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# Female-biased sex ratios under local mate competition: an experimental confirmation

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**Summary**

Experimental work of Nadel and Luck (1992) on a chalcidoid wasp provides a confirmation of sex ratio theory under local mate competition.

*Keywords*: sex ratio; sib mating; local mate competition; chalcidoid wasp

## Introduction

Competition among siblings or among close relatives for reproductive resources (local resource competition: LRC) is an important cause of sex ratio bias (Hamilton, 1967, 1979; Taylor, 1981; Charnov, 1982) and this will be a particularly strong force in species in which there is some offspring mating prior to dispersal. The idea here is that if the parent has control over the sex ratio of her progeny, she should bias this ratio towards the sex that exhibits the least amount of LRC.

A simple example is provided by the following 'partial sibmating' life history. Mated females breed singly; male offspring remain for a time on their native site possibly to mate with their sisters, and then disperse to find additional matings in the population at large. A female offspring mates once, with a brother with some probability $k$, and with a male immigrant with probability $1-k$. Mated females then disperse at random to establish new breeding sites. This life history exhibits LRC between males for matings with sisters (local mate competition: LMC), but no LRC between females, as they disperse at random with no competition between relatives for breeding sites. Thus we expect a female-biased sex ratio.

I show below, with a simple inclusive fitness argument (Hamilton, 1964), that the Evolutionarily Stable Strategy (ESS) sex ratio (proportion of males) depends on the genetic system and is

$$r = \frac{1-k}{2} \qquad \text{(Diploid)} \qquad (1)$$

$$r = \frac{(1-k)\,(2-k)}{4-k} \qquad \text{(Haplodiploid)} \qquad (2)$$

Much attention has been paid to a closely related 'patch structure' life history, in which $N$ mated females breed together on a patch, the offspring mate at random on the patch, and then the mated females disperse at random to form new breeding aggregates. It turns out that this patch structure model is mathematically equivalent to the partial sibmating model described above. The probability of sibmating in the patch structure model is $k = 1/N$, and with this substitution, Equation 1 was obtained by Hamilton (1967) and Equation 2 was obtained by Hamilton (1979: p. 184) and Taylor and Bulmer (1980: p. 416).

Nadel and Luck (1992) have studied a species of parasitic Hymenoptera *Pachycrepoideus vindemiae* (Rondani) which, like many chalcidoid wasps, manifests a female-biased sex ratio.

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Their breeding structure appears to closely fit the partial sibmating model described above. In a laboratory experiment, consisting of 36 broods, Nadel and Luck (1992) estimated the probability of sibmating to be anywhere between 50 % and 75 %, and found a sex ratio of 43/303 = 14 % males. Equation 2, with $k$=50 % and 75 % gives $r$ = 21 % and 9.6 % respectively, so that their results provide a nice fit to the theory.

The inclusive fitness argument for the partial sibmating model proceeds as follows. I let $R_i$ denote the relatedness between a mother and her sex i offspring, and I let $v_i$ denote the reproductive value of the sex i subpopulation. An extra male offspring will increase his mother's inclusive fitness only when he outbreeds ($p = 1-k$); any sibmating simply takes a mating opportunity away from another of her sons. Thus her inclusive fitness gain through an extra male offspring is

$$\Delta W_m = \frac{1-r}{r}(1-k)\ R_m v_m \tag{3}$$

where the multiplier $(1-r)/r$ is the average number of female matings per male. On the other hand, an extra daughter increases her mother's inclusive fitness whether she sibmates or not. In addition, if she does sibmate ($p = k$), she provides an extra mating for a son. Thus the inclusive fitness gain through an extra female offspring is

$$\Delta W_f = R_f v_f + k\ R_m v_m \tag{4}$$

The condition for an equilibrium sex ratio $r$ is that the inclusive fitness gains through extra male and female offspring be equal:

$$\Delta W_m = \Delta W_f \tag{5}$$

To calculate the relatedness coefficients and the reproductive values, we must specify the genetic system, and I assume it is haplodiploid. Then $v_f = 2v_m$ (Price, 1970) and

$$R_m = 1$$
$$R_f = \frac{1+3F}{2+2F} \tag{6}$$

(Hamilton, 1972; Michod and Hamilton, 1980), where $F$ is the inbreeding coefficient, calculated from the recursion

$$F = k\left[\frac{1}{2}\,\frac{1+F}{2} + \frac{1}{2}\,F\right] \tag{7}$$

which calculates $F$ on the left as the probability random alleles from a mated pair are identical by descent. This will happen only if the pair is sibmated ($p = k$) and in this case, the probability of identity is different when the female allele is maternal ($p$ = 50 %) and paternal ($p$ = 50 %). Equation 7 solves to give (Hamilton, 1979)

$$F = \frac{k}{4-3k} \tag{8}$$

When Equations 6 and 8 are substituted into Equation 5, we get the ESS sex ratio (Equation 2).


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