

Research Centre, King's College, Cambridge

Why is Altruism towards Kin so Rare?

By DANIEL I. RUBENSTEIN and RICHARD W. WRANGHAM

With one figure

Received: August 7, 1980

Accepted: September 8, 1980

Abstract

When individuals have the opportunity to invest in offspring or siblings who are equally closely related and helpless, they should invest in offspring. Two reasons are proposed. Both depend ultimately on the fact that if Ego invests in kin other individuals may not behave in Ego's best interest.

I. Introduction

During their lives individuals may value each other for many reasons, but there is ultimately only one important measure of worth: the contribution by another individual to Ego's inclusive fitness (HAMILTON 1964). The magnitude of this contribution is influenced by two variables, the coefficient of relationship (r), and reproductive potential (expected number of future offspring). It follows that in an ultimate sense Ego should value equally an offspring and a full sibling of the same age. Why, then, is parental care so much more common than sibling care? Or in other words, why is altruism towards kin so rare?

There are two principal classes of explanation. First, the parent-offspring relationship is invariably asymmetrical, whereas sibling relationships are often not (ALEXANDER 1974; ESHEL and COHEN 1976; DAWKINS 1979). Parents are significantly older than their offspring and are therefore often able to care for them. Differences between sibling ages, on the other hand, can be small. The implication is that the reason why parents invest more often in offspring is that siblings are only rarely in a good position to help.

Second, there are often differences between Ego's genetic relationship to offspring and siblings. Paternity uncertainty reduces the relatedness of sup-

posed full siblings to between $1/4$ and $1/2$, but mothers and offspring are invariably related by $1/2$. Hence, a mother should prefer to invest in an offspring than in an equally helpless sibling (DAWKINS 1976). It has also been argued that even if the average relatedness of parent to offspring is the same as to full siblings differences in variance in the degree of relatedness should predispose parents to preferentially invest in offspring (BARASH et al. 1978). However DAWKINS (1979) has noted that the difference in variance only exists if r is thought to represent the proportion of shared genes. When r is thought of as the probability of sharing a common gene (HAMILTON 1964) the variance vanishes. Ego should therefore invest indifferently in offspring and siblings in this respect.

In this paper we propose two additional reasons why parental care is common and altruism towards kin is rare. The first is related to the previous argument about asymmetries in investment, whereas the second is concerned with the reliabilities of return on personal investment in offspring versus altruistic investment in siblings. As such the latter argument is concerned with variance, but not with genetic variance.

II. Ensuring Appropriate Investment

Consider the simple case in which Ego has the option of investing its resources in the production of an offspring (O) or an equal-aged full sibling (S) (see Fig. 1). This means that both O and S are related to Ego by 0.5, and have equal reproductive potential. Consequently, we assume that for any given level of investment the change in reproductive potential experienced by O and S will be the same. If so, it appears from previous arguments that Ego should be indifferent as to how it invests its resources (HAMILTON 1964). However this is not so if we assume that selection acts so as to take account of the effects of each strategy on the investment strategies of others.

Suppose that Ego invests in its offspring (O) at a net cost C_E to its own reproductive potential. By doing so it increases O's reproductive potential

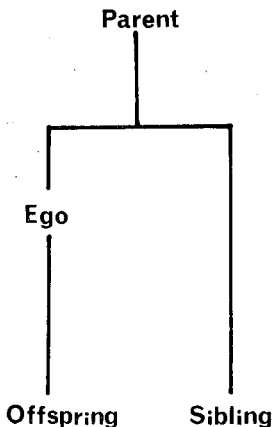


Fig. 1: The pedigree is from Ego's perspective. Offspring and sibling are the same age, and both are related by 0.5 to Ego

by B_O . Ego's inclusive fitness therefore rises by $(B_{Or_{EO}} - C_E)$, where r_{EO} is the coefficient of relationship between Ego (E) and O. Alternatively, by investing equally in S Ego gains $(B_{Sr_{ES}} - C_E)$. Considering only Ego's investment patterns, therefore, Ego's preferred strategy should depend on the sign of $(B_{Or_{EO}} - B_{Sr_{ES}})$. Factors affecting this have been discussed by previous authors (ALEXANDER 1974; DAWKINS 1976, 1979). If the Parent's investment strategy does not affect Ego's strategy and $B_{Or_{EO}} = B_{Sr_{ES}}$, parental and sibling care are equally favoured.

The Parent's investment strategy matters also, however. The Parent (P) can be assumed to be an investor since otherwise S would not exist. Like Ego, therefore, P must decide how to invest. But unlike Ego, P's relatedness to O and S is not symmetrical: r_{PO} is less than r_{PS} (Fig. 1).

This means that although P should invest readily in S, it should not do so as readily in O. For instance, consider what happens if Ego invests in S rather than O. Further investment in S may well lead to diminishing returns, as happens with many forms of investment (e.g. TRIVERS 1974). Although this means that P's optimal strategy may shift from investment in S, the shift is not necessarily towards O. Instead, it may be towards some other individual, X.

The effect of this is seen by calculating the gains to Ego's inclusive fitness through O, S and X simultaneously. First, if Ego invests in O the gain is $(B_{Or_{EO}} + B_{Sr_{ES}})$, where P, being an investor, is assumed to invest B_S in S, at a cost C_P to itself.

If Ego invests in S, on the other hand, there is a probability q that P will invest in X instead of O. Ego's inclusive fitness accordingly rises by $(B_{Or_{EO}}(1-q) + qB_{Xr_{EX}} + B_{Sr_{ES}})$. The difference in gain to Ego between investing in O and investing in S is therefore $q(B_{Or_{EO}} - B_{Xr_{EX}})$. But since neither Ego nor P preferred to invest in X initially, this is greater than zero. Consequently Ego should invest in its offspring, O, rather than in its sibling, S, in other words, parental care is favoured.

III. Minimising Risk

The second explanation for the propensity of individuals to invest in offspring rather than siblings is based on the fact that investments tend to produce uncertain returns. We assume that an animal has a limited amount of resources to invest, and that the return on the investment increases with higher levels of investment, but at an ever declining rate. If so, of two investment strategies yielding the same average return the one with the lower variance in pay-off results in the higher fitness (RUBENSTEIN, in press).

This can be seen by examining the function that describes the fitness (W) of any strategy involving uncertain returns on investment. Fitness is given by

$$W = \varphi(\mu) + \frac{1}{2}\sigma^2\varphi''(\mu) \quad (\text{RUBENSTEIN, in press})$$

where μ and σ^2 are the mean and variance of the return on investment and φ is the function that converts returns on investment into units of fitness. Because

of the assumption of diminishing returns, $\delta'' < 0$. Hence, increases in variance lower a strategy's fitness contribution.

If we assume that given the same resources Ego and her mother have the same expectations of reproduction, the mean benefit to Ego of investing in her own offspring is the same as investing in her sibling (Fig. 1). Ego should therefore invest by the strategy with the smaller variance in reproductive success. The variance associated with investing in her own offspring is likely to be lower than with investing in her mother's offspring because Ego cannot control her mother's behaviour.

Thus, on the one hand the mother may be a poor investor. For example, conflicts of interest could arise, causing the mother to manipulate the use of Ego's investment in ways which decrease its effectiveness from Ego's point of view. On the other hand the mother may be a particularly good investor, perhaps by virtue of her age or experience. Unless Ego can ascertain the outcome of her investment in kin before parting with it, the variance associated with caring for offspring will usually be less than that associated with assisting kin, and parental care should therefore be favoured.

IV. Investment in Kin other than Offspring

These two arguments support the previous conclusions, based on the asymmetry of the parent-offspring relationship and the uncertainty associated with siblings, that personal reproduction is a superior strategy to investing in kin. Furthermore they suggest that even when offspring and siblings are equally related to Ego, and equally helpless, Ego should prefer to invest in its offspring. When, therefore, should individuals invest in their kin?

One class of cases is where siblings or other kin have no alternative investors. This happens when individuals are orphaned. Ego should regard investment in orphans according to a simple cost-benefit analysis unencumbered by the problems considered above. There is evidence from higher animals that individuals do invest in their orphaned siblings (e.g. GOODALL 1968).

Second, if additional investment yields increasing rather than diminishing returns ($\delta'' > 0$), higher fitness will be achieved by investing in the strategy with the higher variance. Increasing returns might obtain when animals are in poor condition and their meagre investment levels yield few returns (RUBENSTEIN in press). When this is so, investing in kin will be superior to reproducing. However, given the paucity of evidence that investment ever leads to increasing returns (SMITH and FRETWELL 1974; WILBUR 1977) this condition seems unlikely to apply.

Third, even if the law of diminishing returns applies, investment in kin might be favoured. This should occur when there is no conflict of interest and when Ego can perceive that its mother will be a more effective investor than itself. Variance about the mother's expected success is then reduced and the expectation is increased. If such perceptions are possible and reliable, Ego should sacrifice its own reproduction and invest in its sibling. However it

seems unlikely that the variance is ever significantly reduced, since parent-offspring conflict can be expected in most circumstances (TRIVERS 1974).

In general, therefore, investment in siblings is not expected. Yet even where kin still have parents individuals may invest in them either as temporary or life-long helpers. Temporary helpers occur in a variety of birds and mammals, and are normally young animals who have not yet bred or attempted to breed (BROWN 1978; MOEHLMAN 1979; REYER 1980). When they do start to breed they stop helping. The problem is to understand why the helpers should prefer investing in offspring which already have investors, rather than producing their own offspring. It seems likely that the solution will often involve a high cost to personal breeding. As long as there is an investment threshold below which attempts to breed result in an expected net loss to Ego's inclusive fitness, Ego should postpone breeding. Such a threshold could occur either because the probability of the offspring surviving is small, or because the costs in terms of diminished reproductive potential are large. In the interim, before gaining adequate resources or opportunities to justify a breeding attempt, young animals may be able to invest a proportion of their resources in the offspring of close kin without incurring prohibitive costs (BROWN 1978).

Life-long helpers represent a less tractable problem. They are known only in the Hymenoptera and termites, and have been explained in three principal ways. First, early workers suggested that altruism was favoured because groups (families) with altruistic offspring would have higher rates of reproduction than those without (DARWIN 1859; WHEELER 1923). This idea relies on evolution by group selection, and hence on the occurrence of rather stringent conditions. In particular, a high proportion of established groups must fail to produce reproductive offspring, and offspring from one group must rarely mate with offspring from another (MAYNARD SMITH 1976). Field data show that the opposite normally occurs (WILSON 1971), indicating that the conditions under which group selection might have effects are not found.

Second is the suggestion that parents manipulate their offspring in such a way that they abandon their own reproductive efforts to assist those of their parents (ALEXANDER 1974). A problem with this explanation when applied to many social insects is that the foundation of the colony by a group of sisters occurs after the death of the mother (CROZIER 1977), and it is difficult to see how the mother can continue to manipulate them. But even if we allow that behavioural suppression of daughters occurs in presocial communities, CRAIG (1979) has shown that unless the cost-benefit ratio is low enough for altruism to arise by kin selection, selection will favour daughters capable of resisting maternal manipulation. Hence, the conditions required for the evolution of parental manipulation are equivalent to those for the evolution of altruism by kin selection.

Third, HAMILTON (1964, 1972) showed that unusually high coefficients of relatedness occurring among Hymenoptera could favour kin-directed altruism by kin selection. An important component of this argument is that females who invest in kin should have lower chances of successfully breeding

on their own than their mothers or sisters do (WEST-EBERHARD 1975). When this is true, the fact that it pays a female to invest in her mother's (or sister's) offspring can be exploited by the mother (or sister). Specifically, she can produce further offspring, which are themselves the objects of further investment by the non-breeding female. Thus an asymmetry in reproductive potential, imposed either ecologically or socially, can induce positive feedback for investment in kin. We know of no evidence yet that investment in kin is favoured unless the costs of personal reproduction are too high for a viable breeding attempt. It would be valuable to know if the high coefficients of relatedness found between hymenopteran sisters can favour investment in kin even where personal reproduction would lead by itself to a probable rise in inclusive fitness. This is an especially pertinent question given evidence that relatedness within Hymenopteran colonies is not as high as expected a priori (WICKLER 1978).

Summary

The problem of how resources are invested so as to maximise probable fitness is sometimes considered without reference to the effect of Ego's strategy on the investment strategies of others. Where such effects are predictable, however, it seems necessary to assume that they influence the evolution of Ego's investment patterns. If so, the conclusion that individuals who invest in their kin at the expense of their own reproductive success suffer a net loss to their inclusive fitness applies even when offspring and other kin are equally related and equally helpless. Hence, the conditions favouring investment in kin are more stringent than previously considered. Our analysis therefore suggests that when individuals make no attempt to breed, environmental constraints on personal breeding will generally be more important than unusually good opportunities for investment in kin. An important problem is to evaluate the conditions favouring investment in kin when kin are more highly related than offspring to Ego.

Zusammenfassung

Bei Überlegungen, wie Individuen investieren sollten, wenn es darum geht, ihre wahrscheinliche Fitneß zu maximieren, bleibt oft unberücksichtigt, welche Auswirkung die vom Individuum verfolgte Strategie auf die Investitions-Strategie anderer hat. Wo dieser Einfluß voraussagbar ist, wird man annehmen müssen, daß er auch die Evolution der Investitionsmuster des Individuums beeinflusst. Wenn das stimmt, dann gilt auch, daß Individuen an Gesamtfitneß einbüßen, wenn sie in Verwandte statt in eigene Nachkommen investieren, selbst wenn sie mit beiden gleich verwandt und beide gleich hilfsbedürftig sind. Die Bedingungen, unter denen sich Hilfe an Verwandte lohnt, sind deshalb enger als bisher angenommen. Wenn demnach — so wird gefolgert — Individuen keine Anstalten machen, sich selbst fortzupflanzen, sind unmittelbare Hinderungsgründe dafür entscheidender als noch so günstige

Gelegenheiten, in Verwandte zu investieren. Wichtig ist, die Bedingungen zu ermitteln, die für das Investieren in Verwandte sprechen, falls der Investierende mit ihnen näher verwandt ist als mit eigenen Nachkommen.

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Authors' addresses: D. I. RUBENSTEIN, Biology Department, Princeton University, Princeton, New Jersey 08544, U.S.A.; R. W. WRANGHAM, Research Centre, King's College, Cambridge CB2 1ST, England.