

# Letter to the Editor

## Maternal Effect as a Cause of Exceptions for HALDANE's Rule

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IN 1922, J. B. S. HALDANE stated: "When in the  $F_1$  offspring of two different animal races one sex is absent, rare, or sterile, that sex is the heterozygous [heterogametic or XY] sex." This is one of a few general rules in evolutionary biology. Indeed, many hybrid crosses obey HALDANE's rule especially in sterility, but exceptions are not rare in inviability: Nine such cases are known in 23 *Drosophila* interspecific crosses that produce only one sex (WU and DAVIS 1993). In this note, I will show that these exceptions are not accountable by the suggestion that "postzygotic isolation often involves a modest number of partially recessive alleles" (TURELLI and ORR 1995) but are mainly caused by the maternal effect. This has been repeatedly pointed out by many authors (*e.g.*, PATTERSON and STONE 1952; SAWAMURA *et al.* 1993a,b; WU and DAVIS 1993). It is important to emphasize this alternative "maternal effect model," because a completely dominant allele(s) are involved in this incompatibility. There is no *a priori* reason to assume that postmating isolation is caused by a loss-of-function type recessive allele(s) (*cf.* ORR 1993; TURELLI and ORR 1995; see WU *et al.* 1996).

Table 1 lists exceptions to HALDANE's rule on hybrid inviability from *Drosophila* studies. The inviability in cross (2) may be caused by the same system as cross (1), since the maternal species is the same and the paternal species are close relatives. In at least four cases (crosses 3, 4, 7, and 8) hybrid females are viable in the reciprocal cross. These cases are not explicable by the involvement of a modest number of partially recessive alleles. When the X chromosome of species 1 ( $X_1$ ) has slightly dominant deleterious alleles above a threshold but  $X_2$  does not,  $X_1X_2$  should be inviable but  $X_2Y_1$  viable, resulting in an exception for HALDANE's rule in one of reciprocal crosses. But if this were the case, we would predict that both  $X_1X_2$  and  $X_1Y_2$  are, in most of the cases, inviable in the reciprocal cross (at least, chromosomally equivalent  $X_1X_2$  should be inviable). The inviability of hybrid males in the reciprocal cross (crosses 4 and 7) is supposed to be caused by a different system than hybrid female inviability (see SAWAMURA *et al.* 1993a,b for cross 7).

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The alternative model for hybrid female inviability postulates two components of incompatibility: a maternal effect and a dominant allele(s) on the paternal X chromosome. In three cases (crosses 3, 7, and 8) it has been shown that hybrid females die as embryos, which is a typical lethal stage of maternal-effect genes. And in two cases (crosses 3 and 7) empirical data, in fact, suggested a maternal effect. Further, in three cases (crosses 2, 3, and 7) the incompatible gene(s) on the X has been identified. In other cases empirical data are not conclusive or data are unavailable. I will discuss the individual cases in which one of these two components has been investigated.

**Cross 2:** When reciprocal  $F_1$  males between ordinary *aldrichi* and *aldrichi 2* were crossed to *mulleri* females, only hybrid females carrying the X chromosome of *aldrichi 2* were inviable. It has been shown that the X-linked element is a dominant gene or cluster of genes by using recombinant X chromosomes between these two strains (CROW 1942). CROW (1942) further showed that no hybrids are produced in the *aldrichi 2* (female)  $\times$  *mojavensis* (male) cross and the *aldrichi 2*  $\times$  *arizonae* cross (only hybrid females are viable when an ordinary *aldrichi* strain is used in these cases). So, the *aldrichi 2* X may have the same effect in these crosses, which means that the incompatible gene(s) of the *aldrichi 2* X interacts with genetic elements other than a maternal (or cytoplasmic) effect of *mulleri*. But this is not conclusive, since there remains a possibility, as mentioned by CROW (1942), that no productivity of hybrid females may be caused by premating isolation.

**Cross 3:** Hybrid females were inviable when males from the *texana*  $\times$  *americana americana*, *texana*  $\times$  *virilis*, or *texana*  $\times$  *lacicola* crosses (these have *texana* X chromosomes) were crossed to *montana* females, while males from the reciprocal crosses (that do not have the *texana* X) produced hybrid females (PATTERSON and GRIFFEN 1944b). This means that the dominant lethal gene(s) of *texana* is X-linked. The gene(s) has been mapped by PATTERSON and GRIFFEN (1944b) using recombinant X chromosomes between multiply marked *virilis* and *texana*. They further investigated the maternal effect factor of *montana*. When hybrid females from the cross of *virilis*  $\times$  *montana*, *texana*  $\times$  *montana*, *montana*  $\times$  *laci-*

TABLE 1  
Hybrid Inviability of *Drosophila*: Exceptional Cases for HALDANE'S Rule

Species cross female × male	Hybrid viability <sup>a</sup>				Components of incompatibility <sup>b</sup>		Reference
	In the cross		In the reciprocal cross		Maternal effect	Dominant gene(s) of parental X chromosome	
	Female	Male	Female	Male			
(1) <i>mulleri</i> × <i>arizonae</i> <sup>c</sup>	X	V	ND	ND	ND	ND	1-3
(2) <i>mulleri</i> × <i>aldrichi</i> 2 <sup>d</sup>	X	V	ND	ND	?	Yes	1-3
(3) <i>montana</i> × <i>americana texana</i> <sup>e</sup>	X (E)	V	V	V	Yes	Yes	4-6
(4) <i>caribiana</i> × <i>similis grenadensis</i>	X	V	V	X	ND	ND	7
(5) <i>crucigera</i> × <i>bostrycha</i>	X (L)	V	X (L)	X (L)	ND	?	8
(6) <i>grimshawi</i> <sup>f</sup> × <i>orthofascia</i>	X (L)	V	X (L)	X (L)	ND	?	8
(7) <i>simulans</i> × <i>melanogaster</i> (or <i>mauritaniana</i> , <i>sechellia</i> )	X (E)	V	V	X (L)	Yes	Yes	9-14
(8) <i>subobscura</i> × <i>madeirensis</i>	X (E)	V	V	V	ND	ND	15, 16

Reference: 1: PATTERSON and CROW (1940); 2: CROW (1942); 3: PATTERSON (1947); 4: PATTERSON and GRIFFEN (1944a); 5: PATTERSON and GRIFFEN (1944b); 6: KINSEY (1967); 7: HEED (1962); 8: YANG and WHEELER (1969); 9: STURTEVANT (1920); 10: DAVID *et al.* (1974); 11: LACHAISE *et al.* (1986); 12: SAWAMURA *et al.* (1993a); 13: SAWAMURA *et al.* (1993b); 14: SAWAMURA and YAMAMOTO (1993); 15: KHADEM and KRIMBAS (1991); and 16: PAPACEIT *et al.* (1991).

<sup>a</sup> V, viable; X, inviable (lethal stage is shown in parentheses: E, embryo; L, larva); ND, not determined because of pre-mating isolation.

<sup>b</sup> Yes, positive data; ?, inconclusive data; ND, not determined.

<sup>c</sup> As *mulleri* × *arizonensis*.

<sup>d</sup> A strain of *aldrichi*. Typical *aldrichi* strains produce both female and male hybrids.

<sup>e</sup> As *montana* × *texana*.

<sup>f</sup> Used different geographical strains in the reciprocal crosses.

*cola*, or *laticola* × *montana* were crossed to *texana* males, hybrid females were viable. This means that the factor of *montana* is recessive.

**Crosses 5 and 6:** YANG and WHEELER (1969) made a backcross of *crucigera/bostrycha* hybrid males to *crucigera* females. Because both of the female and male BC<sub>1</sub> hybrids should be affected by a maternal (or cytoplasmic) effect of *crucigera* without inheriting the *bostrycha* X chromosome, this is a crucial test for the involvement of the X. They observed very few larvae, all of which died at an early larval stage. The paternal X may not be involved in this case. However, there remains a possibility, as mentioned by YANG and WHEELER (1969), that the lack of adult flies may merely reflect the low productivity of hybrids because of the semi-fertility of the F<sub>1</sub> males. In the *grimshawi/orthofascia* case the F<sub>1</sub> males are sterile.

**Cross 7:** This is a well-known exception to HALDANE'S rule (STURTEVANT 1920; DAVID *et al.* 1974; LACHAISE *et al.* 1986). SAWAMURA *et al.* (1993a,b) showed that hybrid females carrying the *melanogaster* X are embryonic lethal when produced by *simulans* mothers, and suggested that the embryonic inviability is caused by the incompatibility between a maternal effect of *simulans* (or *mauritaniana*, *sechellia*) and the X chromosome of *melanogaster*. They further found genes which rescue these inviable hybrids: one is a maternally acting gene located on the second chromosome of *simulans*, and the other is a zygotic acting gene located on the X chromosome of *melanogaster*. Hybrids produced by *simulans* (or *mauritaniana*, *sechellia*) mothers are inviable independent of

their sex, when they carry the wild-type allele of the zygotic acting *melanogaster* gene (SAWAMURA and YAMAMOTO 1993). This indicates that the X-linked gene is completely dominant.

As shown above, almost of all cases of hybrid inviability in *Drosophila* that do not obey HALDANE'S rule are explicable by the incompatibility between a maternal effect and a dominant allele(s) on the X chromosome. The reason is very simple: in XX-XY species, the XX hybrids inherit one of their X chromosomes from the paternal (incompatible) species but the XY hybrids inherit their X chromosome from the maternal (compatible) species.

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