ENVIRONMENTAL REACTIONS OF PHRYNOSOMA

BY

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I HEREBY RECOMMEND THAT THE THESIS PREPARED UNDER MY SUPERVISION BY A. O. Weese

ENTITLED Environmental Reactions of Phrynosoma.

BE ACCEPTED AS FULFILLING THIS PART OF THE REQUIREMENTS FOR THE DEGREE OF Master of Arts.

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ENVIRONMENTAL REACTIONS OF PHRYNOSOMA.

A. O. Weese

Environmental Reactions of Phrynosoma.

I. Introduction

1. General Distribution

The horned lizards, more familiarly known as the "horned toads", of the southwestern portion of the United States and the northern states of Mexico form a very distinct group of the family Iguanidae. Unlike most other comparatively large reptilian genera, this particular genus (*Phrynosoma*) is limited to a very special environment, and it is only in a region of relative aridity that these animals find a favorable habitat. Within the limits set by the above condition the specific habitats of the various species and varieties of the genus vary very greatly, ranging all the way from the extreme aridity and great heat of Death Valley in southern California (*Phrynosoma calidiarum* Cope) to the comparative moisture and cold of the northern Rockies. (*Phrynosoma douglasii* Bell, and varieties.) The species here discussed are all found in the Southwest, and under varying environmental conditions.

Phrynosoma modestum, the specimens of which were taken near Albuquerque, New Mexico, close to the lower edge of the "mesa" or clinoplane region, at an altitude of about 1700 meters, is distributed throughout New Mexico, and to a certain extent in the adjoining states, wherever conditions are similar to those in the above typical habitat. The rainfall here averages about 30 cm. annually, while the yearly evaporation from a free water surface is in the neighborhood of 200cm. The soil is rather

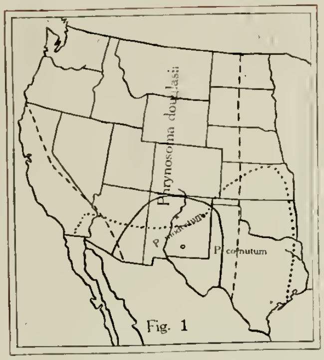

Figure 1. Distribution Map of the Three Species of *Phrynosoma* Discussed in this Paper. The limits of distribution of the species are indicated as follows:

Phrynosoma douglasii, and varieties ---------

Phrynosoma cornutum ....

Phrynosoma modestum ___________

loose and friable, consisting principally of "Tijeras" fine sandy loam and containing, near the surface, a relatively large proportion of fine angular gravel and wind-blown sand. The color is a yellowish or reddish brown. The vegetation is sparse, consisting of scattered grasses, *Chrysothamnus*, *Gutierrezia*, *Salsola*, *Yucca*, etc. This species is not found in the adjoining valley of the Rio Grande, nor in the mountains (Sandias) which border the "mesa" on the east, (2200 meters and above) where moister conditions prevail. In the mountains the rainfall is probably twice as great, on the average, as on the "mesa", although accurate data are not available, and the evaporation is much less, due to the lower temperatures which prevail. In the valley the water table is very near the surface of the soil (actual soil surface or above to 5 meters below the surface). Standing water is not found on the clinoplane except after very heavy rains, which sometimes fail for months at a time, and it is very doubtful if there is any available water supply for the animal other than the small amount obtained with insect food.

Phrynosoma douglasii ornatissimum, the specimens of which were obtained with those of the above species, has a much less restricted habitat, both locally and regionally, as it is distributed over a great deal of the eastern slope of the Rocky Mountains, even as far north as Canada, and, locally, extends into both of the regions described above as bordering on the clinoplane. It is, indeed, more abundant in either of these than in the clinoplane region between, indicating that the determining factor in the distribution, in this case, is similar in the lower valley and on the mountain side. As mentioned above the aridity of these two regions is much

less than that of the clinoplane. The soil differences are also marked, in that the moister soils are more dense and contain more humus, derived from the more abundant vegetation. However, the variation in both the valley and the mountain is very great, from heavy clay to fine sand in the valley and from native rock to fine sand in the mountain.

Phrynosoma cornutum does not occur in the same area as that occupied by the species previously mentioned, although it also is of wide distribution. This species is found throughout Texas and eastern and southern New Mexico, and has been reported from Nebraska, Arkansas, etc. In general, it appears to inhabit regions in which the mean annual temperature is slightly higher than that required by the other two species. The specimens here considered were obtained at Alamogordo, in the Otero basin, New Mexico, where the mean temperature is higher by about 5°C. than at Albuquerque.

2. General Habits

The general habits of the three species here considered are much the same, so no separate description will be attempted. The following discussion will apply, perhaps, more accurately to *Phrynosoma modestum* than to either of the other species, but will, in general, be true of all. They are not, essentially, heat-loving animals, although tolerant of desert conditions. They are found more abundantly during the earlier summer months, and during the autumnal rainy season, when the aerial temperature does not exceed 32°. During these periods the animals move about actively all day, spending the night in protected nooks under vegetation, in the burrows of other animals, or buried beneath the surface of the soil.

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As the daily maximum temperature becomes greater they are to be found only in the early morning and the late afternoon when the heat is less intense. During the heated part of the day the lizard is at rest, almost if not quite buried in the superficial layers of the soil. This position is reached in a characteristic manner. The snout is directed downward and moved rapidly from side to side, the body extremely flattened, while the legs take part in a rapid horizontally clawing movement. The net result of this series of movements is to cover the animal with the loose soil, the depth varying according to the temperature, the soil, and other external conditions, as well as the individual. The same method of burrowing is employed in preparation for hibernation, when the animal may bury itself under several inches of loose soil. In attempting to escape from enemies, other lizards have been observed to dig in a similar manner, and it is probable that *Phrynosoma* also escapes in this way.

3. Food Relations

The food consists of various insects with which the animals come into contact, ants being more readily eaten by the smaller individuals and beetles (*Eleodiini*) forming a considerable portion of the diet of the larger lizards. No food is taken unless it is living, or at least moving. Sand grains set in motion by a heavy wind or otherwise are often snapped up readily and sand grains are accordingly often found in the feces.

4. Water Relations

None of the species of *Phrynosoma* have been observed by the writer to drink water, and it is doubtful if water, independent of

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that contained in the insect food, is ever ingested by the horned lizard. Many individuals are found in situations where there is never any standing water except after the very infrequent heavy rains. Very little water is excreted ordinarily, as when fed on ants, beetles, etc., the feces are eliminated as a dry mass containing practically no water, and the urine is composed of an equally dry mass largely made up of crystals of uric acid. When fed on a moist diet such as grasshopper nymphs from a moist habitat, the feces become softer and are often accompanied by a considerable amount of mucilaginous liquid. The urine, however, remains as usual. The idea that the excretion of waste nitrogen as uric acid is an adaptation on the part of the Reptilia for life in arid regions is well borne out by the conditions in these animals. Analyses made by the writer in the laboratory of Physiological Chemistry of the University of Illinois give the following results (17b):--

Constituents	Milligrams per gram.
Total Nitrogen (N_2)	260.0
Urea+Ammonia Nitrogen	1.4
Ammonia Nitrogen	1.4
Uric Acid	774.0
Uric Acid Nitrogen	258.0
Creatinine	Trace
Ash	87.5
Phosphorus as P_2O_5	3.5

It will be observed that uric acid accounts for practically all of the nitrogen contained in the urine and that urea is entirely absent. In this respect the urine of the horned lizard differs from

that of the aquatic and semi-aquatic reptiles, which contains a considerable amount of urea, as does that of birds, another group in which the uric acid content is high.

5. Reproduction

It is in connection with *Phrynosoma cornutum* that the long disputed question as to the viviparity or oviparity of the members of this genus may be opened again. Cope ('98) states that *Phrynosoma* is oviparous, which is denied by Ditmars ('08) and Watson, ('11) the latter of whom bases his statement on observations of *P. douglasii*. On July 5, 1917, some twenty specimens of *P. cornutum* were received at the Vivarium of the University of Illinois from Alamogordo, N. M., and placed in a sand-bottomed wire screen cage. On July 7, between 11 A. M. and 1 P. M. twenty-three eggs were deposited in the sand on the bottom of the cage. The eggs were about 1 cm. in length, ovoid in shape, and covered with a greyish-white shell of leathery texture. They resembled the eggs of the common painted turtle, and were typical reptilian eggs. Some were opened and found to contain a partially developed living embryo of about 2mm. in length. Several times thereafter, during a period of two weeks, eggs were found in the cage, always in lots of approximately twenty. The deposition of the eggs was never observed. None of the eggs hatched, although living embryos were found in eggs opened a week after deposition. Such embryos were about 6mm. in length. Conditions were evidently not right for the complete development of the embryos. *Phrynosoma douglasii* has not been observed to lay eggs, although a few eggs of *Phrynosoma modestum* were discovered in the cage in which these animals were

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kept. These were found in small numbers only and differed from those of *P. cornutum* in being a light yellow in color and having no leathery shell. As the observations of Watson and Ditmars appear to be well founded, it id possible that the genus is divided with respect to the retention or deposition of the eggs, or that in the same species different conditions may alter the length of time the egg is retained in the maternal body, as is the case among the adders.

II. Environmental Factors

As has been concluded ('17a), it is dangerous to ascribe to any one factor or group of factors the supreme role in determining the seasonal or general distribution of a species. These factors are certainly not the same for all species even in the same environment, and before definite conclusions can be drawn a careful analysis of the habitat must be made, and experimental data must be obtained as to the reactions of the animals in gradients involving the factors capable of variation. Unfortunately, it is not possible or practicable to construct effective gradients involving all environmental conditions, and in such cases we must rely on careful observation and analysis. Such a review as has just been given of the habitat and habits of the horned lizards may indicate to us the probable external conditions variations of which are of importance in the daily and seasonal life of the individual and of the species. The following are the most apparent of such external conditions:--

1. Temperature
   - a- air
   - b- soil
   - c- maxima and minima
2. Water
   - a- relative humidity and evaporating power of air
   - b- soil moisture
   - c- food in relation to its water content

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3. Soil

   a- texture, influenced by

      1- composition

      2- moisture content

      3- vegetation

   b- color

4. Food

   a- character

   b- abundance or scarcity

5. Light

In the natural habitat it is rare that one of the above conditions varies without an accompanying variation in one or more of the others; for example, a variation in temperature of the air is accompanied by a variation in the relative humidity and in the evaporating power of the air, and may be followed by an alteration of soil temperature and soil moisture. Thus it is difficult to consider these conditions separately.

1. Temperature

That temperature affects profoundly the daily life of the animal and limits its activities is shown by the relation of daily variation in temperature to the change from diurnal to crepuscular habit, and to the burrowing activities initiated by high or low temperatures. Minimum temperature is probably associated most closely with the phenomena of hibernation. According to Bachmetjew ('01) the minimum winter temperature which can be survived by hibernating insects depends on the degree of elimination of

water from the tissues and the consequent lowering of the freezing point of the body fluids. Tower ('17) states that in the case of potato beetles those animals acclimated to desert conditions (retention of water) are killed at higher temperatures than those of a more humid climate. In the following experiments gradients in air temperature and in soil temperature (substratum temperature) have been established and the reactions of the animals in such gradients have been recorded.

2. Water

The water relation must always be important in an animal adapted to arid conditions, even though this relation may seem to be a negative one. As indicated by the examination of excreta and observation of the water relations of *Phrynosoma* it would appear that the absence of water as such would not have a limiting effect on the distribution of the animals. It is probably necessary, however, that a certain minimum amount of water be supplied in the food, and that the evaporating power of the air must not exceed a certain maximum for any great length of time. It is to be doubted that any vertebrate may subsist indefinitely without some small water supply in addition to the metabolic water produced internally. As shown in previous experiments (17a) the reaction of *Phrynosoma* in a gradient of the evaporating power of air is not definite unless the gradient be a very steep one. Daily variation in the normal habitat is very large.

3. Soil

The apparent importance of the burrowing reaction in the life

history of the members of this genus points to a corresponding importance of the texture of the soil. Evidently this must be such as to render the success of the burrowing reaction comparatively easy, a condition which would be met only in soils of a low moisture content, and little humus, containing a considerable amount of loosely aggregated particles of sand or fine gravel. In a heavy clay or loam it would be impossible for the animal to burrow deep enough to get below the zone of killing temperatures during hibernation. This would also be impossible in a compact sod. Unfortunately, the problem of the soil relation involves an extensive seasonal study which, so far, it has been impossible to carry out.

While the color and markings of the animals vary with the individual and the species, and the color of the individual changes from time to time, it may be said in general that the color of the horned lizard is very similar to that of the soil of its normal habitat. Experiments of the author and others have shown that a rise of temperature, a condition of darkness, or an increase in the evaporating power of the air causes a centripetal movement of the melanophoric pigment (bleaching) while the opposite conditions cause a darkening. Thus, in general, individuals observed after a rain are darker in color than at other times. The soil is also darker when wet, which might lead the observer to suppose that the change had taken place as a direct adjustment to the color change of the substratum. Within the limits of the conditions of the habitat, variations in the

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evaporating power of the air are the most potent factors producing color change. No direct connection between the color of the animal and that of the substratum has been verified experimentally by the author. Redfield (17), in a recently published paper on color changes in *P. cornutum*, has stated that there is a direct approximation of the color of the animal to that of the substratum, and that the light rays reaching the retina form the stimulus for such changes. The mechanism for the approximation of the color of the animal to that of the substratum is, according to Redfield, subordinate to the daily rhythm of color change occasioned by changes in light and temperature, and to changes brought about by emotional conditions of the animal.

4. Food

An adequate study of this factor would require much more extended observation than has been possible. Some suggestions as to the character of food required have been made above.

5. Light

An estimation of the effect of light of varying intensity and quality in the natural habitat would be very difficult, but it is probable that the relations of light in the life of such animals have been greatly underestimated.

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III. Experimental Results

1. Air Temperature Gradients

Two series of experiments in which air varying in temperature was passed across the experimental cage previously ('17a) described were performed. In the first series the air passing across one third of the cage was heated to a temperature of about 38° by being passed through coils immersed in hot water, that passing across the next third was heated to about 33°, while the remaining third was supplied with air at about 29°. The air was unmodified except as to temperature and the flow was the same in each case. Typical results of this series (*P. modestum* only) are shown statistically in Table I.

In the second series the air for the hottest third was heated to a temperature in the neighborhood of 50°, which is about the maximum soil surface temperature on unprotected sand exposed to the direct rays of the sun. This temperatute was obtained by passing the air through heated iron pipes. A medium temperature was obtained by passing the air through coils immersed in hot water, as above, and remained at about 38°, while the lower temperature was that of the unmodified air, about 30°. These temperatures varied somewhat in the various experiments, but were fairly constant through a single experimental period.

The records of Experiments 34a and 34b show, for *P. modestum*, that the optimum air temperature is in the neighborhood of 35° or 36°. The graphic records of Experiments 86 and 88 (Plate 1) show similar results. It will be noticed in the record of the former

TABLE I.

Experiment 34. Showing the reactions of *Phrynosoma modestum* in an air temperature gradient.

Ten animals were placed in the cage, and observations of their position taken at one minute intervals. The temperatures of the thirds of the cage are indicated at the heads of the respective columns below.

	Experiment 34a			Experiment 34b		
Temperatures	29°	33°	38°	38°	33°	29°
Minutes						
1	3	3	4	3	4	3
2	4	2	4	3	5	2
3	4	2	4	3	6	1
4	4	2	4	4	4	2
5	3	2	5	4	4	2
6	3	2	5	4	5	1
7	3	4	3	4	5	1
8	3	4	3	4	5	1
9	3	4	3	4	5	1
10	3	4	3	4	5	1
11	3	4	3	4	5	1
12	4	3	3	4	5	1
13	2	4	4	4	5	1
14	2	4	4	4	4	2
15	2	4	4	3	5	2
16	2	4	4	3	5	2
17	2	4	4	3	5	2
18	2	3	5	4	5	1
19	2	3	5	4	5	1
20	2	3	5	4	5	1
21	2	3	5	5	4	1
22	1	5	4	5	4	1
23	1	5	4	5	4	1
24	1	5	4	4	5	1
25	1	5	4	3	6	1

that the animal burrowed in the manner previously described, first at a temperature of about 38° and later at a slightly lower temperature. (Indicated by the circles in the first and sixth minutes of the record.) This burrowing reaction was found to take place very often, throughout the whole series, usually at the upper limit of the optimum temperature range. This agrees with the phenomena observed in the field, of burrowing as the air temperature rises in the course of the day.

P. douglasii, as shown in the graphic records of Experiments 82 and 85, (Plate 1) seems to choose a somewhat lower temperature, between 30° and 35°, although there is a considerable amount of individual variation.

P. cornutum, the behavior of which in the gradient is illustrated by the records of experiments 78 and 81, (Plate 1) appears to show a preference for a temperature slightly higher than that shown by the other species.

2. Substratum Temperature Gradients

For the purpose of establishing this gradient the cage was placed in a water bath so arranged that hot water flowed into the latter at one end and cold water at the other, the water being directed backward and forward beneath the cage, and running out near the centre, in such a manner as to produce a gradient in the temperature of the cage bottom. The temperature of the substratum was taken at intervals along the edge of the cage by thermometers whose bulbs were just covered by the sand in the bottom.

The statistical records of Experiments 43, 126 and 127 (Table

TABLE II.

Experiments 43, 126 and 127, showing the reactions of *Phrynosoma modestum* in a gradient of the temperature of the substratum. Temperatures are indicated at the tops of the columns corresponding to the various thirds of the cage, and the number of animals observed in each third at the given time is noted in the respective column.

	Experiment 43			Experiment 126			Experiment 127		
Temperatures	45°	43°	36°	19°	39°	43°	25°	40°	52°
Minutes 1	2	4	2	3	4	3	2	6	2
2	2	4	2	1	5	4	*1* 1	8	0
3	2	4	2	1	4	5	*1* 1	8	0
4	2	5	1	1	3	6	*1*	8	1
5	2	5	1	0	4	6	*1*	8	1
6	2	4	2	0	4	6	*1*	8	1
7	2	5	1	1	4	5	*1*	8	1
8	3	4	1	1	5	4	*1*	9	0
9	1	6	1	2	5	3	*1*	9	0
10	1	5	2	3	4	3	*1*	9	0
11	1	5	2	4	3	3	*1*	*1* 8	0
12	2	5	1	4	3	3	*1*	*1* 8	0
13	2	5	1	2	5	3	Redistributed		
14	1	6	1	1	5	4	21°	36°	46°
15	1	5	2	1	5	4	4	2	4
16	1	5	2	1	5	4	4	3	3
17	0	6	2	1	5	4	3	4	3
18	0	6	2	1	5	4	3	4	3
19	0	6	2	1	5	4	3	5	2
20	0	6	2	1	6	3	3	5	2
21	0	7	1	2	5	3	3	6	1
22	0	7	1	0	7	3	1	9	0
23	1	5	2	1	5	4	0	*1* 9	0
24	0	6	2	1	5	4	0	*1* 9	0
25	0	6	2	0	5	5	0	*1* 9	0
26	0	6	2	0	5	5			
27	0	6	2	0	5	5			
28	0	6	2	1	4	5			
29	0	6	2	0	5	5			
30	0	6	2	0	5	5			

(1) The italic figures indicate that the animal so designated burrowed in the corresponding part of the cage.

II) show an optimum substratum temperature for *P. modestum* of about 40°, or about 5° higher than the optimum air temperature for the same species. In this species the response to changes of temperature of the substratum is very definite, and by varying the temperatures of the gradient the animals could be driven repeatedly from one end of the cage to the other as the temperature was raised or lowered. The lizards often burrowed at or near the upper limit of the optimum temperature, and, less often, at the temperatures below the optimum. The graphic records of Experiments 12 and 28 (Plate 1) give similar results.

The individuals of *P. douglasii* which were taken in the same region as those of the previous species gave practically the same figures for the optimum substratum temperature. The graphic records of Experiments 101 and 26 indicate the behavior of this animal in the gradient. Statistical records of the behavior of *P. douglasii* and *P. cornutum* were not made, because of the size of the animals, which prevented the introduction of any number into the cage at the same time.

P. cornutum, as illustrated by the records of Experiments 45 and 66, (Plate 1) chose a higher substratum temperature than either of the other species, averaging nearly five degrees above that shown by the other curves.

In summing up the results of the air temperature and substratum temperature experiments (over one hundred) in relation to those of the evaporation gradient previously reported ('17a), it is found that the animals choose conditions which are very near the

normal conditions in the usual habitat at the time of greatest activity. These conditions represent the optimum for the animals. For example, as has been noted ('17a), the evaporation optimum for *P. modestum* appears to be near 3cc per hour, as measured by the standard atmometer, which is very near the average outdoor evaporation as observed in the natural habitat of the animal at the season and at the time of day when the animal is most active. If the temperature under such conditions be observed, it will be found that the average atmospheric temperature, 1 cm. from the surface of the soil, in the sun, will be in the neighborhood of 35°, and that of the surface layer of the soil about 40°. These temperatures vary greatly, of course, with other features of the weather, such as air movements, clouds, etc., but in every case when the sun is shining will be found to range from 5° to 10° above the atmospheric temperatures as measured under standard Weather Bureau conditions. Of the variables mentioned here, substratum temperature has a much greater effect on the behavior of the animal than either of the others.

3. Moisture of Substratum Gradient

Although it was impossible to establish and observe an effective gradient of soil conditions, as noted above, several experiments on the direct effect of a moisture gradient were performed. The gradient in water content of the substratum was obtained by placing a layer of "torpedo sand" saturated with water on the bottom of one third of the cage, a mixture of saturated sand and dry sand in the adjoining third, and dry sand in the rest of the cage. In none of

the species observed was any marked preference for any portion of the cage exhibited. Soil moisture, as such, does not seem to effect the movements of the animals, although, in the matural habitat, the high evaporating power of the air produces a considerable degree of temperature difference between dry soil and wet soil by the vaporization of the water from the latter. This difference was not reproduced under experimental conditions. Typical results of this series of experiments are shown in the graphs of Experiments 91 and 97. (Plate 20).

4. Gradient in Color of Light (Wave Length)

Although it would be difficult to estimate the effect of the various light components in the natural habitat, a series of light experiments has been included. For use as a color gradient the cage used in the other experiments was covered with an accessory cover composed of a series of six equal strips of gelatine ray filter in the principal colors (violet, blue, green, yellow, orange, red). Three forty watt electric lamps were placed above the cage within the observation hood, so that the light was approximately equally distributed throughout the cage, each sixth of the cage being illuminated principally by rays of a narrow range of wave length.

Experiment 112 illustrates the movements of *P. modestum* in such a gradient. The longest rays were avoided, as well as the shortest, although the animal remained for greater lengths of time in the red section than in the violet. The optimum seems to lie in the green and the yellow.

P. cornutum (Experiments 116 and 118, Plate 2) avoids both red and violet, with an optimum near the middle of the spectrum. *P. douglasii* did not respond regularly and seemed little affected.

The color reactions are probably not as significant as those involving the other factors here considered, as great variation in the quality of light does not occur in the natural habitat. Direct sunlight there contains a rather larger amount of the light of the shorter wave lengths than elsewhere, and it is possible that the avoidance of violet light as shown in these experiments is of signigicance in explaining the avoidance of sunlight under certain conditions, but it is more probable that heat is the dominating factor in this reaction.

IV. Summary and Conclusions

1. Of the temperature conditions capable of being tested in the gradient, the temperature of the substratum calls forth the most definite responses. In additoon to the indication of an optimum in the movements of the animal, definite motor responses of a specialized character (burrowing) are made to certain temperature conditions just above or just below this optimum. The temperature of the air calls forth similar feactions but not as readily or as definitely as that of the soil or substratum, the reaction to the former being overshadowed by the latter when a difference exists. The temperature of the substratum is evidently of very great importance in the daily movements of the horned lizards and probably plays an important part in the control of distribution. The temperature of the soil is probably also of great importance in connection with the deposition and hatching of eggs in those species which are oviparous. The differences between the optimum temperatures of the various species considered are in the dieection and of the magnitude of the temperature differences normal to their respective habitats. While the limits between which the maxima and minima of environmental temperature may vary and still remain favorable for the completion of the lige cycle of the animal could not be subjected to experiment of the type here used, it is evident that at least the minimum is of great importance in connection with the phenomena of hibernation, and the maximum is probably of similar importance in relation to the aestivation which takes place more or less regularly in these animals.

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2. In the gradient of the evaporating power of air definite responses were obtained only in the case of one species, (*P. modestum*) and here only when the gradient was a steep one. The daily and seasonal variation in this factor is very large in the natural habitat. The reactions of the animals to temperature changes in the environment act in such a way as to prevent the exposure of the organism to excessive desiccation. The effect of soil moisture is apparently felt indirectly, through the alteration of the temperature and the texture of the soil, the latter of which is of importance in relation to the burrowing habit. It is probable that there is a certain minimum water content of food, below which the animal would not survive. This must be very low, however, considering the character of most insects used for food. The excretion of water is reduced to a minimum by the character of the nitrogenous excreta which are almost exclusively in the form of the insoluble uric acid.

3. An important factor in the distribution of these animals is evidently the texture of the soil, which must be suitable for burrowing, as this is the type of reaction of the animal in response to unfavorable conditions generally, ans specifically with respect to hibernation and aestivation. This condition of soil texture is affected adversely by increases in the moisture content, and by increases in the amount of vegetation present. The color of the soil is important from the standpoint of invisibility and it is probable that there is some degree of approximation of the color of the animal to that of the substratum. It is difficult to see how

this fact could be of much use to the species, especially in the case of such profusely armored species as *P. cornutum*.

4. The role of light in the daily and seasonal life of the animals has not been shown, although they are positively phototactic and avoid extremes in the color gradient. The optimum in this gradient lies in the green and the yellow. This may be correlated with the predominant colors of soil and vegetation in the natural habitat.

V. Bibliography

Babcock, S. M. 1912. Metabolic Water: Its Production and Role in Vital Phenomena. Wisconsin Research Bulletin, 22:87-181.

Bachmetjew, P. 1901. Experimentelle entomologische Studien. Leipzig.

Bailey, Vernon. 1905. Biological Survey of Texas. No. Am. Fauna, 25.

Cope, E. D. 1898. The Crocodilians, Lizards and Snakes of North America. Report U. S. N. M. 1898:153-1270.

Dice. L. R. 1916. Distribution of the Land Vertebrates of Southeastern Washington. Uni. Cal. Publ. Zool., 16:293-348.

Ditmars, R. L. 1908. The Reptile Book. New York.

Girard, Charles A. 1853. A Monographic Edsay on the Genus Phrynosoma. Stansbury's Exped. Gt. Salt Lake, :354-365.

Grinnell, Jos. 1917. Field Tests of Theories Concerning Distributional Control. Am. Nat., 51:115-128.

Herrick, C. L., Terry, John, and Herrick, H. N. 1899. Notes on a Collection of Lizards from New Mexico. Bull. Sci. Lab. Dennison Uni., 11:117-148.

Nelson, J. W., Holmes, L. C., and Eckmann, E. C. 1914. Soil Survey of the Middle Rio Grande Valley Area, New Mexico. U. S. D. A., Advance Sheets--Field Operations of the Bureau of Soils, 1912.

Parker, G. H. 1907. Influence of Light and Heat on Melanophores. Jour. Ex. Zool., 3:401-439.

Pritchett, Annie E. 1903. Some Experiments in Feeding Lizards

with Protectively Colored Insects. Biol Bull., 5:271-287.

Ruth, E. S. and Gibson, R. B. 1917. Disappearance of the Pigment in the Melanophores of Philippine House Lizards. Phil. Jour. Sci. Sec. B., 12:181-190.

Shelford, V. E. 1911. Physiological Abimal Geography. Jour. Morph. 22:552-618.

1912. Ecological Succession. V. Aspects of Physiological Classification. Biol. Bull., 23:331-370.

1913a. Animal Communities in Temperate America. Geog. Soc. Chi. Bull. 5.

1913b. The Reactions of Certain Animals to Gradients of Evaporating Power of Air. Biol. Bull., 25:79-120.

1915. Principles and Problems of Ecology as Illustrated by Animals. Journ. Ecol., 3:1-23.

Shelford, V. E. and Deere, E. O. 1913. A Method of Establishing Evaporation Gradients. Biol. Bull. , 25:80-83.

Tower, W. L. 1917. Inheritable Modification of the Water Relation in the Hibernation of Leptinotarsa decemlineata. Biol. Bull., 33:229-257.

Visher, S. S. 1916. The Biogeography of the Northern Great Plains. Geog. Rev., 1:89-115.

Watson, J. R. 1911. A Contribution to the Study of the Ecological Distribution of the Animal Life of North Central New Mexico with Especial Attention to the Insects. Rep. Nat. Res. Surv. New Mex. 1:67-117.

1912. Plant Geography of North Central New Mexico. Bot. Gaz., 54:194-217.

Weese, A. O. 1917a. An Experimental Study of the Reactions of the Horned Lizard, Phrynosoma modestum Gir., a Reptile of the Semi-desert. Biol. Bull., 32:98-116. (bibliography).

1917b. The Urine of the Horned Lizard. Science, N. S. 46:517-518.

Weinzirl, John. 1905. Evaporation from Water Surface at Albuquerque, New Mexico. Bull. Hadley Climatol. Lab., 3:10:1-14.

PLATE 1

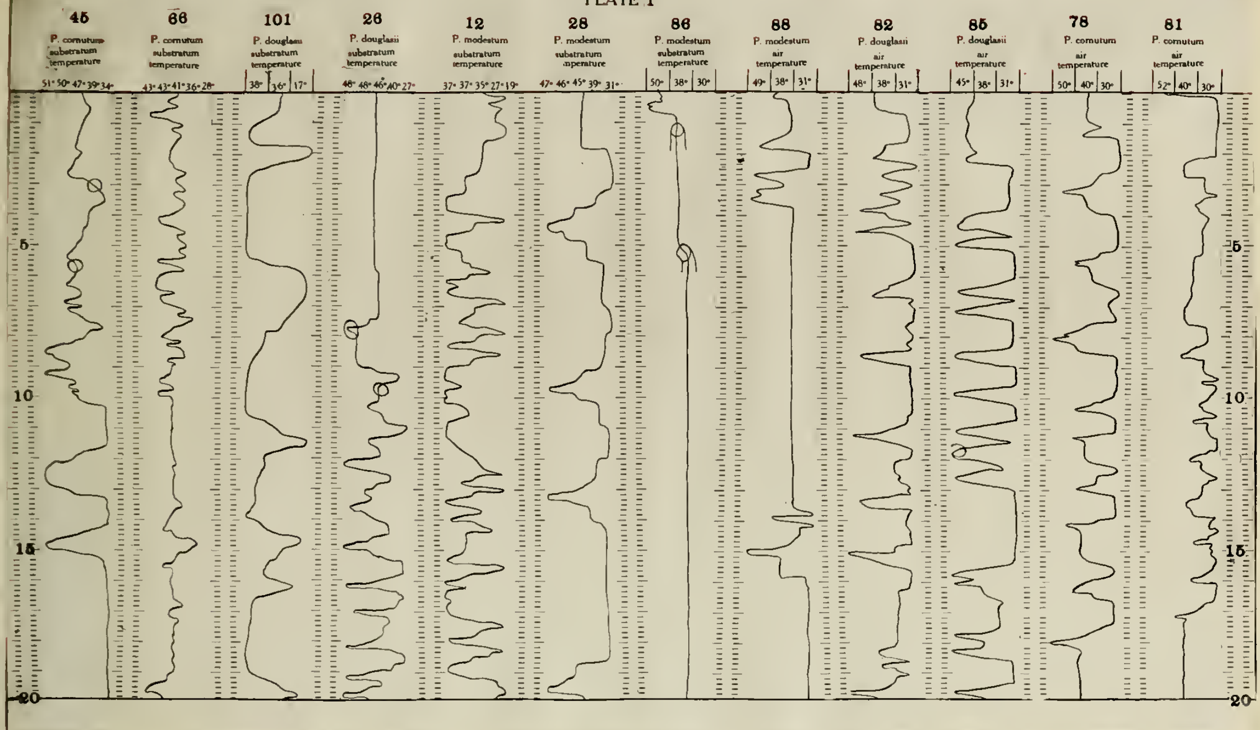

PLATE 2

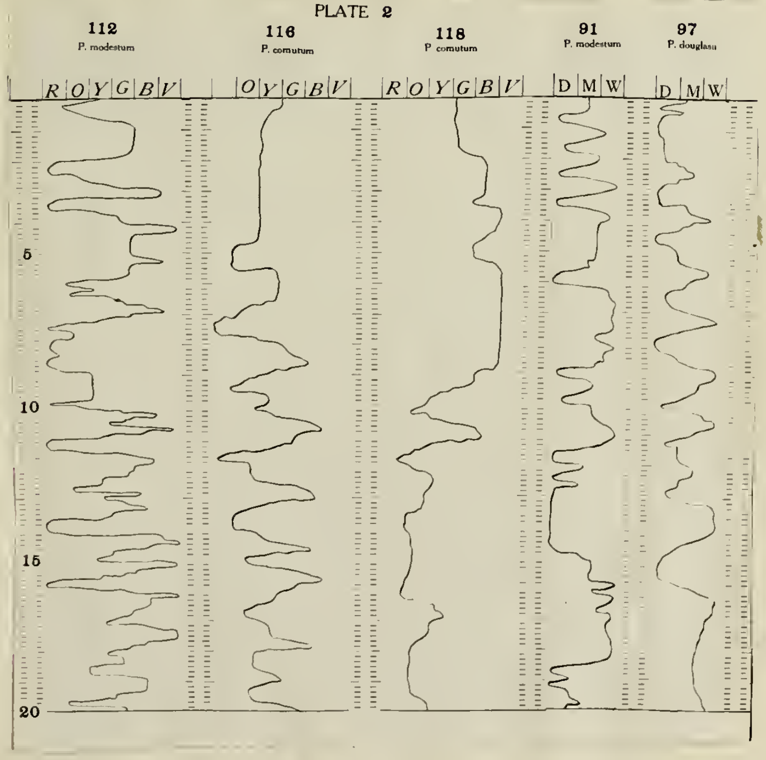

Plate 1, Illustrating the reactions of Phrynosoma in gradients of air temperature and substratum temperature. Experiments No. 45, 66, 101, 26, 12, 28, 86, 88, 82, 85, 78, 81.

In the chart, each section between the numbered scales represents the record of a twenty minute experiment, the distance between the scales representing the length of the cage, and the vertical length of the chart the time, twenty minutes, each division on the scale representing twenty seconds. The curve represents the movements of the animal under observation, and as the time component is vertical and the space component is horizontal, the parts of the curve most nearly horizontal represent the most rapid movements, while the vertical parts of the curve indicate that the animal remained in one spot during the length of time indicated on the adjacent scale. The character of the experiment is in each case indicated above the graph, as is the temperature of the various portions of the cage. In some cases the temperature was taken at five places, and in others only in three places. The circles such as are found in the graphic records of Experiments 45, 26, 86 and 85, indicate that the animal burrowed in the sand on the bottom of the cage at the indicated time.

Experiment 45. For the first two minutes the animal was comparatively quiet, and after the close of this period moved toward the hot end of the cage, to return immediately, and begin to burrow. Just after the fifth minute the animal again moved toward the higher temperature and again burrowed. Thereafter the movements of the animal are of greater amplitude, but become less frequent, and finally it comes to rest near the cooler end of the cage, where it remains until the end of the experimental period.

Experiment 66. This animal at first moves rather rapidly, first toward the warmer end of the cage and then toward the cooler end, never reaching either. After the tenth minute the movements are fewer and shorter, most of the time being spent at a temperature just above 41°.

Experiment 101. The highest temperature here is 38° and the animal spends the most of the time in the warmer end of the cage, with frequent slow excursions to the cooler area.

Experiment 26. This animal remains almost motionless at 46° for nearly eight minutes, and then begins to wander back and forth, spending a little more time in the neighborhood of 40° than elsewhere.

Plate 1, continued.

Experiment 12. This animal first moves toward the cooler end of the cage, finally reaching the warm end during the fourth minute. Thereafter the stays are longer in the 37° regions, although the animal is very active.

Experiment 28. This animal moves more slowly than the preceding one. In this case the gradient is in the other direction from the optimum. The animal reaches the hot end only four times during the period, while the greater part of the time is spent at about 39°.

Experiment 86. This is an example of the very inactive type of animal, which is here stimulated to burrowing by the high temperature encountered in the first trip to the hot end. This animal remained practically covered by the sand throughout the experimental period.

Experiment 88. This animal is active at first, then has a period of rest of about ten minutes at 35°, followed by a short period of activity, which is again followed by a period of rest at 33°.

Experiment 82. This is a good type of the record in which the animal is active, and enters the region of high temperature, but turns back immediately. Most of the time is spent at a temperature just above 31°.

Experiment 85. This is quite similar to the previous record, except that the avoidance of the high temperatures is not so marked, and there is one burrowing reaction at the high temperature.

Experiment 78. This record shows avoidance and turning away from the hot area without entering it. When the animal actually enters the hot area, as in the fourth and ninth minutes, the subsequent stay in the cooler end is longer than when there is an avoidance without entering the warm air.

Experiment 81. This animal is very sensitive to the higher temperatures and never reaches the hot end, although it is very active at times.

PLATE 2. Illustrating the reactions of Phrynosoma in gradients of wave length (color) of light and moisture of substratum. Experiments 112, 116, 118, 91 and 97.

Experiment 112. In this and the two following experiments, the letters R, O, Y, G, B, and V, above the graphs represent the color of the light screen (Red, Orange, Yellow, Green, Blue, Violet) over the corresponding portion of the cage. In this experiment the animal avoids the violet section, turning away from it rather quickly in each instance. The greater part of the time is spent in the green and yellow.
Experiment 116. This animal avoids the violet and even the blue very markedly, and enters the red only twice. The optimum here seems to be in the yellow and the green.
Experiment 118. Avoidance of both the violet and the red is characteristic of this curve. There are two periods, one of which is spent largely in the blue, and another in the orange.
Experiments 91 and 97. Here the letters D, M, and W refer to dry medium and wet thirds of the cage. The graphs show no preference on the part of the animal.