THE EFFECTIVE SIZE OF A NATURAL *DROSOPHILA SUBOBSCURA* POPULATION

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SUMMARY

The effective size of a natural *Drosophila subobscura* population has been computed by drawing together various pieces of ecological information. The value, for both variance and inbreeding effective numbers, is approximately 400. This is largely due to reductions caused by a winter bottleneck and non-random distributions of family sizes.

Areas where such estimates might be refined further are pointed out, and the implications of the results are discussed.

1. INTRODUCTION

POPULATION genetics theory attempts, in general, to increase our understanding of nature by considering ideal populations. It is fortunate, therefore, that Wright (1931, 1938) developed the concept of effective population number: essentially, the size of the ideal population with which an actual population can be equated genetically. As a bridge between theory and the real world, effective population number is a cornerstone of population genetics, and many current controversies involve formulae in which it is an essential parameter (Lewontin, 1974). Yet it is a parameter which subsumes many other parameters, and these must be measured if effective population number is to be quantified. Such quantification has been rare: Greenwood's (1974) study of *Cepaea nemoralis* is the only previous thorough attempt to measure the effective size of a natural invertebrate population.

Drosophila subobscura is the numerically-dominant *Drosophila* species in British woodlands (Basden, 1954; Dyson-Hudson, 1954; Shorrocks, 1975). It has been well investigated genetically (see, for instance, Knight, 1960; Saura *et al.*, 1973; Sperlich and Feuerbach-Mravlag, 1974), but no estimate of effective population size for *D. subobscura* has previously been made. This is remedied in the present paper for the population of Adel Dam Nature Reserve: a mixed woodland of 65,000 m², 8 km NNW from the centre of Leeds, England.

But this paper also has a further purpose. Lewontin (1974) has asserted that effective population number is " impossible to measure " without recourse to tautological genetic techniques. Yet by setting out what is involved in the estimation of effective population number from ecological data, I shall suggest here that Lewontin is unduly pessimistic. Difficulties undoubtedly exist—but this gap between theoretical and empirical population genetics can be bridged.

2. ESTIMATION

Any computation of effective population number should include the following facets: (1) a determination of precisely which individuals should be included within the population; (2) a calculation of the numbers of males and females so included; (3) a determination of the way these numbers change temporally, with direct reference to the breeding cycles of the individuals; and (4) an estimation of the way family sizes are distributed amongst the members of the population. An assessment of the degree of assortative mating might also be useful, but in the present case this is taken as zero.

As regards the first facet, *D. subobscura* shows a marked preference for wooded as opposed to open environments (Dyson-Hudson, 1954), and in the area around Leeds most woodlands are small and distinct. This highlights the twin aspects of determining which individuals to include within a population. The first is the extent to which " sub "-populations are truly separate. This obviously depends on the amount of migration between them, and although there is disagreement on details, it is generally recognised that even low levels of migration can lead to important increases in effective population number (Wright, 1969; Kimura and Ohta, 1971). Unfortunately, no data on interpopulation migration in *D. subobscura* are available.

The second aspect is the " neighbourhood size " of a population in a continuum (Wright, 1969). Using data from a natural population of flies marked with fluorescent dust, I have argued elsewhere (Begon, 1976a) that for *D. subobscura* in the Leeds area, dispersal rates are so high that the neighbourhood size is greater than the woodland itself. In other words, within each woodland, including Adel Dam, mating is potentially random.

Interest is focused, therefore, on the number of individuals in the whole of Adel Dam. The extent to which Adel Dam is simply part of a larger population is unknown, however, and this must be borne in mind throughout. There are, moreover, two important points which should be noted. The first is that male and female numbers must be estimated separately, and recombined using the formula:

$$N_e = \frac{4MF}{M+F} \quad \text{(Wright, 1969)}$$

where N_e is the effective population number, and M and F are the numbers of males and females respectively.

The second point is that these numbers must be calculated for the appropriate stage of each and every generation. Fortunately, in *D. subobscura*, generations are virtually discrete and mating and oviposition coincide (Begon, 1976b). The appropriate stage is, therefore, the period within each generation when mating and oviposition are at their peak. More specifically, a detailed study of reproductive condition in wild *D. subobscura* over a 2-year period (Begon, 1976b) suggests a typical pattern of five generations per year. One generation emerges in late autumn, mates and oviposits in the following spring, and is followed by four further generations over the summer. There are, therefore, peaks of emergence in June, July, August, September and November; and peaks of breeding in April, June, July, August and September. However, there are two

complications. Firstly, over the winter period, a few individuals—probably those emerging first—give rise to two generations, not one. And generations also overlap to an extent during early summer: a small portion of the population passing through two, rather than three, generations. The effects of these complications are discussed below.

The absolute density of *D. subobscura* in Adel Dam has been estimated using the release-recapture technique of Fisher and Ford (1947), once again marking flies with fluorescent dust (Begon, 1976*c*). Values are available for the breeding populations of males and females in April, June and September. Moreover, a re-analysis of Shorrocks' (1975) Adel Dam data has allowed values for the peak breeding populations of July and August to be interpolated from the absolute measures (Begon, 1976*c*). These estimates for the five major breeding populations are presented in table 1.

TABLE 1

Sizes for breeding populations of D *subobscura* in Adel Dam. *Total obtained from male and female values after Wright (1969)*

	Population size for:		
Population breeding in:	Males	Females	Total
April	300	1000	923
June	3900	5900	9392
July	4000	9000	11077
August	4200	11000	12158
September	4800	22200	15787

Effective population number for the *D. subobscura* population of Adel Dam can now be calculated as the harmonic mean of the five totals (Wright, 1969). This value is shown in the first column of table 2, where the importance of the low winter population is readily apparent. But its acceptance

TABLE 2

Effective population numbers for D. subobscura *in Adel Dam*

		Variance-to-mean ratio	
	1	14·78	
Population		Variance number	Inbreeding number
April	923	120	1928
June	9392	1221	133
July	11077	1440	550
August	12158	1581	1373
September	15787	2100	1522
Total (5 generations)	3507	456	445
Total (4 generations)	3217	364	382

involves two assumptions. The first is that there are only five discrete generations each year: that generation overlap in winter and early summer can be ignored. This would certainly be a convenient assumption, because the data needed to calculate the effective size of a growing population with overlapping generations (Felsenstein, 1971) are not available in the present case. It seems reasonable to suppose, however, that if effective population

number is recalculated assuming two (rather than three) early-summer generations, then the true value will lie between the old and the new calculations. This has been done at the bottom of the first column of table 2. The size of the new second early-summer generation has been taken as the mean of the June and July values in table 1. The very small second winter generation has been ignored. Its effect is presumably to reduce the effective population number slightly.

The second assumption, made until now, is that the distribution of family sizes within the population is random. Lifting this assumption can have very important consequences, particularly when, as in the present case, total numbers are changing. Moreover, the estimated effective population number in such a case depends on whether it is the effects on inbreeding or on sampling variance which are being considered (Wright, 1969, after Crow, 1954; Crow and Morton, 1955). Wright's formula for variance effective number is

$$N_e = \frac{N\bar{k}}{1 + \sigma^2_{k/\bar{k}}}$$

where N is the number of parents, $\bar{k}$ and σ^2_k are the mean and variance of their family sizes, and where only those offspring which themselves reach maturity are taken as part of the family. The corresponding formula for inbreeding effective number is

$$N_e = \frac{N'\bar{k}'}{\bar{k}' - 1 + \sigma^2_{k'/\bar{k}'}}$$

where the " prime " refers to the grandparental generation.

One hundred and twenty-three female *D. subobscura* were taken from four newly-established laboratory populations. They were pair-mated in identical near-optimum laboratory conditions in 75 mm × 25 mm tubes of laboratory medium. In the wild, differentials in fecundity, competitive and non-competitive survival and mating propensity are all expected. (Although one factor—the extinction of whole broods—can be discounted because wild females never contain more than a few mature eggs at any one time). Only in their absence would the distribution of family sizes be random ($\sigma^2_{k/\bar{k}} = 1$). However, the 123 families, raised in clement uncrowded conditions, were virtually free from survival and mating differentials, and should, therefore, provide a conservative estimate of the variance-to-mean ratio. Nevertheless, the value obtained was 14·78 ($\bar{k} \simeq 88$). This is surprisingly high, but may indicate that, although laboratory flies are released from many constraints, the laboratory medium is sub-optimal and does not allow the realisation of maximal fecundities in all cases. The variance-to-mean ratio in the wild is still unlikely to be below 14·78, and as the second and third columns of table 2 show, this causes a drastic reduction in effective population number. The new estimate is similar for both inbreeding and variance effective numbers: approximately 400.

3. DISCUSSION

Selection, migration, mutation and drift are the factors which are theoretically capable of affecting gene frequencies. Estimating effective

population number in natural populations is one of the few ways in which their actual importance can be assessed. It is not surprising, therefore, that Wright (1969) has argued that effective population number is " . . . a practical necessity in dealing with natural populations ". Yet to judge by results, and with a few exceptions, practical population geneticists have disagreed. Few attempts have been made to measure effective population number, despite the variety of theoretical controversies to which it is pertinent; and, although Greenwood (1974) has appealed for accurate estimates to supplement his own, the response of theoretical geneticists has been, essentially, despair (Lewontin, 1974).

In the present case the effective population number for *D. subobscura* in Adel Dam *has* been estimated. Of course, this in itself does not negate Lewontin's assertion, because uncertainties still exist. If survival differentials had been measured, or if an exceptionally harsh winter had been encountered, the estimate would have been smaller. On the other hand, interpopulation migration could increase it markedly. (Attention paid in future to any of the factors—particularly the last—would certainly lead to improved estimates.) Nevertheless, overall, it appears that estimating effective population size is worthwhile, and that even the present estimate justifies a re-examination of the relevant theoretical questions. Perhaps, in future, geneticists will study animals and plants with interesting and tractable ecologies, rather than turning despairingly to ecology when their genetic work is complete.

The estimate itself (approximately 400) resolves no controversies. This is not only because it is approximate, but also because it lies within that tantalising range where drift can neither be discounted nor invoked as a definitely potent force. Moreover, the Adel Dam population is probably larger than those nearer *D. subobscura*'s Scandinavian margin, and, in terms of density *per se*, the Adel Dam *D. subobscura* estimates are higher than those of any other temperate *Drosophila* species so far studied (Begon, 1976c). In the past it has generally been the burden of those adherents of drift to prove that natural populations are sufficiently small. Now, for temperate *Drosophila*, this is at least an open question.

4. References

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