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Ecology of Horned Lizards: A Review with Special Reference to *Phrynosoma platyrhinos*

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ing and examining the lizards. The study was partially aided by the Universidad del Valle and the Tulane University International Center for Medical Research (ICMR), grant No. AI-10050 from the United States Public Health Service, National Institutes of Health.

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## Ecology of Horned Lizards: A Review with Special Reference to *Phrynosoma platyrhinos*

ERIC R. PIANKA AND WILLIAM S. PARKER

The diffuse ecological literature on horned lizards (genus *Phrynosoma*) is assembled and condensed. Numerous aspects of their ecology are considered, including time of activity, thermoregulation, diet, stomach volume, foraging behavior, clutch or litter size and number of broods, reproductive effort, expenditure per progeny, testicular cycles, body size, sexual size dimorphisms, seasonal changes in size distributions, survivorship, growth rates, size and age at sexual maturity, movements and homing, predation and broken tails, competitors and selective pressures. Emphasis is given to the desert horned lizard, *P. platyrhinos*, although comparative data on many other species of *Phrynosoma* are also presented and discussed.

Certain aspects of the anatomy, behavior, diet, temporal activity pattern, thermoregulation and reproductive tactics of horned lizards set this genus apart from most other species of lizards. This unique constellation of interrelated phenotypic traits is interpreted as a set of coadaptations that complement one another to make members of the genus ecologically successful.

MANY members of the iguanid genus *Phrynosoma* are characterized by a relatively bizarre constellation of morphological, behavioral and ecological adaptations that tend to set members of this genus apart from most other species of lizards. For example, compared to other lizards, many horned lizards 1) are

strongly dorso-ventrally flattened, 2) are generally armed with sharp spines, particularly around the occipital region, 3) have relatively short legs and are slow and awkward, 4) are noticeably reluctant to run when approached by a large animal, potentially a predator, 5) are typically active over a long time span, 6) often

have more variable body temperatures than other sympatric lizard species, 7) have a conspicuously specialized diet which consists largely of ants and/or, sometimes, beetles, 8) tend to have an exceptionally large stomach capacity for their body size, 9) have a specialized dentition which facilitates ant-eating (myrmecophagy), 10) produce large numbers of relatively small eggs or young and 11) expend a considerable amount of energy on each clutch or litter of young, although expenditure per individual progeny is comparatively low due to the very large clutches and litters in the genus.

Here we consolidate the scattered ecological literature on *Phrynosoma*. We examine and attempt to document the above list of phenotypic traits, and we suggest ways in which this particular constellation of coadaptations could facilitate efficient exploitation of ants as a food source. An integrated view of the ecology of these bizarre lizards is developed, and aspects of *Phrynosoma* ecology are briefly compared with those of the independently evolved, but ecologically somewhat similar, Australian agamid lizard *Moloch horridus*. Data are presented on time of activity, body temperature relationships, diet, stomach size, clutch and litter size, reproductive effort, expenditure per progeny, testicular cycles, body size, sexual size dimorphisms, seasonal changes in size distributions, growth rates, size and age at sexual maturity, movements and homing, predation and broken tails, and competitors. Particular emphasis is given to the desert horned lizard, *P. platyrhinos*, although we also present some comparative data and discussion on eleven other species: *P. asio*, *P. boucardii*, *P. braconneri*, *P. cornutum*, *P. coronatum*, *P. douglassi*, *P. m'calli*, *P. modestum*, *P. orbiculare*, *P. solare* and *P. taurus*.

*Phrynosoma* are restricted to central and western North America, primarily in arid and semi-arid habitats such as desert, thorn scrub and grassland. The desert horned lizard, *Phrynosoma platyrhinos*, occurs throughout most of the Great Basin, Mojave and Sonoran deserts; in the U. S., this wide-ranging species is found in southeastern Oregon, southwestern Idaho, most of Nevada, western Utah, southeastern California and western Arizona (in Mexico, it occurs in northwestern Sonora and extreme northeastern Baja California). Other members of the genus range from northern Guatemala to southern British Columbia [range maps have been published by Smith (1946),

Reeve (1952), Horowitz (1955) and Stebbins (1954, 1966)]. Reeve (1952) recognized 14 species, some of which have extremely restricted geographic distributions and are little known.

Horned lizards are seldom very abundant, and, in fact, are often rather uncommon lizards; as a result there are few detailed ecological studies on them. We examine the ecology of *P. platyrhinos* in as much detail as possible here, combining what has been reported in the literature with new information from our own studies. Data on body temperatures, stomach volumes, diets, clutch sizes and/or reproductive effort are also presented for many other species of *Phrynosoma*, either collected in the field or taken from preserved specimens in the collections of the American Museum of Natural History, the Los Angeles County Museum of Natural History, the Museum of Natural History (Kansas), the Field Museum of Natural History (Chicago), the San Diego Natural History Museum and the Texas Memorial Museum (we thank the curators of these museums, respectively Richard Zweifel, John Wright, William E. Duellman, H. Marx, Thomas Fritts and Robert Martin, for generous assistance).

As noted by Smith (1946), the Texas horned lizard, *P. cornutum*, has attracted the attention of more naturalists than any other species of *Phrynosoma*. Observations on the egg-laying habits of *P. cornutum* have often been reported, as well as various other facets of its life history and reproductive biology (Edwards, 1896, 1903; Strecker, 1908, 1927; Winton, 1916, 1917; Weese, 1919; Givler, 1922; Reese, 1922; Cahn, 1926; Potter and Glass, 1931; Hewatt, 1937; Milne, 1938; Potter and Brown, 1941; Davis, 1941; Kauffeld, 1943; Vincent, 1948; Lewis, 1950; Milne and Milne, 1950; Ramsey, 1956; Ballinger and Schrank, 1970; Prieto and Whitford, 1971; Worthington, 1972; Blaney and Kimmich, 1973; Whitford and Whitford, 1973; Ballinger, 1974).

Papers on the desert horned lizard, *P. platyrhinos*, contain data and discussion on diet, stomach volume, body temperature, time of activity, abundance, reproduction, growth, movements and survivorship (Camp, 1916; Fautin, 1946; Harris, 1958; Dumas, 1964; Pianka, 1965, 1966; Pianka and Pianka, 1970; Medica, Turner and Smith, 1973; and Tanner and Krogh, 1973).

Published accounts of the natural history of the regal horned lizard, *P. solare*, include data

on the testicular cycle (Blount, 1929), oviposition (Schonberger, 1945; Van Devender and Howard, 1973), blood-squirting (Cutter, 1959), movements (Lowe, 1954; Baharav, 1971) and general biology (Parker, 1971, 1974).

Reports on the short-horned lizard, *P. douglassi*, contain observations on molting (Hoffman, 1879), gestation (Schufeldt, 1885), birth of young in these live-bearing lizards (Pack, 1918; Smith, 1941; Tanner, 1942; Dammann, 1949; Milne and Milne, 1950), diet (Knowlton, 1934, 1942; Knowlton and Janes, 1932, 1933, 1934; Knowlton and Thomas, 1934, 1936; Knowlton and Baldwin, 1953), an examination of distribution and allopatry with *P. platyrhinos* (Dumas, 1964), as well as studies of thermoregulation (Heath, 1965; Prieto and Whitford, 1971) and reproduction (Goldberg, 1971).

Some aspects of the distribution and life history of the sand-dwelling, flat-tailed horned lizard, *P. m'calli*, are treated by Klauber (1932), Norris (1949), Norris and Lowe (1964), Mayhew (1965, 1968) and Mayhew and Wright (1971).

Very little ecological information has been published on the Mexican species of *Phrynosoma* (*asio*, *boucardii*, *braconnieri*, *cerroense*, *ditmarsii*, *orbiculare* and *taurus*), although there are a few short reports on *ditmarsii* (Ditmars, 1936; Lowe, Robinson and Roth, 1971; Roth, 1971). Dernehl (1900), Terron (1932), Ochoterena (1932) and Smith (1934) provide limited information on other Mexican species. Neither has much been published on the ecology of the coast horned lizard *P. coronatum*, or the round-tailed horned lizard, *P. modestum* (but see Asplund, 1967; Bundy, Meyer and Neess, 1955; Bundy and Neess, 1958; Dernehl, 1900; Montanucci, 1968; Parker, 1938; and Weese, 1917, 1919).

Bryant (1911) and VanDenburgh (1922) provided early general treatments of *Phrynosoma* biology, which were updated by Smith (1946), Milne and Milne (1950) and Stebbins (1954, 1966). The taxonomy of the genus has been variously treated by Bryant (1911), Klauber (1936), Smith (1946), Reeve (1952), Horowitz (1955) and Presch (1969). Osteological studies of the head and axial skeleton of *Phrynosoma* have clarified relationships within the genus and those with other iguanids (Broom, 1948; Norris and Lowe, 1951; Etheridge, 1964, 1967; and Presch, 1969). Horned lizard chromosomes were described by Gorman, Baptista and Bury (1969). Zug (1971) examined major arteries.

Stuart (1932), Klauber (1932) and Banta (1962a, 1962b) considered various aspects of the zoogeography and distribution of *Phrynosoma*, and Dumas (1964) discussed the generally allopatric distributions of *P. platyrhinos* and *P. douglassi*. Fossil horned lizards, including *P. cornutum* and *P. platyrhinos*, were described by Oelrich (1954) and Brattstrom (1954, 1955). Gigantic specimens of *P. douglassi* and *P. solare*, respectively, were reported by Kerfoot (1962) and Edgren (1948). Miscellaneous facets of reproductive biology of various horned lizards are described by Wood (1936a,b), Tanner (1942), Shaw (1952), Gates (1957), Mayhew (1968), Fitch (1970), Ballinger and Clark (1973) and Parker (1973). Wood (1936b), Milne and Milne (1950) and Lynn (1965) describe aspects of *Phrynosoma* behavior. Meyer (1966) briefly mentions drinking habits of *P. cornutum* and *P. modestum*. Body temperatures have been reported by Brattstrom (1965), Cunningham (1966), Cowles (1940), Cowles and Bogert (1944), Heath (1962a, 1964b, 1965), Mayhew (1968), Pianka and Pianka (1970) and Baharav (1971). Various other aspects of thermoregulation and/or pigmentation were studied by Atsatt (1939), Heath (1962a, 1964b, 1965), Norris (1967), Norris and Lowe (1964), Ballinger and Schrank (1970) and Prieto and Whitford (1971). Color changes, color variation and background color matching were treated by Parker (1938), Lowe (1947), Bundy and Neess (1958), Lawrence and Wilhoft (1958) and Norris and Lowe (1964). *Phrynosoma* diets were studied by Knowlton (1934, 1938, 1942, 1946) and his colleagues (Knowlton and Janes, 1932, 1933, 1934; Knowlton and Thomas, 1934a,b, 1936; Knowlton and Baldwin, 1953). Hottot (1955) surveyed iguanid dentition and noted that *Phrynosoma* have blunt, stout, non-cusped, low-crowned and peglike teeth, which he termed an "ant-eating" dentition. Predators on horned lizards have been reported by Knowlton and Stanford (1942), Vorhies (1948), Stebbins (1954) and Miller (1958). Hay (1892), Winton (1914b), Ruthling (1919), Burleson (1942), Cutter (1959) and Heath (1966) treat blood-squirting from the eyes of horned lizards, thought to function in predator escape. Nocturnal activity is described and discussed by Harris (1958), Williams (1959) and Mays and Nickerson (1968). Other miscellaneous aspects of the life histories of various species of *Phrynosoma* have also been reported by Taylor (1912), Richardson (1915), Camp (1916), Weese (1917, 1919), Pack (1918), Terron

(1932), Ochoterena (1932), Smith (1934), Ditmars (1936), Linsdale (1938), Klauber (1939), Kauffeld (1943), Tevis (1944), Johnson, Bryant and Miller (1948), Lewis (1950), Lowe and Woodin (1954), Tanner (1954), Gates (1957), Tanner and Jorgensen (1963), Gehlbach (1965), Banta (1967) and Mayhew (1968).

#### METHODS

During the course of field work in the western U. S. and northwestern Mexico over the last decade, we observed more than 500 horned lizards of six species in their natural habitat (numbers in parentheses are sample sizes): *cornutum* (12), *coronatum* (24), *douglassi* (48), *modestum* (24), *platyrhinos* (364) and *solare* (54). Many of these were collected and deposited in the Los Angeles County Museum of Natural History: *coronatum* (24), *douglassi* (21), *modestum* (19), *platyrhinos* (274) and *solare* (16). In addition to these specimens, we determined gonadal state and/or stomach contents of the following numbers of preserved museum specimens: *asio* (35), *boucardii* (2), *braconnieri* (7), *cornutum* (462), *coronatum* (199), *douglassi* (125), *m'calli* (121), *modestum* (158), *orbiculare* (69), *platyrhinos* (692), *solare* (227) and *taurus* (4). Thus, the present report is based upon examination of some 2,111 specimens of *Phrynosoma* of 12 species (only *P. cerroense* and *P. ditmarsii* are not represented).

We studied *P. platyrhinos* on 13 desert study areas [previously reported by Pianka and Parker (1972)] scattered over most of its geographic range. A population on an area 3 km west of Grantsville, Utah, was studied in detail; on this area, 96 *P. platyrhinos* and 47 *P. douglassi* were marked by toe clipping and released. These lizards were processed in Salt Lake City and returned to the point of capture the next day. Each animal was sexed, weighed to the nearest 0.1 g, and measured for snout-vent length (SVL) and tail length to the nearest mm. Growth rates were calculated for recaptured lizards after excluding the period from October to April when the animals are inactive. Some lizards were displaced upon return to the field; these were not transported in light-tight containers. Distance between captures was estimated relative to local landmarks for short moves, and measured on an aerial photograph for longer distances. For all active *Phrynosoma* encountered above ground of their own volition, we recorded date, time, approximate size and microhabitat position when first observed.

Most animals on areas other than the above-mentioned Utah site were collected; as detailed below, these specimens provided additional data on cloacal temperature, sex, gonadal state, stomach contents, wet weight, exact size (SVL) and whether or not the tail had been broken and regenerated. Some males were checked for spermatozoa by crushing a section of the vas deferens.

Dissection of preserved specimens supplied information as follows. Testes lengths and widths were measured with vernier calipers or metal millimeter rulers, and ratios of mean testis length over SVL were calculated. Oviparous females (those with eggs in their oviducts) and their eggs were either weighed to the nearest 0.1 g or their volume was estimated by volumetric displacement (a nearly one-to-one correspondence between weight and volume indicates their equivalence). Volumes of intact stomachs were estimated similarly to the nearest 0.1 cc with a small narrow-necked graduated cylinder. Both numbers and volumes of items in various prey categories were estimated for each stomach. Approximate proportional volumes of individual prey items were estimated visually, by the proportion of the total stomach volume taken up by a given item. Prey in each stomach were counted individually, except for ants for which standards were often determined and the number per stomach estimated from the volume. Field methods employed are discussed in greater detail by Pianka (1965, 1967, 1970b), Parker (1971, 1972) and Pianka and Parker (1972), which papers also describe the locations, climates, faunas and floras of most of the study areas.

#### RESULTS AND DISCUSSION

*Time of activity.*—Members of the genus *Phrynosoma* are typically active earlier and later, and over a longer time span, than most other sympatric species of lizards (Smith, 1946; Norris, 1949; Heath, 1965; Pianka, 1966; Pianka and Pianka, 1970). We have found *P. platyrhinos* active as early as 0630 hours (less than 2 hours after sunrise) and as late at 1900 to 2015 hours (a full hour or two after sunset). The possibility of nocturnal activity has been discussed by Harris (1958), Williams (1959) and Mays and Nickerson (1968). In most lizards, time of activity changes seasonally, with somewhat earlier emergence during warmer months (Mayhew, 1968; Pianka, 1973). Such annual changes in activity times have been demonstrated for *P.*



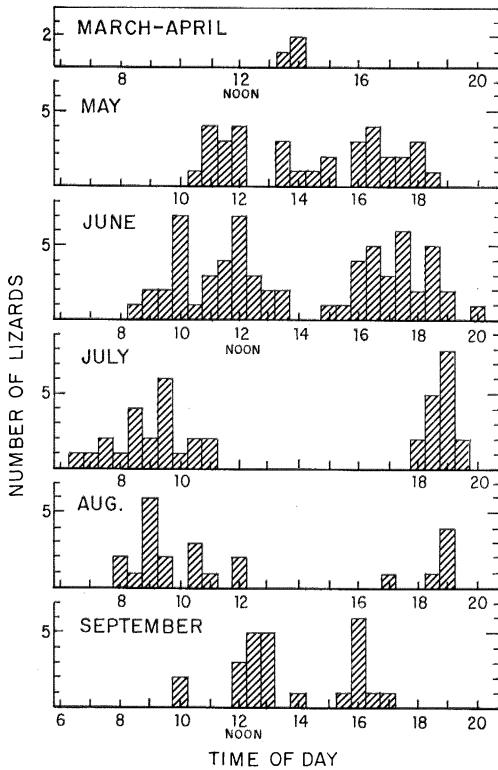


Fig. 1. Frequency distributions of times of activity of *P. platyrhinos* from four northern study sites (areas U, L, G and I), by months, showing seasonal changes in activity patterns. See text.

*m'calli* by Mayhew (1968, p. 235, Fig. 5) and for *P. solare* by Baharav (1971). Fig. 1 shows the times of activity of *P. platyrhinos* on our four northern study areas (I, L, G and U) in the Great Basin desert, by month. During midsummer, the animals emerge early and activity seems to taper off after about 1000 hours. These data (Fig. 1) suggest a bimodal daily period of activity in June, July and August, and a more unimodal activity pattern in May and September (however, without standardizing for diurnal variation in sampling effort, these trends are not conclusive). Expressing times of activity in units of "hours since sunrise" helps to standardize for seasonal shifts in time of activity and facilitates comparisons between species (Pianka, 1973). Table 1 summarizes data on daily activity patterns of nine diurnal species of lizards on ten study areas in the Mojave and Sonoran deserts. To the extent that our collecting was concentrated during the period of greatest lizard activity in the

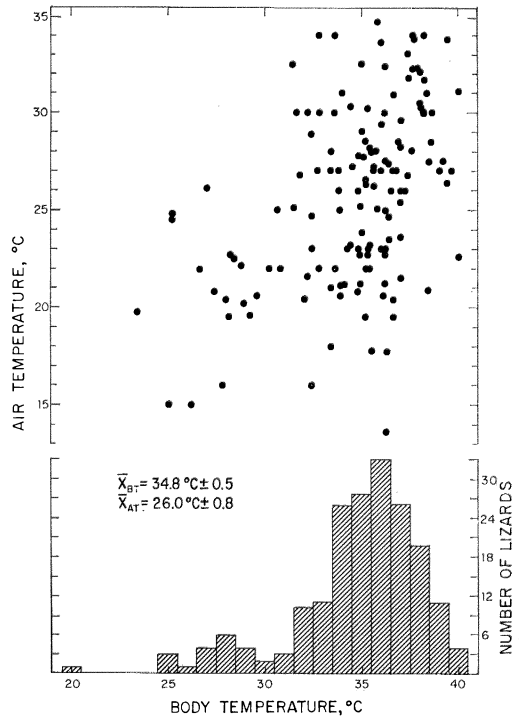


Fig. 2. Body temperatures of active *P. platyrhinos* plotted against ambient air temperature. Frequency distribution of all active body temperatures ( $N = 191$ ) is shown at the bottom of the figure (all study areas plus incidentals lumped).

morning hours, these data are clearly somewhat biased; however, observed differences between species, all of which were sampled over the same time period, presumably reflect real differences in activity patterns (Pianka, 1973). The column at the far right of Table 1 represents the diversity of times of activity, or the "time niche breadth" of Pianka (1973); note that the diversity of the daily pattern of temporal activity is distinctly higher in *P. platyrhinos* than in most other sympatric species listed (Table 1). (Unfortunately, tests of statistical significance have not been developed for this diversity index.)

We discuss these results further in the concluding section on "an integrated view of *Phrynosoma* ecology."

**Body temperature relationships.**—We obtained cloacal temperatures of 211 active *P. platyrhinos*, 18 active *P. douglassi*, and 15 active *P. coronatum*. In addition, Baharav (1971) and Mayhew (personal communication), respec-

TABLE 1. NUMBERS OF LIZARDS ACTIVE AT DIFFERENT TIMES OF DAY IN NINE DIURNAL SPECIES ON TEN STUDY AREAS IN THE MOJAVE AND SONORAN DESERTS. DIVERSITY OF TIME OF ACTIVITY IS GIVEN AT THE FAR RIGHT.

Species	Hours Since Sunrise														Total Number	Diversity of Time of Activity
	1-2	2-3	3-4	4-5	5-6	6-7	7-8	8-9	9-10	10-11	11-12	12-13	13-14	Over 14		
<i>Cnemidophorus tigris</i>	30	229	467	494	238	111	33	12	9	7	10	21	24	1	1686	4.84
<i>Uta stansburiana</i>	24	182	242	166	59	19	13	7	5	3	4	13	17	4	758	4.62
<i>Crotaphytus wislizeni</i>	1	3	10	7	8	1	1	3	1	1	1	1	2	0	40	6.61
<i>Phrynosoma platyrhinos</i>	2	8	12	12	15	7	2	3	4	1	1	3	3	1	74	8.05
<i>Callisaurus draconoides</i>	2	24	66	81	65	26	12	9	4	9	6	20	11	2	337	6.57
<i>Sceloporus magister</i>	3	12	17	18	9	5	3	1	3	0	2	11	4	0	88	7.50
<i>Dipsosaurus dorsalis</i>	0	1	6	10	15	14	6	3	2	5	1	0	0	0	63	6.27
<i>Urosaurus graciosus</i>	0	4	9	15	6	2	5	2	0	0	0	0	0	0	43	4.73
<i>Uma scoparia</i>	1	4	9	11	4	1	1	0	0	0	0	1	0	0	32	4.30
TOTALS	63	467	838	814	419	186	76	40	28	26	25	70	61	8	3121	

tively, provide body temperatures (BTs) for 151 active *P. solare*, and 473 active *P. m'calli*. Statistics for BTs of active *Phrynosoma* are summarized in Table 2. There is a weak positive correlation between body temperature and ambient air temperature in *P. platyrhinos* (Fig. 2). Our mean of 34.9 C ( $S = 3.2$ ,  $N = 211$ ) is somewhat lower than the means of 36.8, 36.0 and 36.4 C, reported by Cowles and Bogert (1944), Brattstrom (1965) and Tanner and Krogh (1973), respectively. We found BTs of active *P. platyrhinos* to be significantly more variable (F-tests,  $.05 < P < .01$ ) than BTs of other sympatric species of desert lizards (Tables 3 and 4; Pianka and Pianka, 1970). Using methods similar to those of Licht *et al.* (1966), body temperature of one recently-captured (2 weeks) *P. platyrhinos* was recorded at 4-min intervals over a full daily period of activity in a laboratory thermal gradient; thus measured, so-called preferred body temperature (PBT) statistics for 204 measurements of this individ-

ual's BT on this day were as follows:  $\bar{x} = 36.0$ ,  $S = 2.1$ ,  $SE = .14$ . Comparison of these PBT statistics with those of active lizards under natural conditions shows that PBTs are significantly higher (t-test,  $P < .001$ ) and less variable (F-test,  $P < .001$ ); this in turn suggests that wild lizards may not thermoregulate as precisely as they might prefer. We discuss such "relaxed" thermoregulation further below in developing an integrated view of horned lizard ecology.

Other aspects of *Phrynosoma* thermoregulation have been studied in some detail by Atsatt (1939), Ballinger and Schrank (1970), Brattstrom (1965), Heath (1962a, 1962b, 1965) and Prieto and Whitford (1971).

*Diet, stomach volume and foraging behavior.*—Among the more salient features of the ecology of *Phrynosoma* is their relatively restricted diet, which is typically composed largely of ants (on occasion, beetles may dominate the diet). The

TABLE 2. BODY TEMPERATURE STATISTICS OF ACTIVE LIZARDS IN SEVEN SPECIES OF *Phrynosoma*, WITH SOURCES.

Species	$\bar{x}$	SE	SD	N	Source
<i>P. cornutum</i>	37.3	0.69	2.85	17	this paper and J. J. Schall, personal communication
<i>P. coronatum</i>	36.7	0.30	1.16	15	this paper
<i>P. douglassi</i>	34.9	0.64	2.72	18	this paper
<i>P. m'calli</i>	37.8	0.13	2.74	473	W. W. Mayhew, personal communication
<i>P. modestum</i>	36.5	0.46	2.53	30	J. J. Schall, personal communication, and this paper
<i>P. platyrhinos</i>	34.9	0.22	3.17	211	this paper
<i>P. solare</i>	34.7	—	—	151	Baharav (1971)

TABLE 3. STATISTICS ON BODY TEMPERATURES OF NINE SPECIES OF ACTIVE LIZARDS IN NATURE. F-TESTS SUMMARIZED IN TABLE 4.

Species	Code	$\bar{x}$	SE	S	N	Source
<i>Cnemidophorus tigris</i>	(C)	39.5	.042	1.8	1848	Pianka (1970)
<i>Uta stansburiana</i>	(U)	35.3	.086	2.4	778	Pianka and Pianka (1970)
<i>Crotaphytus wislizeni</i>	(L)	37.3	.196	2.4	150	Pianka and Pianka (1970)
<i>Phrynosoma platyrhinos</i>	(P)	34.8	.233	3.2	191	this paper
<i>Callisaurus draconoides</i>	(Z)	39.1	.139	2.6	352	Pianka and Parker (1972)
<i>Sceloporus magister</i>	(S)	34.8	.167	1.6	92	Parker and Pianka (1973)
<i>Dipsosaurus dorsalis</i>	(D)	40.0	.297	2.3	60	Pianka (1971a)
<i>Urosaurus graciosus</i>	(T)	36.1	.265	1.5	32	Pianka and Pianka (1970)
<i>Uma scoparia</i>	(F)	37.3	.402	2.2	30	Pianka and Pianka (1970)

myrmecophagous habits of members of the genus set horned lizards apart from most other species of North American lizards which tend to have considerably more catholic diets (Hotton, 1955; Knowlton, 1934, 1938, 1942, 1946; Knowlton and Janes, 1932, 1933, 1934; Knowlton and Thomas, 1934a,b, 1936; Knowlton and Baldwin, 1953; Little and Keller, 1937; Norris, 1949; Milne and Milne, 1950; Pianka, 1965, 1966, 1970b, 1973; Pianka and Pianka, 1970; Reeve, 1952). The diet of *P. platyrhinos* is fairly consistent on our various study areas, usually being composed of about 35 to 65% ants (by volume) and from about 20 to 50% beetles. Table 5 summarizes the stomach contents of 236 specimens from the 13 different study areas. No latitudinal dietary shifts are apparent. Stomach contents of specimens from area M (8 km N of Mojave, California) differed conspicuously from those of horned lizards from most other study areas; on this site which had recently suffered a drought (Pianka, 1970b), in-

sect larvae of various sorts comprised some 22% of the diet by volume. Banta (1961) found *Lycium* berries in the stomachs of 5 *P. platyrhinos* collected in Nevada in June of 1955. On some of our areas, stomachs of *P. platyrhinos* were filled almost entirely with small beetles, particularly when these insects were plentiful. *P. asio*, *P. coronatum* and *P. orbiculare* consume a lot of beetles, too.

Table 6 summarizes the percentages of ants in the diets of samples of 13 species of *Phrynosoma*; in addition, statistics for the ratio of stomach volume over body weight are given for 12 species. Pianka and Pianka (1970) presented data showing that the volume of the stomach of *P. platyrhinos* is significantly larger than that of various sympatric species of lizards. The diet and large stomachs of many horned lizards are considered again below in terms of the overall ecology of *Phrynosoma*.

Stomach contents of 21 *P. douglassi* from area U in Utah are summarized in Table 7;

TABLE 4. UPPER RIGHT: VARIANCE RATIOS OF BODY TEMPERATURES FOR EACH PAIR OF THE NINE SPECIES\* LISTED IN TABLE 3. LOWER LEFT: SIGNIFICANCE LEVELS AS FOLLOWS: NS = not significant, \* =  $P \leq .05$ , \*\* =  $P \leq .01$ , and \*\*\* =  $P \leq .001$ . All F-tests with *Phrynosoma* are highly significant ( $P < .01$  or  $.001$ ), showing that its body temperature is more variable than those of all other species.

	C	U	L	P	Z	S	D	T	F
C	—	1.77	1.77	3.16	2.09	1.27	1.63	1.44	1.49
U	**	—	1.00	1.78	1.17	2.25	1.09	2.56	1.19
L	**	NS	—	1.78	1.17	2.25	1.09	2.56	1.19
P	***	**	**	—	1.52	4.00	1.94	4.55	2.12
Z	**	NS	NS	**	—	2.64	1.28	3.00	1.40
S	NS	**	**	***	***	—	2.07	1.14	1.89
D	**	NS	NS	**	NS	**	—	2.35	1.09
T	NS	**	**	***	**	NS	**	—	2.15
F	NS	NS	NS	**	NS	*	NS	*	—

\* Species Coded as in Table 3.



TABLE 5. SUMMARY OF STOMACH CONTENTS OF 236 *Phrynosoma platyrhinos* COLLECTED THROUGHOUT ITS GEOGRAPHIC RANGE.

Prey Categories	Number	Volume	% Total Number	% Total Volume	Frequency
Aranae	30	2.48	.17	.61	24 (10.2)
Solpugidae	4	7.33	.02	1.82	5 ( 2.1)
Formicidae	15,868	228.12	88.69	56.61	224 (94.9)
Other Hymenoptera	22	1.43	.12	.35	10 ( 4.2)
Orthoptera	16	2.70	.09	.67	15 ( 6.4)
Blattidae	53	9.60	.30	2.38	21 ( 8.9)
Mantidae	1	.50	.01	.12	1 ( .4)
Coleoptera	1,361	89.77	7.61	22.28	183 (77.5)
Isoptera	170	1.20	.95	.30	4 ( 1.7)
Homoptera-Hemiptera	70	4.03	.39	1.00	22 ( 9.3)
Diptera	3	.15	.02	.04	3 ( 1.3)
Adult Lepidoptera	2	.10	.01	.02	1 ( .4)
Insect eggs	15	—	.08	—	2 ( .8)
All insect Larvae	162	29.71	.91	7.37	62 (26.3)
Insect pupae	1	.40	.01	.10	1 ( .4)
Unidentified insects	48	2.64	.27	.65	29 (12.3)
Lizards, sloughed skin	—	10.20	—	2.53	1 ( .4)
Vegetative parts, plant	64	3.07	.36	.76	32 (13.6)
Unidentified material	1	9.58	.01	2.38	58 (24.6)
TOTALS	17,891	402.99			

on this study site, *P. douglassi* is sympatric with *P. platyrhinos* and its diet is dominated by grasshoppers and beetles rather than ants (see also section entitled "competition").

Foraging behavior is quite invariable through-

out the geographic range of *P. platyrhinos*; these horned lizards typically forage by sitting and waiting more or less passively, often near an ant nest. *P. platyrhinos* frequent the open spaces between shrubs; nearly 90% of some 228

TABLE 6. THE PERCENTAGE OF ANTS BY NUMBER OF PREY ITEMS (%N) AND BY VOLUME (%V) IN THE DIETS OF VARIOUS SPECIES OF *Phrynosoma*. STOMACH VOLUME OVER BODY WEIGHT STATISTICS ARE ALSO GIVEN FOR EACH SPECIES.

Species	%N	%V	Number of Stomachs Examined	Stomach Volume/Body Weight			
				$\bar{x}$	SE	SD	N
<i>P. asio</i>	75.3	31.1	23	.078	.0085	.041	23
<i>P. boucardi</i>	71.8	56.8	2	.041	.0127	.018	2
<i>P. braconnieri</i>	80.7	49.1	7	.054	.0089	.023	7
<i>P. cornutum</i>	69.0	61.2	351	.071	.0049	.043	75
<i>P. coronatum</i>	90.3	44.7	214	.064	.0033	.049	222
<i>P. ditmarsii</i> *	85.8	11.3	6(4)	—	—	—	—
<i>P. douglassi</i>	81.0	51.8	50	.070	.0084	.051	36
<i>P. m'calli</i>	97.2	78.0	106	.085	.0032	.032	105
<i>P. modestum</i>	86.1	66.1	130	.072	.0070	.040	32
<i>P. orbiculare</i>	67.5	25.9	67	.087	.0043	.035	67
<i>P. platyrhinos</i>	88.7	56.6	236	.134	.0061	.080	171
<i>P. solare</i>	90.3	88.8	158	.094	.0037	.045	152
<i>P. taurus</i>	47.4	56.5	4	.126	.0546	.109	4

\* From Roth (1971) and V. D. Roth (personal communication).

TABLE 7. STOMACH CONTENTS OF 21 *Phrynosoma douglassi* FROM 3 KM WEST OF GRANTSVILLE, UTAH.

Prey Categories	Number	Volume	% Total Number	% Total Volume	Frequency
Aranae	1	.08	.2	.4	4.8
Formicidae	282	3.18	48.9	15.1	57.1
Orthoptera	13	8.53	2.3	40.6	52.4
Coleoptera	259	7.28	44.9	34.7	52.4
Hemiptera	19	1.38	3.3	6.6	23.8
All insect larvae	3	.20	.5	1.0	14.3
Vegetative parts, plants	—	.20	—	1.0	4.8
Unidentified materials	—	.15	—	.7	9.5
TOTALS	577	21.00			

specimens were in the open when first sighted. Other species of *Phrynosoma* also tend to be found in open spaces.

**Reproduction.**—*Phrynosoma* reproductive tactics are somewhat unusual among lizards. Horned lizards typically expend considerable amounts of matter and energy on reproduction (clutch or litter weights comprise a large fraction of female body weight compared to most other species of lizards); moreover, *Phrynosoma* tend to produce large numbers of eggs or offspring. Finally, many horned lizards probably have delayed reproduction and relatively high survivorship as adults (Medica *et al.*, 1973 show this for *P. platyrhinos*).

Age at sexual maturity. Studies on a marked population of *P. platyrhinos* in Utah (see "a mark and recapture study") show that both sexes near minimal adult size in the late summer of their first year (Table 9, ♂<sub>5</sub> and ♀<sub>8</sub>), but do not breed until the following spring at an age of about 22 months. [Medica *et al.* (1973) also report that sexual maturity is reached at an age of 19–22 months in southern Nevada.] In Utah, the smallest male with spermatozoa during the breeding season was 68 mm SVL, while the smallest female with yolked eggs measured 70 mm SVL. *P. douglassi* follows a similar pattern; a 62 mm SVL male had spermatozoa in May, and a 66 mm SVL female contained yolked follicles. Growth records (Table 9, ♀<sub>12</sub>) show that these sizes are attained at an age of about one year, but, again, breeding does not commence until the following spring. Both *P. platyrhinos* and *P. douglassi* are thus late maturing in northern Utah.

Clutch size and reproductive effort. As indicated above, among lizards *Phrynosoma* are

generally rather fecund. Fitch (1970) summarized available information; mean clutch size (or litter size in viviparous species such as *P. douglassi* and *P. orbiculare*) among species varies from 5.4 in *P. m'calli* to 26.5 in *P. cornutum* (see also Table 11), with desert-dwelling species generally laying smaller clutches or having smaller litters than species from wetter regions.

We collected 46 *P. platyrhinos* females with enlarged yolked eggs 3 mm or larger in diameter during this study, 18 of which contained eggs in their oviducts. Mean clutch size from these data is 8.4 ( $S = 2.8$ ,  $N = 46$ ), although the distribution is somewhat bimodal. We found another 46 gravid female *P. platyrhinos* among the museum specimens examined. Tanner and Krogh (1973) report clutch sizes of another 24 females with a mean of 6.7. The overall mean clutch of 116 gravid females is 7.68 eggs. Clutch size is only weakly correlated with female body size in *P. platyrhinos* (Fig. 3).

Adult female *P. platyrhinos* in Utah measure from 70 to 92 mm SVL. All Utah females had yolked eggs in May and most did in June (Table 8). Ovulation took place in late May and early to middle June. In 1972, females with oviducal eggs were found between 24 May and 12 June, after which no females were ovigerous. (Three females from late June and early July contained yolked follicles, but these may have become atretic since no females with oviducal eggs were encountered either during the same period or later that year.) There may be only one annual clutch in the northern part of the geographic range in some years such as the one described above, but two clutches could occur in other years (see also below). Indeed, Medica *et al.* (1973) found two clutches in some years but only one clutch in other years in

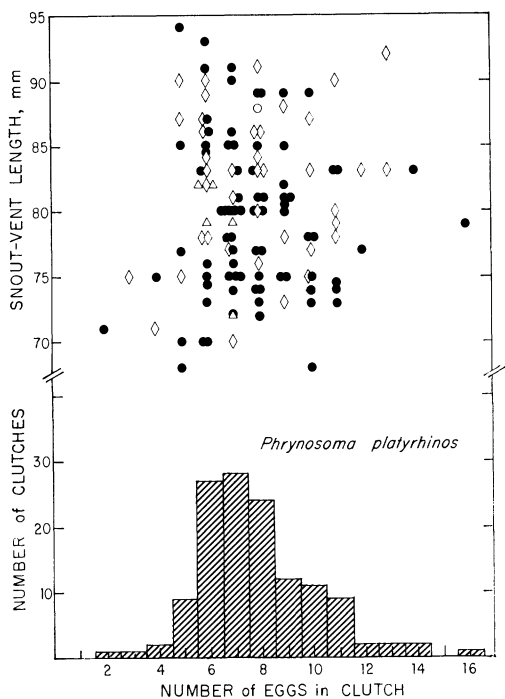


Fig. 3. Plot of clutch size against female snout-vent length in *P. platyrhinos* with frequency distribution of clutch sizes at bottom. Oviducal clutches depicted with diamonds, corpora lutea by triangles, and yolked ovarian clutches by dots.

southern Nevada. We collected females with oviducal eggs during early June through early July on three other northern areas in Nevada (L, G and V). In the Mojave and Sonoran deserts (areas M, S and C), females were found with eggs in their oviducts in early June, late July, and early August, suggesting that two clutches are deposited each season in the south in at least some years (see also below and section on “testicular cycles”).

An 83 mm SVL female *P. platyrhinos* from area U deposited eggs in a one gallon jar during

the night of 10–11 June 1972. This female buried her eggs about 1.5 cm below the surface in 6 cm of moist earth. They were left undisturbed and incubated at 30 C. Ten hatchlings emerged on 29 July and three more on 31 July, an incubation period of 49–51 days. The female was preserved and contained 11 yolked ovarian follicles 6 mm in diameter, suggesting that she may have laid a second clutch under favorable conditions. The short season favorable for incubation and hatchling activity in Utah may, however, often preclude double clutches (see also above).

Hatchling *P. platyrhinos* were first collected in Utah on 18 August 1971 and 11 August 1972. Apparently, no hatching occurred after late August in Utah, and most smaller juveniles did not survive the winter (see also Fig. 6). Hatchlings from the above laboratory clutch of 13 averaged 27.4 (26–30) mm SVL, 12.4 (11–14) mm tail length, and weighed an average of 1.0 (0.8–1.1) g. *P. douglassi* hatchlings appeared on 16 August 1971 and 29 July 1972 on area U in Utah.

Wet weights (or volumes) of oviducal clutches of *P. platyrhinos*, expressed as a percentage of total female wet weight (including the clutch), range from 13.7 to 30.5% ( $\bar{x}$  = 21.9,  $S$  = 3.8,  $N$  = 17), indicating a fairly high reproductive effort in this species. Means of clutch weight over total female body weight are also reported for a number of other *Phrynosoma* species and *Moloch horridus* in Table 11. All but one of these values are relatively high compared to clutch weight over body weight ratios among some 70-odd other species of lizards (range = 5.1 to 30.1%, mean = 17.3; Pianka, in preparation). Due to the large clutches of most horned lizards, however, expenditure per progeny, or egg weight over total female body weight, is relatively low (only about 2 to 3%).

Testicular cycles. In *P. platyrhinos*, male testicular cycles closely parallel the female re-

TABLE 8. SNOUT-VENT LENGTHS (mm) OF GRAVID AND NONGRAVID FEMALE *Phrynosoma platyrhinos* FROM UTAH (1971 AND 1972).\*

Month	N	Gravid		Nongravid		Percent Gravid	Percent Ovigerous
		$\bar{x}$	Range	$\bar{x}$	Range		
May	8	78.4	74–92	—	—	100.0	25.0
June	14	77.5	70–85	78.0	75–80	78.6	50.0
July	5	73.5	71–76	79.0	77–83	40.0	0.0
August	1	—	—	73.0	—	0.0	0.0

\* Data include 5 mark-release adult females.

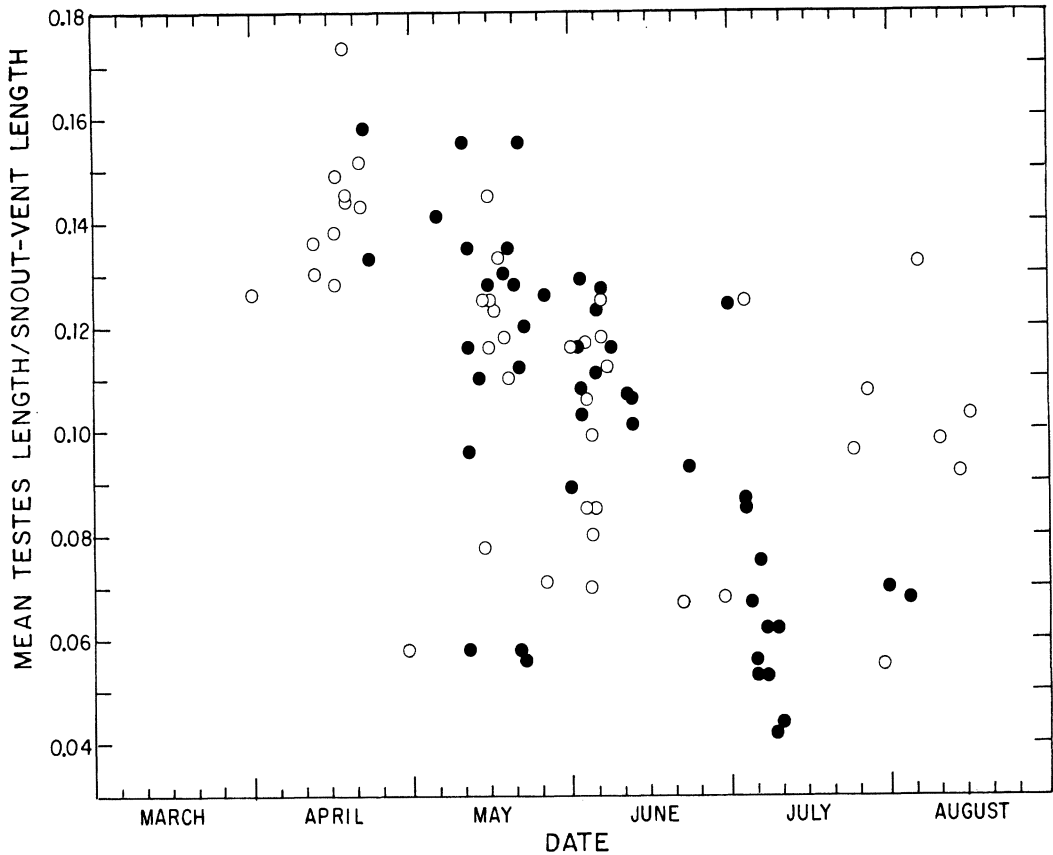


Fig. 4. Seasonal changes in the ratio of mean testis size over SVL of male *P. platyrhinos* that are large enough to be reproductive (65 mm and over in southern animals, 68 mm and over in northern ones). Each point is the mean ratio for both testes of a given male. Dots indicate lizards from the Great Basin desert (areas U, L, G and I); circles represent animals from the Mojave and Sonoran deserts (all other study sites). Note that the breeding season appears to be shorter in the north.

productive cycle. On northern areas, males emerge from hibernation (March–April) with enlarged testes; testicular dimensions peak in mid-May to early June, and then decline rapidly through early July (Fig. 4, dots). Adult activity is also reduced after June. Utah males collected from 22 April through 10 May lacked spermatozoa, while those captured from 15 May through 12 June all had spermatozoa (this corresponds to the period of female ovulation). In the south, testes remain large into early August, further evidence of two (or more) clutches per season (Fig. 4, circles). The general pattern of testicular development and regression in *P. platyrhinos* is similar to that of *P. douglassi* (Goldberg, 1971) and *P. cornutum* (Ballinger, 1974), but differs from that of *P. solare* (Blount, 1929). Of the various temperate lizard testicular

cycle types recognized by Licht and Gorman (1970), *P. platyrhinos* has type IV, *P. douglassi* type III and *P. solare* type I.

*A mark and recapture study.*—One population of *P. platyrhinos* in western Utah (area U) was studied in detail by marking and releasing lizards (see methods). Vegetation on this area is primarily sagebrush (*Artemisia tridentata*), cheatgrass (*Bromus tectorum*), and rabbitbrush (*Chrysothamnus* sp.), along the lower foothills on the east side of the Stansbury Mountains at north latitude 40°36' (Parker and Brown, 1973). *Phrynosoma douglassi* occurs in sympatry with *P. platyrhinos* on this study area, although the former is less abundant than the latter (42 versus 163 individuals captured). The area is apparently the major habitat of *P. platyrhinos*.

TABLE 9. SELECTED GROWTH RECORDS OF JUVENILE *P. platyrhinos* (UPPER) AND *P. douglassi* (LOWER) IN UTAH.

Sex	Capture Dates	SVL (mm)	Tail (mm)	Weight (g)	Growth (mm/day)	Weight change (g/day)
<i>Phrynosoma platyrhinos</i>						
♂ <sub>1</sub>	28 Aug 71	33	14	2.0	—	—
	28 Apr 72	35	16	3.1	0.06	0.03
	14 May 72	44	18	3.7	0.56	0.04
	19 May 72	45	19	4.3	0.20	0.12
	29 May 72	47	20	5.3	0.20	0.10
♂ <sub>2</sub>	30 Aug 71	33	15	2.2	—	—
♂ <sub>3</sub> *	6 Jul 72	64	33	14.5	0.32	0.13
	23 Sep 71	33	16	—	—	—
	19 May 72	41	18	2.9	0.31	—
♂ <sub>4</sub>	21 Jun 72	47	23	5.7	0.20	0.08
	14 May 72	45	21	4.0	—	—
	30 May 72	48	21	5.8	0.19	0.11
♂ <sub>5</sub> *	4 Jul 72	59	29	10.6	0.31	0.14
	9 Jun 72	61	29	10.3	—	—
	12 Jul 72	70	36	15.1	0.27	0.15
♂ <sub>6</sub>	29 Jul 72	26	12	0.9	(hatched in lab)	
	9 Sep 72	37	15	2.2	0.26	0.03
♀ <sub>7</sub> *	26 May 72	40	11	3.0	—	—
	27 Jun 72	52	19	5.2	0.37	0.07
♀ <sub>8</sub>	13 Jun 72	51	23	6.7	—	—
	12 Aug 72	75	37	19.9	0.40	0.22
	30 May 74	81	38	26.6	0.02	0.02
♀ <sub>9</sub>	1 Jun 72	55	24	7.8	—	—
	19 May 73	73	35	20.2	0.05	0.04
	11 May 74	77	39	25.0	0.01	0.01
<i>Phrynosoma douglassi</i>						
♂ <sub>10</sub> *	6 Sep 71	30	14	1.6	—	—
	13 Jun 72	42	21	4.7	0.18	0.04
	23 Jun 72	47	23	5.8	0.50	0.11
	29 Jun 72	47	23	5.7	0.00	-0.02
♂ <sub>11</sub> *	8 Sep 71	36	15	2.6	—	—
	24 Sep 71	38	18	3.4	0.12	0.05
♀ <sub>12</sub>	27 Jun 72	56	24	12.8	—	—
	10 Aug 72	73	33	22.5	0.39	0.22
♀ <sub>13</sub>	13 Jun 72	47	13 + 5	5.2	—	—
	25 Jun 72	49	13 + 5	7.6	0.17	0.20

\* Displaced individuals.

Occasional collections in nearby valleys (*Sarcobatus-Atriplex* associations) and higher in the foothills of the Stansbury Mountains (*Juniperus*) produced only *P. douglassi*. In this restricted geographic area, *P. douglassi* thus occurs in a wide range of habitats, while *P. platyrhinos* is common only in a narrow belt along the lower foothills. It would be interesting to know if the density of *P. douglassi* is

reduced in the zone of overlap with *P. platyrhinos* (see also "competition").

Growth rates. A total of 96 *P. platyrhinos* and 27 *P. douglassi* were marked and released on area U. Seventeen individual *P. platyrhinos* and five *P. douglassi* were recaptured 26 and 7 times, respectively. Average weight gain for 14 juvenile *P. platyrhinos* males was 0.09 g/day (= 2.8 g/month) and for 5 juvenile females was



TABLE 10. RECORDS OF INITIAL AND SUBSEQUENT DIRECTIONS AND MOVEMENTS OF DISPLACED JUVENILE *P. douglassi* AND *P. platyrhinos* IN UTAH.

Sex & Number	Distance (m) and Direction Displaced		Interval (days)	Actual Response (m)		Correct Direction
<i>P. platyrhinos</i>						
♂ <sub>1</sub>	250	NW	309	61	ENE	SE
			4	15	SW	
♂ <sub>2</sub>	250	NW	4	50	SSW	SE
			2	20	SSW	
♂ <sub>3</sub>	400	E	10	152	W	W
♂ <sub>4</sub>	400	E	14	400	W	W
♂ <sub>5</sub>	213	NE	238	37	SW	SW
				31	N	
♂ <sub>6</sub>	400	E	2	40	SSW	W
♂ <sub>7</sub>	1500	WSW	33	55	E	ENE
♂ <sub>8</sub>	1500	WSW	9	107	W	ENE
♀ <sub>9</sub>	1525	WSW	3	20	NE	ENE
			29	20	SW	
<i>P. douglassi</i>						
♂ <sub>10</sub>	400	E	280	400	W	W
			10	30	N	
			6	30	S	
♀ <sub>11</sub>	400	E	16	20	NW	W
♀ <sub>12</sub>	2440	SW	8	40	N	NE

0.23 g/day (= 6.8 g/month). Summer weight gain for seven exclusively summer (June–August) records, averaged 0.11 g/day (both sexes) versus 0.15 g/day for 13 spring and autumn records. Average growth rate of juvenile males was 0.26 mm/day (= 7.9 mm/month), and for females, 0.35 mm/day (= 10.6 mm/month). Summer growth (both sexes) was 0.31 mm/day versus 0.26 mm/day for autumn and spring. Selected growth records are listed in Table 9. Growth rates of *P. douglassi* were 0.20 mm/day for two males and 0.34 mm/day for two females. These data indicate increased summer growth rates in *P. platyrhinos*, and show that females of both species grow faster than males, as might be expected since females attain slightly larger sizes than males in the northern parts of the species' geographic range.

**Movements and homing.** Average distance between successive captures of non-displaced juvenile *P. platyrhinos* was 18.0 meters for 7 male records and 22.5 meters in two females. No adults were recaptured.

Fifty juvenile *P. platyrhinos* and 18 juvenile *P. douglassi* were displaced distances between 50 and 2440 meters (32 *P. platyrhinos* and 13 *P. douglassi* were displaced less than 500 meters;

18 *P. platyrhinos* and 5 *P. douglassi* were displaced more than 1 kilometer). Table 10 shows distances and directions moved by the 12 recaptured individuals, 10 of which moved within 45° of the correct homeward direction. One *P. platyrhinos* and one *P. douglassi* homed a full 400 m to their original capture point, and the *P. douglassi* was recaptured two more times in its original home area. Three *P. platyrhinos* (displaced 213, 250 and 1525 m) recaptured more than once remained in their new areas. These results are somewhat surprising in that homing is rare in lizards and *Phrynosoma* are probably relatively sedentary [see, for example, Baharav (1971)]. Moreover, the ability of some horned lizards to home over relatively long distances contrasts sharply with Weintraub's (1970) results with *Sceloporus orcutti*. Reasons for the evolution of such homing ability in horned lizards remain elusive, but could involve the advantage of being able to return to the relatively permanent location of ant nests.

**Body size and seasonal changes in size distributions.**—Although *P. platyrhinos* attain similar maximum sizes in both north and south (about 90–92 mm SVL for males and 94–95 mm SVL

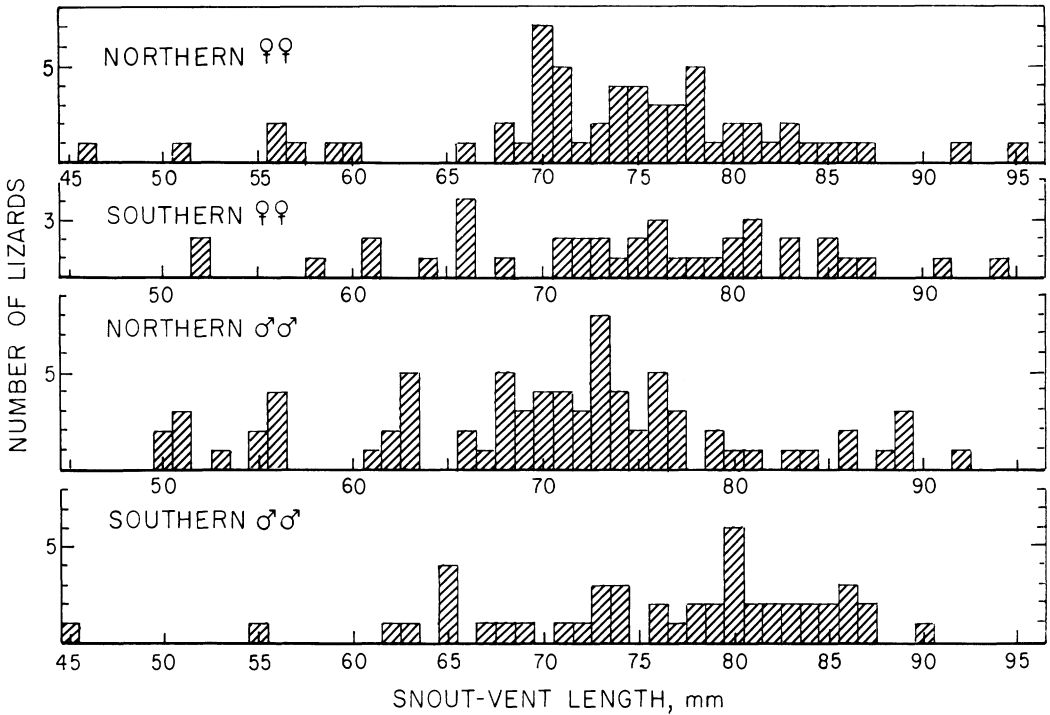


Fig. 5. Frequency distributions of snout-vent lengths of *P. platyrhinos* by sex, in the Great Basin desert ("northern") and in the Mojave plus Sonoran deserts ("southern") to show increased sexual size dimorphism in northern animals. Areas lumped as in Figs. 1 and 4.

in females), an average adult male is considerably smaller in the north than in the south (Fig. 5). Female body size does not change nearly as much with latitude, so that the size difference between the sexes is more pronounced in the north than in the south (Fig. 5). Factors underlying this shift in sexual size dimorphism are obscure; perhaps survivorship of southern males is higher than in the north and an average adult male older in the south.

Monthly changes of SVL size groups for three categories of *P. platyrhinos* in Utah are shown in Fig. 6. Samples are about equally balanced between juveniles and adults in both spring (March–May) and summer (June–July). After July, adults apparently become inactive. We found no statistically significant differences in adult sex ratio in any month. Some juveniles obviously approach minimal adult size during late June, after the breeding season, and all probably reach the size of sexual maturity by the spring of their second year. Parker (1971) presented similar size histograms by months for *P. solare* from Arizona; his data suggest delayed reproduction as well.

*Predation and broken tails.*—While the tank-like, spinily-armoured, body form of horned lizards doubtless confers some immunity from predators, this protection is far from complete. We observed predation on *P. platyrhinos* by the loggerhead shrike (*Lanius ludovicianus*), *Crotaphytus wislizeni*, *Crotalus cerastes* and *Masticophis taeniatus*. Other avian predators, particularly raptors, and other large snakes also prey upon horned lizards (Vorhies, 1948; Miller, 1958).

Broken and regenerated tails have proven to be useful indicators of the intensity of predation on some lizards, and latitudinal gradients in both numbers and density of saurian predators have been documented and correlated with frequencies of broken tails (Pianka, 1967, 1970b). Only 16 of some 330 *P. platyrhinos* had tails which had been broken (4.9%); 6 of 97 (6.2%) southern animals had lost parts of their tails and 10 of 233 (4.3%) northern lizards had broken tails. This latitudinal difference in frequency of broken tails, however, is not statistically significant with a chi-square test.

**Competition.**—Due to their highly specialized and rather unique diet, most *Phrynosoma* are unlikely to experience much interspecific competition for food from other lizards. An exception is area T (22–23 km E Twentynine Palms, Calif.), where *P. platyrhinos* occurs in sympatry with the lizard *Uma scoparia*; the diet of *Uma* on this area is composed of 50% ants by volume and some 81% of these *Uma* were first observed in the open sun (Pianka, 1970b). Food and place niche overlap, and perhaps competition as well, are thus high between these two species on this area. Overlap with six other diurnal lizard species is low in either microhabitat (*Urosaurus graciosus*) or food (*Callisaurus draconoides*, *Crotaphytus wislizeni*, *Cnemidophorus tigris* and *Dipsosaurus dorsalis*), or it is reduced in both microhabitat and food (*Uta stansburiana*). Competition with *Uma* is also suggested by the fact that *P. platyrhinos* is extremely rare on the area.

Usually only a single species of *Phrynosoma* exists on a given study site so that competition from congeners seldom occurs. However, as mentioned above, *P. platyrhinos* occurs in sympatry with the viviparous *P. douglassi* on area U (3 km W Grantsville, Utah). *P. platyrhinos* outnumbers *P. douglassi* by about 4 to 1 at this locality. Dumas (1964) noted that the geographic distributions of, as well as the habitats actually occupied by, these two species of horned lizards are largely allopatric; he also suggested that allopatry is maintained not by interspecific competition, but rather by differences in the thermal ecology and heat requirements of the two species, with the larger *P. platyrhinos* being better able to exploit higher temperatures than *P. douglassi*. Moreover, Dumas argued that viviparity allows *P. douglassi* to inhabit cooler environments, and, by transplanting gravid females, he was able to demonstrate that *P. platyrhinos* eggs laid in *P. douglassi* habitat developed too slowly to hatch before the onset of cool weather. Furthermore, Dumas suggested that the spinier *P. platyrhinos* are better protected from the predatory lizard *Crotaphytus wislizeni*, and he demonstrated that *P. douglassi* of varying sizes are readily eaten by this *Crotaphytus*. He also noted that leopard lizards (*Crotaphytus wislizeni*) are seldom sympatric with *P. douglassi*.

We made a number of observations on area U that are relevant to Dumas' hypotheses. First, we found no horned lizards of either species in the stomachs of 49 leopard lizards

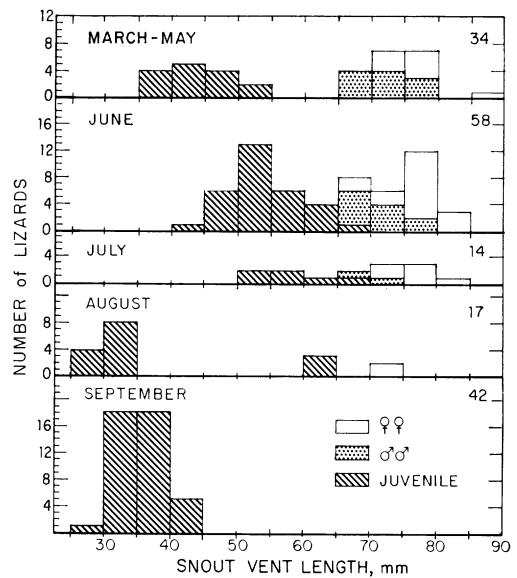


Fig. 6. Frequency distributions of snout-vent lengths of different age and sex groups of *P. platyrhinos* in Utah (area U) by months. Numbers at right are sample sizes. Hatched bars represent juveniles, stippled ones are adult males and open bars represent adult females.

from this area. Second, mean air temperature at the time of collection of some 33 *P. douglassi* (26.1 C) was almost identical to that of 62 *P. platyrhinos* (26.0 C) collected on this study area. Moreover, although our data on *P. douglassi* body temperatures are scant ( $N = 18$ ), they do not differ significantly from body temperatures of *P. platyrhinos* on the same study area ( $t$ -test,  $P < .05$ ). A most interesting fact is that *P. douglassi* on area U consume many fewer ants (only 15% by volume) than *P. platyrhinos* (64%), so that dietary overlap is relatively slight and competition for food is unlikely to be very strong. Notably enough, on other areas *P. douglassi* consumes many more ants [Table 6 and Knowlton and Baldwin (1953)]. Thus *P. douglassi* appears to have shifted its diet on area U in response to competition with *P. platyrhinos*. As indicated earlier, *P. douglassi* may also occur in reduced abundance on this area.

#### AN INTEGRATED VIEW OF *PHRYNOSOMA* ECOLOGY

Many features of the anatomy, behavior, diet, temporal activity pattern, thermoregulation and reproductive tactics of *P. platyrhinos* reported above can be profitably interrelated and interpreted as a series of coadapted phenotypic

traits, whose functions complement one another to make this lizard ecologically successful (Pianka, 1965, 1966; Pianka and Pianka, 1970).

The stomach of *P. platyrhinos*, when expressed as a proportion of total body weight, occupies a considerably larger fraction of the animal's overall body mass (about 13%) than do stomachs of other sympatric desert lizard species (Pianka, 1965, 1966; for data, see Table 6 of this paper and figure 6 in Pianka and Pianka, 1970). Indeed, Pianka and Pianka (1970) found that the mean ratio of stomach volume to body weight of the herbivorous *Dipsosaurus dorsalis* (0.080)\* to be distinctly smaller than the same ratio in *P. platyrhinos* (0.134). The diversity of times of activity, or the "time niche breadth" of *P. platyrhinos* is greater than comparable measures for other sympatric species (Table 1). Related to this broad time niche, variance in body temperature of active *P. platyrhinos* is significantly greater than that of most other species of sympatric lizards (Table 4). The wide fluctuations in *Phrynosoma* body temperatures under natural conditions presumably reflect both the long activity period of these lizards and perhaps their reduced movements into or out of the sun and shade (the vast majority of the animals are in the open when first sighted). More time is thus made available for other activities, such as feeding. Ants are small and presumably contain much unusable chitin (Kitchell and Windell, 1972), so that relatively large numbers of them must be consumed and an ant specialist therefore must possess a large stomach for its body size; this necessitates a tanklike body form. Moreover, possession of such a large gut reduces speed which decreases the ability to escape from predators by movement. As a result, natural selection has favored a spiny body form and cryptic behavior, rather than a sleek body form and rapid movement to cover as in many other species of lizards. A foraging ant-eater must spend considerable time feeding. Food specialization on ants is economically feasible only because these insects usually occur in a clumped spatial distribution and thus constitute a concentrated food supply (MacArthur and Pianka, 1966). To make efficient use of this spatially concentrated, but not overly nutritious, food supply, *P. platyrhinos* has had to evolve a large stomach, expand its time niche and "relax" its thermoregulation. The entire

ecology is dependent upon the animal's cryptic coloration, heavy body and spines, all of which confer some protection from predation, risks of which are increased during long periods of exposure by foraging in the open. A reluctance to move, even when threatened by a potential predator, could be advantageous since movement might attract a predator's attention and negate the advantage of cryptic coloration. Such decreased movement doubtlessly also contributes to the observed high variance in body temperature. The great reproductive potential of horned lizards (Table 11), coupled with relatively high survival of adults, indicates that hatchling and juvenile *Phrynosoma* must suffer extremely heavy mortality. [Medica *et al.* (1973) report annual juvenile survivorship of 26–38% and an annual adult survivorship of from 55 to 75% in *P. platyrhinos* in southern Nevada.] Protection from potential predators arising from the spiny occipital horns is almost certainly much less effective for small horned lizards than for larger ones. High mortality among young horned lizards should favor low parental investment in any given progeny (Murphy, 1968), resulting in low expenditure per offspring and relatively large clutch or litter size. Finally, the very high reproductive effort of *Phrynosoma* is probably a simple consequence of their robust body form. Lizards that must be able to move quickly to escape predators would hardly be expected to weight themselves down with eggs to the same extent as animals that rely entirely upon spines and camouflage to avoid their enemies. Hence the apparent anomalous correlation of a long-lived, relatively *K*-selected, organism with a high reproductive effort is readily explained (see Pianka, 1970a for discussion of correlates of *r* and *K* selection).

Thus, *Phrynosoma platyrhinos*, and perhaps other members of the genus *Phrynosoma*, seem to be characterized by a unique constellation of anatomical, behavioral, physiological and ecological adaptations that facilitate efficient exploitation of ants as a food source and set the horned lizards apart from most other species of lizards. We list these traits again to summarize much of the foregoing discussion. Compared to many other lizard species, *Phrynosoma* 1) are strongly flattened dorso-ventrally, 2) are usually armed with sharp occipital spines, 3) have relatively short legs and are slow and awkward, 4) are noticeably reluctant to move when approached by a potential predator, 5)

\* Herbivores typically have larger guts than carnivores.

TABLE 11. MAJOR ASPECTS OF REPRODUCTION AMONG TEN SPECIES OF *Phrynosoma* AND *Moloch horridus*, WITH AUTHORITIES.

Species	Location	Clutch or Litter Size			Reproductive Effort*			Period of Oviposition or Parturition	Maximum Testes Size	Age at Sexual Maturity	Minimum SVL† at Maturity		Authority or Authorities
		$\bar{x}$	SD	N	$\bar{x}$	SD	N				♀	♂	
<i>P. asio</i>	Mexico	16.9	4.9	7	35.4	1.68	2	mid-August	—	—	91	—	this paper
<i>P. braconieri</i>	Mexico	8.4	2.3	5	21.4	2.81	3	July	—	—	60	—	this paper
<i>P. cornutum</i>	Texas	26.5	6.7	152	30.7	—	30	late May-mid-July	May-early June	—	68	—	Ballinger (1975)
<i>P. cornutum</i>	Texas	23.7	6.0	73	28.8	6.0	41	June-July	May-June	—	69	—	this paper
<i>P. coronatum</i>	Baja and Southern California	12.6	3.8	69	21.3	3.0	16	late May-June	—	—	73	—	this paper
<i>P. douglassi</i>	Arizona	16.7	—	11	—	—	—	August	March-April	—	65	—	Goldberg (1971)
<i>P. douglassi</i>	Arizona, Nevada, New Mexico, Oregon & Utah	16.0	—	56	25.4	8.6	11	August	—	2 years	66	62	this paper
<i>P. m'calli</i>	Southern California-Arizona	5.4	1.3	121	27.0	—	1	—	—	—	66	—	Mayhew (pers. comm.) plus this paper
<i>P. modestum</i>	New Mexico-Texas	10.6	2.3	40	25.8	5.9	18	May-June	May-June	—	50	—	this paper
<i>P. orbiculare</i>	Mexico	9.4	3.6	26	12.8	2.5	15	—	—	—	67	—	this paper
<i>P. platyrhinos</i>	Nevada	6.7	1.4	24	—	—	—	mid-May-mid-July	May-early June	2 years	72	—	Tanner and Krogh (1974); Medica, Turner, & Smith (1973)
<i>P. platyrhinos</i>	Nevada	7.6	—	11	20.5	6.7	5	—	—	—	70	65	this paper
<i>P. platyrhinos</i>	Utah	9.9	2.2	18	25.2	7.7	11	May-June	May	2 years	70	68	this paper
<i>P. platyrhinos</i>	Sonoran and Mojave Deserts	6.8	—	13	24.4	2.0	3	—	May-August	—	70	65	this paper
<i>P. platyrhinos</i>	California, Arizona, Nevada, and Utah (All above plus museum specimens)	7.7	2.1	116	21.0	6.9	36	May-June	May-August	2 years	68	65	this paper
<i>P. solare</i>	Arizona	16.7	3.7	28	32.0	7.2	9	August	June-August	2 years	80	—	Parker (1971) and this paper
<i>Moloch horridus</i>	Western Australia	7.2	1.6	48	15.7	3.5	15	Oct.-Dec.	May-Sept.	3 years	81	75	Pianka and Pianka (1970); Sporn (1965)

\* Mean weight (or volume) of oviducal clutch as a percentage of total female body weight (including clutch).

† In mm.



are often active over a long daily time span, 6) frequently have more variable body temperatures than other sympatric species of lizards, 7) have a conspicuously specialized diet consisting largely of ants, 8) possess an exceptionally large stomach for their body size, 9) have a specialized dentition that facilitates ant-eating (Hotton, 1955), 10) produce large numbers of relatively small eggs or young and 11) expend a considerable amount of matter and energy on each clutch or litter.

*Some comparisons with other species.*—Among horned lizards, *P. platyrhinos* has a relatively small clutch size as well as a fairly low ratio of clutch weight over total female body weight (Table 11). *P. platyrhinos* appear to become sexually mature at about the same size as many other *Phrynosoma* for which there are data, except for the very large species *P. asio* and *P. solare*. Sexual maturity is not reached until the second year in *P. platyrhinos*, *P. douglassi* and *P. solare*; indeed, most *Phrynosoma* may exhibit delayed maturity. In the northern parts of its geographic range, *P. platyrhinos* probably often lays a single clutch each season, although two or more (?) clutches per season may be the rule in the south. Most other *Phrynosoma* for which data exist appear to be single clutched. Thus, *Phrynosoma* probably fall best into the "delayed reproduction, large clutch and single brooded" category of Tinkle *et al.* (1970).

No discussion of horned lizard ecology would be complete without mention of its striking ecological equivalent, the Australian agamid *Moloch horridus*, which has, in at least some ways, evolved convergently with *Phrynosoma* (Pianka and Pianka, 1970). Indeed, after discovering that *Moloch* fed almost exclusively upon ants, Saville-Kent (1897) predicted that *Phrynosoma* would be found to be an ant-eater on the basis of their similarity in body form. As we have seen, his prediction has proven to be correct. *Moloch* is a thornily-armored ant specialist (in nature it eats nothing else!) with delayed maturity (Sporn, 1965) and a single, fairly large clutch for an Australian agamid (mean of 37 *Moloch* clutches is 7.2). A striking difference between the timing of reproduction in *Phrynosoma* and in *Moloch* is apparent from Table 11. Testes of *Phrynosoma* usually reach their largest size sometime during the period from May through August. The equivalent period in the southern hemisphere (Australia) is November through February, dur-

ing which period testes are enlarged and mating takes place in other Australian agamids of the genus *Amphibolurus* (Pianka, 1971a,b). However, *Moloch* appear to mate in the fall (May) and/or late winter (August) (Pianka and Pianka, 1970). Factors underlying the peculiar timing of the reproductive cycle of *Moloch* remain obscure, but early breeding could be necessitated by the relatively long incubation period [average of 5 clutches was 115 days (Sporn, 1965)]. The stomach volume over body weight ratio of *Moloch* (0.051) is much less than that of *P. platyrhinos* (0.134) and similar to that of other sympatric Australian desert lizards (Pianka and Pianka, 1970). Moreover, the variance in body temperatures of active *Moloch* is not conspicuously high among Australian lizards (Pianka and Pianka, 1970). Possible reasons for both these discrepancies between the ecologies of *Moloch* and *P. platyrhinos* are discussed by Pianka and Pianka (1970). Here we simply note that the above integrated view of *Phrynosoma* ecology clearly does not apply in general to all ant-eating lizards.

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## Rates of Heat Exchange in the Lizards *Cnemidophorus sexlineatus* and *Sceloporus undulatus*

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When heated from 21 C to 39 C and subsequently cooled from 39 C to 21 C, both the teiid *Cnemidophorus sexlineatus* (mean weight  $\approx$  6 g) and the iguanid *Sceloporus undulatus* (mean weight  $\approx$  9 g) experienced more rapid heating than cooling. Endogenous heat production, which was estimated from oxygen consumption, could not account for the observed differences between heating and cooling of *Cnemidophorus* at any body temperature, and was sufficient to account for the observed differences between heating and cooling of *Sceloporus* only at high body temperatures. Inasmuch as rates of heating and cooling of dead lizards were similar to the corresponding cooling rates of living animals, changes in thermal conductivity mediated by the cardiovascular system would appear to be primarily responsible for the differential between heating and cooling of live individuals of both species.

Our findings indicate that even the smallest lizards have the physiological capacity to control rates of heat exchange with the environment.

SEVERAL species of lizards, representing the families Agamidae, Iguanidae, Scincidae and Varanidae, possess a physiological capacity to alter rates of heat exchange with the environment (Bartholomew and Tucker, 1963, 1964; Bartholomew and Lasiewski, 1965; Bartholomew *et al.*, 1965; Weathers, 1970). The lizard-like Rhynchocephalia also show different rates of heating and cooling (Wilson and Lee, 1970).

Both endogenous heat production and cardiovascular adjustments during heating and cooling may contribute to the differential between

high rates of heating and low rates of cooling. Endogenous heat production apparently accounts for all of the observed difference between rates of heating and cooling in the scincid *Tiliqua scincoides* (Bartholomew *et al.*, 1965), and for varying percentages of the difference between high heating and low cooling rates in other lizards (Bartholomew and Tucker, 1963, 1964; Weathers, 1970).

Cardiovascular adjustments which increase thermal conductivity during heating and decrease thermal conductivity during cooling have been demonstrated in iguanids and teiids,