Economic Concepts in Biology – Issues with Hamiltons rule

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Economic Concepts in Biology – Issues with Hamilton´s rule

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Hamilton´s rule is considered a cornerstone in evolutionary biology. It is used to understand why organisms help relatives and serves as starting point for the development of cooperation between strangers. The rule is based on a method from economics. It compares a benefit to cost ratio (k) to a genetic relation (r).

The first issue: This rule comes in two versions.

(Eq. 1) $-k>1/r^{\circ}$ ($|k|>1$); Hamilton 1964 I, page 15 and 16 (1)

(Eq. 2) $k>1/\bar{r}$; Hamilton 1964 II, page 20 (2)

The use of r° and $\bar{r}$ should not confuse as the meaning is (Eq. 1) "nearest (greatest) relative" and (Eq. 2) "average genetic relation". In case of offspring both values will be 0.5 (50% similarity of recipient to altruist). More confusing is the absence of the minus sign in the second equation. Equation 1 deals with the inclusive fitness of alarm calls and the negative (-k) benefit to cost ratio for the transmitter of the alarm call (the altruist). The central question to Hamilton is in this context: "*How large must Ikl be for the benefit to others to outweigh the risk to self in terms of inclusive fitness?"* In the second equation k (benefit to cost ratio for the altruist) has lost its minus sign. Hamilton writes: ….*the common detriment to the "altruist" must be high and the ratio of gain to loss (k) correspondingly low.* My interpretation is that the "detriment to the altruist" removes the minus and must always be memorized using this idea. This view is supported by the observation that the benefit to others (recipient) is said to be large (Ikl>1) and therefore b>c. The altruist with -k is -b<c. In Eq. 2 it has become necessary to require a high detriment (loss = cost) to obtain b<c for the altruist.

The second issue: A simple tool to check equations is to observe the use of units. Meaningful equations must have the same dimensions on the right and left sides. To check that is called a dimensional analysis (3, 4). The basic rule of dimensional analysis is dimensional homogeneity. Hamilton´s rule lacks units. His paper deals with fitness but this is a complex concept and not a known physical quality. Nevertheless, we could express fitness benefits and fitness costs in kilojoule (KJ). Then we would compare a dimensionless number based on KJ within one and the same party (benefit of altruist/cost of altruist) with a dimensionless number based on an inverse similarity between two parties (altruist and recipient). This equation has the typical structure of an alogism like the phrase *"At night it's colder than outside".* In case we dig deeper we find that even benefit (revenue) and cost (expenditure) will not stand on the same ground. In case a predator uses glucose in his muscles to catch a prey consisting besides water mainly of fat and proteins we are no longer allowed to only look at KJ consumed compared to the KJ gained. Protein is more than an energy source. Amino acids are in addition important building blocks. Benefits and costs must have different units!

From bad to worse: The now commonly used expression “r*b>c” is Hamilton´s idea resolved (minus sign omitted). This is the misuse of an incomplete equation. Originally Hamilton compared the benefit to cost ratio within one and the same party with an inverse genetic similarity of a second party to the first party. Now the benefit of one party is compared to the cost of a second party at some degree of similarity. This is neither a healthy biologic concept (5) nor a rational economic proceeding where usually profit (revenue minus cost) is compared to profit. No economist would judge the economic state of two companies comparing the benefit in one company to the cost of the other company – whether they hold shares of one another or not. This treatment by economists should guide biologists.

A suggestion: A complete benefit to cost analysis in two related parties must be symmetric with respect to benefit, cost and relatedness.

Party 1: b_1 = benefit of party 1; c_1 = cost of party 1; r_{11} = 1 (relation of party 1 with party 1, e.g. 1); r_{12} = (relation of party 1 with party 2, e.g.0.5)
Party 2: b_2 = benefit of party 2; c_2 = cost of party 2; r_{22} = 1 (relation of party 2 with party 2 e.g. 1); r_{21} = (relation of party 2 with party 1, e.g. 0.5)

$(b_1/c_1)*r_{11} + (b_2/c_2)*_{r12} \sim (b_2/c_2)*r_{22} + (b_1/c_1)*r_{21}$; This equation considers quantity and quality (as biological reciprocity, 5). The equation is symmetric with respect to units and parties and could also be used for a complete net-profit analysis exchanging b/c with b-c.

$(b_1-c_1)*r_{11} + (b_2-c_2)*_{r12} \sim (b_2-c_2)*r_{22} + (b_1-c_1)*r_{21}$; e.g. $r_{11}=r_{22}=r_{12}=r_{21}=0.5$. In this case 50% net profit is paid as dividend and full reciprocity is observed in a purely quantitative consideration.

Literature

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