REACTIONS OF EARTHWORMS TO TEMPERATURE AND ATMOSPHERIC HUMIDITY [1]

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This paper is the record of about one hundred and twenty five experiments carried on at the University of Illinois during 1915 and 1916. It was thought that by comparing the reactions of the various species of earthworms some explanation migh be offered for certain peculiarities of distribution and habitat preference exhibited by some of the species. The species used in one or more experiments, when arranged in order relative to soil moisture, driest first, are: (1) *Diplocardia communis,* (2) *Lumbricus terrestris,* (3) *Helodrilus roseus,* (4) *Helodrilus longicinctus,* (5) *Helodrilus caliginosus,* (6) *Helodrilus foetidus,* (7) *Octolasium lacteum,* (8) *Helodrilus tetraedrus,* and (9) *Sparganophilus eiseni* (nomenclature after Michaelsen). All specimens were collected in the vicinity of Urbana, most of them within twenty-four hours of the time they were used in experiments. Species five. six and seven were available in abundance at all times, and were used in many experiments. *Diplocardia communis* was readily available but was rather unsatisfactory because of its sluggishness and difficulty of locomotion. The four last named species were used in only a few experiments.

The apparatus used was devised by Dr. V. E. Shelford ('14) who suggested the experiments and under whose directions the work was done. It consisted of a cage 45 x 7 x 3 cm. Air entered through a slit in the further side from three fishtail burner shaped chambers, each supplying air to one third of the cage. Double screens separated the slit from the part of the cage in which the animals were confined. The front of the cage was screen. The cage was covered with a glass plate, and during the experiments air flowed slowly across the thirds of the cage, usually at the rate of .016 m. per sec. When different humidities or temperatures were introduced they constituted three different humidity conditions with some mixing at the edges.

In the majority of experiments the floor of the cage was covered with melted wax into the surface of which, after it had slightly hardened, clean sand was pounded. This gave the cage a hard bottom that prevented burrowing which occurred in loose sand. The sand in the surface of the wax gave sufficient roughness for locomotion. In early experiments the bottom of the cage was covered to a depth of about one half inch with moist sand, closely packed so as to offer a smooth hard surface. Under such conditions

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the worms of the control (no air currents) usually lie quiet for a considerable time or move about very little during the entire thirty minutes of observation. The only selection of position within the cage was such as may be attributed to the thigmotactic response. That is, the worms tended to remain in the angles of the cage when they chanced to come there. If stimulated by dry air currents they usually burrowed into the moist sand.

Figure 1 shows several graphs of the movements of the anterior ends of worms, each point in the line representing the exact location of the anterior end of the worm at a given time. These graphs represent only movements lengthwise of the cage. If a worm moved from side to side of the cage, without changing its position with respect to the length of the cage, the line of the graph would be exactly the same as if the worm had remained motionless. Notes indicated whether the specimen was quiet or moving about. Control speciments were observed in the cage with all conditions exactly as in the experiments except that there were no currents of air. Frequently after control observations the air currents were turned on and the same specimens observed under the experimental conditions.

The worms show little sign of stimulation until after a period of exposure, the length of the period depending upon the humidity. In air of between 95 per cent and 98 per cent relative humidity, worms, especially those in corners, often remained quiet for thirty minutes. In air with a relative humidity of a little above 80 per cent worms began to show signs of stimulation within four of five minutes. In dry air (relative humidity of 10 per cent or less) the indications of stimulation were almost immediate. In the graphs sharp points indicate quick changes in direction of locomotion, or avoiding reactions. The worm stopped and immediately withdrew the anterior end by contracting its body. At the same time the anterior end was raised and turned to one side. This is the first indication of stimulation. The body for several somites back from the anterior end is contracted on one side causing this part of the body to bend. The anterior end was then placed in contact with the substratum and locomotion resumed. Thus in a very short time the worm reversed its direction of locomotion. It it merely stopped and remained quiet with the anterior end in one spot for a time and then turned and crawled in the opposite direction, there is no sharp peak in the graph.

When a worm was placed in the middle of the cage with its anterior extremity toward the dry end; it usually moved directly toward the dry end (see broken line graph XI) until it encountered the wall before it changed direction of locomotion. It then followed the end wall until it was in the corner of the cage. Here it remained for several minutes, sometimes attempting to climb up the end wall and sometimes lying quiet with the anterior end pushed down into the corner. If it attempted to climb up the end wall it usually fell to the floor of the cage with its direction of movement reversed, and further locomotion carried it to the opposite end of the cage. With the more active species a second entrance into the dry end of the cage usually re-

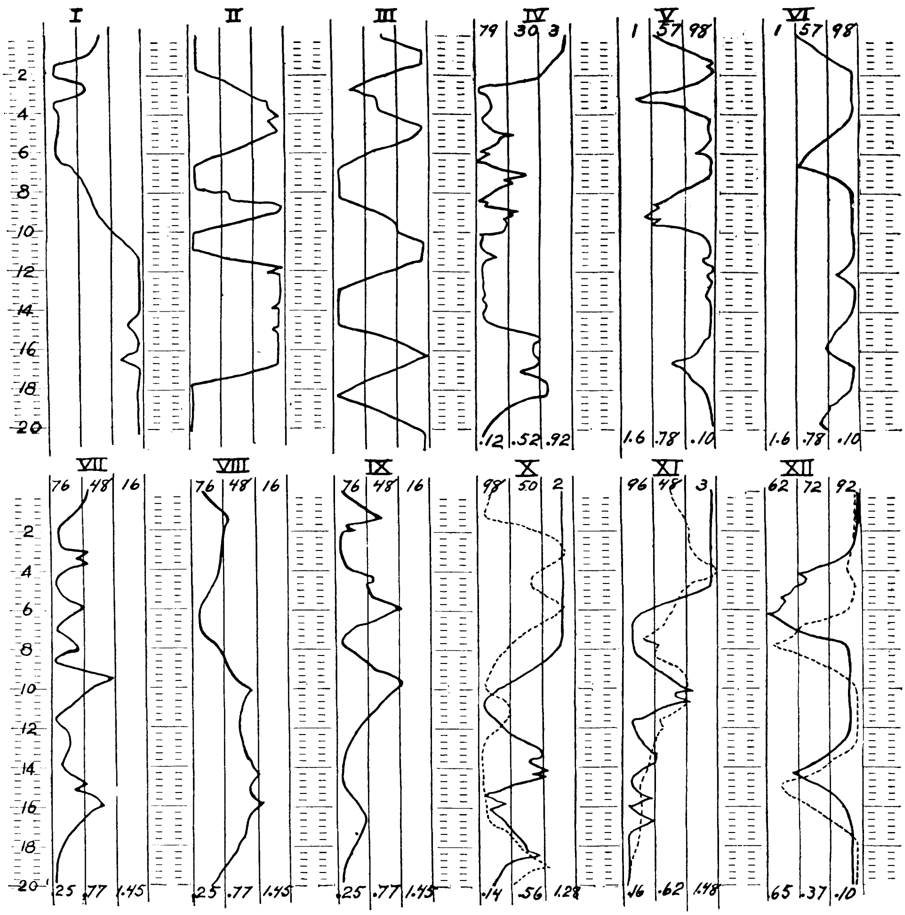

FIG. 1. Graphic representation of the reactions of earthworms in the experimental cage.

The vertical scale indicates time in minutes from the beginning of the experiment. Graphs 1–3 were made when no air currents were passing through to give different conditions in the three parts of the cage; in other respects conditions were exactly as in the experiments. Room temperature 30°. Relative humidity of air in room 58 per cent.

In the other graphs, percentage numbers at the top indicate relative humidity of air currents in each third of the cage. Numbers at the bottom indicate amount of water in c.c. evaporated by each air current in ten minutes, measured by Livingston porous cup atmometers. All sharp peaks indicate avoiding reactions. Temperature of air currents was the same in each third of the cage.

The species used in each graph were: I. *Diplocardia communis.* II. *Helodrilus foetidus.* III. *Helodrilus caliginosus.* IV. *Helodrilus caliginosus.* V. *Helodrilus caliginosus.* VI. *Diplocardia communis.* VII. *Helodrilus foetidus.* VIII. *Diplocardia communis.* IX. *Octolasium lacteum.* X. *Helodrilus caliginosus,* solid line. *Octolasium lacteum,* dotted line. XI. *H. Caliginosus,* solid line. *H. Longicinctus,* dotted line. XII. *H. caliginosus,* solid line. *H. foetidus,* dotted line.

sulted in the avoiding reaction (graph XI) and return to the region of lower evaporation. The second experience in the drier third of the cage was of shorter duration than the first, and after one or two trips to this end, most specimens did not thereafter travel much beyond the middle of the cage (Graphs V, VI, XI). With repeated trials, the worms turned back in air moister than at first endured, thus showing heightened sensibility.

In experiments where the moist air currents approximated saturation, the medium current having a relative humidity of about 50 per cent and the dry air 10 per cent or less, the worms usually did not travel into the dry third of the cage more than once. After one experience and return into the moist third they remained for a long time inactive, or if they did move out toward the dry end of the cage, they turned back as soon as the dry air was encountered.

If the evaporation gradient was not so sharp, that is if the moist air had a relative humidity of 75 per cent to 92 per cent, medium air 50 per cent to 70 per cent, and dry air 25 per cent to 60 per cent (or figures approximating these), the worms traveled back and forth from end to end several times. (Graph XII.) In such cases, after two or three round trips, the worms recoil and return to the moister air when they encounter the drier currents about the middle of the cage.

The tendency to climb up the end wall in the moist third of the cage was shown in relative humidities between 90 per cent and 100 per cent. In air of less than 50 per cent relative humidity, the worms exhibited a nervous activity. The anterior end was frequently lifted and turned from side to side. There were frequent emissions of fluid from the dorsal pores. If the specimen remained for a longer time in the dry end a great degree of irritation was indicated by violent and frequent writhing and twisting movements.

If the bottom of the cage is moistened the reactions to the air currents are not pronounced unless the gradient is very sharp. If the cage bottom is dry the reactions are quite pronounced even with less than 50 per cent difference in relative humidity between the drier and moister ends of the gradient. In a few experiments a sort of double gradient was established. The bottom of the cage was moistened and then the air allowed to flow over the cage until the bottom was dry in the dry end, slightly less dry in the middle and still quite moist in the moist end. In such experiments worms placed in the moist third of the cage sometimes remained within this third during the entire course of an experiment, and worms placed in the dry third, after once finding the moist end of the cage, did not leave it again. The reactions to dry or moist substratum were more definite than the response to air currents of different evaporating power, though contrary to Smith's ('02) observations they do react to air humidity. If the dry end of the cage had the bottom moistened, while the bottom was left dry in the middle and moist air end, worms remained in the dry end until the bottom in this part of the cage had become nearly dry. This does not mean that evaporation of moisture from the cage bottom had so moistened the air that the worms were not stimulated by evaporation. A specimen so situated would exhibit all signs of stimulation: movements of the anterior end of the body, exudation of moisture from dorsal pores, and even violent writhing and twisting movements. The movements of this speciment would carry it to the edge of the moistened substratum but when the worm encountered the dry surface it gave the avoiding reaction and crawled back onto the moistened area (Parker and Pashley '11).

All species of earthworms which we have studied reacted within gradients of evaporation in such a manner as to avoid the air currents of higher evaporating power and tended to select the moister end of the gradient cage. Comparison of different species has not shown any striking differences in behavior. *Helodrilus caliginosus, Helodrilus foetidus, Octolasium* and small specimens of *Lumbricus terrestris* have proven very satisfactory material for experimentation. These species are active and hardy, and have strong powers of locomotion. *Diplocardia communis* appears to be sensitive to evaporation but has such feeble powers of locomotion that in several of our experiments it has been unable to get out of the drier third of the cage after once having travelled there. Several speciments remained in the dry section attempting to force the anterior end of the body down into the corner angle until the body became so dry that locomotion was no longer possible. Other species had such feeble powers of locomotion or dried up so quickly that they made rather unsatisfactory material for such experiments.

A second method of recording experimental results is statistical. Several worms, usually ten, of the same species were placed in the cage at the same time. At each successive minute for twenty or thirty minutes the number of specimens in each third of the cage was recorded. *Diplocardia communis* and *Helodrilus foetidus* were used in these experiments. Records of the statistical experiments cannot be correctly interpreted by computing the total per cent of specimens in each third of the cage during the entire duration of the experiment.

In all the statistical work the gradient was made less sharp than in previous experiments, and the movements of the specimens were for this reason so much reduced that the graph method of record became very tedious and unsatisfactory.

In table I, parts 1, 2, 3 show the reactions of ten specimens of *H. foetidus*. The bottom of the cage was dry. Air currents in each third of the cage had a rate of flow of .016 meters per sec. The specimens were placed in the cage, four in the dry third, three in the medium and three in the moist third. It will be seen that within seven to ten minutes all of the worms had left the dry third and for the six minutes following but one of the specimens reentered this third of the cage. During the entire course of the experiments more than half of the specimens remained in the region of least evaporation. The evaporation is shown for part 3.

Six experiments, with *D. communis* July 21 and 22, 1916, in a humidity gradient are shown in table I, parts 4 and 5. As a rule the drier air is the more avoided. Reactions to temperature are shown in table I, parts 6, 7, and 8, where in all cases the worms avoided the higher temperature.

TABLE I. *Showing the reactions of ten worms in a moisture gradient in five experiments in which the arrangement of the moist, medium and dry was changed*

Parts 1–3 *H. foetidus*, parts 4 and 5 *Diplocardia communis*. Parts 6, 7, and 8 show reactions to temperature. The temperatures are only approximate, as the drafts of air varied somewhat.

Time	Part 1			Part 2			Part 3		
	Medium	Moist	Dry	Moist	Medium	Dry	Moist	Medium	Dry
After mins...	73%	92%	55%	98%	80%	60%	96%	89%	49%
1.....	3	3	4	3	4	3	3	3	4
2.....	2	5	3	5	3	2	3	3	4
3.....	1	6	3	7	1	2	4	5	1
7.....	2	6	2	8	0	2	4	6	0
10.....	4	6	0	8	0	2	4	6	0
15.....	2	8	0	8	1	1	6	4	0
Temp...	27.5° C.	27.5° C.	28.0° C.	30.2° C.	29.7° C.	29.7° C.	.15 cc.	.43 cc.	1.40 cc.

	Part 4			Part 5			
Hum. . .	74%	90%	52%	98%	55%	36%	cc. indicate amt. of water evaporated from Livingston porous cup atmometers in 20 minutes.
10 mins.	1	9	0	7	0	3	
Hum. . .	44%	94%	34%	91%	81%	67%	
9 mins.	4	5	1	6	1	3	
Hum. . .	44%	94%	34%	91%	79%	62%	
10 mins.	5	3	2	3	3	4	

	Part 6			Part 7				Part 8			
	Cage dry, *H. foetidus*			After mins.	Cage wet, *H. caliginosus*			After mins.	Cage wet, *H. foetidus*		
Temp.......	31.8°	32.5°	33.5°		30°	26°	20°		39°	36°	23°
10 mins.....	8	1	1	30	1	1	8	20	0	0	10
Temp.......	33.2°	31.0°	30.1°		36°	34°	25°		48°	41°	20°
10 mins.....	2	6	2	30	0	0	5	20	0	0	10
									33°	29°	17°
								10	2	0	8

One fact brought out by these experiments bears on the question of negative and positive reactions. The statement has commonly been made (suggested by Nagel '94 and later writers) that earthworms never give a positive reaction to chemical substances used in the experiments. It is evident in these experiments where natural stimuli were used and the worm permitted to crawl in a semi-natural environment, that the worm gives no avoiding reaction when entering more favorable conditions, for example very moist air from dry air, the forward movement being merely continued. Worms when entering moderately dry air may give no avoiding reaction the first time that they enter, and in this there is no difference between a reaction of indifference and a positive reaction. The avoiding reaction is given only when extreme stimulation is experienced.

There appears to be a correlation between the degree of moisture of the soil inhabited by the species, but the experiments are too few, and the conditions not sufficiently standardized for comparisons. The observations are however sufficient to indicate that worms react definitely to atmospheric moisture but less sharply than to contact with a moist substratum. Variation in atmospheric humidity occur in the soil where earthworms live, especially in the layers through which the worms must pass in moving to the surface. There is probably some connection, remote or immediate, between the selection of high humidity and the tendency to be most active in the morning when humidity is highest, and nocturnal excursions to the surface which appear to take place when humidity is high and temperature low. The reaction to humidity may be somewhat different in air containing carbon-dioxide and ammonia in the proportions in which they occur in soil air. The investigations of this topic as well as the study of reactions of these gases was omitted because of the interuption of the work.

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