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THE EFFECT OF UNEQUAL MATING FREQUENCIES ON THE VARIANCE EFFECTIVE NUMBER IN RANDOM MATING POPULATIONS

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THE effective number in a random mating population can be described as "inbreeding effective number" or, alternatively, as "variance effective number" (Crow, 1954; Crow and Kimura, 1970). The latter, $Ne(v)$, is defined by the variance of gene frequency change (Δq) per generation:

$$\text{var}(\Delta q) = \frac{pq}{2Ne(v)}, \quad (1)$$

where $p = 1 - q$.

Following Crow (1954), we have

$$\text{var}(\Delta q) = \frac{pq}{4N} \left(1 + \frac{\text{var}(k)}{\varepsilon(k)} \right) \quad (2)$$

in which N is the actual population number and k is the number of effective gametes contributed by a single individual. When k is Poisson-distributed, $\text{var}(k)/\varepsilon(k)$ equals unity and (2) reduces to the expression in the binomial sampling model:

$$\text{var}(\Delta q) = \frac{pq}{2N} \quad (3)$$

so that $Ne(v) = N$.

Now, individual variation in number of matings, whether or not in-

fluenced by competition, leads via $\text{var}(k)/\varepsilon(k) > 1$ to $Ne(v) < N$. Initially it was thought that this discrepancy, arising from multiple matings, could be rather large. However, Crow (1954) gives some empirical data for *Drosophila* males and females to show (see also Crow and Kimura, 1970) that the effective number and the actual number are at least not greatly different (table 1), the ratio of these two being approximately 0.75 for females and 0.50 for males.

TABLE 1

Relation of effective and actual population numbers in experimental data on Drosophila females and males. The adjusted values have been obtained by correcting to constant population size, under random survival of zygotes. Note that the adjusted ratio is larger for males than for females, which reflects a larger var(k) for males. (From Crow, 1954)

	$\varepsilon(k)$	$\frac{\text{var}(k)}{\varepsilon(k)}$	$\frac{\text{var}(k)/\varepsilon(k)}{\text{adjusted to } \varepsilon(k) = 2}$	$\frac{N_e(v)}{N}$
<i>Drosophila females</i>				
Adult progeny	13.9	4.73	1.82	0.71
Egg laying (5 day)	37.2	11.45	1.77	0.72
Eggs, lifetime				
wild type, 25°	714	130	1.36	0.85
wild type, 30°	430	154	1.71	0.74
wild type, 19°	914	111	1.23	0.90
vestigial	432	102	1.46	0.81
<i>Drosophila males</i>	17.9	11.35	3.18	0.48

In the following a realistic model will be proposed and an exact formula presented which accommodates $Ne(v) < N$, resulting from individual variation in mating frequency.

Let, in a virginal population with equal number of both sexes, the variables M_f and M_m be the mating frequencies, in a given time interval of individual females and males respectively, and let x_f and x_m be the number of effective gametes contributed by these individual females and males per mating, that is their number of gametes generating surviving offspring. Then, the total number of effective gametes per female (k_f) is the random sum

$$k_f = x_{f1} + x_{f2} \dots + x_{fM_f},$$

in which each of the M_f terms has the same distribution, so that the mean and variance of k_f are

$$\varepsilon(k_f) = \varepsilon(M_f) \cdot \varepsilon(x_f) \quad (4)$$

and

$$\text{var}(k_f) = \varepsilon(M_f) \cdot \text{var}(x_f) + [\varepsilon(x_f)]^2 \cdot \text{var}(M_f) \quad (5)$$

The statement for males is analogous.

Assume that the probability of a mating event for an individual, within a time interval of unit length, is sufficiently small, so that the distribution of events is Poissonian. Then for individual males the total number of matings (M_m) in a time interval of length t can also be taken to have a Poisson-distribution (with parameter βt , say), so that the probability of no mating is

$$P_0(t) = e^{-\beta t}.$$

However, for individual females it is more realistic to assume that no

multiple matings occur in such a time interval, which means that M_f takes the values 0 or 1. So M_f is binomially distributed with parameter θ , say. Notice that $\theta = 1 - P_0(t)$. Thus, considering any time interval from $t = 0$, M_m has a Poisson-distribution, with parameter α , say; whilst M_f has a binomial distribution with parameter θ , say.

It is reasonable to assume both x_f and x_m to follow a Poisson-distribution (parameters λ_f and λ_m , respectively).

Then, from (4) and (5):

$$\varepsilon(k_f) = \theta \cdot \lambda_f \text{ and } \text{var}(k_f) = \theta \cdot \lambda_f [1 + \lambda_f(1 - \theta)].$$

Similarly $\varepsilon(k_m) = \alpha \cdot \lambda_m$ and $\text{var}(k_m) = \alpha \cdot \lambda_m (1 + \lambda_m)$.

Since $\theta = \alpha$ and $\theta \cdot \lambda_f = \alpha \cdot \lambda_m$, because the offspring originates from equal numbers of maternal and paternal gametes, one obtains, by substitution into (2), followed by adding the expressions for males and females (as can be done with independent samples) and, finally writing λ_f for λ_m (see above) the expression

$$\text{var}(\Delta q) = \frac{pq}{4N} [4 + \lambda_f(2 - \theta)].$$

For constant population size, i.e. $\theta \cdot \lambda_f = 2$, this reduces to

$$\text{var}(\Delta q) = \frac{pq}{2N} \left(1 + \frac{2 - \theta}{2\theta} \right) \geq 1.5 \frac{pq}{2N}. \quad (6)$$

From (2) it follows $\frac{pq}{2N_e(v)} \geq 1.5 \frac{pq}{2N}$, so that $N_e(v) \leq \frac{2}{3}N$.

As an illustration enter in (2) the adjusted ratio's $\text{var}(k)/\varepsilon(k)$ for adult females (1.82) and males (3.18) from table 1.

Averaging over males and females as before, gives

$$\text{var}(\Delta q) = \frac{pq}{4N} \left(1 + \frac{1.82 + 3.18}{2} \right),$$

so that $N_e(v) \approx 0.7N$, which actual value agrees well with $N_e(v) \leq \frac{2}{3}N$ from our model.

Expressions analogous to expression (6) can be derived for the following situations:

1. Females may mate more than once, but the total number of zygotes per female remains the same.
2. Females may mate more than once, which leads to a higher number of zygotes per female.

However, also in these cases, $\text{var}(k) > \varepsilon(k)$ and $\text{var}(\Delta q) > \frac{pq}{2N}$, i.e. $N_e(v) < N$.

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