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HYPOTHESIS

What is enantiotoky, and why doesn't it exist?

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Abstract. Arrhenotoky, in which females arise from fertilized eggs and males from unfertilized eggs, has evolved multiple times in animals, most prominently in the insect order Hymenoptera. An alternative form of haplodiploidy, in which females are haploid and males diploid—here named enantiotoky—is not known to exist. An illustrated thought experiment shows that if it does evolve, it will be very unstable and is expected to disappear very quickly.

Keywords. arrhenotoky; haplodiploidy; parthenogenesis.

Parthenogenesis, in which an unfertilized egg gives rise to a viable offspring, has long been recognized as a widespread minority condition in animals (Siebold 1871; Kirkendall and Normark 2003; Kennedy 2020). Two patterns are most common, thelytoky and arrhenotoky. In thelytoky, diploid unfertilized eggs give rise to females, and there are usually no males. In arrhenotoky, diploid fertilized eggs produce females, while haploid unfertilized eggs produce males (figure 1a). The latter is the most commonly recognized form of haplodiploidy, the pattern in which one sex is diploid and the other haploid. It has evolved repeatedly in invertebrates and is estimated to be present in 12% of animal species (Ross *et al.* 2019). It is the general pattern in the insect order Hymenoptera (Heimpel and Boer 2008), in which thelytoky also has a scattered presence (Haig 1998; Rabeling and Kronauer 2013; Goudie and Oldroyd 2018).

The pattern of descent in arrhenotoky is illustrated in figure 1a. Diploid female '1' produces haploid son '3' parthenogenetically; she also mates with haploid male '2' to produce diploid daughter '4'. As seen in the figure, this pattern can be continued in succeeding generations. In arrhenotoky, then, males have mothers but no fathers. The parentage of females is unremarkable, except that full sisters are identical in the paternal component of the genome, as their father's spermatozoa are identical. Accordingly, they have higher relatedness to each other than do full siblings of diploid species. This feature drew little notice until Hamilton (1964) made it a key point in accounting for the high number of origins of sociality in the Hymenoptera. Wilson (1971: Ch. 17) expanded Hamilton's point to adduce asymmetries of relatedness due to arrhenotoky as an agent in shaping hymenopteran societies, including the fact that workers are invariably females.

Even while there is much that is not yet understood about the evolutionary and ontogenetic origins of arrhenotody, we can conceive on alternative form of haplodiploidy in which fertilized eggs give rise to males and unfertilized eggs to females (figure 1b). After all, we know that haplodiploidy is possible, and there is no evident reason why the sex derived from unfertilized eggs could not just as well be the one that produces the larger gametes. I propose to call this hypothetical alternative form of haplodiploidy enantiotoky, from the greek word εvάvτιος, meaning opposite or reverse. In figure 1b, haploid female '1' produces haploid daughter '3' parthenogenetically and mates with diploid male '2' to produce diploid son '4'. This pattern, likewise is repeated in succeeding generations.

While enantiotoky seems quite possible in principle—and may have arisen just as often as arrhenotoky—a simple thought experiment of its effects (figure 1b) provides a sufficient reason for its apparent nonexistence. Arrhenotoky is a stable pattern, as there must be females in each generation, and males are required for their production. Enantiotoky, on the other hand is flagrantly unstable. While females must be present in every generation, males are involved only in the production of other males, without gene flow from males to females. From the point of view of female alleles, this renders males irrelevant. Accordingly,

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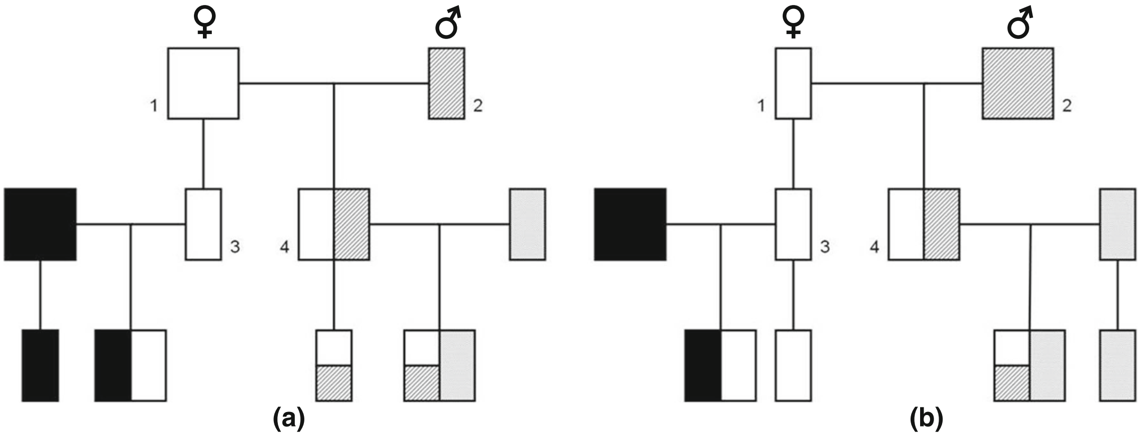

Figure 1. Diagrammatic representation of two alternative forms of haplodiploidy with two generations of descent. (a) Arrhenotoky, with diploid females (full squares) and haploid males (half squares). (b) Enantiotoky, with haploid females and diploid males. Shading indicates identical genome components.

any tendency towards asexuality will have a strong advantage, relative to the cost of producing both sexes, and is expected to invade the population. Populations consisting of haploid females are recorded from one hymenopteran species (Beukeboom *et al.* 2007), although it is not known whether it evolved by way of an enantiotokous phase.

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