COMMENTARY

The economics of altruism and cooperation in class-structured populations: what's in a cost? What's in a benefit?

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Lehmann & Keller (2006, and hereafter referred to as either 'the authors' or L&K) have identified the cost-to-benefit ratio, C/B as being a principal factor in the evolution of altruism and cooperation. The authors argue that this ratio (or some equivalent version) cannot exceed a given threshold if a selective advantage of altruism or cooperation is to exist. Of course, many biologists will readily recognize Hamilton's (1964) rule as a special case of this result. An actor is willing to pay a cost, C, to give a benefit, B, to a recipient whenever

$$C/B < R, \tag{1}$$

where R is a measure of the relatedness between the social partners. Essentially, inequality (1) tells us that, for altruism to be advantageous, the normalized cost of altruism itself cannot be too large.

The simplicity of Hamilton's rule, as it is stated in line (1), certainly understates the tremendous scope of Hamilton's idea. It turns out that Hamilton's rule (1) can be modified so that it applies to the evolution of altruism in a wide variety of situations (Taylor, 1988, 1990). In fact, some important aspects of this variety may have been neglected by the direct fitness model presented by L&K. As we argue below, understanding the costs-to-benefit ratio in general terms can show us that the scope for the promotion of altruism (especially when altruism is mediated by coercion, punishment, or policing) might be different than that suggested by the authors.

Kin selection in a class-structured population

Many interesting examples of kin selection come from class-structured populations. Class structure can occur whenever it is possible to group individuals according to some shared quality. Familiar examples of class structure include sex structure (e.g. class 1 = female, class 2 = male) and age structure (e.g. class 1 = juvenile, class 2 = adult). Class structure can also arise when populations experience inbreeding depression (Denver & Taylor,

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1995), or when populations occur in spatially heterogeneous environments (Leturque & Rousset, 2002). While the authors have presented some examples of class structure in their supplementary material, their work does not address class-structured models in general. Our aim was to do so in a relatively straightforward fashion.

The main challenge in constructing a class-structured kin-selection model comes from the fact that individuals have different components of fitness (e.g. fitness through sons, fitness through daughters; survival, fecundity). In general, a class-structured model requires knowledge of w_{ij}, the expected number of class-i offspring produced by an individual belonging to class j (weighted by genetic contribution).

We can think of w_{ij} as a function of the behaviour exhibited by one or more individuals. A deviant level of behaviour, x will change a number of different w_{ij} expressions. To determine whether a particular (positive) behavioural deviation is favoured in some population we can use either a direct fitness argument (Taylor & Frank, 1996) or an inclusive fitness argument (Taylor, 1988, 1990). In either case, recent work suggests that we should get the same mathematical expression (Taylor & Frank, 1996, P.D. Taylor, G. Wild & A. Gardner unpublished; cf. Frank, 1997).

Consider a relatively simple situation in which all actors belong to the same class (e.g. adult females). In a direct fitness model, we fix attention on a particular recipient (the focal individual, FI to use the terminology of L&K), and consider how each of several actors influences the fitness of that recipient. We express the fitness of a focal recipient chosen from class j as the sum, $\sum_i v_i w_{ij}$, where the coefficients v_i denote the reproductive value of class-i components of recipient fitness, thought of as the asymptotic genetic contribution of class-i individuals to a population in the distant future. Such a notion requires, of course, some assumption about the future trajectory of the population; and for this purpose we suppose that we have a pure monomorphic ecologically stable resident population. Thus reproductive value depends only on the resident behaviour, call it x^*. Of course, if a mutant behaviour, x, is introduced, this assumption will no longer be valid, but for behavioural deviations of small effect (weak selection) the approximation will be reasonable (more precisely it will hold to first-order in mutant deviation $x - x^*$). Reproductive value acts as an 'exchange rate' that allows us to add the w_{ij}'s and express recipient fitness as a scalar quantity.

Even though all actors belong to the same class, we usually have to account for different categories of actor–recipient interactions (e.g. mother interacting with daughter, aunt interacting with niece, etc.). We index actors using integers k, and let x_k denote the behaviour expressed by the kth actor. When the genotype of the recipient is changed, we expect to observe correlated changes in x_k – where the extent of the change is

determined by the degree of relatedness between actor k and recipient j, $R_{k \rightarrow j}$. These behavioural changes result in changes to recipient fitness. In fact, we can express the change in recipient fitness, mathematically, as

$$\sum_{\text{actors } k} \frac{d}{dx_k} \left[\sum_i v_i w_{ij} \right]_{x_k = x*} R_{k \rightarrow j} = \sum_{ik} v_i \frac{dw_{ij}}{dx_k} \bigg|_{x_k = x*} R_{k \rightarrow j}. \quad (2)$$

where the relatednesses are also calculated in the resident population. If the frequency of class-j recipients is u_j we express the expected change in recipient fitness as

$$\Delta W(x*) = \sum_j \left(\sum_{ik} v_i \frac{dw_{ij}}{dx_k} \bigg|_{x_k = x*} R_{k \rightarrow j} \right) u_j$$

$$= \sum_{ijk} v_i \frac{dw_{ij}}{dx_k} \bigg|_{x_k = x*} u_j R_{k \rightarrow j}. \quad (3)$$

The function $\Delta W(x*)$ is often called the 'inclusive fitness effect', and can be derived either using a direct fitness approach (as we have done above), or using a classical inclusive fitness approach (e.g. Taylor, 1988, 1990). As long as selection is weak, the sign of $\Delta W(x*)$ tells us whether selection favours an increase or decrease in the level of behaviour. If $\Delta W(x*) > 0$, then $x*$ is selected to increase over time, if $\Delta W(x*) < 0$, then $x*$ is selected to decrease over time. When $\Delta W(x*) = 0$ the population is said to be at 'evolutionary equilibrium'.

To establish a connection between eqns (1) and (3) we will change our notation slightly. If the derivative $dw_{ij}/dx_k|_{x_k} = x* > 0$, we will place the triple (i, j, k) into a set called **B**, and we will refer to the derivative itself as a 'benefit' of deviant behaviour, B_{ijk}. If the same derivative is negative we label it a 'cost', $-C_{ijk}$ and place (i, j, k) into a set called **C**. The quantities B_{ijk} and C_{ijk} might represent fecundity benefits and fecundity costs, respectively. That is to say, B_{ijk} and C_{ijk} could be the same 'benefits' and 'costs' described by the parameters B and C used by L&K (in fact, fecundity costs and benefits are the only kind considered by the class-structured examples presented in the supplementary material). However, B_{ijk} and C_{ijk} might also be used to represent other kinds of benefits or costs paid through other components of fitness (e.g. survival). It is also useful to point out that B_{ijk} and C_{ijk} can also describe the fitness consequences of some of the other factors considered by L&K, like repeated interactions (e.g. Irwin & Taylor, 2001).

We see now that

$$\Delta W(x*) = \sum_{(i,j,k) \in \mathbf{B}} v_i B_{ijk} u_j R_{j \rightarrow k} - \sum_{(i,j,k) \in \mathbf{C}} v_i C_{ijk} u_j R_{j \rightarrow k} \quad (4)$$

or simply $\Delta W(x*) = b - c$, where b and c correspond to the first and second terms on the right hand side of eqn (4), respectively. Note that, in general, we expect that each term of the summand in b and c will depend on $x*$. Note also that our choice of notation b and c is motivated by the notation introduced by L & K (e.g. their eqn 4), but

our usage differs in that our benefits and costs incorporate relatedness. Our expression (4) may well serve as a more general, and (conceptually) more straightforward framework in which to discuss the evolution of altruism.

If we think of $x*$ as a probability of behaving altruistically, inequality (4) tells that altruism is increasing when

$$\frac{c}{b} < 1 \quad (5)$$

where b and c are overall benefit and cost terms, with components weighted by reproductive value, frequency and relatedness. Certainly, at any particular $x*$, an increase in altruism will not be favoured if the inequality in (5) is reversed. The review by L&K details some of the ways in which a reversal of (5) might be prevented.

L&K concentrate their analysis on ways in which altruism between relatives can be promoted by direct manipulation of benefits B_{ijk} and costs C_{ijk} (e.g. via punishment, coercion). Inequality (5) provides an analogue to the ratio C/B, highlighted by L&K, but the mathematical form of eqn (4) suggests a number of alternative pathways through which the evolution of altruism might be promoted. The economics of the decision to 'help' or 'not help' a relative might also be influenced by a change in reproductive values, v_i, a change in class frequencies u_j, and even through a change in relatedness coefficients $R_{k \rightarrow j}$.

Discussion

The authors have established a set of biological conditions necessary for the evolution of altruism, in particular, if altruism or cooperation has been observed then one of their four conditions must have been met. The factors they identify would presumably appear as terms in our eqn (4) and their conditions for the increase of altruistic behaviour would correspond to our condition (5). The strength of our formulation is that it points to pathways other than through direct manipulation of costs and benefits. This observation might be especially important for examples of punishment, coercion and policing among relatives. Class structure seems to be a key feature of model systems where punishment occurs (Clutton-Brock & Parker, 1995). First, it is possible that 'punishers' (e.g. dominant individuals) are less common than 'punishees' (e.g. subordinates). Secondly, being a 'punisher' rather than a 'punishee' may necessarily influence your genetic contribution to future generations (i.e. your reproductive value). Lastly, it is also possible that punishment/coercion has complicated consequences for the fitness of individuals other than those directly involved in the interaction (e.g. through reduced or increased local competition). These concerns would be naturally addressed by our general class-structured approach (4). As models of punishment, coercion and policing are still in their infancy (L&K), it seems doubly important to point out that other factors, like reproduc-

tive value and class frequency, deserve consideration alongside C and B.

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