

Appendix S1: Extreme inbreeding facilitates haplodiploidy

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Supplementary information to:

*The evolution of haplodiploidy by male-killing endosymbionts:
importance of population structure and endosymbiont mutualisms*

In order to investigate the result from the individual-based simulations in which the male haploidizing endosymbiont persisted for a longer span of generations under conditions of high local relatedness, we analyzed local interactions on a patch by using an analytical model based on a direct fitness approach (Taylor & Frank, 1996). The individual-based simulations showed that evolution towards maximal levels of s preclude the stable persistence of the haploidizing endosymbiont, since this nullifies resource reallocation to infected females. When the haploidizing endosymbiont does not provide any direct survival benefits to the host, stable coexistence of the haploidizing endosymbiont and viable haploidized males is only possible if s does not evolve towards 1, but maintains intermediate levels (i.e., $0 < s < 1$). In this analysis, we investigate the conditions under which such intermediate values of s can be achieved.

We assume that endosymbiont transmission fidelity is maximized ($a = 1$), since this makes it feasible to keep track of the different phenotypes that are interacting in a local population. Our simulations warrant this assumption, since a always evolved towards 1 if the endosymbiont successfully persisted in the population (e.g., see Fig. S1c).

Fitness equations Total fitness over male and female components can be expressed as the sum of male and female fitnesses, multiplied by the class reproductive values for males and females, c_m and c_f , respectively:

$$W = c_m W_m + c_f W_f$$

For $a = 1$, diploid infected females and haploidized males represent the different classes. Their fitnesses are:

$$\begin{aligned} W_f &= R(\bar{s}) \\ W_m &= sR(\bar{s})\frac{1}{\bar{s}} \end{aligned} \quad (S1)$$

in which s is the focal individual's survival probability as a haploidized male, whereas \bar{s}, \bar{s} are the average survival probabilities of the focal individual's brood and the average survival probabilities of haploidized males in the rest of the patch, respectively. The fitness gradient of haploidized male viability from the perspective of a haploidized male then becomes:

$$\left. \frac{dW}{ds} \right|_{s=\bar{s}=\bar{s}} = c_f \frac{\partial W_f}{\partial \bar{s}} r_{\bar{f},m} + c_m \frac{\partial W_m}{\partial s} \cdot r_{m,m} + c_m \frac{\partial W_m}{\partial \bar{s}} r_{\bar{m},m} + c_m \frac{\partial W_m}{\partial \bar{s}} r_{\bar{m},m} \quad (S2)$$

Relatedness coefficients between the focal male as an actor and other males and females in the brood or males in the patch as recipients can be calculated according to:

$$r_{xy}^z = \frac{f_{zy}}{f_{xy}} \quad (S3)$$

in which r_{xy}^z represents the relatedness of individual y to x from the viewpoint of the actor z (Michod & Hamilton, 1980). f_{zy} is the coefficient of consanguinity between the actor z and another individual y , whereas f_{zx} is the coefficient of consanguinity between an individual and himself (or herself). In haploidized males $f_{zx} = 1$. Relatedness from the viewpoint of a haploidized male actor in control of its haploid survival strategy s to the relevant other patch members is given by:

$$\begin{aligned} r_{m,m} &= 1 \\ r_{\bar{m},m} &= \frac{1}{2} + \frac{1}{2}F \\ r_{\bar{m},m} &= \frac{1}{N} \left(\frac{1}{2} + \frac{1}{2}F \right) \\ r_{\bar{f},m} &= \frac{1}{2} \left(\frac{1}{2} \cdot 1 + \frac{1}{2}F \right) + \frac{1}{2}F = \frac{1}{4} + \frac{3}{4}F \end{aligned}$$

in which F is defined as the coefficient of inbreeding of the female part of a fertilized mother. F can be found by solving the following recursion equation:

$$F(t+1) = \frac{1}{N} \left[\frac{1}{2} \left(\frac{1}{2} + \frac{1}{2}F(t) \right) + \frac{1}{2}F(t) \right]$$

yielding:

$$F = \frac{1}{4N-3}$$

The class reproductive values correspond to a normal haplodiploid system if action of the endosymbiont is perfect (Taylor, 1988):

$$\{c_f, c_m\} = \{2, 1\}$$

Based on equation (S2), the fitness gradient therefore becomes:

$$\frac{dW}{ds} = (1+m) \left(2 \frac{dR(\bar{s})}{d\bar{s}} \left(\frac{1}{4} + \frac{3}{4}F \right) + 1 \cdot \frac{R(s)}{s} + 1 \cdot \frac{dR(s)}{d\bar{s}} \left(\frac{1}{2} + \frac{1}{2}F \right) - 1 \cdot \frac{R(s)}{s} \frac{1}{N} \left(\frac{1}{2} + \frac{1}{2}F \right) \right) \quad (\text{S4})$$

Evaluating the fitness gradient at $s = 0$ shows that values of $s > 0$ will always be selected for, since it will always pay off for a haploidized male to have a nonzero chance of survival. When evaluating the gradient at $s = 1$, negative values indicate that selection will lead to intermediate rescue of haploidized males and thus to stable endosymbiont persistence. Investigating the sign of the selection gradient at $s^* = 1$ yields the circumstances under which intermediate haploidized male survival probabilities are selectively favored:

$$\left. \frac{dW}{ds} \right|_{s^*=\bar{s}=\tilde{s}=1} = \frac{(1+m)(2-4N^2(b-2)-N(10-b))}{2N(4N-3)} \quad (\text{S5})$$

In order to have stable persistence of both the haploidizing endosymbiont and haploidized males, the following condition must hold:

$$4N^2(b-2) + N(10-b) > 2 \quad (\text{S6})$$

Fig. S2 illustrates the latter condition by plotting the sign of the fitness gradient against N . This shows that only for values of $N < 2$ selection leads to intermediate values of s and thus stable persistence of the haploidizing endosymbiont. The requirement of high local relatedness in order to obtain stable persistence of haplodiploidy makes sense, since males will only allow themselves to be killed to a certain degree when reallocation of resources to their sisters outweighs the possibility of surviving haploidization in order to fertilize sisters and other females on the patch. The efficiency with which resources are reallocated, b , is crucial in determining the minimally required amount of local relatedness: if reallocation is maximal ($b = 1$), $N < 2$ suffices, but lower efficiencies also require more extreme degrees of local relatedness in order for males to be selected to sacrifice themselves to the good of their sisters. We can conclude that in the case where the host does not accrue any direct benefits from the haploidizing endosymbiont, only extreme levels of inbreeding allow for stable persistence of the haploidizing endosymbiont.

References

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