

in view of the limiting process, the overall frequencies of  $aa$ ,  $aA$  and  $AA$  in the section of the habitat being considered are found to be

$$\bar{p} - \frac{k}{bm} \{p'(0) - p'(b)\}, \quad \frac{2k}{m} \{p'(0) - p'(b)\},$$

$$1 - \bar{p} - \frac{k}{bm} \{p'(0) - p'(b)\}.$$

#### 4. SUMMARY

A situation is considered in which a cline is maintained by the random diffusion of a simply advantageous gene. It is pointed out that Wahlund's formula can be extended to cover this case, and it is applied to obtain overall genotype frequencies in terms of the overall gene frequencies, the selection and diffusion constants, and the rates of change of gene frequency at the boundaries of the section being considered.

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## NATURAL SELECTION THROUGH MATERNAL INFLUENCE

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### 1. INTRODUCTION

In discussions of natural selection at an autosomal locus (Haldane, 1932; Hogben, 1946; Li, 1955) it is usual to assume that genotypes are selected because the zygotes have viabilities or fecundities which depend on their own genotypes. One could suppose, however, that maternal genotypes at one locus might affect offspring fitnesses upon which offspring genotypes, however, have negligible effect. In mammals such an effect can be imagined to operate through intra-uterine environment or post-natal nutrition. Interestingly, Moriwaki and Tobari (1963) have demonstrated a genetic effect which operated through the mother on offspring fitness in *Drosophila ananassæ*. It thus seems worthwhile to report some results in theory of selection through maternal influence.

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## 2. THEORY

It will be supposed that mating is at random and that genotypes AA, Aa and aa have frequencies D, H and R. The maternal genotypes are respectively assumed to confer fitnesses  $W_1$ ,  $W_2$  and  $W_3$  on the offspring. These assumptions lead to table 1. Now, if stars denote frequencies in the

TABLE 1  
*Distribution of matings and fitnesses of offspring*

Mating	Frequency	Fitness	Mating	Frequency	Fitness	Mating	Frequency	Fitness
♀ AA × AA	D <sup>2</sup>	W <sub>1</sub>	♀ Aa × AA	DH	W <sub>2</sub>	♀ aa × AA	DR	W <sub>3</sub>
AA × Aa	DH	W <sub>1</sub>	Aa × Aa	H <sup>2</sup>	W <sub>2</sub>	aa × Aa	RH	W <sub>3</sub>
AA × aa	DR	W <sub>1</sub>	Aa × aa	RH	W <sub>2</sub>	aa × aa	R <sup>2</sup>	W <sub>3</sub>

next generation, if  $P = D + 0.5H$  is the initial frequency of allele A while  $Q = 1 - P$ , and if  $\bar{W} = DW_1 + HW_2 + RW_3$ , it can be seen that

$$D^* = (DW_1 + 0.5HW_2)(D + 0.5H) / \bar{W} = (DW_1 + 0.5HW_2)P / \bar{W}$$

$$H^* = (DW_1Q + 0.5HW_2 + RW_3P) / \bar{W}$$

$$R^* = (RW_3 + 0.5HW_2)(R + 0.5H) / \bar{W} = (RW_3 + 0.5HW_2)Q / \bar{W}.$$

The first point to be investigated is the equilibrium situation in this system. Unfortunately the expression for the new gene frequency  $P^*$  cannot be written in terms of the initial  $P$  and the constants  $W$  alone but must also include terms in  $R$ ,  $H$  or  $D$ . This means that the equilibrium cannot be found by simply setting  $P^* - P = 0$ ; it is necessary to put restrictions on two of the frequencies  $P$ ,  $D$ ,  $H$  or  $R$  simultaneously. The restrictive equations are cumbersome. For instance  $D^* - D = 0$  and  $R^* - R = 0$  imply

$$D^2(3W_2 - 2W_1) + D(2W_1 - 4W_2) + DR(4W_2 - 4W_3 - 2W_1) + (R^2 - 2R + 1)W_2 = 0$$

and

$$R^2(3W_2 - 2W_3) + R(2W_3 - 4W_2) + DR(4W_2 - 4W_1 - 2W_3) + (D^2 - 2D + 1)W_2 = 0.$$

After some attempts at solution, I programmed an electronic computer to calculate  $D^*$ ,  $H^*$ ,  $R^*$  and  $Q^*$  over several generations for arbitrary  $W$ 's and initial  $D$  and  $R$ . In parallel computations from the same  $D$ ,  $R$  and  $W$ 's, genotypic and gene frequencies were also calculated for the usual selection by zygote genotype. From a few runs of this programme it was conjectured that (1) equilibrium gene frequencies are the same for selection by maternal effect or zygote genotype, and (2) at maternal effect equilibrium  $D = P^2$ ,  $H = 2PQ$  and  $R = Q^2$ .

It can be verified from the equations of the system that the genotypic frequencies do not change once the situation  $D = 1$ ,  $H = 0$  and  $R = 0$  or  $D = 0$ ,  $H = 0$  and  $R = 1$  prevails. Thus the kind of equilibrium expected when  $W_2$  is not larger than both  $W_1$  and  $W_3$  is allowed for. Now,

if heterozygotes confer maximum fitness on their offspring, we may conventionally take  $W_1 = 1-r$ ,  $W_2 = 1$  and  $W_3 = 1-t$ . Then the above conjecture is verified for the heterotic situation by noting that setting  $P = t/(r+t)$ ,  $D = P^2$ ,  $H = 2PQ$  and  $R = Q^2$  does indeed imply that  $D^* = D$ ,  $H^* = H$  and  $R^* = R$ . However, algebraic and computational investigations indicate that  $D = P^2$  and  $R = Q^2$  imply  $D^* = P^{*2}$  only if  $P$  has the equilibrium value.

If a common set of fitnesses prevails the maternal influence process has the same equilibrium as the zygote genotype process, but parallel computation showed the latter approached equilibrium more quickly. Another point of difference in the two kinds of process is that genotypic frequencies do not change between birth and sexual maturity under selection by maternal influence but do change under the usual mode of selection. However, these differences in the two kinds of selection will be minor for slow selection near equilibrium.

Of course these conclusions apply only in the context of large population theory. The mathematical difficulties encountered so far make investigation of the presumably more difficult small population situation very uninviting. However, it may be noted that in a large population approach to equilibrium is slower under maternal selection than under ordinary selection with the same reproductive weights,  $W$ . This amounts to a reduction of selection intensity. It thus seems likely that if the population is partially subdivided systematic trend under maternal selection will less effectively counteract genetic drift than under ordinary selection. Consequently it appears that the stable distribution of gene frequencies among small populations will be more variable under maternal selection. Assessment of the importance of the difference would require proper mathematical investigation, but it does seem likely that the two modes of selection will definitely differ in small populations.

### 3. SUMMARY

Selection through maternal influence operates when the mother's but not the offspring's genotypes causes fitness differentials in offspring. Though this type of natural selection is distinct from that usually discussed, equilibrium conditions under the two modes are comparable.

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