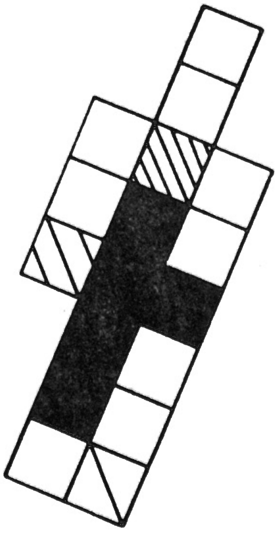
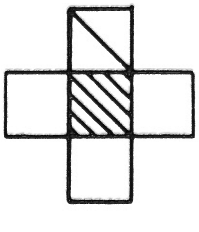

KEY
20- SIGHTINGS/CELL
16-20 SIGHTINGS/CELL
11-15 SIGHTINGS/CELL
6-10 SIGHTINGS/CELL
0-5 SIGHTINGS/CELL

Figure 12. Hotspots of lizard activity at SL. Refer to the key in the preceding figure.









Home Range Size

Convex hull home ranges were calculated for lizards seen at least four times (35 from LCB: 18 juveniles, 11 adult females, and 6 adult males; 31 from SL: 23 juveniles, 4 adult females, and 4 adult males). The number of sightings per lizard seen at least four times at LCB (median = 7, n = 35) was significantly larger (Mann-Whitney U-test: $t = 2.50$, $p<0.05$) than that at SL (median = 6, n = 31). No significant difference (Mann-Whitney U-test: $t = 1.15$, $p>0.05$) was found between the two sites for juveniles seen at least four times but the median trend was the same: 6(n=18) at LCB and 5(n=23) at SL. Seen at least four times, adults (median = 8, n = 25) were sighted significantly more (Mann-Whitney U-test: $t = 3.68$, $p<0.001$) than juveniles (median = 6, n = 41). The number of sightings for adult males and adult females seen at least four times was not significantly different (Mann-Whitney U-test: $U = 83$, $p>0.05$).

Regressions showed a positive relationship between home range area and the number of sightings. Regression slopes for adult males and adult females were compared by covariance analysis. No significant difference between the two slopes was found ($F_s = 0.20$, df = [1, 21], $p>0.05$). This indicates that the number of sightings did not differentially influence the home range sizes of these two groups to any appreciable extent. Similar results were obtained in the comparison of adults and juveniles ($F_s = 0.03$, df = [1, 62], $p>0.05$). Since the number of sightings was significantly different between sites, however, corrections of home range areas seemed necessary.

Home ranges were, therefore, corrected for the number of sightings by the Hatfield (1978) bias factors. Analyses showed no significant differences between adult and juvenile home range sizes (original or corrected) nor between those of adult males and females (Tables 26 and 27). For both original and corrected data, LCB home ranges were significantly larger than those at SL (Tables 26 and 27).

To gain a perspective on individual home range size in relation to the study site, several home ranges were plotted (Figures 13 and 14). Home ranges for two juveniles (J), two adult males (M), and two adult females (F) were plotted for each site. The number of sightings for these lizards was close to the mean number of sightings per lizard of the age/sex group to which each belonged.

Time of Activity

Daily peaks in lizard activity reflect the season. Times of lizard sightings were analyzed by two-month intervals. Adult-juvenile sighting times were compared in August-September; adult male-female sighting times were compared in both June-July and August-September. Sightings per lizard were not averaged before analyses. In August-September, LCB lizards were observed later in the day than SL lizards (Table 28). The age-study site interaction was also significant during these months (Table 28). At SL, juveniles were seen earlier in the day than the adults, while at LCB, juveniles were out later than the adults. At both plots, adults were out at approximately the same time of day. There were no significant differences in the activity peaks of the adult sexes during August-September (Table 29). LCB adults were observed significantly later during the day than SL adults in June-July (Table 29).

Table 26. Two-way Model I analysis of variance tables for the variables uncorrected home range area and Hatfield corrected home range area. The two factors are age (juvenile or adult) and study site.

Variable	Source	DF	Mean square	F
Uncorrected home range area	Age	1	20250.084	0.85
	Study site	1	498277.454	20.81***
	Interaction	1	40756.966	1.70
	Within cells	62	23946.674	
Hatfield corrected home range area	Age	1	322147.399	0.82
	Study site	1	6205801.515	15.82***
	Interaction	1	131730.414	0.34
	Within cells	62	392153.000	

*p<0.05
**p<0.01
***p<0.001

Table 27. Two-way Model I analysis of variance tables for the variables uncorrected home range area and Hatfield corrected home range area. The two factors are adult sexes and study site.

Variable	Source	DF	Mean square	F
Uncorrected home range area	Sex	1	29965.968	0.96
	Study site	1	350679.937	11.21**
	Interaction	1	6702.549	0.21
	Within cells	21	31280.543	
Hatfield corrected home range area	Sex	1	280421.424	1.78
	Study site	1	3502844.890	22.22***
	Interaction	1	114427.687	0.73
	Within cells	21	157636.132	

*p<0.05
**p<0.01
***p<0.001

Figure 13. Home ranges at LCB.

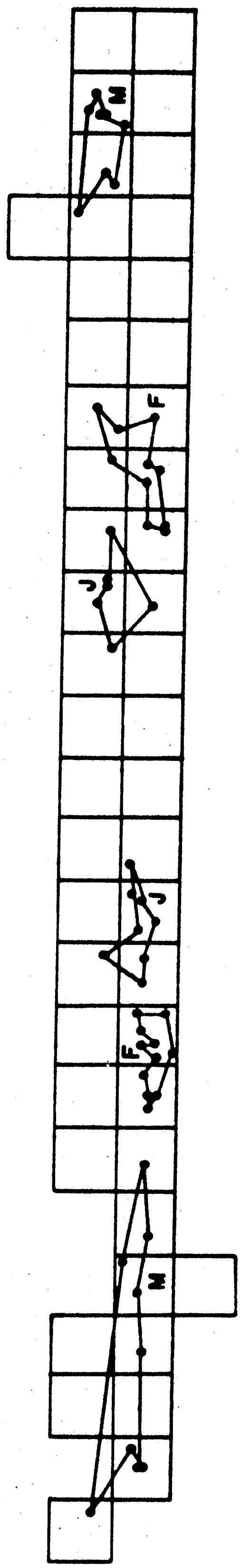
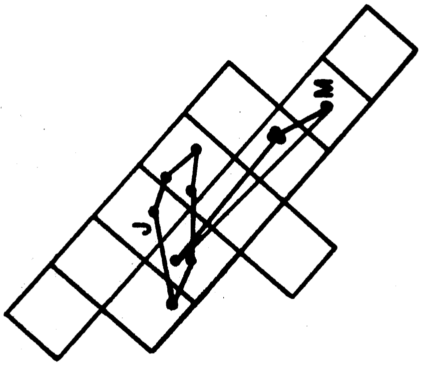
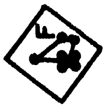
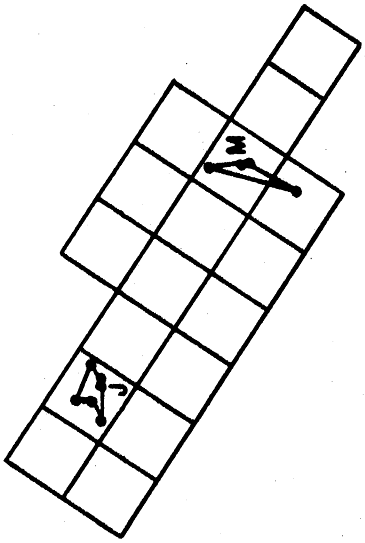

M
F
J
J
F
M

Figure 14. Home ranges at SL.


M
J


F


M
J

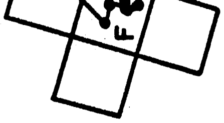

F

Table 28. Two-way Model I analysis of variance tables for the variable time in August-September. The two factors are age (juvenile or adult) and study site.

Variable	Source	DF	Mean square	F
Time	Age	1	2.535	0.40
	Study site	1	80.369	12.71***
	Interaction	1	54.521	8.62**
	Within cells	392	6.323	

*p<0.05
**p<0.01
***p<0.001

Table 29. Two-way Model I analysis of variance tables for the variable time in June-July and August-September. The two factors are adult sexes and study site.

Variable	Source	DF	Mean square	F
Time (June-July)	Sex	1	6.675	0.58
	Study site	1	153.183	13.20***
	Interaction	1	4.363	0.38
	Within cells	95	11.606	
Time (August-September)	Sex	1	1.857	0.24
	Study site	1	1.746	0.23
	Interaction	1	1.964	0.26
	Within cells	93	7.683	

*$p<0.05$
**$p<0.01$
***$p<0.001$

Summary

Collared lizards were captured and marked in a preliminary study during 1978 and an extensive field season (April through November) in 1979. Two study sites, Lake Carl Blackwell (LCB) and Sanborn Lake (SL) were chosen to compare autecologies of different habitats. Characteristics of these habitats, seasonal activity of the lizards, population density and the community sex ratio were noted. The date, time of day, location, and weather data were recorded each time a lizard was observed; if captured, size measurements and sex were also recorded. Home range sizes were calculated via the convex polygon method for lizards with four or more locational data points. All data analyses involved comparisons between the study sites, between adult sexes, and between juveniles and adults, using two-way analysis of variance. For an overall view, major differences were summarized (Tables 30, 31, and 32).

The LCB dam, the larger study site, consisted of large, flat rocks and sparse vegetation (Table 30). In comparison to those at SL, weather conditions for lizard activity included hotter hourly temperatures, higher solar radiation, and less humidity with clearer skies. LCB lizards used more exposed, alert postures in sunnier associations. Cumulative density was lower and individual lizards were seen more frequently than SL lizards. Home range areas were significantly larger.

The SL habitat was more diverse: open sandy areas, fewer rocks, a stream, and thicker vegetational growth than at LCB. Structural associations and lizard postures reflected this diversity (Table 30). A more east-facing site, SL receives the sun's warmth before LCB.

Table 30. Differences between LCB and SL.

Variable	LCB	SL
Median census hour	Later	Earlier
MDBO	Lizards seen more often	Lizards seen less often
Structural association	Sunnier	Shadier
Posture	More exposed, alert	More protected
Hourly temperature	Higher	Lower
Relative humidity	Lower	Higher
Sky conditions	Clearer	Cloudier
Solar radiation	Higher	Lower
Total area	10,800 m^2	7,875 m^2
Area utilized by lizards	10,350 m^2	7,200 m^2
Cumulative density	Lower	Higher
Temporal density	Lower for adult males	Higher for adult males
	Higher for adult females	Lower for adult females
	Lower for juveniles	Higher for juveniles
Transiency	23.9% lizards seen only once	38% lizards seen only once
Number of sightings/ lizard	More	Less
Original home range area	Larger	Smaller
Corrected home range area	Larger	Smaller
Time of activity	Later	Earlier

Table 31. Differences between adult males and adult females.

Variable	Adult males	Adult females
MDBO	Lizards seen less often	Lizards seen more often
Maximum temperature	Lower	Higher
Sky conditions	Cloudier	Clearer
Size	Larger	Smaller
Molting	Less frequent	More frequent
Peak density	Earlier	Later

Table 32. Differences between adults and juveniles.

Variable	Adults	Juveniles
MDBO	Lizards seen less often	Lizards seen more often
Actual/potential sightings	Seen less during span of activity	Seen more during span of activity
Structural association	Sunnier	Shadier
Posture	More exposed, alert	More protected
Hibernation	Began earlier	Began later
Maximum daily temperature	Higher	Lower
Minimum daily temperature	Higher	Lower
Hourly temperature	Higher	Lower
Relative humidity	Higher	Lower
Sky conditions	Cloudier	Clearer
Size - TL SVL MG TAIL	Larger	Smaller
Growth rate	Slower	Faster
Molting	Less frequent	More frequent
Peak density	Earlier	Later
Number of sightings/lizard	More	Less

Lizards seemed more wary and took refuge quicker than at LCB. More lizards were seen only once, perhaps an indication of more transiency.

Adult males were larger than adult females but were seen less frequently (Table 31). Activity of adult males usually occurred on days of cooler maximum temperatures and cloudier skies. Males molted every 40 days; females every 18. Peak density of adult males occurred before that of females. The mean home range size of adult males was larger than that of females, although not significantly.

Juveniles and adults were active during different months of the growing season (Table 32). Adults were seen less frequently during their period of activity than juveniles were during their activity period. More exposed, alert postures in sunnier associations were typical of adults. Hibernation began earlier for adults. Warmer and more humid conditions with cloudier skies characterized adult activity. Adults were larger than juveniles in total length (TL), snout-vent length (SVL), tail length (TAIL), and mouth gape (MG). Growth rates, when significantly different, were slower for adults than for juveniles. A mean of 29 days occurred between adult molts; juveniles molted approximately every 17 days. The mean home range size of adults was larger than that of juveniles, although not significantly.

CHAPTER VI

DISCUSSION

Compared with those at Lake Carl Blackwell (LCB), a significantly greater percentage of Sanborn Lake (SL) lizards were seen only once, an indication of more transiency (or more deaths). Or, structural diversity of the SL habitat may have reduced the probability of seeing a given lizard again. Perhaps, SL was a temporary environment used as lizards passed through the area in search of preferred habitat; SL habitat conformed less well than LCB to published descriptions of collared lizard habitat. Nevertheless, at least two lizards marked at SL in 1978 were resighted there in 1979.

Collared lizards at LCB were individually observed more frequently than SL lizards. This difference in the mean number of days between observations (MDBO) might reflect more activity of LCB lizards which caused them to be out more often. MDBO reflects census frequency; both plots, however, had similar census frequencies so each lizard had an equivalent chance of being seen, irrespective of plot. If most lizard activity at both plots occurred around the later hours typical of LCB censuses, the more frequent observations of LCB lizards might be an artifact. Observation frequencies of juveniles and adults were contrary to expectations: adults were observed less frequently than juveniles. Adult males are the most conspicuous, so one assumes they would be seen more frequently than adult females and juveniles. They were, however, observed less frequently than either adult females or juveniles. Smaller variances show that adult males were more restricted in their times of activity than adult females and so, were probably not active during each census. Juveniles, however, were even more restricted in their activity times than adult males but that probably reflected the cooler fall temperatures when fewer hours of the day were warm enough for lizard activity. Censuses were probably more efficient in the fall due to temperature constraints on lizard activity; thus, juveniles were observed more frequently than adult males because their peak period of activity corresponded to fall census times.

The parameter, actual/potential sightings, also shows that adults were seen significantly less frequently during their months of activity than juveniles were during theirs. Actual sightings of juveniles more nearly approximated their potential sightings (again indicative of weather restrictions on lizard activity and as a consequence, more efficient fall censuses).

Habitat

The two parameters, structural association and posture, reflect the uniformity of the rocky LCB landscape and the relative irregularity of the SL environment. The more exposed, alert postures in sunnier associations characterized LCB lizards better than SL lizards. More rocks and sunnier open areas seem associated with more exposed postures and greater alertness. More activity at LCB (reflected by MDBO) is also congruous with more exposure and greater alertness in sunnier, open areas. These differences can also be partially explained by the census techniques at each site. Rocks on the LCB dam could not be turned over whereas that strategy was used extensively at SL. These differences probably also reflect the later hours typical of LCB censuses. Hours later in the day are usually associated with warmer temperatures, consistent with more exposed, alert postures and sunnier associations.

Adults utilized more exposed, alert postures in sunnier associations than juveniles. This is consistent with the cooler fall temperatures of juvenile activity and the juvenile need for more protection; juveniles were more often found in the adpressed basking posture or under rocks in curled postures. The age-study site interactions revealed different age trends of LCB and SL lizards in their postures and structural associations. More exposed, alert postures in sunnier associations characterized SL adults better than SL juveniles. Again, this reflects the juvenile need for more protection. But also, cooler autumn temperatures forced juveniles to remain under rocks more frequently than was necessary for adults. The lookout posture in sunny associations was typical of LCB adults and juveniles. The more exposed, alert lookout posture would suggest a greater degree of lizard activity at LCB in contrast to SL. The uniform LCB habitat is more exposed to the elements than the irregular SL habitat. Thus, hotter summer conditions would force LCB adults to perhaps seek shadier shelters while juveniles exposed to harsher fall conditions would need sunnier associations conducive to activity.

Seasonal Activity

The significantly later hibernation dates of juveniles in comparison to those of adults, as study site variation was controlled, were due to the different months of activity (Figure 10). Age trends in hibernation dates were complicated by the different study sites. Adults entered hibernacula later at LCB than SL whereas juvenile hibernation began later at SL. Harsh weather conditions stimulate juveniles to enter hibernacula. A greater degree of exposure to the elements at LCB would create harsher fall weather conditions, driving juveniles to hibernate before SL juveniles were forced into hibernacula. Adults, however, begin hibernation before harsh weather conditions prevail; they probably hibernate to reduce predation risk, metabolic energy loss, and/or competition with juveniles once their reproductive activities are completed for the season (Tinkle, McGregor and Dana, 1962; Pianka, 1970; Fox, 1978). Perhaps reproductive activities required more time at LCB, forcing adults to begin hibernation later than at SL. Trends in hibernation dates for the adult sexes were also complicated by the two plots and the reason remains unclear. Hibernation dates for adult males were more similar between plots than those of adult females. Adult female hibernation began later at LCB. Perhaps reproductive duties of LCB females took longer than for SL females.

The rock-turning strategy at SL would presumably suggest later hibernation dates than at LCB, as an artifact. No significant differences were found between study sites when controlling for either the age or sex factor. Thus, beginning hibernation dates were not biased by the different census strategies.

Collared lizard activity at these two Oklahoma sites was first recorded in April. Hatchlings began to appear in August after adults had presumably entered hibernacula. This time schedule coincides with that reported in Kansas (Fitch, 1956).

The density graphs (Figure 10) show that SL females were observed earlier than LCB females. Eggs laid by SL females should have hatched sooner than those laid at LCB. The first hatchlings, however, were discovered at LCB. The more exposed habitat at LCB may have shortened incubation periods. The difference in the first sightings of LCB and SL females may also be emphasized by the two-week intervals on which the density graphs are based. At SL, two females appeared during the first two-week interval but none were observed in the second (Figure 10). Thus, these two females either died without reproducing or returned to hibernacula. Or, if they reproduced, the young did not survive or were not observed in the censuses. Peak female density began during the same two-week interval (midpoint: 20 July) at both plots and most hatchlings appeared during the same time period (midpoint: 31 August) at both plots.

Weather Parameters

Weather comparisons of adult and juvenile sightings were necessarily tempered by different months of activity. Peak adult densities occurred earlier in the summer. The resulting cooler, less humid conditions and clearer skies associated with juvenile activity coincide with peak density in the late summer-early fall. Peak densities of adult males and females may not be temporally distinct enough to explain the cooler maximum daily temperatures and cloudier skies associated with adult male activity; males may simply select such conditions more meticulously than females due to the thermoregulatory constraints of larger lizards.

Lizard activity in terms of certain weather parameters varied between LCB and SL (as age and sex were controlled, separately). Higher hourly temperatures, lower relative humidity, and greater solar radiation were characteristic of lizard activity at LCB in comparison with that at SL. Site-specific lizard activity hinges on the geography of each site. The rising sun warms the more east-facing SL site first since the LCB slope faces west. Thus, the sun's warmth does not affect LCB until later in the day. As afternoon approaches, daily solar radiation increases and then declines as the sun sets. The higher solar radiation and hotter hourly temperatures associated with LCB lizard activity might be due to the later exposure of the site to the sun. The typically later hours of observation at LCB might also have reinforced higher solar radiation and hotter temperatures. LCB lizards were observed under clearer skies than SL lizards (as age was controlled). All these site differences were biased by the fact that under cloudy, cooler, more humid conditions, SL lizards were easier to catch (for re-marking) by overturning rocks.

Significant interactions between age and study site were seen for the parameters maximum daily temperatures and sky conditions. Higher daily maximum temperatures and cloudier skies characterized SL juvenile activity in contrast to LCB juvenile activity. Daily maximum temperatures for adult activity were higher at LCB. Partly cloudy skies were characteristic of adult activity at both plots. Adults were active during late spring-early summer; cloudier skies were probably more prevalent than during the dry late summer-early fall season when juveniles were active. Harsher fall conditions at the more exposed LCB site might have forced juveniles to concentrate their activities on days of clearer sky conditions. In contrast to LCB juveniles, the association of SL juveniles with cloudier skies partially reflects the ease of lizard capture at SL by overturning rocks in cool, cloudy weather when lizard reflexes were more sluggish. Reasons for the higher daily maximum temperatures of SL juveniles and LCB adults are unknown.

Size

Lizard sizes were not significantly different between the two study sites. As expected in a species where males procure and defend territories, adult males of this study were consistently larger than adult females. Also, adults were larger than juveniles except in the tail length percentage of total length (TAILTL). Fitch (1956) reported different tail length percentages of snout-vent length for adult males, adult females, and hatchlings (Table 3). One could, therefore, expect differences in juvenile and adult TAILTL. Perhaps, by October though, the adult proportions of tail length per total length had already been obtained by the half-grown juveniles.

Growth

Lizard growth rates were not significantly different between the two study sites. As expected, when significant differences in growth rate of adults and juveniles occurred, juveniles grew faster. The reason for a significant interaction between study sites and adult sexes in mouth gape (MG) growth rate of June cannot be explained.

Molt

Molting frequencies were not significantly different between study sites. Means show that adult males molted every 40 days, adult females every 18 days, and juveniles every 17 days. These molting frequencies were affected by the fact that adult males were seen less frequently than either adult females or juveniles. Adults (both sexes) molted approximately every 29 days, similar to the 25 days between molts reported by Fitch (1956) for Kansas collared lizards.

Density

At both sites, peak adult male density occurred before that of adult females. This is consistent with documentation on other seasonally breeding temperate vertebrates: territorial establishment by males before females emerge from hibernacula (Crews, 1975) or before females return to the breeding grounds (Wilson, 1975). Density at both sites showed roughly similar forms for each age/sex group.

Cumulative densities showed more lizards per unit area at SL. Temporal densities of juveniles and adult males were also larger at SL. For adult females, however, temporal density was slightly greater at LCB. Larger temporal densities may be due to more lizards and/or a greater seasonal period of activity per lizard. In this study, the larger temporal densities were the result of both (Figure 10).

Spatial Distribution

The preferred habitat of collared lizards, as revealed by the spatial distribution at each site, was rocky. Open sandy areas with decreased vegetation also characterized the preferred habitat at SL. Published descriptions of typical collared lizard habitats substantiate these observations (Fitch, 1956) although SL conforms less well than LCB.

Home Range Size

At LCB, there were consistently more sightings per lizard (for those lizards seen at least four times and for which home range areas were calculated). Perhaps, LCB lizards were more active and, therefore, out more often than SL lizards. Lizards at LCB were also easier to see because they were not so numerous and they inhabited a less diverse landscape (rock and sparse vegetation in contrast to a scatter of rocks, sand, and more abundant vegetational growth at SL). The number of sightings per adult was greater than that for juveniles (actual sightings). This is consistent with the fact that adults were active over a longer time span (potential sightings).

The lower population density at LCB was associated with more available area for individual home ranges. Both original and corrected home ranges were significantly larger at LCB. Perhaps LCB exhibits preferable habitat for collared lizards: rocks and sparse vegetation. Habitat suitable for collared lizards at SL seems restricted by structural diversity between and throughout subplots. None of the SL lizards for which a home range area was calculated ($\geq$ 4 sightings per lizard) moved through the thicker vegetational growth between subplots.

Similarly, Fitch (1956) reported that collared lizards on the University of Kansas Natural History Reservation seldom ventured into the thick vegetational growth surrounding the stone quarry where they lived.

Larger organisms have been reported to possess larger home ranges (Turner, Jennrich and Weintraub, 1969; Yedlin and Ferguson, 1973). Adult home ranges were not significantly larger than those of juveniles in this study. For both original and corrected data, however, the mean adult home ranges were larger than the juvenile means. Juvenile home ranges in this study were cumulative; the last sightings occurred when these young were nearly half-grown. Any enlargements or shifts of juvenile home ranges could have produced overestimations of size. Adult male home ranges were not significantly larger than those of adult females. But the mean adult male home ranges for both original and corrected data were larger than the adult female means; intra-group variation may have precluded any mean statistical differences.

Time of Activity

During August-September, site-specific activity showed LCB lizards active later in the day than SL lizards. In June-July, adults at LCB were observed later in the day than SL adults, as the sex factor was controlled. These time differences in activity were influenced by site geography; the east-facing SL site receives warmth from the rising sun before the west-facing LCB site. But also, the earlier activity of SL lizards could be an artifact of the rock-turning census strategy, and at LCB, later activity might reflect the later hours of observation.

The interaction between age and study site in August-September might reflect a combination of factors: site geography, the warmest time of day through progressing seasons, thermoregulation of different sized lizards, the different census hours, and the different census strategies. Adults were active at approximately the same time of day at both plots. At SL, juveniles were observed earlier in the day than the adults, while at LCB, the reverse was true. The SL habitat warms up earlier than that at LCB because it faces more toward the east. Also, observations at SL took place earlier in the day. The rock-turning censuses at SL could bias times of lizard activity. Larger lizards require more time to reach optimum body temperatures and become fully active. The activity peaks of the adults at both sites and juveniles at SL seem consistent with all these factors. The later activity of LCB juveniles might reflect the sun's warmth reaching LCB later. As fall approaches, maximum daily temperatures occur later in the day. Perhaps, harsher fall conditions at LCB forced juveniles to remain inactive until later in the day. The later observation hours at LCB also affected juvenile time of activity.

Habitat Influences

Parameters of this study were assessed only when lizards were active. Thus, given the physical variations inherent at each site, the following significant lizard differences were intuitively obvious from these site variations. The LCB site is one continuous rock aggregation with lake frontage. Due to the greater degree of exposure and sparse vegetation, lizards would be expected to use sunnier associations and more exposed, alert postures. LCB faces west so the sun's warmth reaches the site later in the day; lizard activity would, thus, be expected to occur later in the day. Higher solar radiation and higher temperatures are also more common at later hours of the day. LCB, as the larger area, should support more lizards, if density was equal at both sites. However, fewer lizards on larger home ranges were found.

The SL site of four subplots exhibits a habitat of greater diversity than that of LCB: sand, fewer rocks, a stream, and more abundant vegetation with taller trees (evidence of more advanced stages of succession). In comparison to LCB, SL faces more toward the east; the sun's warmth reaches SL earlier in the day, so lizard activity would be expected to occur earlier. Lower solar radiation and lower temperatures would, thus, be associated with SL lizard activity. In the smaller area at SL, fewer lizards would be expected, if density was equal at both sites. However, more lizards on smaller home ranges were found. Rocks at SL were readily overturned for ease of lizard capture; sluggish lizard reflexes in cool, cloudy weather aided this strategy. A higher relative humidity, cloudier skies, and more protected postures in less sunny structural associations would, therefore, be expected.

Other significant lizard differences between sites invoke theoretical applications of evolutionary ecology. SL females were characterized by greater productivity than LCB females. The SL population, therefore, was represented by a greater proportion of juveniles (72%) than the LCB population (62% juveniles). But assuming population stability, a smaller percentage of SL lizards survive to adulthood (28% adults at SL and 37% at LCB) even from a larger juvenile base. SL lizards seemed, therefore, to be more transient or more susceptible to death. More lizards at SL were sighted only once, another indication of more transiency or death. Perhaps the habitat at SL is suboptimal and is occupied temporarily by lizards seeking optimal habitat.

The greater diversity of the SL habitat would suggest more predators and more inter-specific competition. Various snakes and insectivorous birds, horned lizards (Phrynosoma) and racerunners (Cnemidophorus) were known to inhabit the SL study site. Few birds and no reptiles other than Crotaphytus collaris were observed at LCB. Lizards appeared more wary at SL, especially as temperatures increased seasonally. They seemed to disappear into hiding places more quickly than LCB lizards, shortening the time of pursuit. This extra-wariness is quantified by fewer sightings per lizard at SL and greater time lapses between observations of individual lizards (MDBO). Perhaps, SL lizards were extra wary because of more predators and the smaller area available in which to escape.

The more abundant vegetational diversity at SL probably supports a more diverse insect population. Such a large diversity of insects might supply less of the preferred prey species for collared lizards; the high cumulative density of lizards at SL in such a situation would intensify intra-specific competition. Both increased competition and predation at SL would heighten mortality or transiency.

If LCB was indeed the more satisfactory environment, what limited the density of collared lizards there? A greater percentage of LCB lizards were older and so, more experienced. Better habitats allow lizards more time for territorial defense and the more frequent observations of LCB lizards in lookout postures on elevated, conspicuous perches do suggest more territorial defense behavior. These older lizards in the optimal habitat of LCB may effectively exclude younger lizards from colonizing. SL may be one suboptimal habitat (in terms of collared lizard needs) to which younger and/or less aggressive lizards are relegated. In attempts to obtain home ranges of higher quality, lizards may constantly travel through these inferior habitats. Those that stay are probably subject to a higher risk of death than lizards living in optimal habitats. During benign conditions, a breeding population can be supported by these suboptimal patches but may be less resistant to periodic, catastrophic reductions than one exploiting an optimal habitat. Recovery from such crashes could occur through local recruitment or immigration from more stable populations like LCB. Either way, more juveniles would inhabit suboptimal patches like SL. These suboptimal habitats, then, may perhaps be considered buffer reserves and overflow for the optimal habitats.

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