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MULTIPLE MATING AND EFFECTIVE POPULATION SIZE IN *CEPAEA NEMORALIS*

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One of the remarkable characteristics of populations of the land snail, *Cepaea nemoralis* (L.), is the ubiquity of the polymorphism for color and banding of the shell. Monomorphic colonies have been found, but they are exceedingly rare. For example, Lamotte (1951) cites only two such cases out of a thousand colonies studied in France. They were samples of 300 from Gergovie (Puy-de-Dôme) and of 100 from Chagny (Saône-et-Loire) made up entirely of yellow unbanded individuals. Even these populations may be polymorphic, since in samples of this size the dominant gene for absence of bands could conceal a low frequency of its allele for banding. Moreover, the gene for absence of bands is epistatic to that for mid-banded, which is normally an important element of the polymorphism.

The rarity of monomorphic colonies is noteworthy since variations in the proportions of the different phenotypes have been attributed by some authors (e.g., Diver, 1940; Lamotte, 1951, 1959) to the action of random genetic drift. If such a dispersive process is responsible for the observed frequencies, then in small, isolated colonies the fixation of genes is to be expected. The rarity of fixation suggests that the effects of genetic drift are somehow reduced in most populations of *Cepaea*.

In order for genetic drift to play a significant role in the alteration of gene frequencies, the effective population size must be relatively small. The effective size may, of course, be very different from the actual number of animals in the population. It is usually smaller but in certain cases can be

larger than the number of breeding individuals.

The mating system of *Cepaea nemoralis* has a profound influence on the effective size of its populations. These snails are hermaphroditic, they mate more than once, and they store sperm for long periods. Each individual may, in a single brood, produce offspring from several matings. I have attempted to discover the number of productive matings per individual in order to investigate the effects of such a mating system on the effective size of populations of *Cepaea*.

The average number of matings from which each animal is producing young can be estimated from a comparison of the frequency of certain forms in a population with the proportions of those forms appearing in the progeny of selected individuals from that population. In a random-mating population where each brood results from a single mating, among broods produced by animals of the recessive phenotype, the proportion of broods containing individuals showing a dominant character will be the same as the proportion of that phenotype in the population. If each brood results from two or more matings, then the number of broods containing individuals showing the dominant character will be proportionally increased.

MATERIALS AND METHODS

A colony of *Cepaea nemoralis* in the south of England was chosen for this study. It is located at the foot of Burderop Down near Wroughton, Wiltshire (Ordnance Survey grid reference SU 158768). An area 50 yards east-west by 10 yards north-south was sampled. It lies between the Ridgeway on the south and a hedge on the

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north. The vegetation consists of long grass, nettles, and umbellifers.

Three pairs of genes suitable for this study are found in the colony. Their phenotypic expressions are yellow/pink, banded/unbanded, and mid-banded/five-banded. All the genes produce clear-cut phenotypes and segregate in a Mendelian manner. The genetics of these forms have been reviewed by Lamotte (1951) and Cain and Sheppard (1954). Additional data are given by Cain and Sheppard (1957) and Cain, King, and Sheppard (1960). Briefly, the universal recessive is the yellow five-banded or 12345 type. Dominant to it are the genes for pink, mid-banded or 00300, and unbanded or 00000. The loci for 12345/00000 and yellow/pink are strongly linked, and 00000 is epistatic to 00300.

This particular colony was chosen because all three dominant genes are found in low frequencies, decreasing in the series: pink > 00000 > 00300. It was hoped that one of the three might be represented in about half the resulting broods. With a dominant at this frequency, the estimate of the number of matings has the greatest precision. Samples were collected on four occasions, three in June, 1960 and one in May, 1961. Fifty yellow banded snails from the first sample were isolated in individual breeding containers. These are flower pots half filled with earth and covered with sheets of glass. The animals were fed on lettuce and occasionally on carrot. Lumps of chalk were always available. The algae growing on the sides of the pots provided an additional source of food. Eggs were allowed to hatch in the breeding pots, but the young snails were transferred to plastic boxes for rearing on a diet of lettuce, oatmeal, and powdered chalk.

During the summer of 1960, 35 snails produced young, 1 died, and 14 others failed to reproduce. It cannot be assumed, however, that the 14 unproductive snails had not previously been fertilized. Seven of them survived the winter, and one produced a brood of 16 young in September,

1961. This represents a storage of sperm for at least 15 months since the last occasion on which this animal could have mated. It confirms reports by Lang (1904, 1911) of sperm storage for more than a year.

RESULTS

Of the 1,630 young removed from the breeding pots, 1,419 lived to an age when they could be scored for color and banding pattern. The scores and the number of broods containing each type are shown in table 1. Two of the possible phenotypes, the double dominants for color and banding pattern, are not represented in the offspring. It is possible that some of the yellow unbanded individuals also carry the gene for 00300, but this is unlikely since the gene is unlinked to the other banding locus and would be assorted at random between the unbanded and five-banded offspring of the broods containing unbanded young.

It is immediately obvious from table 1 that a number of the broods show drastic departures from good Mendelian ratios. Since one parent in each case was homozygous recessive, each brood should be a backcross producing either all dominants, all recessives, or a 1 : 1 segregation of each. In fact, seven of the broods show significant differences from a 1 : 1 ratio with respect to pink, while all of those which are segregating for 00000 and 00300 show similar disturbances. Brood 10 shows departures from 1 : 1 ratio in two segregations, probably as a result of linkage in one "male" parent, with the genes for pink and unbanded in repulsion. There is thus immediate evidence for multiple matings in ten broods.

Although departures from Mendelian ratios demonstrate multiple matings, good ratios do not necessarily represent single matings. Obviously, multiple matings with animals of the same genotype will produce results which are indistinguishable from the broods of single matings. Also a mating with a homozygous dominant followed

TABLE 1. *Offspring of homozygous recessive animals taken as adults from a wild population of Cepaea nemoralis*

Number	Yellow ±12345	Yellow 00300	Yellow 00000	Pink ±12345	Pink 00300	Pink 00000	Total scored	Total hatched	
1	Produced in 1961 only								
2	17			3			20	21	
3	18	8					26	33	
4	15		1				16	18	
5	47						47	56	
7	38			12			50	59	
8	43						43	49	
9	37						37	39	
10	32		2	5			39	41	
12	38						38	40	
13	41						41	45	
14	20						20	23	
16	26			16			42	48	
17	33			13			46	49	
18	12			17			29	32	
19	16			1			17	29	
21	21			22			43	47	
22	29			26			55	56	
23	31			25			56	87	
25	2						2	2	
26	30		10				40	55	
30	17			23			40	40	
31	66						66	69	
32	43			36			79	86	
33	48			4			52	55	
34	35						35	40	
35	48			4			52	53	
36	24			24			48	50	
38	43						43	50	
39	30						30	39	
40	55						55	57	
41	30			22			52	54	
42	51						51	58	
44	63						63	77	
45	11			9			20	41	
46	26						26	32	
Total	1,136	8	13	262			1,419	1,630	
% of total	80.0	0.6	0.9	18.5			Mortality = 12.9%		
No. broods	35	1	3	17					

by one with a homozygous recessive may simulate a single mating with a heterozygous animal. Therefore, it is important to look at the distribution of dominants in the offspring. The proportion of broods containing dominants is very different from the proportions of those dominants found in the parent colony.

Table 2 gives the proportions of dominants in the samples from the parent colony. The samples were tested in two

ways for homogeneity with respect to color. Samples 2, 3, and 4 were each separated into four parts, from the northeast, northwest, southeast, and southwest quarters of the area. When the scores for all three samples are summed, there are no significant differences among the quarters ($P > 0.20$). However, when the total samples from different dates are compared, there is a suggestion that sample 3 differs from the others in having too few pinks (P between

TABLE 2. *The composition of samples of Cepaea nemoralis from the colony from which breeding stocks were obtained*

	% Pink	% 00000	% 00300	N
Sample 1	20.4	4.6	3.7	108
Sample 2	23.8	13.6	0.7	147
Sample 3	10.4	7.5	2.8	106
Sample 4	16.7	11.1	0.0	18
Total	18.7	9.2	2.1	379
Total of 1, 2, and 4	22.0	9.9	1.8	273

0.05 and 0.02). Therefore, comparisons with the breeding results have been made both with and without sample 3.

From the proportion of pink individuals in the parent colony, the expected proportion of broods containing pinks can be calculated. For the offspring of homozygous recessives, fig. 1 shows the expected increase in the proportion of broods containing some pink offspring as the number of matings per individual increases. Let \bar{P} and $\bar{Q} = 1 - \bar{P}$ represent the proportions of the pink (dominant) and yellow (recessive) phenotypes within the colony, and \bar{B} , the proportion of broods, produced by homozygous recessives, containing pink offspring. If the number of offspring per mating is large enough so that all matings with heterozygous pink individuals produce some pink offspring, and if an individual has mated n times, then the probability that a brood from this individual will fail to produce some pink offspring is \bar{Q}^n . Therefore, if each individual has mated n times, the proportion of broods, produced by homozygous recessives; containing pink offspring is

$$\bar{B}_n = 1 - \bar{Q}^n .$$

In fig. 1 the solid curve represents the expected increase in the proportion of broods containing pinks, based on the total of all the samples (% pink = 18.7). If sample 3 is omitted, then the increase is represented by the broken curve.

The horizontal solid line shows the observed proportion of broods which contain pink individuals among the offspring. Each brood is counted here as a single ob-

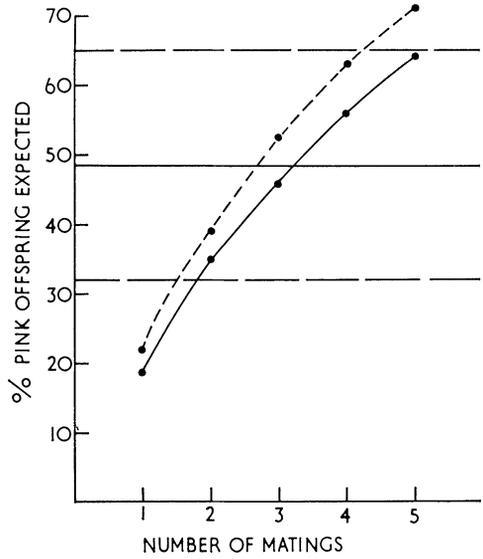


FIG. 1. The relation between the mean number of matings in *Cepaea nemoralis* and the expected proportion of broods containing pink individuals. The continuous horizontal line gives the observed proportion of broods containing pinks. The 5% confidence limits of the proportion are indicated by the horizontal broken lines.

servation. For this reason the 5% confidence limits, represented by the horizontal broken lines, are rather wide.

An attempt was made to use more of the available information by considering the proportions of pink to yellow offspring within each brood. Unfortunately, it soon became apparent that unjustifiable assumptions were necessary for such an estimate. It is very doubtful, for example, whether two matings separated by long periods of time would contribute equally to the subsequent offspring of a particular individual. If sperm from more recent matings fertilize a higher proportion of the eggs in a clutch than sperm which have been stored for some time, then an estimate of multiple mating based on the proportion of types within that brood would be highly misleading.

This objection does not apply to estimates based on the *proportion of broods* containing dominants. Matings in the distant past, from which no sperm remain viable, will, of course, be ignored; but they

are of no biological interest. The important thing to measure is the number of matings which are capable of contributing contemporaneously to the offspring of an individual. Therefore, I shall consider each brood as a single observation.

From fig. 1 it is possible to obtain an estimate of the average number of productive matings per individual in *C. nemoralis*. The average for the observed broods is between two and five matings per individual with 3.2 as the most likely value. If population sample 3 is excluded, then the estimates are reduced by about one-third of a mating. Since it is to be expected that the number of matings per individual will be distributed as a Poisson series, and since the zero term of the distribution cannot be determined (see above), then the mean of the Poisson series will be slightly smaller. If \bar{X} is the mean of the truncated distribution, and m is the Poisson mean, then

$$\bar{X} = \frac{m}{1 - e^{-m}}.$$

If \bar{X} is 3.2, then the mean of the Poisson distribution is 3.

The average number of matings can be estimated by a second method. It is a useful check since it is independent both of the proportion of broods containing pinks, from which the first estimate is derived, and of the proportions within the broods. The broods are divided into those which conform to good Mendelian ratios and those which do not. The two groups seem to be distinct. If the numbers of matings follow a Poisson distribution, then the proportion of good Mendelian ratios is related to the mean of the distribution. For a truncated Poisson distribution, if each animal has mated r times, then the probability that all r matings are with individuals of the same genotype (and therefore that the offspring will conform to a Mendelian ratio) is (Bulmer, personal communication):

$$\frac{e^{-m}}{1 - e^{-m}} \left(\frac{m^r}{r!} \right) (D^r + H^r + R^r)$$

where D , H , and R are the proportions of dominant homozygotes, heterozygotes, and recessive homozygotes in the population. The sum of all r terms for the whole distribution is then:

$$\frac{e^{-m}}{1 - e^{-m}} \left[(e^{mD} - 1) + (e^{mH} - 1) + (e^{mR} - 1) \right].$$

Among the 35 broods, 28 or 80% show good Mendelian ratios for the pink/yellow segregation. Equating this percentage with the summation above and substituting the values of D , H , and R (0.01, 0.18, and 0.81) derived from the samples from the colony, the value of m is found to be 1.3, corresponding to a mean of 1.8 for the truncated distribution.

This value is considerably smaller than that derived from the proportion of broods containing pinks. There are several factors which may contribute to the discrepancy. The most important of these is probably the sampling variance both of the proportion of broods containing pinks and of the proportion of good Mendelian ratios. The overlap in the confidence limits for these two proportions would allow values of m from 1.4 to 2.3.

Another factor could be the omission, from the sum of the probabilities of like matings, of one class of matings capable of producing good Mendelian ratios. A double mating with equal contributions from a dominant homozygote and a recessive homozygote would produce a 1:1 ratio simulating a single mating. There are also triple matings which might produce such a result; although as the number of matings rises, the possibility of unequal contributions and therefore of a detectable disturbance increases. These types of matings were excluded from the summation because (a) dominant homozygotes are rare (1%) in the population, (b) the contributions of different matings may or may not be equal, and (c) the summation becomes much more difficult if they are included.

Another source of error may be the occurrence of multiple matings of the type

$H + R$ in which the contribution of the R mating is reduced. Of the ten good Mendelian ratios for pink/yellow, six show a deficiency of pinks and only three a deficiency of yellows. This is striking since the overall proportion of pinks exceeds expectation (see below). Although the numbers are small, it suggests that some of the excess yellows could result from small contributions from R matings in the relatively distant past.

For these reasons it seems that the estimate based on Mendelian ratios is subject to a greater variety of errors than the estimate based on brood proportions. It is likely, therefore, that the true mean value for the number of matings is closer to 3 than to 1.3. However, since the null hypothesis is that each animal produces young from only one mating at a time, a conservative estimate of the mean value of m is two matings.

DIFFERENTIAL FERTILITY

The overall phenotypic proportions in the offspring of the sample should bear a definite relationship to the proportions in the population from which the sample was drawn. Since in this case only the offspring of recessives have been reared, the expected proportion of individuals of dominant phenotype among the offspring will be:

$$\frac{pq}{q^2 + pq} = p.$$

Therefore, the expected overall proportion of any dominant is equal to the gene frequency of that dominant in the parent population.

From tables 1 and 2 it can be seen that the pink offspring make up 18.5% of the total instead of the expected 10%. There are at least two possible explanations for the discrepancy. The first is that the gene frequency of pink in the population is indeed 18.5% and that the population samples are significantly deficient in pinks compared with the parent population. The

only evidence in favor of this hypothesis is the slight heterogeneity of the successive samples (see above). On the other hand, the most extreme sample does not approach the proportions demanded by a gene frequency of 18.5%.

An alternative explanation for the excess of pink young is differential fertility of pink and yellow parents. The broods containing pink offspring tend to be slightly larger than those which do not. Omitting the very small brood, number 25, the mean brood size of all-yellow broods is 39.8, while that of the broods containing some pinks is 43.5. It might be argued that the brood size of the all-yellow broods is biased, since small broods would be expected to lack pinks through sampling errors more often than large broods. However, if only the broods which contain pinks are compared, the mean of the eight broods with the highest proportion of pinks is 46.3, compared with a mean of 39.8 for the eight with the lowest proportions.

The effect is not very great, for the regression of brood size on the proportion of pinks within the brood (in angular measurement) is not significantly different from zero ($t_{(15)} = 0.82$). There may be other factors contributing to the discrepancy; but it is interesting that there is an indication of differential fertility in yellow and pink individuals, particularly as the difference is being expressed by means of the contributions of the "male" parents.

The disturbance of the overall pink/yellow ratio in the offspring is another compelling reason for using the proportion of broods containing pinks, rather than the proportions within broods, for the estimates of multiple matings.

DISCUSSION

The concept of effective population size has been discussed by Wright in a series of pioneering papers (e.g., 1931, 1938, 1939, 1940). The effective size of a population is "the number of individuals that would give rise to the sampling variance or the rate of inbreeding appropriate to the con-

ditions under consideration, if they bred in the manner of the idealized population" (Falconer, 1960). Usually the effective population size is smaller than the number of breeding individuals, but in special circumstances it may actually be larger.

The effective population size N_e is not equal to the actual population size N (1) when self-fertilization is excluded, (2) when the numbers of the sexes are unequal, (3) when the population fluctuates in numbers, or (4) when family size is non-random. The mating system of *Cepaea nemoralis* has a direct effect on the relation of N_e to N in all of these situations.

In *Cepaea*, cross-fertilization is obligatory. Since the probability of self-fertilization in the ideal population is equal to that of any other possible mating, obligatory cross-fertilization results in a slight decrease in the rate of inbreeding and hence an increase in effective population size (Falconer, 1960):

$$N_e = N + 1/2 \text{ (approx.) .}$$

Unless the population size is very small it is unlikely that this change will be of any importance.

Of considerably greater significance to the effective size of populations of *Cepaea* is the fact that these snails are hermaphrodites. In populations of animals with separate sexes, an inequality of the sexes will reduce the effective population size to twice the harmonic mean of the numbers of males and females (Wright, 1938):

$$N_e = \frac{4N \delta N \text{♀}}{N \delta + N \text{♀}} .$$

In the extreme case of a very few individuals of one sex and unlimited numbers of the other, the effective size is approximately four times the number of the least numerous sex. With hermaphroditic animals, however, the equality of the sexes is automatically adjusted so that there is no reduction in population size.

If the population fluctuates in size from time to time, then the effective size will be closer to the minimum than to the maxi-

imum value. For n successive population sizes, the effective population size is the harmonic mean of the numbers at each time (Wright, 1938):

$$N_e = \frac{n}{\sum_{i=1}^n \frac{1}{N_i}} .$$

It is in the case of short-term fluctuations that the system of multiple matings and sperm storage in *Cepaea* will have its greatest effect. If each animal produces offspring from an average of two matings and is capable of sperm storage for more than a year, then the effects of a severe reduction in population size will be mitigated. Without this system, the maximum number of diploid sets of genes that can be present when the population is at its smallest is $2N$, provided that each animal has been previously fertilized. In a population with separate sexes the maximum is $1.5N$.

In the case of *Cepaea*, each animal is storing the sperm contribution of an average of two other animals. Thus, if a reduction of population size occurs, the number of male contributions will be larger than the number of animals in the population. The population size will be equivalent to that of a unisexual population which contains $3N/2$ males and $N/2$ females. According to Wright's equation, the effective population size is then $3N/2$. Thus, if a "crash" of population numbers in *Cepaea* is followed by a swift recovery, the effective population size will be the harmonic mean of the population sizes before and after the disaster and 1.5 times the population size at the time of minimum size.

$$N_e = \frac{3}{\frac{1}{N_{\max}} + \frac{1}{1.5N_{\min}} + \frac{1}{N_{\max}}} .$$

In this way the mating system provides a reservoir of variability during temporary depletions in numbers.

Finally, the effective population size is affected by the distribution of family size.

In the ideal population, where the population size is stable, the mean number of gametes contributed by each individual is 2. Since the contributions vary according to a Poisson distribution, the variance of gamete contributions is also 2. If the variance is larger or smaller than 2, then the effective population size is not the same as the actual population size. Wright (1938, 1940) shows the relation to be:

$$N_e = \frac{4N - 2}{2 + \sigma_k^2}$$

where σ_k^2 is the variance of the number of gametes contributed by the parents. When $\sigma_k^2 =$ the mean $m_k = 2$, then N_e is almost the same as N . In the special case when each animal provides exactly two gametes, the variance becomes zero and the effective population size is very nearly $2N$. When the variance is larger than the mean, then the effective population size is smaller than the actual population size.

Crow and Morton (1955) have shown that if the survival of young is at random, the variance of brood size tends to approach the mean as the numbers of surviving offspring decrease. Laboratory populations of *Drosophila* appear to conform to the assumption of random survival, yielding estimates of N_e of from 0.35 to $0.90N$. However, if each brood tends to survive or perish as a unit, then the variance tends to increase with decreasing numbers of survivors. For example, if the variance of family size among the offspring of the 35 individuals recorded here for *Cepaea nemoralis* is adjusted to a mean of 1 (for a population of hermaphrodites), it becomes 1.12 if survival is assumed to be at random and 52.20 if survival is by broods (for the method of adjustment, see Crow and Morton, 1955). In the absence of modifying conditions, the latter value would represent an effective population size of only 4% of the actual population size!

There is no direct evidence in *Cepaea* for the validity of one model of survival rather than the other in natural conditions.

It seems likely that a change takes place at hatching. A clutch of eggs may survive or perish as a unit; but once an individual has hatched, its survival, if not random, is unlikely to be highly correlated with the fate of other members of the same brood.

The breeding structure of the *Cepaea* population operates in two ways to limit the restriction of effective population size by an increased variance of brood size. First, the offspring of each individual are divided into a number of broods produced over a period of months or even years. It is highly unlikely that the fates of members of different broods will be correlated with each other. Second, each brood is composed of contributions from one "female" parent and an average of two "male" parents. The result of such a brood composition is to reduce the effects of any tendency for unit survival of groups of offspring from single parents. Consequently, there will be a reduction of the variance of the gametic contributions of individuals.

In general, therefore, the mating system of *Cepaea nemoralis* minimizes the effects of the several factors that reduce the effective size of populations. Since processes having a dispersive action on gene frequencies depend on a restriction of population size [I exclude changes in the magnitude and direction of the systematic forces (Wright, 1949, 1955), which are not random], populations of *Cepaea nemoralis* are buffered against random changes in gene frequency. It seems likely that in *Cepaea*, and probably in other species of snails as well, the system of multiple mating and sperm storage has been evolved to protect organisms of rather limited mobility from impoverishment of the gene pool. Even in the extreme case of a population founded by a single fertilized individual, the gene pool will consist of an average of six haploid sets of genes. The homeostatic action of the mating system can be invoked as a factor contributing to the rarity of monomorphic colonies in this highly variable species.

SUMMARY

1. The land snail, *Cepaea nemoralis* (L.), is hermaphroditic with obligatory cross-fertilization. The breeding system of its populations includes both multiple mating and sperm storage.

2. The mean number of matings contributing to each brood is estimated to be not less than two.

3. There is some evidence of differential fertility between yellow and pink "male" parents.

4. Multiple mating and sperm storage serve to minimize the effects of population fluctuations and of increased variance of brood size which might otherwise reduce the effective size of populations.

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