

# Effects of inbreeding depression on relatedness and optimal sex ratios

JACO M. GREEFF<sup>1\*</sup> and PETER D. TAYLOR<sup>2</sup>

<sup>1</sup>Department of Zoology and Entomology, University of Pretoria, Pretoria 0002, South Africa

<sup>2</sup>Department of Mathematics and Statistics, Queen's University, Kingston, Ontario K7L 3N6, Canada

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When parents are related, their offspring will receive genes that are identical by descent. The effect of such inbreeding is to increase the relatedness of each parent to the offspring (Hamilton, 1972; Michod and Hamilton, 1980). In some taxa, inbreeding leads to reduced fecundity (inbreeding depression) resulting from recessive deleterious genes that become homozygous. The result is that inbred diploid offspring will make a smaller contribution to the gene pool, and this will tend to decrease the population-wide average relatedness of parent to offspring. That is, while inbreeding increases this relatedness over its outbred value, the added factor of inbreeding depression will moderate this increase. In a diploid population, this will apply to both sexes of offspring equally, but under haplodiploidy, this will affect only the relatedness of a mother to her diploid daughters, her relatedness to her sons being fixed at 1, independently of inbreeding or inbreeding depression. Thus in a haplodiploid population, inbreeding depression will provide an additional source of relatedness asymmetry of a mother to her two offspring sexes, and this will have an effect on any sex-specific behaviour towards her offspring; in particular, this will modify the sex ratio bias due to relatedness asymmetry. Denver and Taylor (1995) recently examined the effects of inbreeding depression on the sex ratio, but failed to account properly for its effects on the relatedness of a mother to her daughters. Here we derive the correct relatedness formula, and calculate the sex ratio in a partially sibmating haplodiploid population.

Consider a very large haplodiploid population where a proportion  $p$  of all females sibmate and their diploid offspring suffer an inbreeding penalty of  $s$ . Let  $q = p(1-s)/(1-ps)$  be the probability that a female has sibmated parents. We define  $F$  as the coefficient of inbreeding of a random female,  $G$  as the coefficient of consanguinity between a random female and her brother, and  $H$  as the coefficient of consanguinity between a random female and her mate. It then follows that  $F = qG$  and  $H = pG$ . If  $G'$  is the value of  $G$  one generation later, then we get an expression for  $G'$  in terms of whether the mating female has sibmated parents or not:

$$G' = q[(1 + F)/4 + G/2] + (1 - q)[(1 + F)/4] \quad (1)$$

Setting  $G = G'$  and remembering that  $F = qG$  and  $H = pG$ , we get:

$$\begin{aligned} F &= q/(4 - 3q) \\ G &= 1/(4 - 3q) \\ H &= p/(4 - 3q) \end{aligned} \quad (2)$$

\*Author to whom all correspondence should be addressed.

We can now obtain  $r_f$ , the relatedness of a daughter to her mother, as the ratio of the coefficient of consanguinity between the female and her daughter to the coefficient of consanguinity of the female with herself (Michod and Hamilton, 1980):

$$r_f = \frac{(1 + F)/4 + H/2}{(1 + F)/2} = \frac{(2 - ps - p^2s)}{(4 - 2p - 2ps)} \tag{3}$$

It can be shown that  $r_f$  is an increasing function of  $p$  and a decreasing function of  $s$  (Fig. 1).

Denver and Taylor (1995, Equation 1) provide a general formula for the evolutionarily stable (ES) sex ratio  $\alpha$  (proportion of males) under partial sibmating:

$$\alpha = \frac{1}{2} \cdot [1 - p] \cdot \left[ \frac{2r_m v_m}{r_f v_f + r_m v_m} \right] \cdot \left[ \frac{V_o}{(1 - p)V_o + pV_s} \right] \tag{4}$$

where  $v_i$  is the reproductive value of sex  $i$  and  $V_o$  and  $V_s$  are the reproductive values of a single outbreeding and sibmating respectively. The three terms in square brackets identify the three routes through which sibmating can bias the sex ratio. The first is the local mate competition factor, the second is the effect of inbreeding on relatedness asymmetry, and the third is the effect of inbreeding on the relative reproductive value of the two types of matings. Using this formula and our value of  $r_f$  in Equation (3), we obtain the sex ratio in a haplodiploid population as:

$$\alpha = \frac{1}{2} \cdot [1 - p] \cdot \left[ \frac{2(2 - p - ps)}{4 - p - 2ps - p^2s} \right] \cdot \left[ \frac{3}{3 - 2ps - p^2s} \right] \tag{5}$$

The relatedness term obtained by Denver and Taylor (1995) (the middle square bracket) is the same as ours with  $s = 0$ ; thus we provide the correction due to inbreeding depression. The  $V$  term (the last square bracket) was calculated by Denver and Taylor, and it is seen to be unity when there is no sibmating ( $p = 0$ ) or if there is no inbreeding depression ( $s = 0$ ).

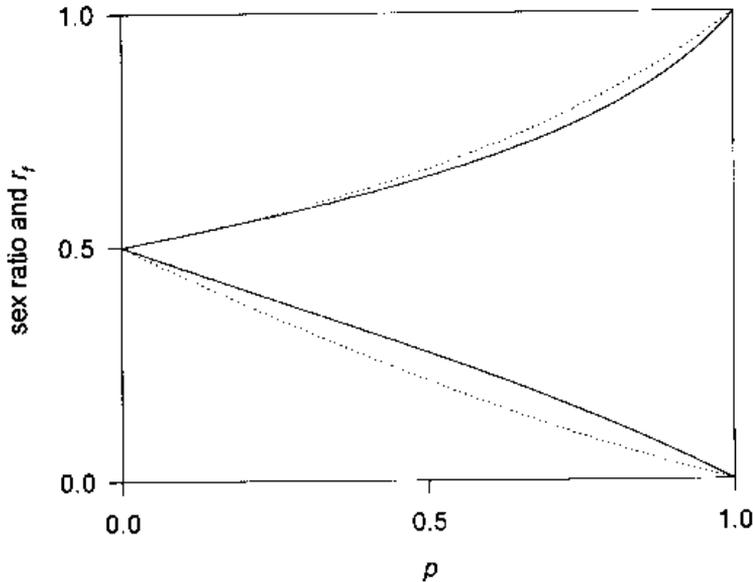


Figure 1. The ES sex ratio (lines below 0.5) and  $r_f$  (lines above 0.5) as a function of  $p$  where  $s = 0$  (dotted lines) and  $s = 0.5$  (solid lines).

The form of the last two terms shows that increases in  $s$  lead to increases in the sex ratio. The last two square brackets of Equation (5) increase as  $p$  increases, whereas the first square bracket decreases. This has the ultimate effect that the difference in the ES sex ratio of two populations with different values of  $s$  will first increase and then decrease as  $p$  increases (Fig. 1). In other words, the effects of  $s$  on the sex ratio are small when few individuals sibmate, and at the other extreme, when  $p$  is close to 1, the effect of  $s$  on the ES sex ratio is overshadowed by that of  $p$ .

Presently, there are many inclusive fitness models with partial sibmating. If these models are to be extended to incorporate the effect of inbreeding depression, it is important to incorporate this change in  $r_f$ . Especially for Hymenoptera with complementary sex determination, where the penalty for sibmating is  $s = 0.5$  (Cook and Crozier, 1995), these effects of inbreeding depression are very important.

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