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A Correlation of the Environmental Reactions of Various Animals of the Arid Steppe*

The animals of a given animal community are bound together because of their similar or equivalent reaction to the factors of the environment. This agreement need not extend to the reactions to all factors of the environment and need not involve agreement in specificities of reaction, but, in so far as the normal environment of two species in the same biome is the same, the reactions are necessarily equivalent in character. This has been amply demonstrated for aquatic communities by Shelford (1914), for terrestial mammalian communities of the moist forest by Chenoweth (1917) and for certain other communities by Shelford and others, in various papers.

The work of the author on the horned lizards (Phrynosoma) (1917, 1919) points in the same direction, so far as these animals are concerned, in the semi-arid steppe community. The present paper is the result of an attempt to extend the inquiry to certain other constituents of the biome, belonging to the class Insecta. Darkling beetles (Tenebrionidæ) have been chosen as the most representative insects of the arid region.

1. General Distribution. The horned lizards or "horned toads" of the genus Phrynosoma are limited in their distribution to regions of relative aridity. The various species and varieties of the genus, however, are found everywhere from regions of excessive aridity and great heat, such as Death Valley in southern California (*Phrynosoma calidiarum* Cope), to the comparatively cold and moist regions of the northern Rocky Mountains (*Phrynosoma douglassii* Bell, and varieties). The two species here discussed are found in central New Mexico. The members of the tribe *Eleodiini* of the family Tenebrionidæ, comprising the darkling beetles, are also found throughout the arid and semi-arid regions of North America.

All specimens of both lizards and insects were taken near Albuquerque, New Mexico, close to the lower edge of the mesa or clinoplane region, at an altitude of about 5,000 feet. The

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rainfall here averages about eight inches annually, while the yearly evaporation from a free water surface is nearly ten times as great. The soil is loose, except where the "Tijeras fine sandy loam" has been washed or blown away, exposing the harder "adobe." The color of the soil is a yellowish or reddish brown. The vegetation is coarse, consisting of scattered grasses, *Chrysothamnus. Gutierrezia, Salsola, Yucca*, etc. The faunal realm is, therefore, that of the warm temperate arid steppe.

The lizards studied were *Phrynosoma modestum* and *Phrynosoma douglassii ornatissimum*, the former restricted as a species to this region, and the latter of somewhat wider distribution. In the case of the insects, no attempt was made to separate individual species in the experiments, but in all cases several individuals of different species were grouped together. As all individuals were taken from the same habitat and as there was no observable specific difference in their behavior, this procedure seemed justifiable. The species used experimentally included: *Eleodes carbonaria, E. caudifera, E. sponsa, E. hispilabris* and *E. longicollis*.

2. *General Habits.* The daily and seasonal occurrence of the two groups of animals is very similar. All are found more abundantly during the later spring months and during the late summer rainy season, when the maximum aerial temperature does not exceed 32°C. (90°F.). During these periods the animals move about actively, the horned lizards spending the cooler nights in protected nooks under vegetation, in the burrows of other animals, or buried beneath the surface of the soil. The darkling beetles are more crepuscular and nocturnal in their habits than the lizards. They are sensitive to low temperatures, however, and spend their inactive periods in clumps of vegetation or in other sheltered positions. Both protect themselves from extreme heat by "digging in." During those months of the year when the daily maximum temperature rises above 32°C. lizards and beetles are abroad in abundance only during the less heated portions of the day.

3. *Food Relations.* The food of the lizards consists of various insects with which they come into contact, chiefly ants for the smaller individuals, and *Eleodiini* for the larger ones. No

food is taken unless it is living or at least moving. The beetles feed mostly on dead or decaying vegetable matter, although they also eat green vegetation and fungi, and collect in large numbers about the carcasses of dead vertebrates.

4. *Water Relations.* Standing water is very infrequent on the "mesa," being found only after heavy rains; so the amount of free water available is very limited. Very little water is excreted ordinarily by the lizards, 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 soft bodied insect larvæ, the feces become softer and more liquid, but there is no change in the character of the urine. The only water excreted by the beetles is found in the ill smelling fluid ejected from the anal glands when disturbed. Uric acid is the sole nitrogenous constituent of the dry urine of these insects, also. Urea, which is the principal nitrogenous constituent of the urine of most vertebrates, is soluble and requires a considerable amount of water for its elimination. Uric acid, on the other hand, is insoluble, and may be excreted in the solid form. This is of distinct advantage in arid desert conditions, as it enables the animal to exist without the ingestion of free water, the entire water requirement of the animal being met by the small amount of water contained in the food and the larger amount produced in metabolism by the oxidization of the hydrogen of the food. Both groups of animals also have an impervious integument, thus reducing the water loss from evaporation to a minimum.

We cannot ascribe to any one factor or group of factors the supreme role in determining the distribution of a species. These factors are certainly not the same for all species 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 cases where the construction of such a gradient is impossible, we must rely on careful observation and analysis. Such a review of the habitat and habits of the horned lizard and the darkling bettles may indicate to us the probable external conditions, variations of which are of importance in determining their association. 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.
3. Soil.
    - *(a)* Texture as influenced by
        1. Composition.
        2. Moisture content.
        3. Vegetation.
    - *(b)* Color.
4. Food.
    - *(a)* Character.
    - *(b)* Abundance or scarcity.
5. Light.
    - *(a)* Quality.
    - *(b)* Quantity.
    - *(c)* Rhythm.
6. Miscellaneous.

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, as well as soil texture. Thus it is difficult to consider these conditions separately.

1. Temperature. That temperature affects profoundly the daily life of the animals considered and limits their activities is shown by the relation of the daily variation of temperature to the diurnal, crepuscular or nocturnal habit, and to the digging activities associated with high and low temperatures. Minimum temperature is probably very closely associated with the phenomena of hibernation. According to Bachmetjew (1901) the minimum winter temperature which can be survived by hibernating insects depends upon the degree of elimination of water from the tissues and the consequent lowering of the freezing point of the body fluids. The findings of Tower (1917) in the case of the potato beetles lead to the same conclusion. He found that potato beetles acclimated to the desert conditions of Tucson and consequently retaining more water in the body tissues, were killed by higher winter temperatures than those living in the more humid climate of Illinois.

2. Water. The water relation must always be important in animals adapted to arid conditions, even though this relation may seem to be negative. As indicated by the examination of the excreta and observation of the habits of the animals in relation to water it would appear that the absence of water as such would not have a limiting effect on distribution. 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 has been shown that Phrynosoma reacts in steep gradients of the evaporating power of air (1917a). While some insects of the family Tenebrionidæ (Babcock, 1912) are known to exist indefinitely without any imbibition of water, it is to be doubted that any vertebrate may subsist indefinitely without some small water supply in addition to metabolic water. As shown in previous experiments (1917a, see table 1) the reaction of Phrynosoma in a gradient of the evaporating power of air is not definite unless the gradient is very steep. The Eleodiini give no definite reaction in such a gradient. (Table 2.)

3. Soil. The apparent importance of the "digging in" reaction in the life history of both animals points to a corresponding importance in the texture of the soil making this response possible. Evidently the texture of the soil must be such as to render the digging process comparatively easy. This condition is met only in soils of a low moisture content and little humus. In a heavy clay or loam it would be impossible for the animals to get below the zone of killing temperatures during hibernation. The color of the soil may have something to do with the relations of Phrynosoma, but this would not apply to the uni formly black Eleodiina.

4. *Food.* An adequate study of the food problem with respect to either species would consume far more time than has been available. Such a study would be very valuable. Some suggestions as to the character of the food relations have been made above.

5. *Light.* An estimation of the effect of light of varying intensity, direction and quality in the natural habitat would be difficult. It is probable that the relations of light in the life of such animals have been greatly underestimated. The horned lizards, in a cage in a room lighted by windows along one side, very often collect on the sides of the cage next to the windows, crawlling up the screen walls of the cage. This reaction does not occur when the cage is in the direct rays of the sun. Experiments with color, intensity and direction have been carried out with both species and results will be given in the course of this paper.

6. *Miscellaneous.* There are doubtless many environmental conditions not mentioned above having their effect on the animals. Among these might be mentioned wind, electrical conditions, parasitism, other community relations, etc. Our knowledge of these various conditions as they affect Phrynosoma and Eleodes is practically nil.

EXPERIMENTAL METHODS.

1. *Air Temperature Gradients.* The apparatus used in this series of experiments consisted of a cage of suitable size allowing perfect freedom of movement on the part of the animals, divided into three rectangular areas, each supplied with a current of air at a different temperature moving at the same rate across the area. As the air passing over the three parts of the cage came originally from the same source, the only difference in the air in

the different thirds of the cage was in temperature and relative (not absolute) humidity.

2. *Substratum Temperature Gradients.* The same cage was used, but in this series the bottom of the cage was heated by the use of currents of water flowing across a pan underneath the bottom. The course of the currents was so directed by baffle plates that the temperature of the bottom of the cage varied evenly from hot at one end to cool at the other.

3. *Gradients in the Evaporating Power of Air.* The same arrangement was used as in (1), but, instead of being heated to different temperatures the air passing across the various thirds of the cage was passed through driers or moisteners, so that the air passing across one end of the cage was moist, across the other end, dry, and across the middle third of the cage, intermediate in its moisture content.

4. *Gradient in Intensity of Light.* A sixty-watt Mazda lamp was so placed above the cage that one end of the cage was partially shaded, while the other end received the full force of the illumination. As the light came from above, direction did not enter into consideration.

5. *Gradient in Wave Length of Light.* The cage was covered by an accessory lid composed of a series of six equal strips of gelatine ray filter in the principal colors of the spectrum—(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 being illuminated by rays of a narrow range of wave length.

6. *Direction of Light.* The cage was illuminated by a sixty-watt Mazda lamp placed near one end. This is not an accurate method, as, of course, the intensity of the light varies inversely as the square of the distance from the source of illumination.

Results of Experiments.

Results were recorded in two different ways. In the statistical method of recording several animals were distributed over the cage, and then subjected to the gradient. Readings were then taken at definite intervals and the number of individuals in each part of the cage recorded at such intervals. In the graphic method, a single individual was placed in the gradient cage and its subsequent movements recorded graphically. In such a graphic record a vertical scale represents time and the space between such vertical scales represents the length of the cage. The curve in this space, then, 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 curves more nearly horizontal represent the most rapid movements from end to end of the cage, while the vertical parts of the curve indicate that the animal was at rest during the length of time indicated on the scale. Both methods of recording were used, and gave the same results, apparently as well as actually.

1. Air Temperature Gradients. A characteristic reaction of Phrynosoma is illustrated by the record of Experiment 88, in which the temperatures of the thirds of the cage were respectively 49°, 38° and 31°, and Experiment 82, in which the temperatures were 48°, 38° and 31°. (Fig 1.)

At the beginning of this experiment the animal was introduced into the central section of the cage, made a slight movement toward the hot end during the first few seconds, returned, then, in the second minute, made an excursion nearly to the hot end, to return immediately nearly to the cool end. Two subsequent incursions into the hot end were made, then the animal remained at a temperature of about 35° until nearly the end of the fourteenth minute when the same process was repeated. The animal finally came to rest at a temperature of about 31°. Similar results are indicated in the statistical record of Experiment 34b. (Table III.)

The darkling beetles react in very much the same way in similar gradients. A characteristic graphic record of the reactions of a darkling beetle in an air temperature gradient is shown in the record of Experiment 304. Here the movements are much more rapid than those of Phrynosoma in the chart illustrated, but not more rapid than those shown by other lizards. The records of Experiment 296 (same individual as 304) show an appearance much more like the record of the movements of the lizard. In these experiments the temperatures were 38°, 32°, 30° and 36°, 30°, 27°, respctively. The temperature most sought by the animal was in the neighborhood of 27° and 26° in these experiments. The same results are indicated in the statistical records of Experimnet 302. (Table IV.) The beetles thus show a "preference" for a temperature about four or five degrees below that sought by the lizards.

2. *Light Gradients.* The movements of the horned lizard in a color gradient are shown in the graphic records of Experiment 112 (Fig. 1), where the animal avoided the violet section, spending the greater part of the time in the green and the yellow. The beetles do not seem to react at all in gradients of the wave length of light.

In a gradient of light intensity, however, they react very definitely, as shown by the statistical records of Experiments 311 and 312. (Table 5.) They are equally active in relation to the direction of light, as illustrated by the records of Experiments 321 and 322. (Table 6.) In both cases the insects seek the region of least illumination, reacting negatively to both direction and intensity of light. The horned lizard, as previously mentioned, reacts negatively to light of great intensity, e. g., sunlight (perhaps on account of the heat rays), and positively to diffuse light.

Summary and Conclusions.

In experiments with Phrynosoma and Eleodes the conclusion is reached that of the environmental conditions capable of being tested by means of gradients, only two seem to affect both animals—temperature and light. Evaporating power of air, except as included in temperature, seems of very slight effect. The reactions in temperature gradients are very similar, with only slight differences in the optimum. This difference is in the direction which accords with the difference in the daily habits of the animals. The reactions with respect to light, also, differ in the manner that might be expected from the observed differences in the period of activity.

What role other environmental conditions may have in the daily and seasonal life of the two groups may be very difficult to determine, but the effect of two, at least, of the most important of these has been shown, and the reactions in gradients of these two are similar in the degree that the daily life of the animals is similar, and differ in the direction of the difference in daily life habits.

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Fig. 1. Illustrating the reactions of Phrynosoma and Eleodes in gradients of air temperature and the reactions of Phrynosoma in a gradient of wave-length (color) of light. Experiments No. 88, 82, 296, 304 and 112.

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 ten seconds. The curve represents the movements of the animal under observation, and as the time component is vertical and the space component 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 the same position during the length of time indicated on the adjacent scale. The animal used in the experiment is in each case noted above the graph, as is the temperature of the various parts of the cage.

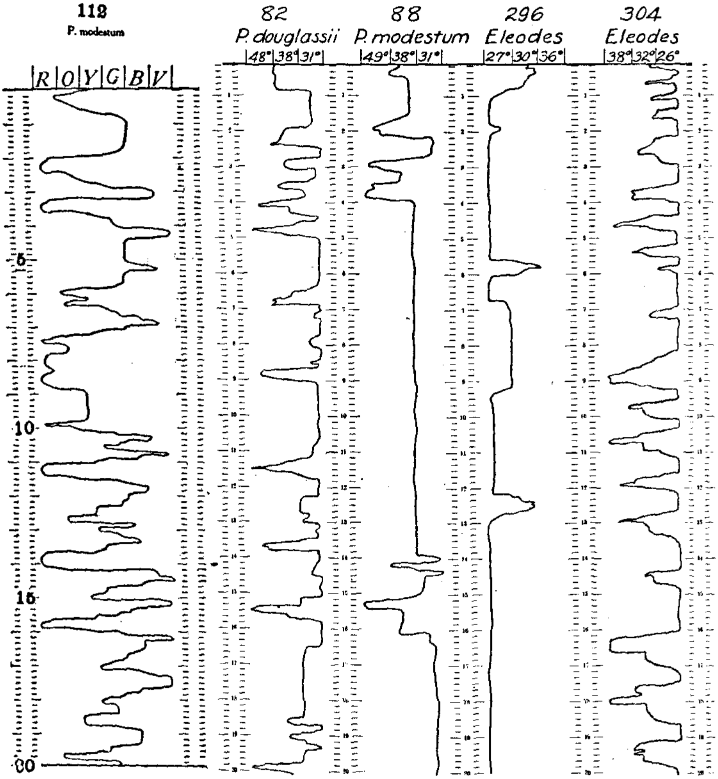
Controls, i. e., experiments in which all portions of the cage were at the same temperature, were carried out in all cases, but the regular curves obtained have been omitted to save space.

Experiment 88.—This animal showed alternate periods of rest at an optimum temperature and activity involving incursions into both temperature extremes represented in the gradient.

Experiment 82 is a good example of the type in which there is great activity, but very short stays in the unfavorable temperatures.

Experiment 296.—The animal, introduced into the cage in the 30° section, moved a short distance toward the warm end of the cage, but turned and thereafter made only a few excursions from the 27° region. The record of this experiment is very similar to that of Experiment 88.

Experiment 304.—This beetle was much more active than the one used in the previous experiment. The record is very similar to that of Experiment 82. In both experiments with Eleodes, the temperature at which the animal remained the greater part of the time, was a few degrees below the optimum temperature chosen by Phrynosoma.



(Fig 1.)

Experiment 112.—In this and the two experiments following, the letters R, O, Y, G, B and V above the graphs represent the color of the light screen over the corresponding portion of the cage. The graphs may be interpreted in the same manner as those illustrated in Plate I. In this experiment the animal avoided the violet section, turning away from it rather quickly in each instance. The greater part of the time was spent in the green and the yellow.

TABLE I.

Showing the Reactions of Phrynosoma in Gradients of Air Humidity.

The method of procedure here was the same as that pursued in the experiments illustrated in Chart 1., except that ten individuals were used in each experiment and numerical readings were taken at half-minute intervals. The summation of the results is indicated in numbers and in percentages at the foot of the columns.

	Experiment 12.			Experiment 13.		
Humidity	98%	57%	6%	6%	57%	98%
Evaporation	0.3	0.8.	2.0.	2.0.	0.8,	0,3,
Minutes						
	3	3	4	3	3	4
1	4	2	4	2	5	3
	3	4	3	1	7	2
2	4	3	3	1	7	2
	4	4	2	2	7	1
3	5	4	1	4	5	1
	5	4	1	3	3	4
4	5	3	2	1	3	6
	5	4	1	2	4	4
5	4	6	0	2	2	6
	4	6	0	4	2	4
6	3	6	1	3	3	4
	5	4	1	1	4	5
7	5	4	1	2	3	5
	5	5	0	2	3	5
8	5	4	1	1	3	6
	5	4	1	3	2	5
9	4	5	1	3	5	2
	2	5	3	2	5	3
10	6	2	2	2	3	5
	4	3	3	4	4	2
11	4	4	2	4	4	2
	5	4	1	2	4	4
12	5	4	1	3	4	3
	3	5	2	5	2	3
13	3	5	2	3	3	4
	3	4	3	1	4	5
14	4	4	2	4	4	2
	3	5	2	4	3	3
15	4	4	2	3	2	5
	5	4	1	2	5	3
16	5	3	2	1	4	5
	6	3	1	3	2	5
17	5	2	3	2	4	4
	4	3	3	2	5	3
18	3	6	1	4	5	1
	5	4	1	1	7	2
19	5	2	3	0	7	3
	5	4	1	2	5	3
20	5	3	2	2	5	3
	172 43%	157 39%	71 18%	97 24%	160 40%	143 30%

TABLE II.

Showing the Reactions of Eleodes in a Gradient of Air Humidity.

The method of procedure here was the same as that pursued in experiments 12 and 13. Twelve individuals were used.

EXPERIMENT 301.

Humidity	98%	57%	6%	Humidity	98%	57%	6%
Evaporation	0.3.	0.8.	2.0	Evaporation	0.3.	0.8.	2.0
Minutes				Minutes			
	6	0	6	11	6	2	4
1	6	0	6		7	1	4
	6	0	6	12	7	3	2
2	6	0	6		6	2	4
	6	0	6	13	6	2	4
3	6	0	6		5	2	4
	6	0	6	14	6	2	4
4	6	0	6		5	3	4
	5	1	6	15	6	3	3
5	5	1	6		5	3	4
	5	0	7	16	7	1	4
6	5	1	6		7	1	4
	5	2	5	17	5	3	4
7	5	2	5		5	3	4
	5	2	5	18	6	3	3
8	5	3	4		6	2	4
	5	3	4	19	6	1	5
9	6	2	4		6	1	5
	6	1	5	20	6	2	4
10	5	2	5				
	5	2	5				

TABLE III.

Experiment 34b. 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 taken at intervals along the cage are indicated at the heads of the respective columns.

Minutes	Temperatures			Minutes	Temperatures		
	38°	33°	20°		38°	33°	20°
1	3	4	3	16	3	5	2
2	3	5	2	17	3	5	2
3	3	6	1	18	4	5	1
4	4	4	2	19	4	5	1
5	4	4	2	20	4	5	1
6	4	5	1	21	5	4	1
7	4	5	1	22	5	4	1
8	4	5	1	23	5	4	1
9	4	5	1	24	4	5	1
10	4	5	1	25	3	6	1
11	4	5	1	26	3	6	1
12	4	5	1	27	3	6	1
13	4	5	1	28	3	6	1
14	4	5	1	29	3	6	1
15	3	5	2	39	3	6	1

TABLE IV.

Experiment 304. Showing the Reactions of Eleodes in an Air Temperature Gradient.

Minutes	Temperatures			Minutes	Temperatures		
	37°	31°	27°		37°	31°	27°
	5	5	2		3	2	7
1	2	3	7	11	3	1	8
	1	1	10		1	1	10
2	1	1	10	12	1	2	9
	1	1	10		1	1	10
3	1	1	10	13	2	1	9
	1	2	9		1	3	9
4	1	1	10	14	1	0	11
	1	1	10		1	2	9
5	2	2	8	15	1	3	8
	1	2	9		2	3	7
6	1	3	8	16	2	3	7
	3	1	8		2	0	10
7	1	0	11	17	1	2	9
	1	1	10		2	1	9
8	2	2	8	18	2	2	8
	2	2	8		1	3	8
9	2	2	8	19	1	1	10
	1	2	9		0	1	11
10	1	3	8				

TABLE V.

Showing the Reactions of Eleodes in a Gradient of Intensity of Light.

The method of procedure here was the same as in the previous experiments. Six individuals were used. The letters, D, M, L, (Dark, Medium, Light) at the heads of the columns indicate the relative amount of light.

EXPERIMENTS 111 AND 112.

	111			112				111			112		
Min	D	M	L	D	M	L	Min	D	M	L	D	M	L
			1			6		1	1	4	6		
1		1	5	1	1	4	11	1	2	3	5		1
		1	5	3	1	2		1	2	3	5		1
2		1	5	3	1	2	12	2	2	2	5	1	
		1	5	3	1	2		3	1	2	6		
3		1	5	3		3	13	3	1	2	6		
	1	1	4	5		1		3	1	2	6		
4	1	1	4	4	1	1	14	3	1	2	6		
		1	5	4	1	1		4		2	6		
5		1	5	5		1	15	4		2	6		
		1	5	4	1	1	16	4		2	6		
6	1	1	4	4		2		4		2	6		
		3	3	5		1		4		2	6		
7	1	1	4	5		1	17	4		2	6		
	1	1	4	5		1		4		2	5		1
8	1	1	4	5		1	18	5		1	6		
	1	1	4	5	1			5		1	6		
9	2	1	3	6			19	5		1	6		
	3	1	2	6				5		1	5	1	
10	1	1	4	6			20	5		1	6		

TABLE VI.

Showing the Reactions of Eleodes to the Direction of Light.

The method of procedure was the same as in previous experiments. Six individuals were used. The hands indicate the direction of the rays of light.

EXPERIMENTS 321 AND 322.

Min.	321		☜	☞ 322			Min.	321		☜	☞ 322		
	2	1	3	6				5	1		2	1	3
1	2		4	6			11	4	1	1		3	3
			6	4	1	1		4	1	1	1	2	3
2		1	5	2	1	3	12	4	1	1	1	2	3
	1	2	3	3	3	3		4	1	1	1	2	3
3	2	1	3	3	2	1	13	4	1	1	1	1	4
	2	1	3	5	1			4	1	1		1	5
4	3	1	2	4	1	1	14	4	1	1	1	1	4
	3	1	2	2	3	1		4	1	1	1	1	4
5	2	3	1	2	3	1	15	4	1	1	1	1	4
	2	3	1	2	3	1		4	2		1	1	4
6	3	3		3	2	1	16	4	2		1	1	4
	3	1	2	2	2	2		4	2			1	5
7	3	1	2	2	1	3	17	5	1			1	5
	4	1	1	3	2	1		5	1			1	5
8	5	1		3	2	1	18	5	1			1	5
	5	1		2	1	3		5	1			1	5
9	5	1		2	1	3	19	5		1		1	5
	4	1	1	2	1	3		5	1		1	1	5
10	5	1		2	1	3	20	6				1	5