

Supporting information for Journal of Evolutionary Biology article *Natural selection. VII. History and interpretation of kin selection theory* by Steven A. Frank

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Contents: Notes written and distributed by William D. Hamilton for his graduate course at the University of Michigan, Fall 1979. Class attended by Steven A. Frank. Notes scanned by Frank in October 2012.

Comments by Steven A. Frank: These notes show Hamilton's Price equation analysis of sex ratios for group structured populations. The approach was explicitly formed as a group selection analysis, following Price's (1972, see main article for full citations) methods. Hamilton (1975) developed Price's methods. The derivation here was motivated by Hamilton's interests in fig wasp sex ratios, published as Hamilton (1979) but without these mathematical details.

Hamilton  
10/31/79

Ess sex ratios for a sperm-storing animal with local competition for mates


Recapitulation of Price equation

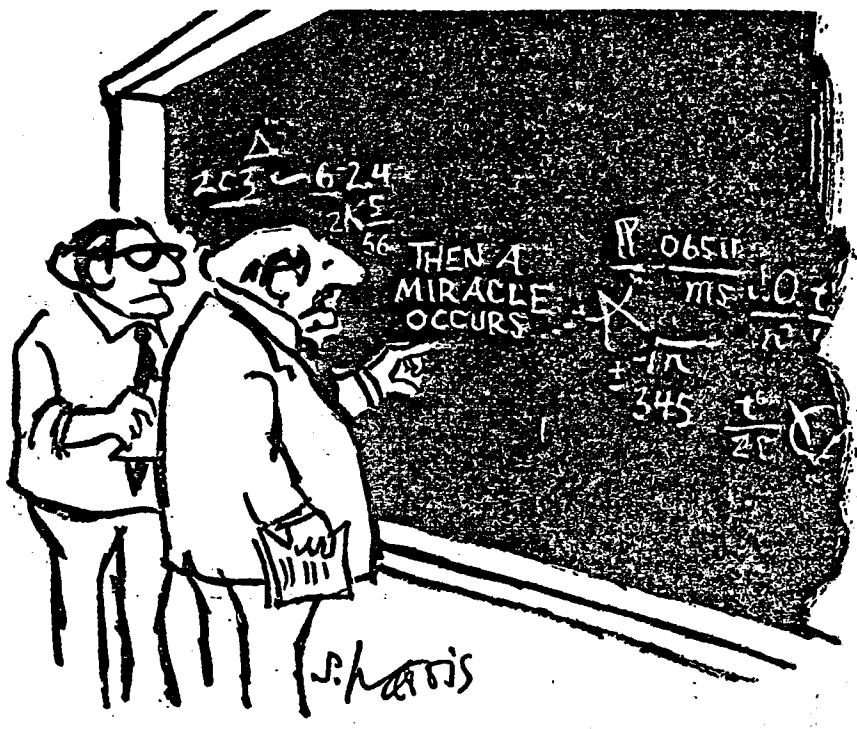
$$w \Delta q = C_{\text{ov}}(w_s, q_s) + E(w_s \Delta q_s)$$

1. Use the equation to expand its own second term.
2. Replace covariances by product of regression and variance.
3. Change significance of subscript so that it indexes the class of groups having exactly  $S$  of its members of type  $b$  (instead of indexing particular groups). Then:

$$w \Delta q = R(w_s, q_s) V(q_s) + \sum_{s=0, n} P_s \{ R_s(w_{si}, q_{si}) V_s(q_{si}) + E_s(w_{si} \Delta q_{si}) \}$$

where  $P_s$  is the frequency of groups having exactly  $S$  members of type  $b$ .


Type  $a$  and Type  $b$  are going to refer to colonising composites, i.e. a female plus the stored sperm that she carries . It is assumed that a sex-ratio gene can be in either part of the composite and carried in any part of the genome. The  $w_{si}$  will be made up as inclusive fitness and this means that the  $\Delta q_{si}$  can be treated as zero. This step may seem dubious at this stage but some justification for it will be explained later.



"I think you should be more explicit here in step two."

Thus the prepared form of the Price equation is

$$w_{\Delta} = R(w_s, q_s) V(q_s) + \sum_{s=1}^n P_s R_s(w_{si}, q_{si}) V(q_{si})$$

We are assuming that individuals (colonising composites) come together in groups of  $n$ ; they give rise to equal broods; these mate together; then the products -- new colonising composites  -- take off for the new dispersal phase.

Thus if  $b'_u$  is the relatedness of a son with respect to a genetic element in the composite, and  $b'_v$  is the relatedness of a daughter, using <sup>a sense of</sup> inclusive fitness we have:

$$\text{fitness} \propto b'_u \times \text{expected number of inseminations by sons} + b'_v \times \text{expected number of daughters.}$$

We now assume that the genetic element actually affects the sex ratio. We hopefully disregard complexities of those cases of control where the genetic element can be paired with a homologue and assume that there are just two sex-ratio types  $a$  and  $b$  producing sex ratios  $x_a$  and  $x_b$ .

Since the number of females among progeny in an  $s$ -type group (group with  $s$  members type  $b$ ) is  $1 - X_s$  where  $X_s = p_s x_a + q_s x_b$ , and since in the male progeny sons of a particular parent composite form a fraction  $x_b / X_s$  of the total, the expected number of inseminations by sons is  $\propto$  (proportional to)

$$\frac{x_b}{X_s} (1 - X_s)$$

Expected daughters are  $\propto 1 - x_b$

Thus we define the fitness of an individual type  $b$  settler to be

$$w_{si(b)} = \frac{x_b}{X_s} (1 - X_s) b'_u + (1 - x_b) b'_v$$

Similarly

$$w_{si(a)} = \frac{x_a}{X_s} (1 - X_s) b'_u + (1 - x_a) b'_v$$

By the difference of these the regression in an S-type group is

$$R_s(\omega_{si}, q_{si}) = -(x_a - x_b) \left\{ \frac{1}{X_s} b'_u - (b'_u + b'_v) \right\}$$

The total number of inseminations by sons in a group is obviously the same as the total number of daughters in the group. Hence

$$\omega_s = (1 - x_s) b'_u + (1 - x_s) b'_v = (1 - x_s)(b'_u + b'_v)$$

(see dotted underlined expression below)

Substituting for  $X_s$  (and considering the gradient of the linear function so obtained with respect to  $q_s$ ) we find  $R(\omega_s, q_s) = (x_a - x_b)(b'_u + b'_v)$

Noting that  $V(q_{si}) = P_s q_s$  we can now substitute in the prepared Price equation and obtain

$$\omega \Delta q = (x_a - x_b) \left[ B V(q_s) - \sum P_s \left\{ \frac{1}{X_s} b'_u - B \right\} P_s q_s \right]$$

where  $B = b'_u + b'_v$ .

With this we are ready to find the ess sex ratio—this being that which if ascribed to one of the types renders the other type, producing any differing sex ratio, certain to have a selective disadvantage.

Let  $x_a - x_b = \delta$  (with  $\delta \neq 0$ ). Then  $x_b = x_a - \delta$   
and  $X_s = P_s x_a + q_s x_b = \underline{x_a - q_s(x_a - x_b)} = x_a - q_s \delta$

It can also easily be shown that

$$\frac{1}{X_s} = \frac{1}{x_a} + \frac{q_s \delta}{x_a X_s}$$

and this will also yield a helpful substitution. (Note: how one guesses in advance that this will be helpful is a somewhat obscure point. Really, the usefulness of setting up such an expression only becomes apparent in retrospect after following through a longer process of algebraic manipulation, as in my first derivation of the results below). Making these substitutions in the last equation for the gain

of type b:

$$\begin{aligned} \omega \Delta g &= \delta \left[ BV(g_s) - \sum P_s \left\{ \frac{b'_u}{x_a} + \frac{b'_u \delta g_s}{x_a x_s} - B \right\} P_s g_s \right] \\ &= \delta \left[ BV(g_s) - \left\{ \frac{b'_u}{x_a} - B \right\} \sum P_s \beta_s g_s - \frac{b'_u \delta}{x_a} \sum P_s \frac{\beta_s g_s^2}{x_s} \right] \end{aligned}$$

Here we note that  $\sum P_s \beta_s g_s$  is the "within group variance".

So, since  $P_g$  is the total variance and  $V(g_s)$  the between group variance,

$$\sum P_s \beta_s g_s = P_g - V(g_s). \quad \text{Hence}$$

$$\begin{aligned} \omega \Delta g &= \delta \left[ BV(g_s) - \left\{ \frac{b'_u}{x_a} - B \right\} \{ P_g - V(g_s) \} \right] - \delta^2 \frac{b'_u}{x_a} \sum P_s \frac{\beta_s g_s^2}{x_s} \\ &= \delta \left[ B P_g - \frac{b'_u}{x_a} \{ P_g - V(g_s) \} \right] - \delta^2 \frac{b'_u}{x_a} \sum P_s \frac{\beta_s g_s^2}{x_s} \end{aligned}$$

We note that  $\delta^2$  and every other item in the last term is positive; thus the last term as a whole is negative. The involvement of  $\delta$  in the first term, however, indicates that this term can be positive or negative. But it is possible to select  $x_a$  such that  $[ ]$  in the above equation is zero; then the second term determines that  $\omega \Delta g$  is certainly negative. Hence with such an  $x_a$  it is seen that any differing  $x_s$  results in counterselection of type b. Hence such an  $x_a$  must be the ess.

$$\text{If } x_a = x^* \text{ gives } [ ] = 0 \text{ then } B P_g = \frac{b'_u}{x^*} \{ P_g - V(g_s) \}$$

$$\begin{aligned} \text{This gives } x^* &= \frac{b'_u}{b'_u + b'_v} \cdot \frac{P_g - V(g_s)}{P_g} \\ &= \frac{1}{2} \left( 1 + \frac{b'_u - b'_v}{b'_u + b'_v} \right) P_{ST} \end{aligned}$$

where  $P_{ST} = \frac{P_g - V(g_s)}{P_g}$ . ( $P_{ST}$  can be considered an index of panmixia. Symbol and definition are from S. Wright -- see volume 2 of his treatise. Note that use of  $P$  here is quite different from its use in  $P_s$  for frequency of types of group).

Now the various cases of genomic control of sex ratio can be considered, providing various pairs of formulas for the  $b'$  coefficients. With a further decision as to the settling behavior so as to fix  $V(g_s)$  in relation to  $\beta_s$ , sex ratios can be evaluated. The obvious standard case for settling is that it occurs at random. Then  $V(g_s) = \beta_s/n$  and  $P_{ST} = (n-1)/n$

The above argument has had two somewhat heuristic steps -- firstly that where we ignored  $E_s(A_s)$  and secondly that where we ignored potential special sex ratios produced in heterozygotes and assumed just two sex-ratio types.

The first can be justified by pointing out that  $\Delta g_{s_i}$  is really only concerned with heterozygotes like  $A_a A_b$  and  $X_a X_b$  and provided that in these neither element is driving then we do not need to worry about other "heterozygotes" like  $X Y_a, X_b Y$ , etc., where drive against the other chromosome may be occurring. This is because as inclusive fitnesses the  $\omega_{s_i}$  are being designed to set out the just set of equipotential replicas of  $Y_a$  or  $X_b$  or other elements. Each replica has the capability to produce a composite the same as the parent, so the set measured by  $\omega_{s_i}$  is equivalent to a set of parthenogenetic offspring; so, as for such offspring,  $\Delta g_{s_i} = 0$ .

The second weak point is obviously no problem at all in cases where effects are caused by the Y chromosome, whether the Y occurs in males or females. This is because heterozygotes like  $Y_a Y_b$  can't occur. As it turns out it seems not to be a problem either for the other potentially more complex cases of sex-ratio control. This fact is known to me from checks by computer simulation. At present I cannot give a complete rationalisation, but if we take the case where the sex ratio of the het is always between the homs and try to reason about the direction of selection rather than about quantitative gain of alleles, the success of the method in locating the sex does not seem very surprising.

Coefficients of relatedness of offspring to parents,  
 $b'_u$  and  $b'_v$  (see Hamilton, 1972)

In the case of autosomes we only need note that by symmetry of inheritance  $b'_u$  and  $b'_v$  must be equal. Thus the ess sex ratio for autosomal control is simply  $\frac{1}{2}P_{ST}$  or  $(n-1)/n$ . We may call this the standard sex ratio of the model and notate it  $x^{(n)}$ .

In the case of Y-linked control we have, for control in heterogametic males,  $b'_u = 1$  and  $b'_v = 0$  and for control by Y in heterogametic females  $b'_u = 0$  and  $b'_v = 1$ . These give  $x^* = 2x^{(n)}$  and  $x^* = 0$  respectively.

For an active element on the X we need the following table:

		Offspring		Difference	Sum	Diff./Sum
		XY	XX			
Active parent	XY	F	1+F	1	1+2F	$\frac{1}{1+2F}$
	XX	1/2	$\frac{1+3F}{2(1+F)}$	$\frac{F}{1+F}$	$\frac{1+2F}{1+F}$	$\frac{F}{1+2F}$

F is the coefficient of inbreeding. If we assume random settling (as above in setting  $P_{ST} = (n-1)/n$ ) it is quite easy to show by methods explained originally by S. Wright (and later in various textbooks) that for this type of an "Island" model  $F = 1/(4n-3)$ . This leads to

$$1/(1+2F) = (4n-3)/(4n-1) \text{ and } F/(1+2F) = 1/(4n-1)$$

These expressions for  $(b'_u - b'_v)/(b'_u + b'_v)$  are being prepared for evaluation of the ess. But before we can decide which coefficient in a row of the above table is to be  $b'_u$  and which is to be  $b'_v$  we again have to decide which sex is heterogametic. It is easily seen that this decision determines whether "diff./sum" is to be added or subtracted from unity to provide the relatedness factor for  $\frac{1}{2}P_{ST}$ . Thus finally we can draw up the following table of ess sex ratios for the model, all being conveniently treated as modifications to the standard sex ratio:

Active agent

Male heterogamety

Female heterogamety

Autosomes, either sex

$$x^{(n)}$$

$$x^{(n)}$$

Y

$$2x^{(n)}$$

0

X in XY

$$\left(1 - \frac{4n-3}{4n-1}\right)x^{(n)}$$

$$\left(1 + \frac{4n-3}{4n-1}\right)x^{(n)}$$

X in XX

$$\left(1 - \frac{1}{4n-1}\right)x^{(n)}$$

$$\left(1 - \frac{1}{4n-1}\right)x^{(n)}$$

↑

~~(1 - \frac{1}{4n-1})x^{(n)}~~

x<sup>4</sup>

x<sup>0</sup>

$$4n-1 - 4n+3$$



UNDEATABLE SEX RATIOS FOR DIFFERENT COMPONENTS OF THE GENOME  
 WITH EITHER MALE HETEROGAMETIC (—) OR FEMALE HETEROGAMETIC (.....)

