GENETIC STUDIES ON WILD POPULATIONS OF MELANDRIUM

II. FLOWERING TIME AND PLANT WEIGHT

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1. INTRODUCTION

MANY studies have shown that there is often considerable heritable variation to be found in wild species (see Stebbins, 1950). Much of this variation is of a quantitative, rather than a qualitative, nature which suggests that the genetic variation between wild populations is largely polygenic (Mather, 1953). Few studies, however, have analysed the variation in any detail. In the following account, quantitative variation between samples from four populations of *Melandrium album* and two of *M. rubrum* has been examined and its inheritance studied in a set of diallel crosses. The genetic activity of the sex chromosomes has also been examined in these dioecious species particularly in relation to differences arising between male and female plants.

2. MATERIAL AND METHOD

The locations of the populations studies are given in table 1. Samples of seed were collected from ten randomly chosen plants at each location. The seed from any one location was mixed and from the resulting plants three males and three females were taken at random to be used in the crossing programme. Males and

TABLE 1
Location of material

Sample	Habitat	Location
W ₁	Cultivated field	Bayford, Herts
W ₅	Hedgerow	Essendon, Herts
W ₇	Uncultivated field	Hertford, Herts
W ₈	Cultivated field	Whitacre, Warwicks
R ₄	Hedgerow	Whitacre, Warwicks
R ₅	Hedgerow	Aberystwyth, Cards

W = *M. album*. R = *M. rubrum*.

females from the same sample were crossed together in all possible ways, and those from different samples in six random but independent pairs, using each male and female once only. A total of $(6 \times 9) + (15 \times 6) = 144$ crosses was therefore made. Each pollination was carried out with an excess of pollen. Two randomised plots

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of ten plants from each cross were planted in one block. Since a number of crosses gave poor or delayed germination, the data from duplicate plots was pooled.

Three metrics were taken from the plants :—

- (i) Flowering time ; the number of days from an arbitrary date to the opening of the first flower.
 - (ii) Plant weight ; the wet weight in ounces.
 - (iii) The proportion of females in the progeny.
- 1918 plants were examined.

3. RESULTS

The data were first examined by means of analyses of the variance within and between groups of intra- and inter- population crosses, male and female progeny being treated separately. The sex differences, expressed as the mean difference between males and females within a single plot, was also analysed in this way. The methods of Jinks (1954) and Hayman (1958) for the analysis of diallel tables were then employed. As before (Lawrence, 1963) the groups of intra- and inter-population crosses are called "parents" and " F_1 's" respectively.

(i) Flowering time

The average flowering time of the different groups of male and female progeny are given in table 2, and the corresponding results

TABLE 2

The average flowering time for each parent and F_1 group

$\begin{smallmatrix} \delta \\ \backslash \\ \text{♀} \end{smallmatrix}$	W ₁	W ₅	W ₇	W ₈	R ₄	R ₅
W ₁	$\begin{smallmatrix} 36.5 \\ 26.2 \end{smallmatrix}$	$\begin{smallmatrix} 34.2 \\ 24.2 \end{smallmatrix}$	$\begin{smallmatrix} 26.8 \\ 23.0 \end{smallmatrix}$	$\begin{smallmatrix} 21.7 \\ 24.1 \end{smallmatrix}$	$\begin{smallmatrix} 27.9 \\ 27.0 \end{smallmatrix}$	$\begin{smallmatrix} 23.3 \\ 25.6 \end{smallmatrix}$
W ₅	$\begin{smallmatrix} 37.8 \\ 28.8 \end{smallmatrix}$	$\begin{smallmatrix} 46.7 \\ 29.8 \end{smallmatrix}$	$\begin{smallmatrix} 32.1 \\ 26.9 \end{smallmatrix}$	$\begin{smallmatrix} 31.8 \\ 25.4 \end{smallmatrix}$	$\begin{smallmatrix} 29.5 \\ 24.0 \end{smallmatrix}$	$\begin{smallmatrix} 26.6 \\ 23.3 \end{smallmatrix}$
W ₇	$\begin{smallmatrix} 32.4 \\ 30.8 \end{smallmatrix}$	$\begin{smallmatrix} 41.5 \\ 35.5 \end{smallmatrix}$	$\begin{smallmatrix} 31.8 \\ 27.4 \end{smallmatrix}$	$\begin{smallmatrix} 29.3 \\ 25.2 \end{smallmatrix}$	$\begin{smallmatrix} 31.9 \\ 33.7 \end{smallmatrix}$	$\begin{smallmatrix} 24.1 \\ 26.4 \end{smallmatrix}$
W ₈	$\begin{smallmatrix} 32.5 \\ 28.2 \end{smallmatrix}$	$\begin{smallmatrix} 47.0 \\ 30.4 \end{smallmatrix}$	$\begin{smallmatrix} 28.3 \\ 22.5 \end{smallmatrix}$	$\begin{smallmatrix} 34.0 \\ 33.5 \end{smallmatrix}$	$\begin{smallmatrix} 32.5 \\ 45.6 \end{smallmatrix}$	$\begin{smallmatrix} 31.8 \\ 29.6 \end{smallmatrix}$
R ₄	$\begin{smallmatrix} 42.3 \\ 38.6 \end{smallmatrix}$	$\begin{smallmatrix} 37.0 \\ 33.1 \end{smallmatrix}$	$\begin{smallmatrix} 33.1 \\ 29.7 \end{smallmatrix}$	$\begin{smallmatrix} 22.4 \\ 30.4 \end{smallmatrix}$	$\begin{smallmatrix} 35.8 \\ 37.0 \end{smallmatrix}$	$\begin{smallmatrix} 25.8 \\ 32.8 \end{smallmatrix}$
R ₅	$\begin{smallmatrix} 31.3 \\ 29.1 \end{smallmatrix}$	$\begin{smallmatrix} 36.2 \\ 27.9 \end{smallmatrix}$	$\begin{smallmatrix} 23.8 \\ 22.0 \end{smallmatrix}$	$\begin{smallmatrix} 31.9 \\ 30.1 \end{smallmatrix}$	$\begin{smallmatrix} 37.5 \\ 43.2 \end{smallmatrix}$	$\begin{smallmatrix} 30.5 \\ 32.9 \end{smallmatrix}$

Top figure = female plants. Bottom figure = male plants.

of analyses of variance in table 3. It can be seen that in both sexes there is considerably more variation between groups than within them, and that these differences are significant (table 3, item 1). Table 2 shows that the action of at least several, and probably many, genes is indicated by the variation.

Despite this superficial similarity in the analyses of males and females, a great difference between them is revealed when the distribution of the variation is examined in detail. In the females there is highly significant variation among both parents and F_1 's (table 3, items 1 (i) and (ii) and also a consistent deviation of the F_1 's from the mid parent (item 1 (iii)). The significance of these items shows that there is both additive and dominance variation between the samples in female flowering time. None of these items is significant in the males, but unlike the females there are highly significant differences between the groups of reciprocal crosses (item 1 (iv)). This contrast between the sexes shows that much, and possibly all, of the variation in flowering time in these samples resides in the sex chromosomes. The absence of consistent paternal inheritance in male progeny suggests that only the X chromosome is active.

W_r/V_r (Jinks, 1954; Dickinson and Jinks, 1956) and $W'r/V_r$ (Hayman, 1958) graphs of male and female flowering time are shown in fig. 1. The presence of sex chromosome activity does not disturb the expectations for these graphs in either sex if F_1 values are obtained by pooling reciprocal data (Jinks unpub.).

For female data both the W_r/V_r and $W'r/W_r$ regressions are significant ($P = 0.01-0.001$ in both cases), indicating that the samples differ in their properties of dominance. R_4 and R_5 have the greatest number of dominant alleles among these samples, or possibly the dominant alleles of greatest effect. W_5 , W_7 and W_8 have the greatest number of recessive alleles, and W_1 is intermediate between the two groups. The relatively greater scatter of points about the W_r/V_r , compared with the $W'r/W_r$, regression probably arises from heterozygosity. Differences in the level of heterozygosity among the various samples lead to an arrangement of the points on parallel lines of unit slope on the W_r/V_r , but not the $W'r/W_r$, graph (Dickinson and Jinks, 1956). The significance of these differences cannot however be tested in the present data, and greater scatter about the W_r/V_r regression may also in part arise from purely statistical considerations. In the presence of heterozygosity the slope of the W_r/V_r regression does not have a precise expectation (Dickinson and Jinks, *loc. cit.*) but the observed slope of $+0.840 \pm 0.258$ is close to the approximate value of $+0.9$ which is expected in the absence of non-allelic interaction. The slope of the $W'r/W_r$ regression ($b = +0.580 \pm 0.074$) does not deviate significantly from the expected $+0.5$ (Hayman, 1958).

The contrast between male and female data in the analyses of variance is maintained in the W_r/V_r and $W'r/W_r$ analyses. The W_r/V_r regression for male flowering time is not significant, but

TABLE 3
Analyses of variance in flowering time

Item	Females			Males			Females—Males		
	MS	N	VR	MS	N	VR	MS	N	VR
1. <i>Between groups</i>									
(i) between parents	1133	35	2.85***	863	35	2.39***	1041	35	1.34
(ii) between F ₁ 's	2246	5	5.66***	732	5	2.01	2490	5	2.23
(iii) P. v. F ₁	1075	14	2.71**	566	14	1.57	1322	14	3.04***
(iv) between reciprocals	3132	1	7.89**	806	1	2.23	85	1	<1
	683	15	1.72	1188	15	3.29***	359	15	<1
2. <i>Within groups</i> †									
(i) within parents	397	87	...	361	88	...	708	77	...
(ii) within F ₁ 's	393	43	...	425	41	...	776	37	...
	401	44	1.02	306	47	1.39	1115	55	2.56**
3. <i>Total</i> †	...	122	...	...	123	...	...	112	...

† As some plots contained plants of only one sex, the degrees of freedom vary in the three analyses.

‡ Including reciprocals.

*** P<0.001

** P<0.01

unexpectedly there is a significant ($P = 0.05-0.01$) linear relation between $W'r$ and Wr . This presumably arises from a small autosomal activity or activity of the pairing segment of the sex chromosomes which

FIG. 1.— Wr/Vr and $W'r/Wr$ graphs for male and female flowering time. Broken lines on the Wr/Vr graphs have unit slope and have been fitted to the data by eye. Broken lines in the $W'r/Wr$ graphs have a slope of $+0.5$ and pass through the origin.

was not detected by the analysis of variance. In this case the insignificance of the Wr/Vr regression arises from heterozygosity and/or non-allelic interaction. Heterozygosity is suggested by the distribution of five of the points on two parallel lines of unit slope. The difference between the sexes is further emphasised by the dominance ranking of the samples. Among the males W_7 and W_5 are the most dominant, W_1 and R_4 are intermediate, and R_5 and W_8 the most recessive. This order is quite different from that in the females. Since a few crosses gave progeny of only one sex, the results of the analyses are

not strictly comparable. It is, however, unlikely that the differences between the sexes arise from this source. Both the analyses of variance and the Wr/Vr and $W'r/Wr$ analyses strongly indicate that the majority of the variation between the samples arises from the action of the sex chromosomes.

Further information on the activity of the sex chromosomes was obtained from the examination of the sex difference. The mean difference between the sexes varies considerably from group to group, and the analysis of variance (table 3) shows that some of the variation is significant. In addition there is a two and a half fold difference

FIG. 2.— Wr/Vr and Wr/Wr graphs for the sex difference in flowering time. Broken lines as in fig. 1.

between the mean variance within parent, as compared to F_1 groups (table 3, items 2 (i) and (ii)). The parent and F_1 variances are homogeneous among themselves (Heterogeneity of parent variances $P = 0.5-0.3$, of F_1 variances $P = 0.7-0.5$). In so far as this variation is genetic, the presence of dominance is indicated (Mather, 1943, 1960; Breese and Mather, 1960). It was argued previously (Lawrence, 1963) that smaller variation within F_1 groups also probably arises from the action of some form of epistasis.

Both the Wr/Vr and the $W'r/Wr$ regression for the sex difference (fig. 2) is significant ($P = 0.01-0.001$ and $P = 0.05-0.01$ respectively). The distribution of the six points on two parallel lines of unit slope in the Wr/Vr graph suggests that the samples differ with respect to heterozygosity. The positive intercept of the Wr/Vr regression on the Wr axis appears to arise from these differences in heterozygosity, and not from incomplete dominance (cf. Lawrence, 1963). The order of dominance differs from that in either the male or female progeny.

(ii) *Plant weight*

The average weights of the groups of male and female plants are given in table 4. The results of the analyses of variance (table 5) show that, as with flowering time, there is considerably more variation between, than within, groups in both sexes. In contrast to the flowering time data, however, the distribution of variation is very similar in males and females. In both there is significant variation

TABLE 4
The average plant weight of each parent and F_1 group

$\begin{smallmatrix} \delta \\ \backslash \\ \text{♀} \end{smallmatrix}$	W ₁	W ₅	W ₇	W ₈	R ₄	R ₅
W ₁	10.2 8.7	12.6 8.2	9.9 10.9	10.8 7.9	17.5 15.7	14.3 13.4
W ₅	15.6 10.9	14.9 13.8	18.4 14.9	14.0 14.5	21.4 21.5	17.6 16.7
W ₇	15.2 13.9	16.3 11.6	14.8 12.1	14.7 10.6	15.3 13.6	16.2 17.2
W ₈	13.4 11.0	15.3 13.8	10.5 9.1	10.8 8.7	17.5 14.0	16.5 15.5
R ₄	14.0 10.5	16.3 10.7	20.8 12.1	12.8 8.1	17.6 12.2	12.3 17.1
R ₅	14.9 11.8	19.3 14.9	18.8 16.0	18.3 13.7	20.7 21.2	17.0 16.4

Top figure = female plants. Bottom figure = n

among parents, F_1 's and also a consistent deviation of the F_1 's from the mid parent (table 5, items 1 (i), (ii) and (iii)). Additive and dominance variation between the samples is therefore found in both sexes. Unexpectedly there are significant differences between reciprocal F_1 groups in female, but not male, progeny (item 1 (iv)). Despite this, it appears that the majority of the variation in weight in the samples is autosomal in origin.

Wr/Vr and W'r/Wr regressions (fig. 3) are highly significant in both sexes (males Wr/Vr and W'r/Wr $P = 0.01-0.001$, females Wr/Vr and W'r/Vr and W'r/Wr $P < 0.001$), showing the high heritability of plant weight. The slopes of the regressions are all close to the expected values. There is no evidence of different levels of heterozygosity among the various samples in the female data, but the scatter

TABLE 5
Analyses of variance in plant weight

Item	Females			Males			Females—Males		
	MS	N	VR	MS	N	VR	MS	N	VR
1. <i>Between groups</i>	230	35	3.1***	217	35	3.8***	292	35	1.42
(i) between parents	555	5	7.5***	517	5	8.6***	498	5	2.70*
(ii) between F_1 's	185	14	2.5***	256	14	4.3***	297	14	1.16
(iii) P. v. F_1	480	1	6.4*	194	1	4.9*	269	1	1.26
(iv) between reciprocals	148	15	2.0*	75	15	1.3	251	15	1.22
2. <i>Within groups</i> †	75	87	...	57	88	...	206	77	...
(i) within parents	74	43	...	48	41	...	151	37	...
(ii) within F_1 's	77	44	1.0	67†	62	1.4	255	55	1.69*
3. <i>Total</i> †	...	122	...	...	123	...	...	112	...

† See note to table 3.

*** $P < 0.001$.

** $P < 0.01$

† Including reciprocals.

* $P < 0.05$

of the points about the male W_r/V_r regression may arise from this cause.

Despite the lack of significant variation between reciprocal F_1 male progeny, the dominance ranking in the two sexes differs to a certain extent, suggesting sex chromosome activity. The results of the analysis of variance (table 5) of the sex difference in plant weight

FIG. 3.— W_r/V_r and W_r'/W_r graphs for male, and female weight. Broken lines as in fig. 1.

support this conclusion. There is significant variation among the parents (table 5, item 1 (i)), and also significantly greater variation on the average within F_1 than within parent groups. The different F_1 and parent variances are homogeneous among themselves (heterogeneity of parent variances $P = 0.5-0.3$, of F_1 variances $P = 0.7-0.5$). This indicates the presence of dominance (Mather, 1943, 1960; Breese and Mather, 1960). Despite such evidence, it is clear that the variation between groups is not great. It is probably for this reason

that variation between reciprocal F_1 male progeny was not detected. The insignificance of the W_r/V_r and the $W'r/W_r$ regressions (fig. 4) also agrees with this conclusion.

FIG. 4.— W_r/V_r and $W'r/W_r$ graphs for the sex difference in weight. Broken lines as in fig. 1.

(iii) *Variance within and between intra-population families*

The ratio of the variance of family means to the mean variance within intra-population families for each character is given in table 6.

TABLE 6

Rates of the variance between families to the average variance within them

Sample	Chiasma† frequency	Cell† variance	Flowering time		Plant weight	
			♀	♂	♀	♂
W1	...	...	4.95***	1.60	5.11**	7.35***
W5	...	...	3.90***	1.01	2.09	5.74*
W7	2.66*	1.93	1.94	2.60*	0.98	1.12
W8	2.76*	1.24	2.78**	3.92***	1.84	0.99
R4	0.69	0.62	2.92*	0.65	1.49	1.13
R5	1.99	1.13	2.62*	7.62*	2.44*	3.81**

*** $P < 0.001$ ** < 0.01 * < 0.05

† Taken from Lawrence 1963.

In twenty-seven of the thirty-two cases the variation between families is the greater, and is significantly so in fifteen cases.

(iv) *Sex ratio*

The average proportion of females varies considerably from group to group (table 7). In most, but not all, cases there is a significant excess of females over males. An analysis of variance, of the

TABLE 7
Per cent. females in the parent and F₁ groups

$\begin{array}{c} \diagup \text{♂} \\ \text{♀} \end{array}$	W ₁	W ₅	W ₇	W ₈	R ₄	R ₅
W ₁	41	81	62	48	77	61
W ₅	60	83	68	52	85	60
W ₇	41	79	51	68	60	62
W ₈	36	56	42	54	51	61
R ₄	24	66	36	50	68	48
R ₅	47	73	53	21	61	54

TABLE 8
Analysis of variance in sex ratios (per cent. females transformed to angles)

Item	MS	N	VR
1. <i>Between groups</i>	4271	35	2.34**
(i) Male parent	17,724	5	9.69***
(ii) Female parent	5201	5	2.84*
(iii) Male $\times$ female	1395	25	< 1
2. <i>Within groups</i>	1829	97	...
(i) within parents	1741	47	} 1.10
(ii) within F ₁ 's	1912	50	
3. <i>Total</i>	...	132	...

*** $P < 0.001$ ** $P < 0.01$ * $P < 0.05$

percentage females converted to angles (Fisher and Yates, 1957), shows that the differences between the crosses are significant (table 8). Further the majority of the variation is attributable to the male parent. However, a small, significant, influence of the female parent is also found.

4. DISCUSSION

It has been shown that with regard to both flowering time and plant weight greater genetic variation existed between the population samples than within them. The two characters exhibited both additive and dominance variation between the samples, but differed in the

distribution of activity among the chromosomes. The variation in flowering time arose largely, possibly exclusively, from the activity of the sex chromosomes. Of these, only the X chromosome appears to have activity. No evidence was found to indicate a direct effect of the Y chromosome. An indirect effect, although unlikely, cannot, however, be entirely excluded. The dominance variation among male progeny, indicated by the significant $W'r/Wr$ regression, may be autosomal in origin, or arise from the pairing segment of the sex chromosomes. It appeared to be of relatively minor importance as it was not detected by an analysis of variance. In contrast to flowering time, the variation in plant weight was largely autosomal with only a small effect of the sex chromosomes.

Apart from the different gene frequencies in the samples, differences in the level of heterozygosity with regard to flowering time and possibly also weight are suggested by the Wr/Vr analyses. The differences are shown by the distribution of points on parallel lines of unit slope in the Wr/Vr graphs. These parallel lines have been fitted by eye, and no attempt has been made to test the fit statistically. However, the distribution of points bears a striking resemblance to that expected theoretically (Dickinson and Jinks, 1956).

Insofar as the samples are adequate and representative, the conclusions reached concerning the nature of the differences between the samples can be extended to the populations from which they were drawn. Extrapolation becomes more reliable the greater the number of genes by which the samples differ in each gene system. It is clear from the results that there are at least several, and most probably many, genes influencing either flowering time or weight in these plants.

The marked effect of the sex chromosomes on flowering time and negligible activity of the autosomes points to the adaptive importance of particular relations between males and females. Analysis of the sex difference demonstrated that the various groups of crosses did in fact possess characteristic relations between the sexes. In general males flowered earlier than females, but the average sex difference varied widely. At one extreme, in the W_5 group of intra-population crosses, males flowered an average of nearly seventeen days earlier than the females. At the other extreme, the males in the R_4 and R_5 intra-population families flowered at the same time as the females, or even, perhaps, a little later. Wr/Vr and $W'r/Wr$ analysis suggests that the sex difference is controlled by a polygenic system exhibiting ambidirectional dominance and heterozygosity. In the production of the sex difference the action of the sex chromosomes can be of two principal kinds. First, direct action; that is the difference between the average effect of a pair of chromosomes and the average effect of a single chromosome. This presumably depends largely on dominance, although other interactions may also occur. Second, indirect action or sex limitation (Morgan, 1914), where there is an

interaction between the gene system controlling flowering time and that determining sex. The first alternative, that of direct action, does not appear likely in the present material. If the sex difference depended on dominance, it would be expected that on the average the size of the difference would be greater in the inter-population than in the intra-population hybrids. This is not found. Further, if the autosomes and the Y chromosome can be neglected, as is suggested by the data, it should be possible to predict the relative sizes of the sex difference in the inter-population hybrids from the W_r/V_r graph of the females since this gives the dominance relation of the X chromosomes. This does not, however, prove to be possible. On the other hand no positive predictions can be made to test the hypothesis of sex limitation. A factor complicating the attempt to distinguish between the two alternatives is shown by the significant differences between the groups of reciprocal families with respect to female weight. These probably arise from maternal or cytoplasmic inheritance.

The sparse evidence for genetic variation in flowering time of male plants from different populations, even though such variation is found in female plants, may be due to gene-environment interaction which has been shown to be an important factor in the flowering of populations of grasses (Cooper, 1955). The early flowering of males relative to females presumably ensures that an adequate supply of pollen is available when the stigmata are receptive. The variation in the extent of this earliness may arise from variation in the conditions of pollination.

The six groups of intra-population families are closely similar to the biparental progenies of Mather (1949). If the parents of such groups of families have been drawn from randomly mating populations, the mean genetic variation within families is expected to be larger than, or at least equal to, that between family means (Mather, 1949; Hayman and Mather, 1955). The reverse was found, which indicated that a certain amount of inbreeding took place in the parent population. The variances compared in table 6 contained components due to environmental or error variance, and thus the comparisons are not entirely valid. However, the environmental variance associated with the observations within families will be greater than that for family means, and thus the ratios of true genetic variance will be larger than those given in table 6.

Departures from equality in the numbers of males and females, generally giving an excess of the homogametic sex, have been reported for a number of plant species possessing XY sex chromosome mechanisms (Lewis, 1942). In *Melandrium*, Correns (1928) showed that this departure resulted from gametic rather than zygotic selection. X bearing pollen grew faster down the style than Y bearing pollen, giving an excess of female plants when there was pollen competition. The differential growth rates of X and Y pollen was shown to be controlled by the genotype of the male parent (Correns *loc. cit.*). In

the present experiment, all pollinations were carried out with excess pollen, and thus maximum departures from a one to one ratio will have been obtained. The results demonstrate the importance of the male parent in determining the sex ratio, and further show that there are genetic differences between populations with regard to this character. The small effect of the female parent shown by the results may arise from an influence of the style on the differential growth rates of X and Y pollen, or possibly from zygotic selection.

Different sex ratios in the various populations may reflect the different efficiencies of pollinating agents in different environments. This in turn could be related to the density of plants or the predominant pollinating insect species. Alternatively different sex ratios may be concerned with recombination, since recombination is often higher in the homogametic sex (Haldane, 1922).

5. SUMMARY

Greater genetic variation has been found between samples from four wild populations of *Melandrium album* and two of *M. rubrum* than within them, for flowering time and plant weight. Both characters show additive and dominance variation, and the populations also probably differ in the level of heterozygosity in the two gene systems. Weight was found largely to be an autosomal character, while flowering time was determined almost entirely by the sex chromosomes in these plants. The characteristic differences in flowering time of male and female plants in the various populations appeared to result from an indirect action of the X chromosomes, that is by sex limitation, rather than from a direct action. The populations have different sex ratios and inbreed to a certain extent.

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