

SHORT COMMUNICATION

SEX DETERMINATION IN BEES. XXV. ADAPTIVE VALUE OF THE xo^1 GENE IN ITS ORIGIN

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ABSTRACT

An algebraic treatment shows that an xo^1 mutation (which produces diploid xo^1xo^1 drones) of the xo sex genes, will become automatically established in a panmictic Hymenoptera population whenever the adaptive value of xo/xo females or xo males is smaller than the adaptive value of xo/xo^1 females or xo^1 males. By computer simulation it was shown that in endogamous populations the new xo^1 mutation will not be commonly established because of the severe conditions: xo/xo^1 needs an adaptive value $1/3$ greater than that of xo/xo , or xo must have an adaptive value of 0.50 or less (xo/xo^1 and xo^1 being 1).

INTRODUCTION

According to Kerr (see references in Kerr, 1987), sex determination in bees occurs during two phases: the first, a few hours after the egg is laid and the second, in the prepupa before most imaginal discs and the integument are determined. In both phases, the process occurs by a balance between regulator genes that act on a set of femaleness determining genes that are additive (non-compensated or complementary) and maleness determining genes that are non-additive (compensated).

Bull (1981) elaborated a hypothesis proposing the origin of Hymenoptera

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from a primitive group in which sex would be determined by $xx = \delta$ and xy or $xx' = \text{♀}$ plus complementary genes. This model is in opposition to Hartl and Brown (1970) who derive the Hymenoptera from a sexual system in which females are XX. We think the Hartl and Brown model looks closer to the true answer because of the following reasons: a) the orders phylogenetically closer to the Hymenoptera, such as Strepsiptera, Coleoptera, Diptera, Megaloptera, and Siphonoptera, all have xx females (Makino, 1951); b) all known haplodiploid insect groups or species that in the closer group or species have diploid species have XX females, such as 1) *Micromalthus debilis* (Coleoptera); 2) Acarina (near to Araneida); 3) Coccidea e Aleyroidea (near to Hemiptera), and 4) Thysanoptera; c) Devlin *et al.* (1985) indicated that *Drosophila melanogaster* has genes that are compensated (non-additive) and genes that have a dosage effect (additive); d) diploid species with sex determination by a series of multiple alleles are not known. Therefore, we favor the model of Hartl and Brown (1970). Under this assumption, one of the primitive female-determining genes is x_0 , which in haploids is overcome by maleness genes and, therefore, determines testes and in diploids overcomes the maleness genes and determines ovaries. In the entire group of panmictic Hymenoptera, this gene tends to mutate to x_0^1 and then to x_0^2 , x_0^3 , . . . x_0^{19} , etc. forming a series of x_0 -heteroalleles.

What may have been the characteristic of the first x_0^1 mutation when it first occurred in the various groups of panmictic Hymenoptera? Why have no endogamous Hymenoptera been found with x_0 -heteroalleles?

FATE OF A MUTATION FROM x_0 TO x_0^1 IN PANMICTIC POPULATIONS OF HYMENOPTERA

Data obtained by Kerr (1986) have shown that the rate of mutation at the x_0 locus agrees with $\mu = 1.6 \times 10^{-6}$; by generalizing, this means that in every x_0/x_0 Hymenopteran species, populations receive one x_0^1 allele in about 1,600,000 x_0 -genes. Let us see what happens in a panmictic population with the new mutant.

Let us assume a panmictic population of Hymenoptera with a pair of genes A and a at frequencies p and q . There is no selection. At equilibrium the genotypic frequencies will be: $AA = p^2$, $Aa = 2pq$, $aa = q^2$ for females and $A = p$, $a = q$ for males. If survival (1-s) is R_1 , R_2 , R_3 , R_4 and R_5 for AA , Aa , aa , A and a , respectively, and gametic frequencies are p (A) and q (a) for females and r (A) and s (a) for males, then the zygotic frequencies will be $AA = prR_1$, $Aa = (ps + qr) R_2$, $aa = qs R_3$ for females; and $A = pR_4$ and $a = qR_5$ for males. The gametic frequencies of this ($T + 1$) generation will be:

$$\left[pr \cdot R_1 + \frac{(ps + qr) R_2}{2} \right] (A) + \left[qsR_3 + \frac{(ps + qr) R_2}{2} \right] (a).$$

At equilibrium the gametic frequencies of generation T are equal to those of generation (T + 1) (Kerr, 1952). Therefore:

$$\frac{p}{q} = \frac{pr \cdot R1 + \frac{(ps + qr) R2}{2}}{qs \cdot R3 + \frac{(ps + qr) R2}{2}} \quad (1)$$

$$p = \frac{pr \cdot R1 + \frac{(ps + qr) R2}{2}}{pr \cdot R1 + qs R3 + ps R2 + qr R2} \quad (2)$$

$$q = \frac{qs \cdot R3 + \frac{(ps + qr) R2}{2}}{pr \cdot R1 + qs R3 + ps R2 + qr R2} \quad (3)$$

$$r = \frac{p \cdot R4}{p \cdot R4 + q \cdot R5} \quad (4) \quad \text{and} \quad s = \frac{q \cdot R5}{p \cdot R4 + p \cdot R5} \quad (5)$$

Substituting r and s from (4) and (5) into (1)

$$\frac{p}{q} = \frac{2p^2 \cdot R4 \cdot R1 + pq \cdot (R5 + R4) R2}{2q^2 \cdot R5 \cdot R3 + pq \cdot (R5 + R4) \cdot R2}$$

Calculating p, since $q = 1 - p$:

$$p = \frac{R5 \cdot R2 + R4 \cdot R2 - 2 R5 \cdot R3}{2 (R5 \cdot R2 + R2 \cdot R4 - R4 \cdot R1 - R5 \cdot R3)} \quad (6)$$

In the case of xo mutating to xo^1 the adaptive value of $xo^1 xo^1$ should be $R3 = 0$, since diploid males are either killed or are semi-sterile. Thus, when $R1 = R2 = 1$ and $R4 = R5 = 1$,

$$p = \frac{1 + 1 - 0}{2 (1 + 1 - 1 - 0)} = 1, \text{ i.e.}$$

gene xo^1 will not be established in the population. If $R_2 = 1$, $R_4 = R_5$ and $R_1 < 1$, e.g., 0.9, then: $p = \frac{2}{2.2} = 0,91$, i.e. xo^1 will be maintained independent of new mutations.

The same will happen if $R_5 = 1$ and $R_4 < 1$, e.g. $R_4 = 0,9$, $p = 0,95$. This means that for xo^1 to become established in a panmictic hymenopteran population it is sufficient that selection against the female xo/xo^1 be less than that against xo/xo and or that selection against the male xo^1 be less than that against xo .

FATE OF AN xo^1 MUTATION IN AN ENDOGAMOUS HYMENOPTERAN POPULATION

Using the method of approximation, i.e. drawing several graphs in a PCXT computer with different values of R_1 , R_2 , R_4 , R_5 and with $R_3 = 0$ (diploid drones), and running for 750 generations of brother x sister matings, it was found that for the gene xo^1 to be maintained in a population of endogamous Hymenoptera the adaptive value of AA, i.e., R_1 , should be smaller than $2/3$ or R_4 , i.e. $1-s$ for A should be smaller than 0.5.

CONCLUSION

In a panmictic population of Hymenoptera it is sufficient that either the xo/xo^1 female or the xo^1 male be slightly better adapted than xo/xo or xo , respectively, for xo^1 to become maintained in the population independent of new mutations. However, in endogamous populations, the conditions suffer more constraints since the adaptive value of xo/xo^1 should be more than $1/3$ greater than that of xo/xo , or the adaptive value of xo^1 should be double or more than that of xo . This suggests that a series of xo -heteroalleles can evolve more easily in a panmictic than in an endogamous species.

ACKNOWLEDGMENTS

Research supported by the Brazilian National Research Council (CNPq). We thank Dr. Robert E. Page Jr. for correcting the original manuscript.

RESUMO

Um tratamento algébrico mostra que o gene determinante do sexo xo^1 , mutante de xo , poderá estabelecer-se numa população panmítica de himenópteros desde que os respectivos valores adaptativos das fêmeas xo/xo ou dos machos xo sejam levemente menores que 1 (sendo xo^1 e/ou xo^1/xo igual a 1). Já numa população endógama o gene xo^1 só entrará em equilíbrio se xo/xo tiver

valores adaptativos inferiores a 0.66 e/ou xo for menor que 0.50, em relação a xo/xo^1 e xo^1 cujos valores adaptativos (R2 e R5) são iguais a 1.

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(Received September 17, 1987)