

## TAYLOR AND FRANKS MODEL FOR KIN SELECTION

Let  $y$  be the phenotype of our focal (or target) individual

Let  $z$  be the mean phenotype in the population. Keep in mind that a change in  $y$  might also change  $z$ . Also keep in mind that individual fitness is affected by the mean phenotype in the population,  $z$ . Thus, individual fitness could be a function of both  $y$  and  $z$ .

$$W_i = f(y, z).$$

Now let  $x$  be the genic value or breeding value underlying the phenotype,  $y$ , of our focal individual.

We want to know how individual fitness ( $W_i$ ) is affected by changing  $x$ . In other words we want to know

$$\frac{dW_i}{dx},$$

which is the change in fitness with respect to the change in  $x$ . (Note we have the total derivative here.)

By the chain rule, we get

$$\frac{dW_i}{dx} = \frac{\partial W_i}{\partial y} \frac{dy}{dx} + \frac{\partial W_i}{\partial z} \frac{dz}{dx}$$

Have a close look at the right-hand side of the equation. The red part ( $dy/dx$ ) takes into account how the phenotype,  $y$ , changes with the genotype,  $x$ . Note that it is multiplied by how individual fitness changes with a change in  $y$ . So  $y$  affected by a change in  $x$ , and fitness is affected by a change in  $y$ . Now look at the blue part ( $dz/dx$ ). It gives the change in the mean phenotype with respect to a change in  $x$ . And it (the blue part) is multiplied by the change in fitness with respect to the change in population mean phenotype,  $z$ .

As we already know, the red and blue derivatives can be written as regression coefficients, giving.

$$\frac{dW_i}{dx} = \frac{\partial W_i}{\partial y} \beta_{y,x} + \frac{\partial W_i}{\partial z} \beta_{z,x}$$

By simple reorganization, we can write the equation as

$$\frac{dW_i}{dx} = \left[ \frac{\partial W_i}{\partial y} + \frac{\partial W_i}{\partial z} \frac{\beta_{z,x}}{\beta_{y,x}} \right] \beta_{y,x}$$

Finally, since the regressions coefficients are ratios of covariances to variances, the expression becomes

$$\frac{dW_i}{dx} = \left[ \frac{\partial W_i}{\partial y} + \frac{\partial W_i}{\partial z} \frac{\text{cov}(z,x) / \text{var}(x)}{\text{cov}(y,x) / \text{var}(x)} \right] \beta_{y,x},$$

which simplifies to

$$\frac{dW_i}{dx} = \left[ \frac{\partial W_i}{\partial y} + \frac{\partial W_i}{\partial z} \frac{\text{cov}(z,x)}{\text{cov}(y,x)} \right] \beta_{y,x}.$$

Queller (1992, available on course web site) has shown that this ratio of covariances is, in fact, relatedness, giving:

$$\frac{dW_i}{dx} = \left[ \frac{\partial W_i}{\partial y} + \frac{\partial W_i}{\partial z} R \right] \beta_{y,x}$$

Can you see how the ratio of covariances is relatedness?

Now let us ask: when will an increase in altruistic behavior in our focal individual spread in the population given that it decreases the fitness of the focal individual. In other words, when will the trait spread, given that

$$\frac{\partial W_i}{\partial y} < 0 ?$$

This will happen when the term in square brackets is positive (assuming  $\beta_{y,x} > 0$ ), which is when

$$\frac{\partial W_i}{\partial y} + \frac{\partial W_i}{\partial z} R > 0$$

$$R \frac{\partial W_i}{\partial z} > -\frac{\partial W_i}{\partial y}$$

Note the relatedness (no pun intended) to Hamilton's rule:  $Rb > c$ . But also note how the  $R$  "falls out" of the model by Taylor and Frank.

There is one other thing to see in the model. From above we have

$$\frac{dW_i}{dx} = \frac{\partial W_i}{\partial y} \frac{dy}{dx} + \frac{\partial W_i}{\partial z} \frac{dz}{dx}$$

If  $z$  does not change with  $x$ , or  $W_i$  does not change with  $z$ , we have

$$\frac{dW_i}{dx} = \frac{\partial W_i}{\partial y} \frac{dy}{dx}$$

Candidates for the ESS are found by setting

$$\frac{dW_i}{dx} = \frac{\partial W_i}{\partial y} \frac{dy}{dx} = 0$$

If  $y$  varies positively with  $x$ , in other words if there is a genetic basis for the phenotype,  $y$ , then

$$\frac{\partial W_i}{\partial y} = 0 \text{ at the ESS.}$$

As such, Taylor and Frank's model collapses on our old model for finding the ESS when the phenotype is continuously distributed, such as for sex ratio. See these steps, I think, makes clear some of the assumptions that went into the method.