

Opportunity Cost, Benefit and Degree of Relatedness

Hamilton's rule states that an animal (henceforth 'giver' for convenience) should perform an act towards another individual ('receiver') if the gain to the receiver ($= B$) devalued by the giver's degree of relatedness to it ($= r$) is greater than the cost to the giver ($= C$) of performing the act; that is, if $rB > C$ (W. D. Hamilton, *J. theor. Biol.*, 7, 1-16, 1964). This rule has been widely cited and applied in explanations of behaviour towards relatives. The purpose of the present note is to caution against too simple an understanding of the word 'cost'.

The cost of performing an act must include a term for each of its consequences. Sometimes one consequence will be the missing of an opportunity to perform some other act. This may be because acts require time and energy, or because it is in the nature of the act that it can be performed only once (e.g. sacrificing one's life) and so to perform the act today in one set of circumstances is to miss the opportunity to perform it ever again under any circumstances. This forgoing of opportunities has a cost known as the opportunity cost of an act, and it is equal to the highest net benefit ($rB - C$) which can be attained by any alternative act. It is clear that with cost interpreted in this way, when choosing one act from several, only the one with the highest net benefit will be chosen by Hamilton's rule.

But surely this is all very obvious, and no one would be misled for long by neglecting opportunity costs? Consider the following argument about paternal care compared across species with varying degrees of certainty of paternity: males in species with lower certainty of paternity should show less paternal care because their lower expected relatedness to their mates' offspring means that fewer acts qualify as evolutionarily advantageous, by Hamilton's rule (i.e. lower r makes $rB > C$ less likely to be satisfied). This argument is at best incomplete: if the only alternative use for the time and energy the males save by denying help to present offspring is to help later offspring of equally doubtful paternity, then the optimal allocation of their resources will not depend on how certain they are of their paternity.

We can consider the effects of different sets of options on the male's optimal allocation of resources. If a male cannot mate with other females while caring for the young of his present mate but can desert his mate and her offspring at any time to search for another mate, then certainty of paternity will not affect the male's optimal degree of paternal care. (Uncertainty of paternity in this case could arise through sperm storage by females.) To see why this is so in terms of a model by Grafen & Sibly (*Anim. Behav.*, 26, 645-652, 1978), consider Fig. 1. The graphs show expected benefit (ordinate) to a male who deserts his mate and her offspring, as a function of the time at which he deserts (abscissa) during the rearing of the offspring. Under the assumptions of the model, males act to maximize the rate of accrual of expected benefit. The upper graph shows the case with perfect certainty of paternity, and the lower graph the case with 50% certainty of paternity. The expected benefit is exactly halved in the latter case, but the figure demonstrates that the optimal staying time for the male is completely unaffected by this halving. For decreased certainty of paternity to generate decreased paternal care in this model, the time between broods would have to decrease as certainty of paternity decreases. There seems to be no general reason to expect this. If, on the other hand, a male can spend part of each day feeding his mate's offspring and part trying to copulate with other females whose offspring he will never care for, then lower certainty of paternity will bring

about less paternal care. Thus we see that the effect of certainty of paternity on paternal care cannot be evaluated without knowing what opportunities males give up when they spend time and energy caring for their mates' offspring.

It is also inadequate to argue that simply because females are surer of their maternity than males are of their paternity, female care should evolve. It is inadequate to argue that of two individuals the more altruistic towards a third should be the more closely related to it. It is inadequate to argue that across species, increased relatedness between classes of individuals should mean increased altruism between them. In all these cases the argument is inadequate because it is incomplete: the opportunity cost has been neglected. To find out what the opportunity cost is, we must find out about the alternatives which face

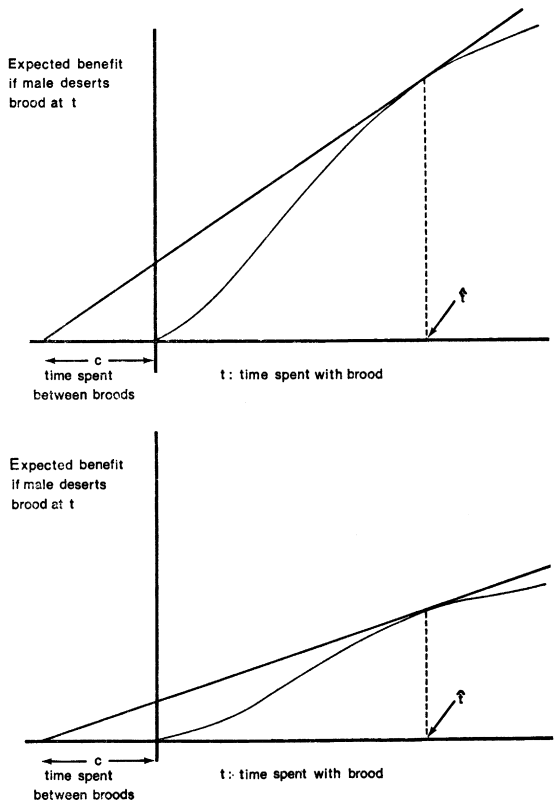


Fig. 1. After Grafen & Sibly (1978, op. cit.). The upper graph shows the case with full certainty of paternity, the lower the case with 50% certainty. In both cases, the optimal staying time is found by taking a tangent to the curve from a point c to the left of the origin. The point of tangency gives the optimum because that value of t maximizes the rate of accrual of expected benefit. It is a simple matter of geometry that when the whole benefit curve is halved the point of tangency corresponds to the same value of t , t_1 , as before. There is nothing special about halving; the same result holds whenever the whole benefit curve is multiplied by any positive constant.

each individual concerned. The alternatives may be affected just as much by lack of certainty of paternity, or other variable of interest, as is the altruistic act itself.

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