
ABSTRACT. — Hymenoptera is the order of insects where eusociality has arisen more frequently. The propensity of this order to evolve complex eusocial traits has been linked to their haploidioidy (i.e. diploid females and haploid males). In this paper we propose a new theory explaining why eusocial traits evolve more frequently in haploidioidy than in diploid species. The probability to fix an allele(s) in haploidioidy systems may be orders of magnitude higher than in diploid species and the ratio of the two probabilities is inversely correlated with allele frequencies and with the number of genes involved. This property of the haploidioidy system should greatly facilitate the evolution of complex multigenic altruistic traits as those present in the eusocial systems. This theory is not incompatible with that proposed by Hamilton (1964), but foresees much higher advantages in the evolution of sociality both by kin and group selection.

KEY WORDS: Haploidioidy; Eusociality; Evolution; Hymenoptera.

RIASSUNTO. — Aplodiploidia ed evoluzione dell’eusocialità negli insetti. L’ordine degli Imenotteri è quello in cui l’eusocialità è sorta più frequentemente. La tendenza di questo ordine ad evolvere caratteri eusociali complessi è stata correlata con l’aploidioida (cioè femmine diploidi e maschi aploidi). In questo lavoro proponiamo una nuova teoria la quale spiega perché i caratteri eusociali si evolvono più frequentemente nelle specie aploidioidi rispetto a quelle diploidi. La probabilità che si fissi un alele (alleli) in sistemi aploidioidi può essere ordini di grandezza maggiore rispetto alle specie diploidi ed il rapporto delle due probabilità è inversamente correlato con le frequenze alleliche e con il numero di geni coinvolti. Questa proprietà del sistema aploidioidide dovrebbe grandemente facilitare l’evoluzione di caratteri multigenici complessi come sono quelli che operano nei sistemi eusociali. Questa teoria non è incompatibile con quella proposta da Hamilton (1964) ma prevede vantaggi molto maggiori nell’evoluzione dell’eusocialità sia attraverso la «kin selection» che la selezione di gruppo.

It is well known that eusocial insects belong to Hymenoptera Aculeata, with the only exception of Isoptera (termites) and the recently discovered case of Thysanoptera (Crespi and Mound, 1997). Eusociality arose independently at least 11 times among Hymenoptera but only once in Isoptera (Wilson, 1971). Hamilton (1964) suggested that the propensity of Hymenoptera to evolve eusociality is related to their haploidioid mechanism of sex determination, in which fertilized eggs give origin to diploid females, while unfertilized ones originate haploid males. Haploidioidy is shared by Hymenoptera Aculeata and few other insect groups, including Thysanoptera, but not Isoptera. According to Hamilton, the evolution of altruistic characters is easier in haploidioid animals because the relatedness value \( r \) between sisters is 75% in the haploidioid species instead of 50% in the diploid ones \( (\text{kin selection}) \).

In these years many papers have tried to prove or disprove the Hamilton’s theory (Breed, 1989; Strassmann and Queller, 1989; Pamilo et al., 1997), but the issue is still open because in many haploidioid species \( r \) value was found to be lower than \( \frac{3}{4} \), due

(*) Nella seduta del 13 maggio 2005.
to the multiple insemination of fertile females (i.e. the insemination of a female by more than one male). A different theory on the role of haplodiploidy in the evolution of euociality has been proposed by Reeves (1993), the so called «Protected invasion model». Reeves suggests that in haplodiploid species the probability of fixation of an altruistic character is higher than in diploid ones if the character is determined by a dominant allele and the genetic drift is one of the driving forces of fixation. In these conditions the character is more easily fixed in females and this would partly explain why males are drones.

In the present paper we propose a new hypothesis (which does not exclude Hamilton’s one) that explains how haplodiploidy greatly facilitates the evolution of euociality. Our hypothesis is much simpler than Reeve’s one; it is valid with dominant as well as recessive alleles, and it does not require genetic drift. The only required prerequisite is that the foundress is homozygous for the allele(s) conferring the social trait and that it is fertilized by a male hemizygous for the same allele(s). If this condition is not met, the individuals of the colony will be genetically and phenotypically heterogeneous for the social trait, due to the independent segregation of genes in meiosis, and the colony will become anarchic.

Let us consider the simplest possible case: the social trait is determined by the recessive allele \( a \) of a single polymorphic gene (the hypothesis remains valid also if the social trait is determined by a dominant allele). According to the postulate, a stable colony is obtained when a \( a/a \) female mates with an \( a/a \) (diploid system) or an \( a \) (haplodiploid system) male. The probability of having a full homozygous recessive colony depends on the frequency of the \( a \) allele, and it can be estimated with the following formulae:

\[
\begin{align*}
P_D &= X^4 \\
P_{HA} &= X^3
\end{align*}
\]

where \( P_D \) and \( P_{HA} \) are the probabilities, in diploid and haplodiploid species respectively, that the individuals of the progeny are homozygous for the \( a \) allele, and \( X \) is the frequency of \( a \). In table Ic the values of \( P_D \), \( P_{HA} \) and \( R \) (\( P_{HA}/P_D \)) are calculated for frequencies of \( a \) varying in the population from 0.5 to 0.001. Two points are immediately apparent: 1) the probability to obtain a homogeneous progeny is always higher in the haplodiploid system; 2) the ratio between the two probabilities (\( P_{HA}/P_D \)) increases as allele frequency decreases. This is due to the fact that in diploid populations males and females have three genotypes (\( AA, Aa, aa \)), while in haplodiploid populations the genotypes are three in females but only two \( (a \) and \( A \) \) in males, and this facilitates the cross between an \( a/a \) female and an \( a \) male.

In tables Ib and Ic the values of \( P_D , P_{HA} \) and \( R \) are calculated assuming that the social trait is determined by the recessive alleles of two (tab. Ib) and three (tab. Ic) independent genes. In these cases the \( X \) values are obtained by multiplying the allele frequencies at the genes involved. The frequency of the recessive alleles in the population is assumed to be the same for the genes considered. However, the formulae remain valid for any allele frequencies combinations, as well as for any possible number of genes. The probability to obtain a homozygous progeny for independent recessive allele(s) is higher in haplodiploid