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DEMOGRAPHY OF A BARRIER ISLAND POPULATION OF THE KEELED EARLESS LIZARD, *HOLBROOKIA PROPINQUA*

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In recent years, emphasis has been placed on the quantitative approach to the study of the structure and function of natural populations of animals. Blair (1960) emphasized that because most lizards are diurnal, large enough to be observed at a distance, and of relatively low mobility they are perhaps the best vertebrates for studying the function of natural populations. Despite these advantages, knowledge of the life histories of lizards remains meager (Tinkle, 1973).

Holbrookia propinqua is a relatively small iguanid lizard that occurs on aeolian sand deposits in Texas and Mexico. Seemingly, it is most abundant on the barrier islands off the coast of Texas and Mexico (Smith, 1946). Oosting (1954) pointed out that the sand strand is a distinctive habitat that supports a characteristic vegetational cover, the zonation and life forms of which are repeated around the world. On South Padre Island, Cameron County, Texas, this habitat presents extremely rigorous conditions. The topography is being modified constantly by wind action; consequently, vegetation is also in constant flux due to transportation and deposition of sand. Periodically, hurricanes and storm tides create cuts or passes connecting the Laguna Madre and Gulf of Mexico. In the process, large expanses of the island are denuded, thereby initiating new successions of vegetation. In the summer, temperature fluctuations are extreme. Furthermore, due to the proximity of the Gulf of Mexico and Laguna Madre, island populations are exposed to salt spray in the air and salt that accumulates on vegetation and prey. Thus, the populations of *H. propinqua* on South Padre Island presented an opportunity to study the adaptation of a saurian population to a unique set of environmental variables.

Despite the local abundance of this species (Axtell, 1954, 1958; Smith, 1946), little information is available concerning its demography. Axtell (1954) commented on relative abundance and escape behavior. He also reported clutch sizes and laying dates of two females kept in captivity and recorded the events of a courtship encounter between a male and a gravid female. Selander *et al.* (1962) reported oviductal eggs in females collected in July and recorded observations made of a courtship and copulation encounter. They also presented data showing sexual dimorphism in snout-vent length and tail length. Clarke (1965) described and compared the display patterns and social behavior of species of *Holbrookia* (including *H. propinqua*) maintained in enclosures.

The purpose of this study was to provide quantitative information on the structure and function of populations of *H. propinqua* in nature. This information should facilitate comparison of life history strategies between *H. propinqua* and other lizard species and should provide insight into the adaptations that permit *H. propinqua* to exploit the rigorous barrier island habitat.

MATERIALS AND METHODS

In July 1969, two study areas were established on South Padre Island, Cameron County, Texas, 12.1 kilometers north of the Brazos-Santiago Pass (Fig. 1). Each study area included 0.368 hectare subdivided into 6.1 by 6.1-meter quadrats by lettered and numbered stakes. The two areas were situated 67.1 meters apart and encompassed dissimilar habitats, as described below. On 2 June 1971, a third study area of equivalent size was established 26.1 kilometers north of the Brazos-Santiago Pass. Surveys of the gridded areas were concentrated during the spring and summer months from May to September. Occasional checks were made at other times of the year.

Each study area was surveyed by walking between two rows of stakes until the entire area was covered. The grids were worked in random fashion, starting at different positions so as to reduce the possibility of lizards becoming habituated to the path of the observer. Each study area was surveyed a similar number of times in a given year; however, due to the inclusion of unfavorable habitat, grid 2 required much less time to work. I attempted to work the areas at every hour of the day, but in order to obtain a maximum number of captures, most man-hours were spent during the maximum activity periods of the lizards.

A net approximately 30 centimeters in diameter attached to a 1.5-meter wooden handle was used to facilitate capture of lizards. Tinkle's

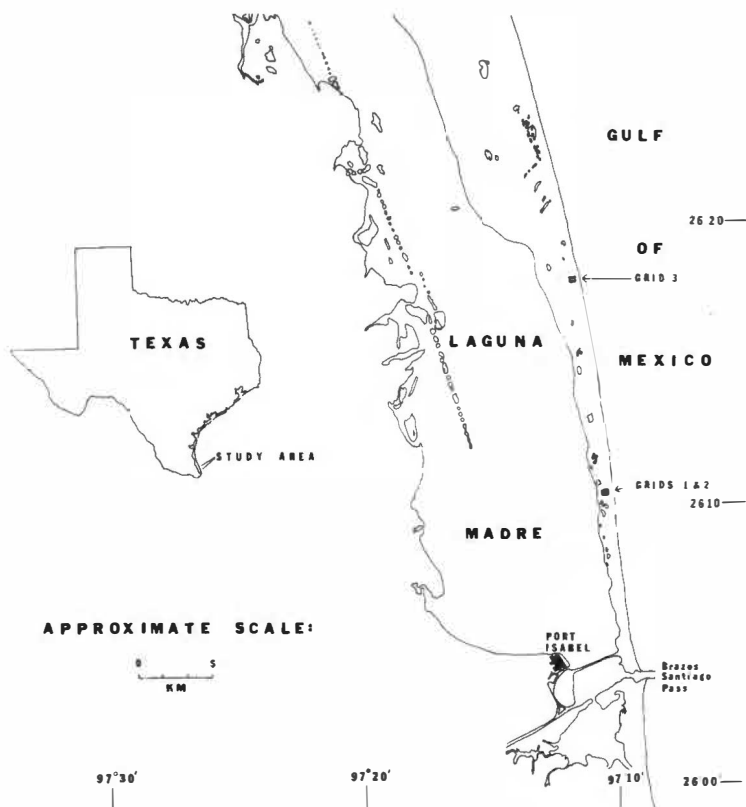


FIG. 1.—Map showing location of study areas.

(1967*b*) method was used to mark each lizard permanently by toe clipping. No more than one toe on each foot was removed. Captured lizards were painted dorsally with a unique, colored symbol so that they could be identified at a distance, thereby making capture unnecessary to record subsequent positions. When shedding removed or obliterated the symbol, the lizards were captured and repainted.

On each capture, the following data were recorded: date, time of day (Central Standard Time), position, sex, weight, snout-vent length (SVL), and tail length (both original and regenerated parts). All measurements are in millimeters and all weights are in grams. Information on shedding, scars, coloration, reproductive condition, and behavior immediately preceding capture were recorded also. Individuals were processed near the site of capture and then released immediately so as to minimize any adverse effects of captivity. No animal was away from its territory for more than two hours.

All study areas were surveyed at least every third day. In 1970, grids 1 and 2 usually were surveyed every other day and sometimes daily. To reduce the effects of possible temporal shifts in home range, I utilized only those captures made during the reproductive season (March to September) in calculating home range size.

The minimum polygon (convex polygon) and probability density function methods were employed to estimate home range sizes. Jorgensen and Tanner (1963), Tinkle (1967*a*, 1967*b*), Tinkle and Woodard (1967), Turner (1971), and Milstead (1971, 1972) have discussed in detail the assumptions, limitations, and relative merits of these two methods.

The sex of adults was ascertained easily by the presence in males of hemipeni, bold lateral bars, a relatively longer tail, and larger body size. In August 1970, I discovered that the sex of juveniles could be determined by the presence, in males, of an enlarged pair of postanal scales. Prior to this time, sex was not determined for lizards with a snout-vent length less than 40 but they were included in a common class. However, many lizards first marked as juveniles subsequently were captured as adults so that their sex could be determined.

Dissection of specimens collected from near the grids and from locations on the Texas mainland provided information on reproductive cycles. A year's sequence of samples was collected from May 1970 to May 1971 for analysis of seasonal variation in the reproductive ecology of *H. propinqua*. An attempt was made to collect approximately 15 males and 15 females each month; however, in winter months this objective proved extremely difficult to accomplish, and a December sample was not obtained.

In order to assess yearly variation in reproductive characteristics, samples were collected in the spring and summer of 1969, 1970, and 1971 on South Padre Island. In addition, samples were collected from Brazos Island, Cameron County, Texas, and from the following localities on the Texas mainland to determine whether geographic variation in reproductive effort existed: *Brooks County*: 4.8 km. N Encino; 3.2 km. S Falfurrias. *Kenedy County*: 35.4 km. N Raymondville; 54.7 km. N Raymondville; 46.7 km. S Sarita; 39.4 km. S Sarita; 37.8 km. S Sarita; 33.8 km. S Sarita; 27.4 km. S Sarita; 16.1 km. S Sarita; 9.7 km. S Sarita; 8.0 km. S Sarita; 7.2 km. S Sarita; 4.8 km. S Sarita; 8.0 km. S Armstrong; 0.8 km. S Armstrong; 1.6 km. N Armstrong; 2.4 km. N Armstrong; 3.5 km. N Armstrong; 9.7 km. N Armstrong; 10.3 km. N Armstrong; 10.5 km. N Armstrong; 14.5 km. N Armstrong; 23.3 km. N Armstrong. *Willacy County*: 1.6 km. N, 2.4 km. W Port Mansfield; 15.3 km. N Raymondville.

Animals were autopsied and the number and size of yolking ovarian follicles, oviductal eggs, and corpora lutea were noted. Weights of oviductal eggs, lengths of both testes, and the relative size of seminiferous tubules and vas deferens were noted. Size of corpora adiposa were scored qualitatively with the criteria proposed by Ruibal *et al.* (1972).

Statistical procedures employed are those of Sokal and Rohlf (1969). A probability value of less than 0.05 is considered significant.

DESCRIPTION OF STUDY AREAS

Physical Aspects and Climate

Padre Island extends approximately 193 kilometers along the gulf coast of Texas, from Corpus Christi south to the Brazos-Santiago Pass at Port Isabel. It is a classic example of a barrier island and varies from about 450 meters to approximately 5 kilometers in width. It is separated from the Texas mainland by a shallow estuary, the Laguna Madre, which has a maximum width of 15 kilometers. Padre Island National Seashore occupies most of the north and central portion of the island and extends southward to the Port Mansfield Cut. That portion of Padre Island which extends from the Port Mansfield Cut to the Brazos-Santiago Pass is customarily referred to as South Padre Island.

Study areas on South Padre Island (Fig. 1) and collection sites on the Texas mainland were situated in the semiarid climate of extreme southern Texas (Thorntwaite, 1948). Predominant winds are southeasterly. The normal annual rainfall of 60.9 centimeters is poorly distributed with a peak in September and October. Most of the precipitation is a result of thunderstorm activity, and often a single thunderstorm will account for an entire month's rainfall. Air temperatures in summer and autumn are not extremely high but are usually in the lower thirties (centigrade) during the daytime and the middle twenties at night. The prevailing onshore winds from the Gulf of Mexico moderate the high temperatures. Surface sand temperatures in summer regularly exceed 60° centigrade during the hot part of the day and fall below 30° at night. Winter temperatures are mild, with the normal daily minimum for January, the coldest month, being 11.5°C. Frequently, an entire winter will pass without a temperature as low as the freezing point; however, damaging cold does occur occasionally.

Generally, tides are less than 1 meter, and waves along the beach are usually 0.5 to 1.0 meter in height, but, during storms and hurricanes, waves may be 3.0 to 5.0 meters high and tides 5.0 meters above average sea level (Milling and Behrens, 1966).

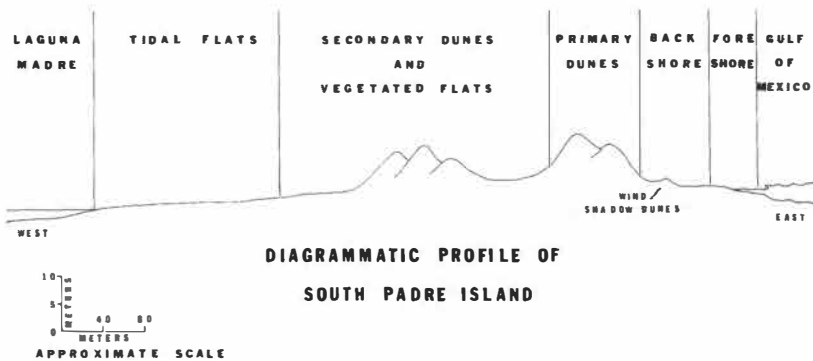


FIG. 2.—Transverse profile of South Padre Island showing major topographic zones.

Tourism is the major industry of the island and various human activities may affect the distribution of *H. propinqua*.

Topography and Vegetation

I subdivided South Padre Island into five major topographic zones (Fig. 2). From the gulf westward these were: 1) foreshore, 2) back-shore, 3) primary dunes, 4) secondary dunes and vegetated flats, and 5) tidal flats. Lizards occurred in all zones except the foreshore and tidal flats. Censuses in spring and early summer of 1969 indicated that earless lizards were most numerous in the secondary dune zone and along the margins of washovers where pioneer plant communities were present. The study areas, all located in the secondary dune zone, were chosen primarily because they supported large populations of *H. propinqua*. The secondary dune and vegetated flat zone was in the lee of the taller primary dunes and thus less exposed to environmental stresses. Consequently, the dunes here were partially to completely stabilized. This zone also varied markedly in width and vegetational composition. Sea oats (*Uniola paniculata*) and bluestem (*Schizachyrium scoparium*) were the most common plants on the dunes. Where the secondary dunes bordered washovers, sea oats, croton (*Croton punctatus*), and beach morning glory (*Ipomoea stolonifera*) were most common. In the absence of dunes, marshes may occur in the hollows. These areas were covered with dense vegetation consisting primarily of sedges (*Dichromena colorata*, *Carex* sp., *Fimbristylis castanea*, *Eleocharis* sp.) and cordgrass (*Spartain patens*).

Grid 1 was situated along the margin of a washover. A pioneer plant community comprised the northern half of the grid. Grid 2 included stabilized dunes and relatively dense vegetation. An area cor-

responding roughly to the southeast one-fourth of this grid included a portion of the vegetated flat zone. Here, cover approached 100 per cent and constituted unfavorable habitat for lizards. Grid 3 included partially stabilized secondary dunes; however, the eastern margin comprised a portion of the leeward side of the primary dunes, and here the vegetation consisted almost entirely of widely scattered clumps of sea oats.

To determine plant composition, a series of three line transects was run across each grid. The transects corresponded to the lettered rows of stakes; therefore, each transect was 67.1 meters long and subdivided into eleven 6.1-meter intervals. Transects were selected by drawing random numbers, but those intersecting the southeast one-fourth of grid 2 were excluded. Cover and frequency were determined for each plant species. Also, an estimate of the total percentage of ground surface covered by vegetation was obtained.

Bluestem was dominant on all three study areas (Judd, 1973). Croton and beach morning glory made significant contributions to cover and community structure only on grid 1. Grid 2 exhibited a 12.0 per cent increase and grid 1 an 18.7 per cent increase in total cover from 1970 to 1971.

RESULTS AND DISCUSSION

Age Class Nomenclature

Hatchling earless lizards were seen first in 1970 on 26 June and in 1971 on 23 June. Averages, followed by ranges in parentheses, for selected measurements of five males captured on these dates were: SVL, 24.4(24-25); tail length, 32.2(29-35); weight, 0.50(0.44-0.45). Four females also captured on these dates measured: SVL, 24.8(23-27); tail length, 30.3(24-34). Weights for three hatchling females were 0.65(0.58-0.78).

Based on this information, I considered any lizard 27 SVL or less a recent hatchling. Prior to its first winter, a lizard larger than 27, but less than 45, was called a juvenile. Between emergence from the first winter and entrance into the second winter, a lizard was called one-year-old. Very few lizards lived longer than one year; those that did were termed two-year-old or three-year-old, as the case might be.

Dixon (1967) stated that hatchling *H. maculata* were seen for the first time on 17 August at White Sands, New Mexico. Gennaro (1974) reported that hatchling *H. m. maculata* first appeared in eastern New Mexico on 6 July. This is about two weeks later than the first appearance of hatchling *H. propinqua*. Difference in time of hatchling appearance might be related to latitudinal temperature differences.

TABLE 1.—Size relationships of *Holbrookia propinqua* at known ages.

Age category	Snout-vent length			Tail length			Weight		
	N	X	SE	N	X	SE	N	X	SE
<i>Males</i>									
Hatchling	27	25.7	0.21	27	32.5	0.33	24	0.61	0.05
One-year-old (240-280 days)	6	51.7	0.84	5	75.6	2.28	4	4.16	0.20
One-year-old (305-365 days)	9	54.7	0.97	6	78.0	2.11	8	5.03	0.21
Two-year-old (700 days)	7	56.4	1.29	5	79.8	2.40	7	5.60	0.45
Three-year-old (975 days)	1	58.0		1	81.0		1	6.36	
<i>Females</i>									
Hatchling	28	25.2	0.25	24	30.6	0.57	24	0.65	0.03
One-year-old (240-280 days)	8	50.8	0.53	7	64.6	1.33	6	4.11	0.19
One-year-old (305-365 days)	11	50.6	0.82	7	65.0	1.10	11	4.36	0.11
Two-year-old (700 days)	3	49.0	1.15	3	62.3	3.53	3	4.19	0.13

Hatchling *H. m. maculata* ranged from 19 to 22 SVL (Gennaro, 1974), which is markedly smaller than hatchling *H. propinqua*. Clarke (1972) listed a minimum SVL of 21 for hatchling *H. propinqua*, which is within the range for *H. m. maculata*. In any event, the SVL of *H. propinqua* at hatching (21-27) is similar to that reported by Engeling (1972) for *Cophosaurus texana* (24-30), by Pianka and Parker (1972) for *Callisaurus draconoides* (26-32), and by Tinkle (1967b) for *Uta stansburiana* (18-23).

Size Relationships at Known Ages

Periodic recapture of marked animals provided considerable information on size and growth (Table 1). There was no significant difference in SVL or weight of hatchling males and females, but males had significantly longer tails than females ($t=4.614$, 49 df, $P<0.001$). Lizards 240 to 280 days old exhibited the same size relationships as did hatchlings. Males continued to exhibit significantly longer tails than did females ($t=3.892$, 10 df, $P<0.01$) but were only slightly larger in SVL than were females. Once females reached a SVL of about 50, growth became exceedingly slow, as evidenced by the almost identical mean SVL and tail length values of the 240 to 280-day-

old and 305 to 365-day-old age classes. Males at an age of 305 to 365 days were significantly longer in SVL ($t = 3.300$, 18 df, $P < 0.01$) and tail length ($t = 5.700$, 11 df, $P < 0.001$) than were females. The few individuals that lived longer than one year showed the same relationships as did adult one-year-old lizards. Males were markedly larger than females in all measurements. Two-year-old males were slightly larger than one-year-old males, but the difference was not significant. Two-year-old females were not larger than one-year-old females. One male was known to have been marked first on 13 September 1969, at a SVL of 55, and last captured on 19 May 1971, at a SVL of 58. The largest snout-vent lengths recorded were 57 and 60 for females and males, respectively. The longest tail length recorded for a female was 74; the longest recorded for a male was 89. The heaviest male, a two-year-old individual with a SVL of 60 and a regenerated tail 60 millimeters long, weighed 6.9 grams. The heaviest female weighed 6.1 grams and was a gravid one-year-old individual of 55 in SVL. Gennaro (1974) found one, two, and three-year-old age groups in *H. m. maculata*; however, as in *H. propinqua*, three-year-olds were extremely rare. Gennaro (1974) also found no evidence of sexual dimorphism in SVL of adults, but males had significantly longer tails than females of the same size. Maximum SVL and weight of both sexes of *H. m. maculata* were similar to those attained by *H. propinqua*, but one-year-old males of *H. m. maculata* were markedly smaller than one-year-old males of *H. propinqua*.

Growth Rates

Variation in daily mean growth increments is shown in Table 2. Lizards were grouped according to size at first capture. During the first 45 days after hatching, males increased in SVL at a faster rate than did females, but growth of the tail was only slightly more rapid in males. Growth rates during the first season of growth were much more rapid than after the first winter. During the second growth season, males and females had similar rates for SVL, but the rate of increase of tail length for males was almost four times that for females. The growth rate decreased markedly once lizards attained a SVL of 50. Growth rates for tail length and weight then became similar in males and females, but the rate of growth in SVL for males was double that for females; thus, males became much larger in SVL than did females of a similar age (Table 2).

One may check the validity of these data by using growth rates to estimate the increase in size that would accrue in a hypothetical individual and by then comparing the size of this lizard with that of

TABLE 2.—Daily growth rates of *Holbrookia propinqua* (mean followed by sample size, in parentheses).

Age group and time period for determining rates	Snout-vent length	Tail length	Weight
<i>Males</i>			
Hatchlings			
first 45 days after hatching	.278(5)	.264(5)	.016(5)
Juveniles (SVL 31-40)			
first 45 days after capture	.146(5)	.294(4)	.033(4)
Juveniles (SVL 31-40)			
first year's growth, 8-10 months	.069(5)	.097(3)	.012(5)
One-year-old (SVL 41-50)			
second season's growth			
first capture to October	.059(18)	.098(18)	.009(16)
Adults (SVL > 50)			
2 to 700 days	.014(73)	.016(62)	.002(64)
<i>Females</i>			
Hatchlings			
first 45 days after hatching	.187(6)	.209(6)	.021(6)
Juveniles (SVL 31-40)			
first 45 days after capture	.173(5)	.402(5)	.029(5)
Juveniles (SVL 31-40)			
first year's growth, 8-10 months	.069(3)	.085(3)	.010(5)
One-year-old (SVL 41-50)			
second season's growth			
first capture to October	.057(62)	.025(60)	.003(47)
Adults (SVL > 50)			
2 to 700 days	.007(25)	.016(23)	.001(26)

known age lizards. For example, if the observed growth rate for the first 45 days after hatching was 0.278 millimeters per day, the increase in SVL during this period would be 12.5. Hatchling males had a mean SVL of 25.7; therefore, a male hatching on 1 July should measure 38.2 in SVL by 15 August. With this value as the size of a juvenile male and given a growth rate of 0.146 millimeters per day, the hypothetical male would have a SVL of 44.8 on 1 October. If this same growth rate of 0.146 millimeters per day prevailed throughout the month of October, this individual would have a SVL of 49.2 on 1 November. Thus, a male hatching 1 August would have a SVL of 44.8 on 1 November. If the assumption is made that little or no growth occurred during the winter months of November, December, January, and February, males emerging in March could be expected

to have a SVL of 45 to 49. Ten males, captured on 4 and 18 March 1972 on grid 3, exhibited a mean SVL of 45.0 (42-51). Therefore, the observed growth rates appeared to be very reliable.

Growth in early spring was slow. Daily growth rates for selected characters in five males captured in March and recaptured in April were as follows: SVL, 0.048; tail length, 0.160; weight, 0.017; for two females: SVL, 0.095; tail length, 0.071.

Applying these rates to a hypothetical male and female hatching 1 July, these individuals would be expected to be 51.3 and 50.7 in SVL, respectively, on 15 April. Lizards hatching 1 July would reach an age of 288 days on 15 April. Males known to be from 240 to 280 days of age had an average SVL of 51.7 whereas females of the same age had an average SVL of 50.8. It appears that the estimated growth rates are relatively accurate.

Males and females had similar weights at a given SVL throughout the first season of growth. During the second season, females showed a slightly greater average weight than did males of the same SVL. This was due to the fact that females were gravid at this time. Variation in weights of females at a given SVL was largely due to the presence or absence of eggs. Because males grew at a faster rate than did females, during the second growing season, males that attained snout-vent lengths greater than 55 weighed more than most females.

Growth rates for snout-vent lengths of *H. m. maculata* (Gennaro, 1972) were apparently greater than those for *H. propinqua* of all age and size categories. However, because *H. propinqua* hatched earlier and had a longer season of growth, the size of *H. m. maculata* and *H. propinqua* was similar at onset of the first winter.

A comparison of growth rates for SVL of all animals in their first season of growth among *H. propinqua* (0.20), *H. maculata* (0.24, Gennaro, 1974), *C. texanus* (0.27, Engeling, 1972), and *C. draconoides* (0.24, Pianka and Parker, 1972) showed that closely related species all had similar growth rates and that the rates fell within the range of 0.2 to 0.3 millimeters per day suggested by Tinkle (1967b) as average for lizards.

Variation in Size of One-year-old Lizards

A comparison of SVL of one-year-old lizards on the study areas during May, June, July, and August for 1970 and 1971 is shown in Fig. 3. There were no significant differences in SVL of females between areas or years. However, males of grid 2 were significantly smaller than males of grid 1 in both 1970 and 1971 (graphical test, Fig. 3). This is interesting because the two areas were situated only 67

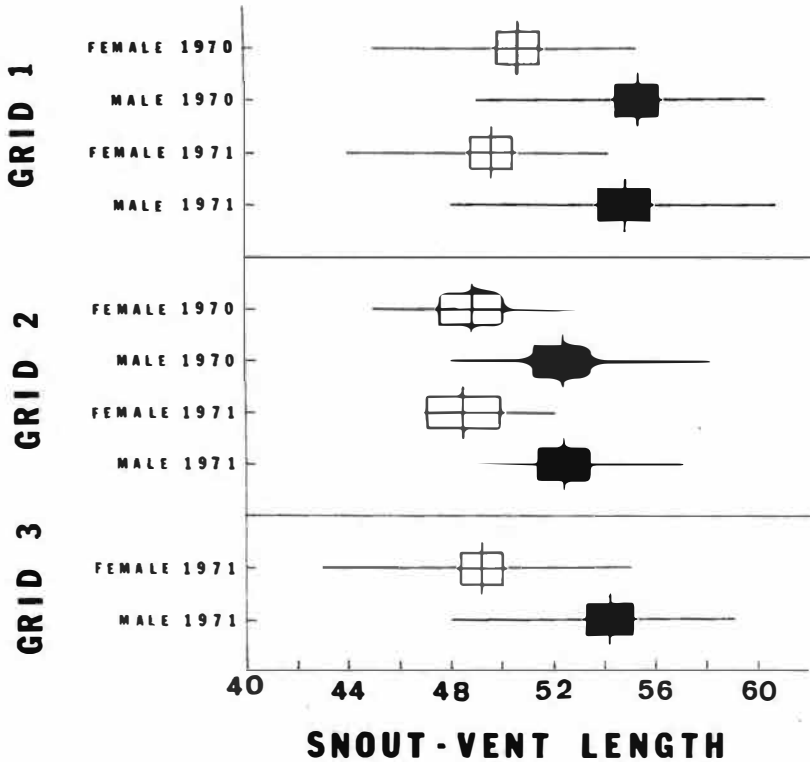


FIG. 3.—Comparison of snout-vent length of one-year-old lizards between areas and years. The horizontal line represents the range; the vertical midline, the mean. Rectangles indicate the 95 per cent confidence intervals of the mean. Open rectangles represent females. Black rectangles represent males. Sample sizes are indicated above the rectangles.

meters apart. Possible explanations are offered below. Males of grid 2 were not significantly smaller than males of grid 3, even though the two areas were 14 kilometers apart. All males together averaged 54.1 in SVL, which is very similar to the mean SVL of 54.7 obtained for males known to be 305 to 365 days old. All females combined had an average SVL of 49.6, which is similar to the mean SVL of 50.6 for females 305 to 365 days of age.

Axtell (1954) presented information on size of *H. propinqua* from the Texas mainland (one locality given was Boca Chica Beach, Brazos Island, Cameron County, Texas) and Selander *et al.* (1962) reported size data for *H. propinqua* from a barrier island off the coast of Tamaulipas, Mexico. Samples from the Texas mainland, South Padre Island, and the Tamaulipas barrier island fell along a north-

south transect through the range of the species. Average snout-vent length and standard error, when applicable, are followed by range, in parentheses, and sample size: *Texas mainland*: males, 49.8(45-57)56; females, 48.1(45-55)56 (Axtell, 1954); *South Padre Island*: males, 54.1 \pm 0.23(48-60)170; females, 49.6 \pm 0.21(43-55)162; *Tamaulipas barrier island*: males, 56.0 \pm 0.50(49-62)33; females, 50.9 \pm 0.50(47-53)14 (Selander *et al.*, 1962). Axtell (1954) failed to include a value that would allow one to calculate the variance of his sample so that a statistical comparison between mainland and island populations was not possible. In any event, the differences between the mean SVL values of mainland and island populations of females were small. However, the mean SVL of males of the Texas mainland sample was markedly smaller than that of the Padre Island sample (difference, 4.3) and the Tamaulipas barrier island sample (difference, 6.2). The difference in the means of the Tamaulipas barrier island males and Padre Island males was only 1.9. Furthermore, males of the Tamaulipas barrier island sample were not significantly larger in SVL than males of grid 1 from South Padre Island ($t = 1.810$, 112 df, $P > 0.05$). Thus, it appears that variation between the two different island samples of *H. propinqua* was of a magnitude that regularly occurs among populations on the same island. On the other hand, the difference in mean SVL of island males and mainland males was of a much greater magnitude than regularly occurs among island populations. The mean SVL of Texas mainland males was markedly smaller than the mean SVL of males from grid 2 of the Padre Island population.

Size and Age at Maturity

The following statements pertain to Padre Island lizards. I followed Tinkle (1972) in considering age at maturity as the age at first breeding rather than age at which mature size is attained. The smallest female examined that exhibited yolked follicles measured 44 SVL. Examination of marked females revealed that the smallest gravid individual also had a SVL of 44. Females reached a SVL of 44 in their first season of growth, approximately three months after hatching. Early hatchlings reached this size at about the first of October, a time inappropriate for reproduction. Thus, females did not become sexually mature until the following spring at an age of approximately 10 months. Some females became sexually mature at relatively small body sizes, but the majority (91.7 per cent) did so at a SVL of 47 or greater. Nevertheless, females with a SVL of 44 or more in May, June, July, August, and September were considered adults.

TABLE 3.—*Monthly variation in reproductive condition of female H. propinqua from South Padre Island. (Numbers represent individual lizards).*

Date	Unyolked follicles only	Yolked follicles	Yolked follicles and corpora lutea	Unyolked follicles and corpora lutea	Oviductal eggs and corpora lutea	Total
1970						
May	6	5			2	13
June	1	10			2	13
July		5	3	1	2	11
August		5	1	3	7	16
September	4	2		8	1	15
October	22				1	23
November	13					13
1971						
January	2					2
February	10					10
March	10					10
April	15					15
May		11	1		3	15

The smallest male with enlarged testes (>5.0 in length), enlarged ducts, and motile sperm measured 51 in SVL. Males reached this size at about nine months of age.

Female Reproductive Cycle

Unless indicated otherwise, comments pertain to Padre Island females. Ovaries of immature females contained eight to 14 translucent follicles measuring about 0.2 to 1.0 in diameter. Yolking follicles were observed first in females collected on 28 May (1970 and 1971); however, two females in 1970, and three in 1971, contained oviductal eggs during May, which indicated that vitellogenesis in some females occurred at an earlier date. Apparently, vitellogenesis of ovarian eggs began in late April or early May, because 15 females collected from 17 to 24 April 1971 were all prereproductive whereas all of 15 females collected on 28 May 1971 were in some reproductive stage (Table 3). About 1 May was the time at which a majority of females would be undergoing vitellogenesis for the first clutch of eggs. Vitellogenesis was not initiated in all at the same time; yolked follicles were found in only five of 13 females collected on 28 May 1970. After this date, only one female of 40 collected in June, July, and August failed to exhibit evidence of yolked follicles, oviductal eggs, or

corpora lutea (Table 3). Females captured on the same day often differed markedly in the size of their respective yolked follicles, again an indication that there was individual variation in onset of vitellogenesis. Yolking follicles could first be recognized at a diameter of about 1.7. The largest yolked follicles observed were 8.55 in diameter. Yolking follicles appeared throughout the reproductive season and were last noted in a female collected on 18 September.

The time required for follicular development probably approximates 30 days because all females collected between 17 and 24 April 1971 lacked yolked follicles whereas they were present in 80 per cent of the females collected on 28 May 1971. This conclusion was also supported by information gained from weighing and palpating females in the field. Three females that were known to have recently oviposited took an average of 28 days (22-37) to develop their next clutch.

Evidently, follicular development of succeeding clutches rarely began before egg deposition had occurred, inasmuch as only three females were found with oviductal eggs and yolked follicles. Two of these females were in the South Padre Island sample of August 1969, and one occurred in the mainland sample of June 1971.

By 18 September, 80 per cent of the females examined were post-reproductive (Table 3). All but one of 23 females collected on 24 October were postreproductive. Thus, the reproductive season may be assumed to extend from about 1 May to approximately 1 October, a period of approximately 150 days.

Clutch Frequency and Size

Clutch frequency can be determined exactly only by weighing and palpating selected females at regular intervals (Tinkle, 1973). If the first clutch of eggs were produced on 28 May, and assuming 30 days elapsed time between clutches, five clutches might be produced with oviposition occurring on 28 May, 27 June, 27 July, 26 August, and 25 September. However, autopsy information indicated that the September laying date was too late for most females. Furthermore, allowing time for incubation, 42 to 56 days (Clarke, 1972), would mean that hatchlings should be present in the population during October; no hatchlings were found after September. The conclusion that no more than four clutches are probable appears compelling. Even though a maximum of four clutches is possible, I think this figure is too high for most females. Change in weight of marked females indicated that most laid their first clutch about 14 June, a second clutch about 12 July, and a third clutch about 7 August. A fourth clutch

TABLE 4.—Number of adult (*M*=males, *F*=females) and juvenile (*J*) lizards of *Holbrookia propinqua* in 1970 and 1971 based on number of animals marked on the study areas.

Month	Grid 1			Grid 2			Grid 3		
	M	F	J	M	F	J	M	F	J
1970									
May									
June	25	23	0	14	13	2			
July	15	12	10	13	10	13			
August	6	4	30	6	3	20			
1971									
May	21	22	0	12	8	0			
June	21	25	2	10	5	0	27	30	0
July	17	13	21	11	6	10	18	28	4
August	11	4	15	5	2	9	15	21	6

might be laid about 6 September, but because there were usually few females in the populations in August and September (see Table 4), I think this would be an unusual situation. Furthermore, some late maturing females probably produced only two clutches (July and August). These conclusions were supported by information gained from marked females.

Dixon (1967) reported that females of *H. maculata* had bright colors on the hind limbs, sides of the body, and top of the head during the last week of June while clutches were developing. Females of *H. propinqua* also developed reproductive coloration either during or soon after ovulating their first clutch of eggs. Thus, the presence of yellow and red coloration indicated that females were reproductively active. Generally, larger females (more than 50 in SVL) became reproductively active earlier than smaller females. Many of the smaller females did not ovulate their first clutch of eggs until July.

Local populations varied considerably in the synchrony of reproductive events. Reproductive events were delayed approximately one month in the grid 3 population, as evidenced by the small proportion (22 per cent) that had ovulated in June and the large number of females present in August (23 females on grid 3 compared to three on grid 2 and four on grid 1).

In summary, there was conclusive evidence for at least two clutches based on weight changes of marked females and simultaneous presence of yolked follicles and corpora lutea in four females. All available evidence indicated that most females laid three clutches of eggs.

TABLE 5.—Clutch size in *H. propinqua* from South Padre Island in 1970. The number of follicles, eggs, and corpora lutea is followed by the number of individuals, in parentheses, possessing this count. In the summary statistics, the mean is followed by the standard deviation and the sample size, respectively.

Date	Yolked follicles	Oviductal eggs	Corpora lutea	Summary statistics
May	3(4)	3(1)	3(1)	3.25 ± 0.463,8
	4(1)	4(1)		
June	2(1)	3(1)	4(2)	3.43 ± 0.646,14
	3(5)	4(2)		
July	4(3)			3.00 ± 0.707,13
	2(1)	2(1)	2(1)	
	3(4)	3(1)	3(2)	
August	4(3)			3.00 ± 0.426,23
	3(5)	2(1)	2(1)	
September	4(1)	3(6)	3(8)	2.75 ± 0.754,12
			4(1)	
	2(1)	2(1)	2(3)	
	3(1)		3(4)	
Summary				
statistics	3.167 ± 0.592,30	3.00 ± 0.646,25	3.00 ± 0.655,15	3.07 ± 0.621,70

A maximum of four clutches is probable. Clutch size can be estimated by counting the number of yolked follicles, oviductal eggs, or corpora lutea (Ballinger *et al.*, 1972; Tinkle, 1961, 1967*b*). Clutch size data for South Padre Island populations are presented in Table 5. An average clutch size of three was indicated by all three counts. There was no seasonal difference in clutch size. Clutch size for small (SVL 44-50) and large (SVL 51-57) females in May and June were (mean and standard deviation followed by range, in parentheses, and sample size): $3.00 \pm 0.354(2-4)17$ and $3.38 \pm 0.619(2-4)16$; in July through September, $2.79 \pm 0.588(2-4)24$ and $3.36 \pm 0.497(3-4)14$, respectively. However, large females produced significantly larger clutches than did smaller females ($t = 3.839$, 69 df, $P < 0.001$).

Geographic Variation in Clutch Frequency and Reproductive Potential

Clutch frequency is not known exactly for mainland populations, but the available data suggest a frequency higher than that of island populations. Three of seven mainland females collected on 24 March 1971 exhibited small yolking follicles, the largest follicle measuring 2.4 in diameter, whereas of 11 mainland females collected on 28 May 1971, seven had oviductal eggs, one had corpora lutea and yolk-

ing follicles, and three had yolking follicles only. In the island population, only four of 15 females collected on 28 May 1971 had oviductal eggs or yolking follicles and corpora lutea.

A similar time of 30 days for clutch development was indicated for mainland females because a majority of females (nine of 13) collected one month later (28 June) also had oviductal eggs or yolking follicles and corpora lutea. Based on the large proportion of females that had oviductal eggs or had already oviposited by 28 May, I think that most mainland females could produce four clutches of eggs during the reproductive season.

I followed Ballinger *et al.* (1972) in considering reproductive potential as the total zygotic contribution of a female during one reproductive season. It is probable that a majority of South Padre Island females produced three clutches of three eggs each, resulting in a reproductive potential of nine eggs per female. A few females might produce four clutches of four eggs each, but 16 eggs per female should be considered the maximum potential possible for this population.

If mainland females produced only three clutches per season, a low estimate of 13 to 15 eggs per female was indicated. If mainland females produced four clutches, their reproductive potential (18 eggs) was double that of island females.

Because mainland females are devoting more energy to reproduction than are island females, one might reason that they would have less energy available for growth and hence might be smaller than island females. Mean snout-vent lengths (followed by standard deviation and sample size) for mainland and South Padre Island females were, respectively: $49.2 \pm 2.207, 42$ and $50.1 \pm 2.389, 108$. Although the difference is statistically significant ($t = 2.035, 148$ df, $P < 0.05$), I do not think it is biologically meaningful, for the difference in means was only 0.9, and measurements were made to the nearest millimeter so that an error of one millimeter would be quite possible in any measurement. Furthermore, many of the mainland females were collected early in the breeding season, but island females were collected throughout the reproductive season, thereby introducing the possibility of additional growth in females comprising late season samples. SVL ranges were 44 to 57 for island females and 44 to 54 for mainland females; only three of the 108 island females exceeded a SVL of 54. These three large island females may have been two-year-olds.

Yearly variation in clutch size of South Padre Island females was: 1969, $3.17 \pm 0.592(2-4)30$; 1970, $3.07 \pm 0.621(2-4)70$; 1971, $3.08 \pm 0.682(1-4)52$. Thus, the mean clutch size was essentially three for all three years. Comparison of clutch sizes of the Padre Island ($3.09 \pm$

0.634(1-4)152), Brazos Island ($3.52 \pm 0.731(3-5)23$), and Mainland ($4.63 \pm 0.935(3-7)67$) populations over a period from 1965 through 1971 showed significant geographic variation in clutch size. Padre Island lizards produced significantly smaller clutches than either Brazos Island ($t = 2.968, 173 \text{ df}, P < 0.01$) or Mainland ($t = 14.233, 217 \text{ df}, P < 0.001$) populations. Clutch size in the mainland population was significantly larger than that of both island populations.

Characteristics of egg samples from South Padre Island compared with those from the mainland follow, respectively: length, 11.5(9.0-13.3), 11.2(8.9-12.3); width, 6.8(5.5-7.8), 6.6(5.8-7.2); egg weight, 0.26(0.18-0.35), 0.24(0.19-0.34); clutch weight, 0.75(0.54-1.05), 1.13(0.77-1.77). Clutch weight averaged 17.3 per cent of the total weight of females from South Padre Island; mainland, 25.8. Thus, although clutch size was significantly greater in mainland than in South Padre Island populations, egg size was similar.

The size of corpora lutea ranged from 3.40 in females that had ovulated recently to 1.40 in females that had oviposited. All corpora lutea were of approximately the same size.

Male Reproductive Cycle

A detailed study of the testicular cycle and reproduction of male *H. propinqua* will be presented elsewhere. The following comments pertain to the South Padre Island population. Testis size remained relatively constant from May through August, although the testes of some individuals began to decrease in August (Fig. 4). By September, regression had occurred in most individuals although a few males retained enlarged testes. By October, regression was complete; no males were reproductively active. Mean testis size of juvenile males was only slightly smaller than that of one-year-old males in October and November. Testis and tubule enlargement were gradual from January to May. In April, a majority of the males examined were reproductively active, as evidenced by large testes and the presence of active spermatozoa in the epididymides. By May, almost all males were reproductively active.

When reproductively active, males developed a pink coloration on the underside of the tail and a variously colored dewlap spot. Coloration was much more extensive in mainland males. No island male less than 51 in SVL possessed reproductive coloration. Nonreproductive males on the study areas in 1971 (areas combined) comprised 13 per cent of the male population in May, 18.2 per cent in June, 8.3 per cent in July, and 2.0 per cent in August.

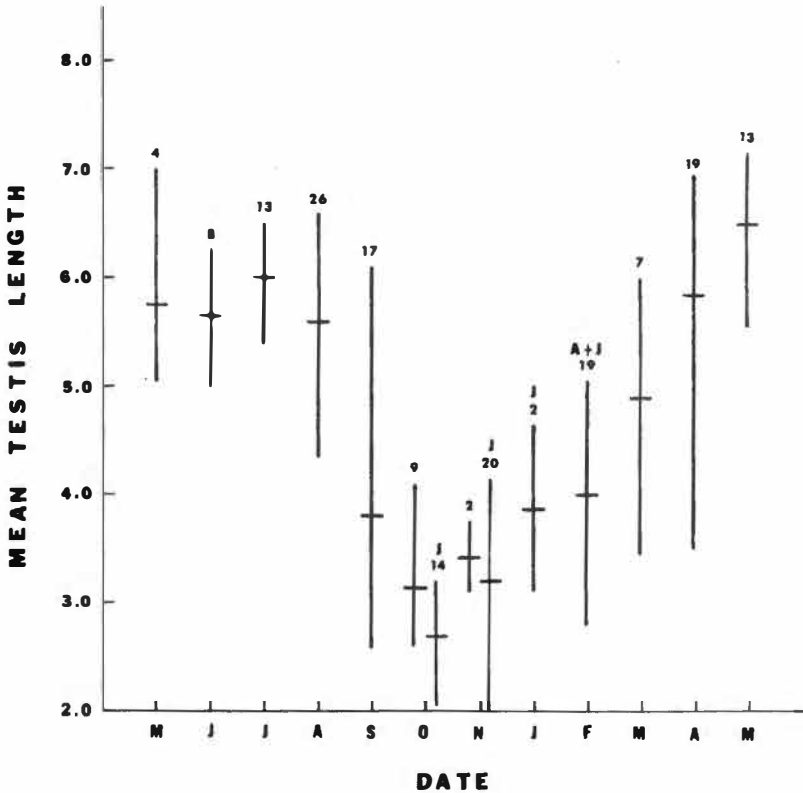


FIG. 4.—Seasonal variation in testes size of *H. propinqua*. Numbers above the vertical lines indicate sample size. Ranges (vertical lines) and means (horizontal lines) are based on averages of both testes. J indicates juveniles.

Males of other species of the genus *Holbrookia* appear to exhibit similar cycles. Parker (1973) reported the presence of spermatozoa in male *H. maculata* from 31 May to 1 August and in all male *H. texana* examined between May and July, but he noted that spermatozoa were absent in *H. texana* in August and September. Schrank and Ballinger (1973) stated that spermatozoa were recorded first in the seminiferous tubules of *Cophosaurus texanus* (= *Holbrookia texana*) near the end of March and that spermatozoa were absent after the first of August.

Fat Body Cycle

Hahn and Tinkle (1965) demonstrated the functional importance of stored fat to reproduction in lizards. Large fat bodies were rare in

adult females from May through September (Judd, 1973). However, in October, most of the females examined had large fat bodies. Females with small, medium, and large fat bodies were represented in the February sample. Most females had small fat bodies after the first clutch of eggs was laid and did not store significant amounts of fat in corpora adiposa again until after the reproductive season was ended (Judd, 1973).

No male exhibited large fat bodies from March to September (Judd, 1973). In September, three size categories (small, medium, and large) were represented. In the months from October through February, most males had moderate or large fat bodies. Males with large fat bodies were observed first in September, and this was the same sample wherein testis size showed marked regression (see Fig. 4). By October, almost all males had large fat bodies.

Schrank and Ballinger (1973) reported that fat bodies were depleted almost completely in male *Cophosaurus texanus* during the reproductive season and suggested that stored fat reserves are important in the male reproductive cycle. Parker (1973) reported that fat bodies were small in six and not detectable in five of 11 male *H. maculata* collected during the reproductive season. Thus, the data indicated that *H. propinqua* and these closely related species have similar fat body cycles that are related to the reproductive cycle.

Population Density

Intensive work, combined with the relatively small size of the study areas, small home range, and the fact that these lizards are not easily disturbed by human activity, made it possible to mark virtually all resident adults on the study areas each summer. It was not possible to mark all hatchlings.

In estimating adult density, it was necessary to determine which of the lizards initially marked on the study areas were marginal or transient individuals. I followed Tinkle (1967a) in considering residents as those lizards that were captured at least three times within the boundaries of the study areas (Table 6), but there was an additional temporal problem. A lizard captured the requisite three times in June, for example, could be killed or emigrate and be replaced by an immigrant that was subsequently also captured the requisite three times. Therefore, in an effort to compare density throughout the breeding season, I employed the minimum numbers method (Table 4).

Because of the late (July) initiation of field work, data for 1969 were excluded from density calculations. Numbers of juveniles listed in Table 4 are those actually captured and are not estimates of ju-

TABLE 6.—*Adult density (lizards per 0.368 hectare) of Holbrookia propinqua in 1970 and 1971.*

Grid	Sex	N	Absolute density	Ecological density
<i>1970</i>				
1	Male	23	25	25
	Female	18	20	20
	Total	41	45	45
2	Male	14	15	21
	Female	10	11	15
	Total	24	26	36
<i>1971</i>				
1	Male	19	21	21
	Female	21	23	23
	Total	40	44	44
2	Male	13	14	19
	Female	7	8	10
	Total	20	22	29
3	Male	21	23	23
	Female	29	32	32
	Total	50	55	55

venile density. Adult numbers began to decline on the study areas when large numbers of juveniles appeared in the populations in July. By August, the number of adults was reduced markedly. As will be shown below, this probably was due to adult mortality and not to emigration.

By the end of June, sufficient censuses were completed to mark all the adults on the study areas (compare Tables 4 and 6). The total number of adults known to be present in June slightly exceeded the average number of residents in all cases, except on grid 2 in 1971. This was to be expected because of the inclusion of marginal individuals in the total captured.

Tables 4 and 6 show marked variation in adult density between study areas. Density of grid 2 was markedly less than that of grid 1 in 1970 and less than those of grids 1 and 3 in 1971. Grid 2 contained only 0.276 hectare of suitable habitat, but calculation of ecological densities still showed that the number of adults on grid 2 was markedly less than that of the other two study areas (Table 6).

There was no change in adult density from 1970 to 1971 on grid 1, but grid 2 showed a slight reduction in numbers. In absolute numbers, only four lizards were involved. This loss could have resulted from a reorganization of the spatial relationships so that a greater number of

marginal individuals were excluded. However, I do not think this is true for an examination of total numbers marked revealed a similar decline in population density.

Even when allowance was made for unsuitable habitat on grid 2, a comparison of numbers of resident adults on the three study areas (Table 6) showed considerable variation. Grid 3 supported 20 per cent more lizards than grid 1 and 47 per cent more adults than grid 2 (based on ecological density). It is tempting to try to relate densities of lizards to per cent cover. Areas where cover approached 100 per cent were not occupied; however, the relationship between cover and density was not a simple inverse relationship. For example, grid 1 had a lower per cent cover in 1970 than in 1971 but showed no decrease in population density. Grid 1 had less cover in 1970 than grid 3 in 1971, yet grid 3 supported 20 per cent more adults.

Perhaps the most critical factor is the way in which the vegetation is distributed. The size of vegetational clumps may increase without affecting lizard density markedly so long as the clumps do not become contiguous. However, lizard density decreased when an increase in cover resulted from grasses, sedges, or rushes coming to occupy the bare areas between clumps of vegetation.

Examination of data provided by Judd (1973) supports this view. Sixty-seven per cent of the increase in total cover on grid 1 from 1970 to 1971 was due to increase in the per cent cover contributed by bluestem whereas only 11.2 per cent of the increase was due to star rush, which occupies areas between clumps of grasses. But on grid 2, more than 50 per cent of the increase in total cover was due to rushes (31.7 per cent) and red lovegrass (21.7 per cent), which came to occupy the areas between clumps of bluestem and sea oats.

On grid 3, 76.3 per cent of the total cover in 1971 was due to the clumping grasses, bluestem, and sea oats whereas another 17.6 per cent of the total cover was contributed by *Oenothera* sp., which grew singly. There were no rushes or red lovegrass on grid 3.

It seems reasonable to conclude that the decrease in number of adults on grid 2 from 1970 to 1971 was due, in part, to an increase in plant cover in areas between clumps of bluestem and sea oats.

Sex Ratios

Sex ratios based on total number of adult and juvenile lizards (males precede females) marked on the study areas were: grid 1: 1969, adults 10, 7; 1970, adults 34, 31; 1971, adults 31, 33; juveniles 15, 15; grid 2: 1969, adults 7, 5; 1970, adults 23, 17; 1971, adults 17, 12; juveniles 8, 7; grid 3: 1971, adults 41, 45; juveniles 4, 6. None of the pop-

ulations departed significantly from a 50:50 ratio in a given year. Grid 2 consistently supported more males than females, but a chi-square test of the sex ratio for all years combined was not significant ($X^2 = 1.048$, 2 df, $P > 0.5$).

Table 4 shows the number of males and females known to occur on the study areas during each month of the summer in 1970 and 1971. Although grids 1 and 2 had more males than females in July and August, the ratios for a given month and area did not differ significantly from 50:50. Likewise, combined samples of grids 1 and 2 during July and August did not depart significantly from equality.

Age Structure

Hatchlings and juveniles were recognized easily by size even though juveniles of several sizes were present simultaneously in the population. Adults could not be assigned reliably to age classes on the basis of size. Lizards known to be two-year-olds were not larger than many one-year-old lizards. The only way one could assign adults accurately to age categories was to know their previous history in the population.

Biomass

I have taken the number of adults marked on a study area in a given month as the density of adults for that month and then have totaled the weights of these individuals to arrive at an estimate of adult biomass. Each lizard was weighed on the initial capture, and most were weighed several times subsequently. If a weight record was absent for a given month, I considered the last recorded weight as the weight of the individual for that month. If two or more weights were available for an individual in a given month, a mean was taken and was used in the accumulation of adult biomass.

I calculated juvenile biomass in a similar manner, except when a weight record for a given month was absent. In this case, I compensated for growth in mass during the elapsed time from the last weighing by using the growth rates presented in an earlier section of this paper.

The greatest biomass supported on the study areas (Table 7) was about 240 grams (grid 1 in June 1970 and grid 3 in June 1971); it appeared that the probable maximum biomass that could be supported in optimum habitat was approximately 653 grams per hectare.

Biomass reached a peak in May and June before hatchlings appeared. The addition of juveniles to the population did not increase biomass significantly, for adults began to disappear from the popula-

TABLE 7.—Estimates of biomass (B) and density (D) for adult and juvenile *Holbrookia propinqua* on the study areas in 1970 and 1971. Density and biomass figures are numbers and grams per 0.368 hectare respectively.

Month	Grid 1						Grid 2						Grid 3					
	Adults		Juveniles		Total		Adults		Juveniles		Total		Adults		Juveniles		Total	
	D	B	D	B	D	B	D	B	D	B	D	B	D	B	D	B	D	B
	1970																	
June	48	236.0	00	0.0	236.0	27	109.6	2	1.0	110.6								
July	27	136.9	10	6.2	143.1	23	99.6	13	7.0	106.6								
August	10	49.0	30	21.3	70.3	9	34.2	20	15.3	49.5								
	1971																	
May	43	190.4	0	0.0	190.4	20	76.3	0	0.0	76.3								
June	46	196.6	2	1.0	197.6	15	59.9	0	0.0	59.9	57	241.0	0	0.0	241.0			
July	30	136.0	21	17.6	153.6	17	69.5	10	8.4	77.9	46	197.8	4	2.8	200.6			
August	15	71.6	15	16.2	87.8	7	27.5	9	10.1	37.6	36	154.3	6	5.1	159.4			

TABLE 8.—Comparison of home range size (Probability Density Function, in hectares) for sex and age categories of *Holbrookia propinqua*. Means and standard deviations are given in meters.

Sex and age	N	Mean recapture radius	SD	PDF Area
Adult males	80	7.96	3.21	0.065
Adult females	76	5.04	2.06	0.028
Subadult males	15	9.81	3.93	0.097
Juvenile males	8	4.86	1.60	0.020
Juvenile females	10	3.66	2.48	0.020
Juveniles (males, females, and unsexed)	43	4.68	1.86	0.020

tion at the same time so that, in fact, biomass was lowered as juveniles entered the population.

Monthly and yearly variation in biomass is related primarily to variation in the number of adults present. Average adult weight was similar throughout the reproductive season on a given study area; therefore, adults did not exhibit weight loss as the summer progressed. Because survival figures (presented below) indicated about 90 per cent mortality each year, a maximum of about 588 grams per hectare was available to predators.

Home Range

From July 1969 to September 1971, a total of 538 lizards was marked, including 191 adult males, 170 adult females, 46 juvenile males, 53 juvenile females, and 78 unsexed juveniles. These lizards were recaptured 2279 times for an average of 4.2 captures per lizard.

Table 8 compares mean recapture radii and home range sizes (probability density function method) among sex and age categories. Subadult males exhibited larger mean recapture radii and home ranges than did adult males, but the difference was not significant. Apparently, juveniles did not increase significantly the size of their home range during the first six weeks of life because juveniles less than 30 in SVL and juveniles 30 to 39 in SVL had almost identical mean recapture radii ($t=0.162$, 37 df, $P>0.8$). In addition, the mean recapture radius of adult females was not significantly larger than that of juveniles ($t=0.412$, 87 df, $P>0.6$). However, the mean recapture radius of adult males was significantly larger than that of adult females ($t=6.761$, 154 df, $P<0.001$).

There was a direct relationship between number of captures and home range size when the minimum polygon method was employed. However, in both sexes of *H. propinqua*, increasing the number of captures beyond 10 did not result in any appreciable increase in mean home range size. Consequently, I have utilized only those individuals captured 10 or more times in calculating home range size. No juveniles were captured 10 or more times so it is not possible to estimate accurately their home range size by this method.

Home range sizes, in hectares (minimum polygon), between males and females on the three study areas (mean followed by sample size; males precede females) were: grid 1: 0.024, 11; 0.010, 16; grid 2: 0.042, 13; 0.019, 6; grid 3: 0.026, 5; 0.008, 7. Mean home range size for the 29 males was 0.033; for the 29 females, 0.012. As with the probability density function, males of each area exhibited markedly larger home ranges than did females of the same area. Male home ranges were 2.8(2.2-3.0) times as large as those of females of the same grid. Mean values for males of grids 1 and 3 were almost identical whereas the mean for males of grid 2 was considerably, but not significantly, larger. The same relationship existed for females.

Shifts in individual home ranges have been assessed by calculating the distance between centers of activity and per cent area overlap in successive years. The results of these calculations are summarized in Table 9. The mean distance between activity centers of males as juveniles and adults is similar to the mean distance between activity centers of adult males from one year to the next. The distance between activity centers was less for females. Although data are limited for males as subadults and adults in successive years and for females as adults in successive years, some indication of the relative permanence of the home range can be gained by comparing mean distance between activity centers (Table 9) and the mean recapture radius (Table 8). These comparisons indicate some reorganization in the spatial relationships of individuals from one year to the next because mean distance between activity centers exceeds mean recapture radius in all cases, except for adult females in successive years. However, the degree of reorganization appears to be slight for comparison of per cent area overlap shows 50 per cent or more overlap in all cases except for males as subadults and adults.

Twenty-three naturally occurring male versus male aggressive encounters were observed in the field. These were supplemented by 13 staged encounters wherein nonresident males were introduced to resident males (males within their home ranges). In addition, eight naturally occurring female versus female aggressive encounters were ob-

TABLE 9.—Distance between activity centers (in meters) and per cent area overlap of home ranges in successive years for selected age and sex groupings of *Holbrookia propinqua*.

Age classes compared	Distance between activity centers			Average home range overlap (%)
	Range	Mean	N	
<i>Male</i>				
Juvenile and adult	3-21	11.0	7	54.50
Subadult and adult	7-27	17.1	2	
Adult and adult	6-19	11.6	6	50.73
Total	3-27	12.0	15	45.75
<i>Female</i>				
Juvenile and adult	3-22	9.2	11	54.50
Adult and adult	1-5	3.0	2	78.74
Total	1-22	8.3	13	58.27

served and these were augmented with 14 staged encounters involving introduction of nonresident females. The details of these observations will be reported elsewhere, but it was apparent that both sexes of *H. propinqua* actively defended a territory.

The data suggest that both sexes defend at any point within their home ranges, but sufficient observations to detail the extent of even one lizard's territory are lacking. Therefore, it is suspected, but unsubstantiated, that home range and territory are equivalent in this species.

Home ranges (minimum polygon) of males overlapped considerably. Often, this was due to the presence of a subadult male within the confines of the home range of one or more adult males, but the home ranges of adult males also commonly overlapped, although slightly, and there was no evidence of a hierarchical social structure among males. Home ranges of females rarely overlapped at all, and when it occurred, it was very small.

Based on the data presented here, juveniles of both sexes confined their movements to relatively small areas from hatching to their first winter retreat. Emerging the following spring, subadult males increased their movements markedly and established territories. Males that hatched from late clutches might not have reached adult size at the onset of the breeding season. These males did not possess territories and tended to wander considerably but were tolerated within the territories of adult males if they exhibited submissive behavior. Females did not increase significantly their movements the following spring; thus, their adult home range was only slightly larger than

their juvenile home range. Engeling (1972) noted that in the closely related species *Cophosaurus texanus* the mean home range size of juvenile males was greater than that of adult males. He attributed this to the probability that some of the juvenile males did not have an established home range and, consequently, tended to wander over a relatively large area. He also stated that large males tolerated small males that ranged into their territories.

Home range size appeared to be affected by variation in habitat. In areas where vegetation was relatively dense, such as grid 2, home range size was relatively larger in both sexes. This relationship may be explained by the fact that lizards in these areas were able to move farther without encountering another lizard than was possible in areas of sparse vegetation.

An alternative explanation may be that habitats, such as the one represented by grid 2, are marginal ecologically. Consequently, productivity in terms of lizard biomass was lower. This hypothesis makes the assumption that lizards would maintain larger home ranges in order to obtain necessary food. It is supported in part by the fact that males of grid 2 were significantly smaller than males of grid 1, although the two grids are only 67 meters apart.

Still another possibility is that home range size is inversely related to density, that is, as density of lizards increases, home range size decreases. Quite probably, all of these factors are involved and are responsible for the variation in home range size among the study areas.

It is extremely difficult to compare home range size among lizard species. Spoecker (1967) and Tinkle (1967*b*) discussed, in detail, reasons for this difficulty. Home range size of *Holbrookia propinqua* falls within the range of variation for iguanid lizards reported by other investigators (Blair, 1960; Brooks, 1967; Engeling, 1972; Gennaro, 1972; Jorgensen and Tanner, 1963; Tinkle *et al.*, 1962; Tinkle, 1967*a*, 1967*b*) and is also quite similar to values reported by Tinkle (1967*a*, 1967*b*) for *Uta stansburiana* (mean: 0.044 for 143 males and 0.012 for 171 females). This is not surprising in view of the similarities in size and ecological requirements of the two species.

Gennaro (1972) studied the home range size and movements of *Holbrookia maculata* in eastern New Mexico. He employed the minimum polygon method of estimating home range size and reported that home range size could be estimated with a minimum of four captures for both males and females. Gennaro (1972) found the average home range size of male *Holbrookia maculata* (0.100 for 10 males) was larger than that of females (0.060 for 10 females), but that the difference was not significant. The home range size of male *Holbrookia maculata* is over three times that of male *H. propinqua* whereas the

home range size of female *H. maculata* is over five times that of female *H. propinqua*. The home range size of the one juvenile *H. maculata* (0.010) reported by Gennaro (1972) is very similar to that of adult female *H. propinqua*.

Gennaro (1972) compared movements among sexes and age classes by comparing the average distance moved between captures. He found that the mean distance moved by juvenile males did not differ significantly from the average distance moved by juvenile females, but that the mean distance moved by juveniles (sexes combined) was significantly lower ($P < 0.01$) than the mean distance moved by adults.

These data suggest that juvenile *H. maculata* and juvenile *H. propinqua* have similar home range sizes, but that unlike *H. propinqua*, both sexes of *H. maculata* significantly increase the size of their adult home ranges.

The larger home range size in *H. maculata* may be a function of differences in productivity of the habitats and the amount of lizard biomass per unit area. On South Padre Island, only two species of lizard occurred on the study areas, *H. propinqua* and *Cnemidophorus sexlineatus*. In eastern New Mexico, five species of lizard were found on the study area: *H. maculata*, *C. sexlineatus*, *Sceloporus undulatus*, *Phrynosoma cornutum*, and *Eumeces obsoletus*.

Other factors that could have contributed to differences in home range size include structural differences in the habitat and differences in population structure and density.

Engeling (1972) studied the home range ecology and movements of *Cophosaurus* (= *Holbrookia*) *texanus* in Comal County, Texas, and employed the minimum polygon method of estimating home range size. Mean home range sizes in hectares were: 0.022 for two males, 0.011 for four females, and 0.024 for nine juveniles. Although *C. texanus* is markedly larger than *H. propinqua*, the home range sizes of these two species are similar. Engeling (1972) found that males moved significantly greater distances than females, but no significant differences existed in comparisons of distances moved by adult females versus juvenile females, juvenile males as opposed to juvenile females, or hatchling males versus hatchling females.

Gennaro (1972) observed that home range overlapped between both sexes of *H. maculata*. Engeling (1972) reported results for *Cophosaurus texanus* similar to those obtained here for *H. propinqua*, that is, home ranges of males overlapped considerably whereas those of females were usually exclusive.

Data presented here show that as young *H. propinqua* reach sexual maturity they simply range more widely in the same area. The juvenile

range normally is overlapped broadly by the adult home range. Late maturing males (subadults) tend to disperse farther and hence may come to occupy an entirely different area. Females are more sedentary than males.

Engeling (1972) showed that as young *Cophosaurus texanus* increased in size they occupied a larger area. He also presented data that indicated the distances moved by males and females were similar until sexual maturity was attained, after which time males moved farther than females.

The data confirmed the presence of home range behavior in *H. propinqua*. With the exception of subadult males, all sex and age categories restricted their movements to a limited area. Apparently, a given lizard recognizes its home range, for numerous field observations confirm that disturbed lizards often run directly to the nearest rodent or crab burrow. Also, when chased, a lizard will turn or double back as it approaches the presumed home range boundary. Numerous authors have pointed out that a knowledge of the home range is of a selective advantage for it facilitates escape from predators.

Blair (1960) showed that per cent area overlap in successive years for adult female and male *Sceloporus olivaceous* was 34.5 and 23.8 per cent, respectively. He further stated that once a *S. olivaceous* reached sexual maturity it usually remained in the same area for the remainder of its life, although the details of the boundaries varied from year to year. The same statements hold true for *H. propinqua*.

Dispersal

Movement of young lizards away from the hatching site as they grew larger was used to estimate relative dispersal in *Holbrookia propinqua*. The hatching site was considered to be the first capture of a lizard 27 or less in SVL. The average maximum distance from the hatching site of 45 juveniles (sexes combined) was 7.7 meters. This figure was calculated for juveniles during their first season of growth. The distance is only 1.6 times the average recapture radius of juveniles and is less than the mean recapture radius of adult males. Based on this information, it seems unlikely that significant immigration or emigration of juveniles takes place.

Information on dispersal from hatching sites to the adult home range is available for six males and nine females. Dispersal in this case has been determined by calculating the distance from the hatching site to the center of the adult home range. Males moved an average of 11.7 meters ($s=7.2$) and females an average of 10.3 meters ($s=7.0$) from their hatching site. The difference between the two

means is not significant ($t=0.400$, 13 df, $P>0.9$). The pooled mean is 10.9 meters.

Very little information is available in the literature concerning dispersal of lizards. Tinkle (1967b) reported male *Uta stansburiana* shifted the center of the adult home range 25.6 meters from the hatching site whereas for females this shift averaged only 16.2 meters. Harris (1964) reported that all hatchling males of *Agama agama* left the areas they utilized as juveniles; however, hatchling females often remained in the same areas and eventually mated with the dominant resident male. Blair (1960) reported mature male *Sceloporus olivaceus* moved an average of 71.3 meters from their hatching sites and females an average of 48.8 meters from theirs. Engeling (1972) presented data showing that adult *Cophosaurus texanus* averaged 30.2 meters distance from their hatching site.

Comparison of dispersal of *Holbrookia propinqua* with data available for other lizard species emphasizes the sedentary nature of *H. propinqua*. Absence of significant dispersal in *H. propinqua* did not result in intense competition between age groups, for there was essentially an annual turnover in the population.

Immigration and Emigration

A boundary area 30.5 meters wide around the perimeter of the study areas was marked with stakes and was traversed at frequent intervals in 1970 and 1971. Juveniles were considered to be immigrants if originally marked outside the grid and subsequently recaptured at least twice on the grid. Adults were classified as immigrants if originally captured outside the grid and subsequently captured three or more times on the grid. Juveniles were considered to be emigrants if originally marked on the grid, recaptured at least once on the grid, and subsequently recaptured outside the grid without returning to it. Adults were regarded as emigrants if captured three or more times on the grid and subsequently recaptured outside the grid without returning to it.

Combining the data for all three study areas for 1970 and 1971 showed that only four lizards could be classified as immigrants and only five as emigrants. No juveniles were involved in these movements, although one immigrant and one emigrant were originally marked as juveniles. Three of the immigrants were males and four of the emigrants were males. All males measured 54 or less in SVL and two were 48. All but one of the movements occurred in July and August at a time of relatively low adult density.

A total of 284 adults were marked in 1970 and 1971 on the study areas and boundary areas so that the frequency of immigration was 1.4 per cent and the frequency of emigration was 1.8 per cent. These figures suggested that the two processes were balanced and that the percentage of immigration and emigration was quite low. Tinkle (1967a) reported estimates of 6 per cent for emigration of *Uta stansburiana*, and Blair (1960) estimated about 5 per cent emigration for young *Sceloporus olivaceus*.

The rates presented herein might be low estimates for two major reasons. First, not all juveniles on the study areas and boundary areas were marked; hence, there might have been some movements of juveniles that were not detected. Second, some immigration and emigration might have occurred before all resident adults were marked on the study areas, although I do not think this would produce a significant change in the estimates because virtually all resident adults were marked within one month.

Survivorship

Egg survivorship can be measured accurately by determining the total number of eggs produced on an area and the total number of hatchlings resulting from them (Tinkle, 1972). Because it was not possible to mark all hatchlings, egg survivorship could be estimated only indirectly. A knowledge of the number of resident females on each study area and their reproductive potential allowed an estimate to be made of the number of eggs produced each season. I then used the one-year-old lizards as the cohort from which to determine survivorship from egg to an age of one year.

In calculating the number of resident females, I took the monthly totals presented in Table 4 and assumed a density in May 1970 equal to that of June 1970. For calculations of reproductive potential, it was assumed that each of the females present in a given month produced a clutch of three eggs. This was a realistic estimate of reproductive potential of the population inasmuch as it accounted for loss during the breeding season and assumed that only about 25 per cent of the females produced four clutches. The average number of resident one-year-old lizards present in 1971 (Table 6) was used for the density of the one-year-old cohort. Allowance was made for known two-year-old animals in these groups, however. No known two-year-olds were present on grid 2 in 1971. Two males and one female were two-year-olds on grid 1, so that the number of resident one-year-old adults on grid 1 in 1971 was 37 and the number on grid 2 was 20.

TABLE 10.—*Survivorship among marked Holbrookia propinqua on South Padre Island, Cameron County, Texas. Data for 1969 to 1971 combined.*

Age class and study area	Sex	Total marked	Total recovered in subsequent year	Per cent survival
Grid 1				
Hatchlings		35	4	11.4
Juveniles		21	8	38.1
One-year-old	Male	45	5	11.1
	Female	46	1	2.2
Two-year-old	Male	3	1	33.3
	Female	0	0	00.0
All adults		94	7	7.5
Grid 2				
Hatchlings		27	3	1.1
Juveniles		28	11	39.3
One-year-old	Male	28	3	10.7
	Female	22	2	9.1
Two-year-old	Male	3	0	00.0
	Female	2	0	00.0
All adults		55	5	9.1
Totals				
All hatchlings		62	7	11.3
All juveniles		49	19	38.8
All one-year-old		141	11	7.8
All two-year-old		8	1	12.5

Reproductive potential of grid 1 females in 1970 was 186 eggs, and the reproductive potential of grid 2 females was 117. Thus, egg survival to an age of one year on grid 1 was 20.4 per cent, and on grid 2 it was 17.1 per cent. The mean egg survival for the two grids was 19.1 per cent.

Juvenile lizards were divided into two age categories: hatchlings or juveniles marked in their first summer or autumn. The data in Table 10 are for hatchlings and juveniles marked in 1969 or 1970 and recovered in the following year.

Obviously, juveniles had a distinct advantage in survival over hatchlings. It appeared that significant losses occurred largely in the first two to three weeks of life, for it would take the smallest hatchlings approximately 18 days to reach a SVL of 28 (the minimum juvenile SVL).

Per cent survivorship of hatchling and juvenile categories combined equals 23.4. Assuming this figure accurately reflected juvenile survival, subtraction of percentage egg survival to one year would give an estimate of the percentage egg hatching. These calculations sug-

TABLE 11.—Life table for a Padre Island population of *Holbrookia propinqua*.
 $lx \times mx =$ contribution to replacement rate (R_0) by animals of age x .

Age class	Age in years (x)	Survivorship (lx)	Fecundity (mx)	Product (lx × mx)
Egg	0.00	1.000	0	0.0
Hatchling	0.13	0.957	0	0.0
One-year-old	1.12	0.234	4.5	1.053
Two-year-old	2.12	0.018	4.5	0.081
Three-year-old	3.12	0.002	4.5	0.009
				$R_0 = 1.143$

gested that 95.7 per cent of the eggs laid by resident females hatched. This percentage might be considerably lower if females from outside the grids sometimes lay eggs within the study areas and if a portion of the resident adults included in the 1971 populations are immigrants. Tinkle and Ballinger (1972) reported an egg survivorship of 85 per cent for Texas populations of *Sceloporus undulatus*. Using similar methods, Tinkle (1973) arrived at a hatching success of about 100 per cent for *Sceloporus graciosus*.

Few adult lizards live for more than one year (Table 10). Thus, there is essentially an annual turnover in the population. Due to the small number of one-year-old animals recovered in the following year, the observed difference between males and females of grid 1 probably was not significant.

Survival figures reported here should be considered minimal for there was some loss, although small, due to emigration.

Life Table for Holbrookia propinqua

The egg was chosen as the first age class (Table 11). Survival (lx) from egg to hatching was considered equal to the difference between egg survival to an age of one year and the mean of hatchling and juvenile survival to an age of one year. Survival of hatchlings to age one year was based on the mean of the independently determined survivorship of hatchlings and of juveniles. Survival of one-year-old and older lizards was based upon figures presented in Table 10 for all one-year-old and two-year-old lizards and a survival rate for females equal to that of males. Each female was assumed to produce three clutches of three eggs each, and one-half of the eggs were assumed to be female.

The calculated replacement rate (R_0) was close to unity (Table 11). It was apparent that R_0 was affected little by the contribution of two

and three-year-old females. The replacement rate would remain near unity if there were no females older than one year in the population.

Frequency of Broken Tails and Predation

Pianka (1970a), Pianka and Parker (1972), Tinkle (1972), and Tinkle and Ballinger (1972) assumed that the frequency of tail loss in lizards indirectly measured the frequency of encounters with predators. Some tail breaks may occur as a result of intraspecific fighting; however, if there is no positive correlation between population density and the percentage of broken tails, one may reasonably assume that a difference between populations reflects a real difference in frequency of encounters with potential predators.

Tinkle (1972) pointed out that tail break frequencies need to be adjusted to account for life expectancies and lengths of activity seasons when comparing frequencies between populations. I assumed an activity season of 12 months, based on the collection of lizards in all months of the year except December, and also that lizards of all populations matured at the same age and had life expectancies similar to those of the Padre Island population.

Table 12 compares tail break frequency among males, females, and juveniles of three populations. These figures were based on frequencies at first capture of marked lizards plus frequencies among lizards collected for reproductive studies. In all populations, tail break frequency was highest among adult males, next highest in adult females, and lowest among juveniles. Tail break frequency may be higher among males than among females because of the more frequent movements and greater distances moved by the former. Males might be more susceptible to predation inasmuch as their movements take them farther away from concealing vegetation and burrows and attract the attention of potential predators. Females tend to remain near concealing vegetation and move less often. Tail breaks among juveniles were probably few for the same reasons that applied to adult females, plus the fact that their life span, and, hence, exposure to possible predation has been much shorter than that of adults.

The higher frequency of breaks among mainland lizards suggested greater predation pressure on the mainland population than on the island populations. A comparison of the number of different potential predators for the South Padre Island population and the mainland population supported this hypothesis. The list of potential predators occurring on the mainland was derived from personal observations and published sources. As shown in Table 13, the number of potential predators on the mainland far exceeds the number present on Padre

TABLE 12.—Tail break frequencies in three populations of *Holbrookia propinqua*. M = males, F = females, and J = juveniles.

Population	N	M	Per cent	N	F	Per cent	N	J	Per cent
Padre Island	295	53	18.0	287	26	9.1	181	11	6.9
Brazos Island	14	2	14.3	15	1	6.7	4	0	0.0
Mainland	63	17	27.0	54	11	20.4	48	3	6.3

Island. *Coluber constrictor* is probably the most important predator of earless lizards on the island. On two occasions, I observed individuals in the process of eating earless lizards. I also saw *Cnemidophorus sexlineatus* and adult male *Holbrookia propinqua* capture and swallow hatchling *H. propinqua*. It is perhaps questionable whether ground squirrels or coyotes take active earless lizards, but they may locate and eat buried individuals. I have not seen badgers or skunks on South Padre Island, but Raun (1959) reported them from North Padre Island. If these mammals are present on South Padre Island, they doubtlessly prey on earless lizards. Hirth (1963) reported seeing ghost crabs eating *Ameiva quadrilineata* and *Basiliscus vittatus* on a Costa Rican beach. Both *Ocypode albicans* and *Gecarcinus lateralis* are large enough to capture buried earless lizards. The use of crab burrows as retreats by *H. propinqua* may increase the frequency of encounters between lizards and crabs.

I never observed gulls preying on earless lizards but I have seen them capture *Sceloporus olivaceous* on the mainland adjacent to South Padre Island. No hawks were seen on the island during the course of the study, and I have never seen them capture earless lizards on the mainland, but do not doubt that they do so. Although road runners were not seen on South Padre Island, Selander *et al.* (1962) reported them on the Tamaulipan barrier island. Road runners are present on the mainland and probably capture *Holbrookia propinqua*.

It seems likely that snakes are the primary predators of earless lizards on the mainland, and the larger number of predatory snake species alone (Table 13) may easily account for the increase in predation pressure suggested by tail break frequency. Supportive evidence for decreased predation pressure on island lizard populations is given by Rand's (1954) study of an island and mainland population of *Cnemidophorus lemniscatus*. Rand found the frequency of tail breaks to be eight times higher in the mainland population.

TABLE 13.—*Known and potential predators of Holbrookia propinqua for Padre Island and South Texas mainland populations.*

Predators	Island	Mainland
Mammals	<i>Didelphis marsupialis</i>	<i>Didelphis marsupialis</i>
	<i>Conepatus leuconotus*</i>	<i>Conepatus leuconotus</i>
	<i>Taxidea taxus*</i>	<i>Spilogale putorius</i>
	<i>Canis latrans</i>	<i>Mephitis mephitis</i>
	<i>Spermophilus spilosoma</i>	<i>Taxidea taxus</i> <i>Canis latrans</i> <i>Urocyon cinereoargenteus</i> <i>Spermophilus spilosoma</i>
Birds	<i>Larus argentatus</i>	<i>Elanus leucurus</i>
	<i>Larus atricilla</i>	<i>Circus cyaneus</i>
	<i>Larus delawarensis</i>	<i>Falco sparverius</i>
	<i>Larus pipixcan</i>	<i>Lanius ludovicianus</i>
		<i>Corvus cryptoleucas</i> <i>Cassidix mexicanus</i> <i>Geococcyx californianus</i>
Reptiles	<i>Cnemidophorus sexlineatus</i>	<i>Cnemidophorus sexlineatus</i>
	<i>Holbrookia propinqua</i>	<i>Holbrookia propinqua</i>
	<i>Coluber constrictor</i>	<i>Coluber constrictor</i>
		<i>Masticophis flagellum</i>
		<i>Salvadora lineata</i>
		<i>Arizona elegans</i>
		<i>Pituophis melanoleucus</i>
		<i>Lampropeltis calligaster</i>
		<i>Lampropeltis doliata</i>
		<i>Lampropeltis getulus</i>
		<i>Cemophora coccinea</i>
	<i>Rhinocheilus lecontei</i>	
	<i>Hypsiglena torquata</i>	
	<i>Sistrurus catenatus</i>	
	<i>Crotalus atrox</i>	
Invertebrates	<i>Gecarcinus lateralis</i>	
	<i>Ocyrode albicans</i>	

*Literature records only.

Life History Strategy

Tinkle (1969) and Tinkle *et al.* (1970) suggested that the evolutionary reproductive strategies of lizards could be grouped into early-maturing, multiple-brooded species, and late-maturing, single-brooded species. Pianka (1970*b*) and Ballinger (1973) pointed out that this dichotomy reflects the well-known theoretical strategies of *r* and *K*

selection. Pianka (1970b) argued that these are not exclusive alternate strategies but are simply endpoints of an r - K continuum. Subsequently Tinkle and Ballinger (1972) and Tinkle (1972) demonstrated that in both relatively r -selected and K -selected populations of *Sceloporus undulatus* multiple broods might be produced. Ballinger (1973) showed that early maturity may occur in the otherwise relatively K -selected species *Sceloporus jarrovi*.

Turner *et al.* (1970) pointed out that all long-term studies of lizard populations have shown year-to-year variation in reproductive success because of changes in clutch size and the frequency of clutch deposition. They also showed significant year-to-year variation in survivorship in a Nevada population of *Uta stansburiana*. Tinkle and Ballinger (1972) and Tinkle (1972) showed that variations occur in life history characteristics among populations of *Sceloporus undulatus* that are as great as those among species. Parker (1972), in a study of the western whiptail lizard *Cnemidophorus tigris gracilis* in Arizona, indicated that temperate species of the lizard genus *Cnemidophorus* seem to have a narrow range of similar reproductive strategies. Parker (1972) compared abundance and reproductive patterns of nine lizard species from South Mountain, Maricopa County, Arizona, and suggested that parallel evolution may have involved selection for similar types of reproductive strategies, feeding habits, and other factors in pairs of flatland-montane ecological equivalents. He raised two related questions: 1) has selection for parallel reproductive strategies occurred because of environmental demands or from innate, inflexible reproductive characteristics? and 2) is a particular reproductive strategy intimately tied to a particular saurian niche? Tinkle and Ballinger (1972) argued that the differences in life history characteristics between populations of *Sceloporus undulatus* resulted from selection that favored one set of life history genotypes in one population and other genotypes in another population. However, they pointed out that the question of whether the observed differences exist because of different ecologies or genetic adaptations to these ecologies is not resolved.

Information presented in this study showed interpopulation variation in clutch size. However, a comparison of life history characteristics of *Holbrookia propinqua* and closely related species showed great similarity. Species of the genera *Callisaurus*, *Holbrookia*, *Cophosaurus*, and *Uma* are regarded as a closely related group and are collectively referred to as sand lizards because of similar morphological adaptations. Some of the salient features of the reproductive strategies in these lizards are compared in Table 14. I have included information

TABLE 14.—Summary of reproductive strategies for *Holbrookia propinqua* and related lizards. Format of the table and much of the data are from Pianka and Parker (1972).

Species	Location	No. of clutches	Mean clutch size	Periods of egg laying	Max. testis size	Age at maturity (years)	Min. SVL at maturity		Authority
							M	F	
<i>Holbrookia propinqua</i>	Texas	3	3.1 Is. 4.6 Mn. Range (4-12)	May-Aug.	May-Aug.	1	50	44	This paper
<i>Holbrookia lacerata</i>	Texas		6.1	May-Aug.	May-Aug.				Axtell (1956)
<i>Holbrookia maculata</i>	Texas	?(2)	4.9	?(May-Aug.)		1	45		Tinkle <i>et al.</i> (1970)
<i>Holbrookia maculata</i>	New Mexico		7.0	May-Aug.		1	44	45	Gennaro (1974)
<i>Holbrookia maculata</i>	Kansas			Apr.-Sept.					Fitch (1970)
<i>Holbrookia maculata</i>	Arizona & Mexico								Fitch (1970)
<i>Holbrookia texana</i>	Texas		5.3	Jun.-Aug.			53	55	Cagle (1950)
<i>Holbrookia texana</i>	Texas		5.0	Apr.-Aug.			48		Johnson (1960)
<i>Cophosaurus texanus</i>	Texas	3	6.0	Apr.-Aug.	Apr.-Jun.	1		50	Ballinger
(= <i>Holbrookia texana</i>)									<i>et al.</i> (1972)
<i>Cophosaurus texanus</i>	Texas	Multiple	6.1	Apr.-Aug.	May-Jun.	1	50	51	Engeling (1972)
<i>Callisaurus</i>	Calif. & N. Nevada	?	4.2	Jun.-Jul.	May-Jun.		70	65	Kay <i>et al.</i> (1970)
<i>druconoides</i>		Multiple							Pianka & Parker (1972)
<i>Callisaurus</i>	Arizona, Calif., & S. Nevada	?	4.3	May-Aug.	Jul.-Aug.	1	67	63	Pianka and Parker (1972)
<i>druconoides</i>		Multiple							
<i>Uma inornata</i>	California		2.4	May-Sept.	Apr.-May	1-2	80	70	Mayhew (1965)
<i>Uma notata</i>	California		2.0	May-Aug.	Apr.-May	1-2	80	70	Mayhew (1966b)
<i>Uma scoparia</i>	California		2.6	May-Jul.	Apr.-May	1-2	80	70	Mayhew (1966a)
<i>Uta stansburiana</i>	Texas	3	4.0	Mar.-Aug.	Mar.-Jun.	1		38	Tinkle (1961)
<i>Uta stansburiana</i>	Colorado	3	3.2	Apr.-Jul.	Apr.-Jul.	1-2	?(42)	37	Tinkle (1967b)
<i>Uta stansburiana</i>	Nevada	2-5	3.5-4.0	Apr.-Jul.	Apr.-Jul.	1-2		?(36)	Turner <i>et al.</i> (1970)
<i>Uta stansburiana</i>	Arizona			Feb.-Jul.	Dec.-Jan.				Asplund and Lowe (1964)

TABLE 15.—Comparison of life history characteristics of the Australian agamid *Amphibolurus isolepis* and the North American iguanid *Holbrookia propinqua*.

Characteristic	<i>Holbrookia propinqua</i>	<i>Amphibolurus isolepis</i>
Habitat	Aeolian sand dunes	Sandy deserts
Dominant vegetation	Perennial grasses	Perennial grasses
Location	In open, between shrubs or grass clumps or in open shade adjacent to plant	In open, between shrubs or grass clumps or in open shade adjacent to plant
Mode of escape	Male, long runs Female, short dash to vegetation	Long runs
Annual activity	All year	All year
Diel activity	Aut. and Win.—Unimodal Spr. and Sum.—Bimodal	Aut. and Win.—Unimodal Spr. and Sum.—Bimodal
Mean Tb (all active lizards)	37.5° C	37.7° C
P Tb	37.9° C	37.0° C
Feeding strategy	Sit and wait	Sit and wait
Food	Opportunistic insectivore Ants predominate in juveniles	Opportunistic insectivore Ants predominate
Coloration	Sexually dimorphic Females more colorful	Sexually dimorphic Males more colorful
Male cycle	Active—mid spring through late summer	Active—early spring through midsummer
Female cycle	Gravid—late spring to early autumn	Gravid—early spring through late summer
No. of clutches	2-4, mode 3	2 or 3
Clutch size	Range=1-7, X=3.1 Island, 4.6 Mainland	Range=1-6, X=3.3
Minimum size at maturity	Male 51 mm. SVL Female 44 mm. SVL	Female 51 mm. SVL
Hatching	Summer and autumn	Summer and autumn
Age at first breeding	9 to 10 months	6 to 9 months
Survival	Annual turnover	Annual turnover

for *Uta stansburiana* because this species has been extensively studied and is similar in size and ecological position to species of the genus *Holbrookia*. It is apparent that the Padre Island population of *H. propinqua*, other species of the genus *Holbrookia*, and *Callisaurus draconoides* conform closely to the early-maturing, small size, short life expectancy characteristics associated with an *r*-selected strategy. Pianka and Parker (1972) discussed the similarities and differences in the reproductive cycles of *Callisaurus*, *Holbrookia*, and *Uma*. They emphasized that the mean clutch size in *Callisaurus* and *Holbrookia* was two to three times the clutch size of *Uma*; that the age at first breeding was one year or less in *Callisaurus* and *Holbrookia*, in contrast to probable maturity at two years for most *Uma*; and that *Callisaurus*, and especially *Holbrookia*, reached sexual maturity at consistently smaller body sizes than did *Uma*. They also predicted a rapid

population turnover and low longevity for *Callisaurus* and *Holbrookia*, which was confirmed for *H. propinqua* in this paper and for *H. m. maculata* by Gennaro (1974). Thus, the variation in life history strategy in the genus *Holbrookia* is much less than that exhibited by the various species of *Sceloporus* (Ballinger, 1973; Blair, 1960; Crenshaw, 1955; Tinkle and Ballinger, 1972; Tinkle, 1972, 1973; Woodbury and Woodbury, 1945).

Throughout this study, I have been impressed by the ecological similarities of *H. propinqua* and *Uta stansburiana* in western Texas (Tinkle, 1961, 1967a, 1967b). Certainly, *H. propinqua* and *U. stansburiana* are more similar in life history characters than are *H. propinqua* and any of the several species of *Uma*. Pianka (1971a, 1971b) and Pianka and Parker (1972) discussed the ecological convergence of several phylogenetically disparate desert lizards. Pianka (1971b) discussed similarities of the ecology of *Amphibolurus isolepis* (Agamidae) of western Australia and *Uta stansburiana* and concluded that, in terms of place niche, *A. isolepis* appeared to be intermediate between *Uta* and *Callisaurus*. I have used data presented by Pianka (1971b) in constructing Table 15 wherein I compared salient features of the ecology of *Amphibolurus isolepis* and *Holbrookia propinqua*. The ecologies of the two lizards are extremely similar. The similarity in the ecology of *H. propinqua*, *U. stansburiana* (in western Texas), and *A. isolepis* supports the view that similar life history strategies develop in response to similar environmental demands.

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