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SELECTIVE MATING IN THE EARTHWORM (LUMBRICUS TERRESTRIS L.)*

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INTRODUCTION

Selective or assortative mating has been discussed under the term "homogamy," which has been defined by Harris (3) as "the mating of physically or psychically similar individuals." The phenomenon has been observed in the plant kingdom [see D. F. Jones (5)] and in several phyla of the animal kingdom, including Protozoa and Chordata. Willoughby and Pomerat (9) have reviewed homogamy with respect to physical characters, and the evidence for influence of psychic factors in mate selection has been summarized by H. E. Jones (6) and Schiller (8).

This paper will report (1) certain quantitative findings on the existence and degree of assortative mating in *Lumbricus terrestris* L., a representative of the phylum Annelida, the homogamic tendencies of which have not previously been investigated; (2) the significance of the mechanism of mating in another hermaphroditic form; (3) the effect of environmental factors on the intensity of homogamy in this particular species; and (4) evidence for the role of homogamy in establishing or maintaining new populations of earthworms.

METHODS

Two hundred seventy-six mating pairs of earthworms were collected between 10 P. M. and 4 A. M. on the campus of Clark University and private lawns in the vicinity of the campus. The dates of collection fall into two groups, May 31 to June 19, 1933 and September 7 to September 24 of the same year.

The worms were washed, dried on a blotter, killed in 15 per cent alcohol and preserved in 95 per cent alcohol. The weights and volumes were taken immediately after drying, the former to the nearest .01 gram and the latter to the nearest .01 cc. Volumes were measured by determining the weight of displaced water from a standard 25 cc. pycnometer. Segment count, including pre-

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clitellar count as a taxonomic check, and length to the nearest millimeter completed the series of measurements.

In making the correlations between measurements of the pairs of worms each measurement was entered on each axis of the correlation diagram [the double-entry method of Pearl (7), Jennings (4) and others] since it is impossible to distinguish systematically between the members of hermaphroditic pairs. The direct correlations are given in Table I.

Table I. Direct Correlations

	SUMMER	FALL	TOTAL
Wt-Wt	.19 ± .04	.30 ± .04	.34 ± .02
Vol-Vol	.25 ± .04	.30 ± .03	.33 ± .02
Lgt-Lgt	.08 ± .03	.61 ± .02	.53 ± .02
Seg-Seg	.05 ± .05	.04 ± .02	.02 ± .02

It is apparent not only that there is a significant correlation for all characters save segment count but also that there is a possibly significant difference between the correlations for summer and fall worms. An attempt to evaluate both the positive correlations and the seasonal differences is made below. The low correlation with respect to number of segments is due to the narrow range of distribution for the number of segments; 88 per cent of the worms had between 136 and 152 segments, with the mean at 143.4. The low length correlation between mates of the summer group is due to the fact that there was not a great variation in size of the worms, and moreover, those worms which were longer, being relatively few and scattered, were unable to secure mates of their own size. As might have been anticipated, the degree of similarity of mates with respect to weight and volume is approximately the same.

Possible Causes of Selection

Data are available to test the role of the following factors in the homogamy observed: chance association; barometric pressure; relative humidity; temperature; and regional and seasonal influence. In the evaluation of these factors, segment count will not be included since it is patently irrelevant; and volume will be omitted since it so closely approximates weight.

Chance. Several correlations were made for the characters of weight and length. The "mates" for these correlations were determined by arbitrarily drawing from a box pairs of weight and length data, respectively. The average weight correlation after such randomization was .10 ± .07, and the mean length correlation was .03 ± .04. No measurement was used twice for the computation of these coefficients. The low degree of correlation found by this method conclusively points to some factor other than chance which was operating to produce the statistically sound evidence for mate selection revealed in Table I.

Barometric Pressure. The habit of earthworms of appearing in greater numbers during damp or rainy weather, presumably a period of low barometric pressure, necessitated a rather narrow pressure range. Coefficients of correlation for groupings of the animals according to pressure range, indicated in Table II, showed no consistent effect of this variable.

Table II. Barometric Pressure in Inches

	28.95-29.05	29.06-29.30	29.31-29.55
Lgt-Lgt	.61 ± .04	.13 ± .08	.53 ± .04

Relative Humidity. Although there was a considerable range for humidity groupings this factor appears to have little influence on homogamy. See Table III.

Table III. Relative Humidity

	40%-60%	61%-80%	81%-98%
Wt-Wt	.36 ± .07	.33 ± .05	.29 ± .06
Lgt-Lgt	.17 ± .06	.26 ± .04	.67 ± .02

The differences between the weight correlations are not statistically reliable (Diff/s diff = 0.35 for low vs. middle range, and 0.51 for middle vs. high range). The high length correlation of the upper humidity range is apparently indicative, but this high degree of homogamy is actually due to the fact that this group is composed almost entirely of worms collected from the private lawns during the fall (Cf. Table V). There is likewise a high degree of similarity of mates for the middle group, in which the greatest difference between members of a pair is 3.5 cm., but this is not evident from the coefficient of correlation because of the limited range of measurements. The opposite effect of high or low relative humidity on the trend of weight and length correlations nullifies any conclusion that humidity might have a consistent effect on the selection of mates. No logical explanation can be offered at this time for the reversal of trend with respect to the two characters.

Temperature. Increase in temperature causes a marked decrease in direct homogamic weight and length correlations as shown in Table IV.

Table IV. Temperature

	40°-55°	56°-65°	66°-80°
Wt-Wt	.42 ± .06	.31 ± .05	.11 ± .09
Lgt-Lgt	.76 ± .04	.59 ± .04	.41 ± .06

The critical differences between length coefficients are 3.04 for low vs. middle range, and 3.67 for middle vs. high range; although the differences for the weight coefficients are not so reliable statistically they corroborate in general those between the length coefficients for the same temperature ranges (Diff/σ diff = 1.41 and 2.00 respectively). These values are based on all of the worms collected from both the campus and private lawns during June as well as September. As such they indicate that temperature is a vital and important factor in selection of mates by earthworms. However, those animals which fall into the low temperature group are predominantly Private-Lawns worms, which were collected in the fall. An analysis of the data subdivided according to region and season is necessary, therefore, before assigning any conclusive role to temperature in mate selection.

Region and Season. The homogamic indices for groups arranged according to collecting area are recorded in Table V.

Table V. Area and Season of Collection

	Campus (Summer)	Campus (Fall)	Campus (Total)	Private Lawns (Fall)
Wt-Wt	.19 ± .04	.25 ± .05	.25 ± .04	.22 ± .04
Lgt-Lgt	.08 ± .03	.46 ± .05	.31 ± .03	.66 ± .02

The difference between the length coefficients for the fall campus group and for the summer campus group suggests that season is influential in mate selection, and again this is supported by weight data. There is, however, no significant difference between the weight coefficients for the fall worms which are separated according to locality. But the extremely high coefficients for length in these subgroups and the divergence between them are indicative of a real factor. It is possible, then, that both region and season, as well as temperature (Table IV), may be factors in determining the similarity of mates.

From the Private-Lawns group no worm which was more than 19 cm. in length was found to have a mate less than 17 cm. long. Of the fall campus group only four cases exist where worms 15 cm. or more in length mated with worms of less than 15 cm. In other words, relatively long worms tend to mate with worms of approximately their own length, regardless of area of collection. The selective mating of long worms accentuates the degree of correlation by virtue of their deviation from the mean size of the population, and in doing so might provide a means of speciation, tending to produce a larger race if size in itself were heritable.

When the campus and Private-Lawns populations are analyzed with respect to size and weight, it is at once obvious that the two are distinct, as pointed out in Table VI.

Table VI. Weight

	Mean	s	$_sM$	Diff	Diff/$_s$ diff
Priv. Lawns (Fall)	4.96	0.92	0.06	0.56	6.22
Campus (Fall)	4.40	0.84	0.07	0.40	4.44
Campus (Summer)	4.00	0.84	0.06		
Length					
Priv. Lawns (Fall)	14.92	2.09	0.16	0.59	2.23
Campus (Fall)	15.51	2.57	0.18		

It is clear from this table firstly, that the two populations differ with respect to both length and weight, but not in the same way. The Private-Lawns worms are heavier than the campus worms, but are at the same time shorter; the ratio of weight to length is 0.33 for Private-Lawns and 0.29 for campus worms. Secondly, as observed in Table VI, there is a seasonal variation in weight. Unfortunately, no collections were made from the private lawns in June so that neither confirmation nor refutation for the campus data can be offered. Histological comparisons of spring and fall worms have not been made, but the increase in weight of worms in the fall might be due to the deposition of fat or other food substance in anticipation of the hibernating season.

Two other points have been made from the data presented, namely, that long worms tend to mate with long worms, irrespective of locality, and that temperature possibly causes an increase in homogamic tendencies. The fact that similarity of mates is greater among worms from the relatively short, stout population of the private lawns would suggest that, having a greater diameter, adjustments of length between mates is less easily accomplished by them. It is likewise reasonable that warmer temperatures in reducing viscosity of the protoplasm would increase mutual adaptability, and that lower temperatures would correspondingly reduce it. The significant feature, however, seems to be that the larger individuals (fall campus and private lawns) are the ones which have the higher degree of homogamy. It would be presumptuous to conclude that homogamy has caused a new population to be distinguished from a stock group, particularly in this instance when the two populations are several hundred yards apart in a modern city. But, it can be said with certainty that the Private-Lawns group, being larger, will be so maintained through the forces of assortative mating. It might be further concluded that the campus population, in increasing its size toward fall has also inadvertently provided a mechanism for maintaining racial dimensions, again assuming that size is inherited.

Since the two lowest temperature classes were collected in the fall, and since all of the high temperature group except 14 pairs were collected in the summer it may be that temperature in itself is secondary in the modification of mate selection. The results noted in Table IV are in part at least contingent upon seasonal size variation of individuals and local variation in mean weight and length of discrete populations.

Cross-Correlations

Cross-correlations were calculated for the various measurements of the worms divided according to season of collection to test the possibility that there might be a relationship between different characters of the mating worms. In such correlations weight of one worm is correlated with volume, length and segment number of its mate; volume is correlated with length and segment number of the mate, and length is correlated with the mate's segment number. These results are presented in Table VII.

Table VII. Cross-Correlations

	SUMMER	FALL	TOTAL
Wt-Vol	.21 ± .04	.28 ± .03	.35 ± .02
Wt-Seg	−.05 ± .05	−.01 ± .03	.01 ± .03
Wt-Lgt	.05 ± .03	.31 ± .03	.30 ± .02
Vol-Seg	−.03 ± .03	.01 ± .03	.002 ± .03
Vol-Lgt	.04 ± .03	.33 ± .03	.31 ± .02
Seg-Lgt	−.17 ± .03	.07 ± .03	.01 ± .03

The correlations involving number of segments range from a low of .01 to a high of .07; obviously mate selection is completely independent of segment number, either directly or indirectly. The results of all of the correlations, save weight-length, might have been reasonably predicted from the direct correlations. The correlation for these characters of .31, which is not sensibly different from the direct weight correlation for the same group of worms, indicates an interdependence between weight and length of mates which is probably artifactitious, as examination of Table VIII will reveal. Here the weight-length self correlation of .58 is relatively low. The degree of interdependence between weight and length of mates mentioned above is interpreted as being relatively high by comparison with other homogamy coefficients, but relatively low statistically, for with r = .31, the coefficient of alienation is .94, describing the predictability of a measure from that of the correlated measure of only 6 per cent better than chance. The coefficients of correlation involving volume must, of course, approximate those for weight. In summary, there seems to be no basis for mate selection beyond those expressed in the direct correlations and the subsequent analyses of with regard to climatic and geographical agents.

Self Correlations

In order to evaluate more intelligently the cross-correlations and direct correlations previously reported, self correlations for the characters used have been determined. These consist of comparisons between different characters of the same worm, in which the worms are treated as individuals of a population rather than as mates. The results of these calculations are recorded in Table VIII.

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Table VIII. Self Correlations

	SUMMER	FALL	TOTAL
Wt-Vol	.95 ± .003	.98 ± .003	.96 ± .002
Wt-Seg	.29 ± .04	.20 ± .03	.19 ± .02
Wt-Lgt	.63 ± .03	.58 ± .02	.61 ± .02
Vol-Seg	.28 ± .04	.22 ± .03	.22 ± .03
Vol-Lgt	.61 ± .03	.57 ± .02	.60 ± .02
Lgt-Seg	.49 ± .03	.27 ± .03	.30 ± .03

As previously, all correlations with which segment number is concerned must be low because of the relatively narrow range of variation of this measurement. With regard to the self correlations alone this would suggest that, at least among sexually mature animals, the seasonal fluctuation in size is accomplished by distribution of the weight and length variations among the segments, rather than by any increase in segment number. It further points to a genetically constant number of segments for this species within rather narrow limits. It is significant that among the deviates from the mean, far more are found below than above, perhaps pointing to accidental loss.

The slight variation between the summer and fall groups with respect to weight and volume is probably due to the differential earth content in the two categories. Although the relationship between weight and length is conspicuous as may be deduced from the substantial coefficient of .61, the discrepancy from a correlation of 1.00, which would exist if worms were perfect protoplasmic cylinders, points to a considerable individual variation in body contour. Of the variations which can be found, it is justifiable to suppose that the relatively long and slender worms are better able to adjust themselves to the size of their mates than the relatively short, stout animals (p. 8).

Discussion

A mean value of .31 ± .02 for homogamic coefficients of correlation was obtained for the earthworm on the basis of the four characters studied. This value, however, is considerably influenced by the segment correlations, which have been previously shown to exert no influence in mate selection. Exclusive of this character, the mean is .40 ± .02.

In the discussion of the environmental factors in homogamy, it was observed that temperature varied inversely with the degree of homogamy. If valid, this is suggestive of a chemical or metabolic agent in the phenomenon, whose efficiency in producing a high degree of similarity in mates is decreased at the higher temperatures. This, at best, is a mere hypothesis whose counterpart has been found to hold true in other physiological activities in other species. The decreased efficiency of this questionable agent may also be simply increased mobility of the worm, providing greater facility in the apposition of the proper parts during copulation.

A consideration of the manner of insemination in the earthworm suggests that this relatively high degree of homogamy is of considerable importance in the transfer of sperm. Grove (2) points out that there is a firm union between segments 9-11 of each worm with the clitellum of its mate, and a weaker point of contact between segment 16 of that worm and segment 26 of its mate; each point is secured by secretion of mucus and by modified setae. The seminal fluid is mutually exchanged through a pair of lateral seminal grooves and pit-like depressions formed by special muscles lying in the lateral blocks of the longitudinal musculature. He states, "These pits are produced by rhythmically occurring waves of further contraction passing backwards along this sheet of muscle-fibers.

"A point of difficulty which may be raised is that the action of these muscles produces two grooves in the integument, whereas only one—the dorsal or uppermost—conveys the seminal fluid and constitutes the seminal groove. During congress . . . . . the lower groove is hidden from view by the adposed ventral surfaces of the two worms so that it could not be determined whether similar waves of contraction to those which are present in the upper one appear in this case, also, though, since no conveying function is effected by this groove, it would seem to be unlikely. It may be, since the position of this lower groove in each worm would be more or less coincident during the union, that their apposition may serve as a point d'appui for the muscles during contraction, whereby the effect produced in the upper groove may be more marked."

Even though the juxtaposition of the proper segments might be effected by virtue of the highly mobile body, it seems probable that such an arrangement might interfere with the proper formation of the pits through which the sperm is transferred (by maladjustment of the "points d'appui"). In the event that the pits be not perfectly formed, a loss or inadequate conduct of seminal material might occur. It therefore follows that homogamic mating is of distinct advantage to the species in that the proportionality between eggs and sperm is better maintained by mates of similar size. Any differential interference with transfer of sperm would affect the probability of insemination of the eggs of the mate.

These conclusion corroborate those of Crozier (1) in his study of the nudibranch mollusc, *Chromodoris zebra*. Crozier has further pointed out that the number of eggs deposited is almost directly proportional to the length of the animal; it is consequently of advantage to the species that homogamic matings should occur, since the number of eggs fertilized is probably greater (assuming that there is a superabundance of sperm and that the number of eggs is proportional to the size of the animal).

Homogamy, then, might be said to be a causative agent in maintaining the numbers of an earthworm population directly, and in augmenting both size and numbers of individuals indirectly through the tendency of larger worms to seek mates of their own size. If the mean size of a population is governed by inheritance through homogamic, large individuals it is also necessary to postulate that speciation with respect to other characters, which may be genetically linked to the genes regulating size, may also occur. For the genes which may not be linked with the size-genes homogamy provides a means for genetic dispersal among individuals.

Conclusions

1. Direct homogamic correlations with a mean value of .31 ± .02 were found for *Lumbricus terrestris* L.; these values are actualities and cannot be explained on the basis of chance association of the animals.

2. It is unlikely that barometric pressure is influential in assortative mating; the role of relative humidity in mate selection is uncertain, although evidence is presented which indicates that it may have some function in this connection. There is an inverse relationship between temperature and the degree of homogamy, but this relationship may be secondary to seasonal or local effect.

3. Season and localities studied seem to have a marked effect on the selection of mates in this species because of the tendency toward increased weight in the fall and variation of size with the locality. Long worms tend to mate with long worms *irrespective* of locality.

4. In view of the complexity of the mechanics of mating in the earthworm, the high degree of homogamy would seem to depend chiefly upon mechanical factors, and these may be influenced by climatic or geographical agents.

5. It is suggested that homogamy in *Lumbricus terrestris* L. has a definite survival value for the species in that it provides for the fertilization of a maximum number of eggs, for the maintenance of individual size variation in a population and for genetic diversity within such a group.

6. Since homogamy has been proven for several somatic characters, it undoubtedly plays a significant part in speciation, and hence in general evolutionary changes, either directly through the characters studied or through others which may be genetically linked with them.

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