

Fig. 1 a, Isotopic ratio distribution for geological lead samples from Africa and Europe from the Tables of refs 13-15 (small box corresponds to range shown in b); b, lead isotope ratios for Nigerian 'bronze' objects listed in Table 1 (probable errors for all measurements are as shown for object Q). A-Q, Objects listed in Table 1.

• Could the Ife piece be a mixture of the sources used by the Igbo-Ukwu culture which may have preceded it, and the Benin culture which may have followed it?

• What were the actual sources of the lead and the patterns of its trade? Were the sources local (Nigerian) or were the raw materials brought from elsewhere in Africa (perhaps on trans-Saharan trade routes) or did they arrive from Europe?

Work is continuing to attempt to answer some of these questions.

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## Parental investment, mate desertion and a fallacy

TRIVERS<sup>1</sup> defines parental investment as "any investment by the parent in an individual offspring that increases the offspring's chance of surviving . . . at the cost of the parent's ability to invest in other offspring". He has cleverly used this definition to elucidate many outstanding problems in social ethology<sup>1-3</sup>. But one of his most appealing usages of it is fallacious.

He states<sup>1</sup>: "At any point in time the individual whose cumulative investment is exceeded by his partner's is theoretically tempted to desert". The context is that of a mated pair of birds, cooperating in the rearing of young. At various times during incubation the female has invested more in the offspring than the male, and the male is said to be tempted to desert. At other times the male's cumulative investment is higher, and the female is then said to be tempted to desert.

If true, this idea would have interesting consequences. A female, in danger of being deserted after copulation, might force a male to invest heavily in her offspring before they are conceived. The price of copulation might be a well built nest and plenty of courtship feeding. Even useless 'labours of love' might be imposed as a means of increasing the male's investment before copulation, and therefore of reducing his temptation to desert afterwards. The theory also neatly uses the difference in gamete size to explain why females make better parents than males. As Trivers says<sup>1</sup>: ". . . her initial very great investment commits her to additional investment more than the male's initial slight investment commits him".

The idea has been influential<sup>4</sup>, and it appeals to economic intuition. A government which has invested heavily in, for example, a supersonic airliner, is understandably reluctant to abandon it, even when sober judgment of future prospects suggests that it should do so. Similarly, a popular argument against American withdrawal from the Vietnam war was a retrospective one: "We cannot allow those boys to have died in vain". Intuition says that previous investment commits one to future investment.

The fallacy can be demonstrated by analogy. Suppose a female has an orphaned baby brother, the same age as her own son. She has only enough food to keep one of the two infants alive. Which should she prefer? Intuition points to the son, but this is not necessarily correct. There are no genetic grounds for preferring either infant: the mother's relatedness<sup>5</sup> to both is the same, 0.5. A naive application of parental investment theory predicts that the female should prefer the son on the grounds that she has already invested heavily in him: she should not

let all her earlier investment go to waste by preferring the brother, in whom she has invested nothing.

This argument is wrong for it misunderstands why quantity of previous investment is important. A child in whom more has already been invested should be preferred only because he is going to need less investment in the future. This means he can be fledged (or weaned) sooner, and the parent will therefore be free to invest in new children sooner. Our hypothetical female should prefer whichever of the two children has already had most invested in him, regardless of who did the investing, because his future life can be bought more cheaply.

We now return to the original quotation from Trivers. The father and mother have an equal genetic stake in each offspring. Either parent's reluctance to desert at any moment should be related to the quantity of investment still needed to bring the offspring to maturity. This quantity will be negatively related to the amount that has already been invested: it does not matter who did that investing. Trivers almost acknowledges this in another part of the same paper<sup>1</sup>, when he suggests that it may pay either partner, even the one who has so far invested most, to desert. This forcible closure of options puts the deserted partner in "a cruel bind". But Trivers's characterisation of the cruel bind is misleading: "... the deserted partner ... has invested so much that he loses considerably if he also deserts the young, even though, which should make no difference to him, the partner would lose even more". The true nature of the cruel bind is this. Regardless of who did the previous investing, the young have had so much poured into them that either partner alone has a good chance of rearing them. To desert after one's partner has deserted is to condemn the young to death; to desert first merely condemns one's partner to make the difficult decision. Genes for deserting first are favoured by natural selection, precisely because genes for deserting second are not. But in either case, the important quantity influencing the decision is quantity of future investment which will be required.

It is of course true that previous investment by a particular parent is relevant to how much he or she can invest in the future: this is the basis of Trivers's definition. But for each particular parent this is a lifetime's calculation: the amount invested in the current offspring is only a small part. There is thus no justification, other than sheer coincidence, for Trivers<sup>1</sup> to draw the cumulative investment curves of his male and female with the same starting baseline. A parent should value the life of a particular child as a function of the proportion that this child represents of his total future reproductive prospects. These future prospects will be negatively correlated with the total amount he has invested in his lifetime, but only negligibly with the amount he has invested in the current particular child.

Does the theory that female coyness might evolve as a means of forcing males to invest early, thereby reducing their temptation to desert later, survive our objection to its parent assumption? This depends on how the majority of females in the population behave. If the majority play the same coy game, desertion tactics will not pay a male: he commits himself to a period of prolonged and costly courtship with a new female before she will let him copulate. If conditions are such that it would pay females to renounce coy tactics, however, the optimal strategy for a male could well be different. This is one of those cases of conflict of interest where the best strategy depends on what others are doing. We therefore suggest that the appropriate conceptual tool is Maynard Smith's<sup>6-8</sup> "evolutionarily stable strategy" (ESS). The contest is "asymmetric"<sup>8</sup>, the basis of the asymmetry being sex. We seek a stable combination of male and female strategies, for example, a ratio of 'coy' to 'fast' females which is stable against an equally stable ratio of 'faithful' to 'philanderer' males. Preliminary analysis<sup>9</sup> suggests that there are conditions in which a stable equilibrium, consisting largely of coy females and faithful males, could evolve. More work is required (J. Maynard Smith, unpublished), but the point we make is that these are the lines along which the thinking must be. We must not simply assume that the partner who has in-

vested least in the current offspring is the one most tempted to desert.

The other suggested consequence of Trivers's theory which we have already mentioned was that the female's high initial investment commits her to continued high investment: thus viviparity, milk-secretion, highly developed maternal care, and so on. Once again, the idea is wrongly expressed. A female is 'committed' to future investment in a child, not because of how much she has already invested in that child, but because of the cost of finishing the task, in relation to how much she would have to invest in order to bring a new child up to the same age.

In any case, the idea of past commitments leading to future commitments had difficulties in explaining the high incidence of paternal care among teleost fish<sup>10</sup>. Instances among birds and mammals where the father plays the main parental role are extremely rare; in the teleosts they are commonplace. Why the difference? The following theory makes use of Trivers's "cruel bind" idea, referred to earlier.

Gametes dry up in air, so this has forced terrestrial animals to copulate rather than practise external fertilisation as many fish do. After copulation, the female is left physically in possession of the zygote and while it is still in her body she cannot desert it, but the male can. However fast she lays it, the male is still offered the first opportunity to desert, thereby closing the female's options and forcing her into Trivers's cruel bind. For the reasons already discussed, this tends to lead to the evolution of maternal care.

Fish are not similarly obliged to copulate since there is no danger of their gametes drying up. In such externally fertilising species there is no automatic sense in which the female is left in possession, allowing the male to make his escape. Either sex might thus use the quick-desertion strategy. But there is a possible reason why the male might be more vulnerable to being left 'holding the baby'. Whichever partner spawns first is likely to be one jump ahead, but there is danger in spawning too early; the partner may not be ready. Sperm being lighter than eggs, tend to diffuse faster and so males have more to lose from premature spawning than females. Females can therefore afford to spawn earlier than males, putting them in a strong position to leave the male in possession of the newly conceived zygotes, forcing him into Trivers's cruel bind. This explains the widespread evolution of paternal care in fish. A comparative analysis of the incidence among teleosts<sup>10</sup> of external fertilisation against intromission, in relation to paternal against maternal care, might be rewarding.

In conclusion, a parent 'deciding' whether to desert a child should ask the following questions. How closely related<sup>9</sup> is this child to me? How likely is it to survive if I do, and if I do not, desert it? What proportion of my total future reproductive potential does this child represent? How much would it cost me to make a new child equivalent to this one? The parent should ignore its own previous investment in the particular child, except in so far as it affects the answers to these questions. Trivers is largely right, but partly for the wrong reasons.

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## Nitrate reductase as a possible predictive test of crop yield

NITROGEN supply is one of the key factors affecting the quality and quantity of crops. The amount of nitrogen fertiliser used is increasing year by year; on a worldwide basis we now use seven times the total fertiliser used in 1939 (ref. 1). In many developed countries the use of excess nitrogenous fertiliser is already causing environmental disturbance, especially in inland rivers and lakes, and represents a potential danger to drinking water supplies. By contrast, in much of the world crops are grown in conditions of nitrogen deficiency. Lacking in each situation is the availability of a reliable method for determining the amount of nitrogenous fertiliser, if any, which should be applied for optimal yield with minimum cost and environmental side effect, or for maximum use of limited resources. We have found that early season assays of nitrate reductase provide such a method.

Usually, whatever the source of nitrogen fertiliser, soil conditions ensure that nitrogen enters the plant predominantly as nitrate. The first and rate limiting step in nitrate utilisation is catalysed by the inducible enzyme, nitrate reductase<sup>2</sup> and Hageman's group in Illinois have demonstrated a correlation between nitrogen supply, nitrate reductase activity integrated throughout the year and grain yield in wheat<sup>3</sup> and maize<sup>4</sup>. In these experiments, which were conducted in suboptimal nitrogen conditions, addition of further nitrogen, especially during the early part of the growing season, led to increases in nitrate reductase activity and in final grain yield.

We have examined the possibility of using nitrate reductase assays, early in the development of the crop, as a predictor of ultimate grain yield. In the first series of experiments wheat plants (Hope/Chinese Spring substitution line 7B) were grown in sand culture in controlled conditions in growth rooms, at a number of defined nitrate levels. Nitrate reductase activity in the uppermost fully expanded leaf (which was found to have the highest nitrate reductase activity (R. Hallam and G. C. Blackwood, unpublished results)) was measured weekly *in vitro* and the effect of nitrate concentration on nitrate reductase activity was compared with the effect on the final yield. The data are shown in Fig. 1. There is a good correlation between nitrate reductase and yield ( $r=+0.90$ ,  $n=7$ ) at the earliest date of measurement, except at high (50 mM) nitrate concentrations. Similarly, there was a good correlation between grain yield and grain protein ( $r=+0.969$ ,  $n=8$ ) indicating that increasing nitrogen supply had no effect on the protein content of the grain. Furthermore, there were no significant changes in amino acid composition. Thus early nitrate reductase activity provides a good estimate of ultimate grain yield.

The critical test of a predictive assay is its successful use on crops growing in the field. To be sure of nitrogen deficient conditions for such a test, experiments were carried out (in collaboration with Dr. A. E. M. Hood of ICI's Jealott's Hill Research Station) on long standing nitrogen deficient plots at West Isley, Berkshire. Plots were treated with 0, 75, 112 or 150 kg ha<sup>-1</sup> of nitrogen and measurements of nitrate reductase made early, in the middle and late in the growing season. The crop was spring barley var. Julia. As before, samples for assay consisted of the uppermost fully expanded leaves and these were collected in the morning and stored at ambient temperature

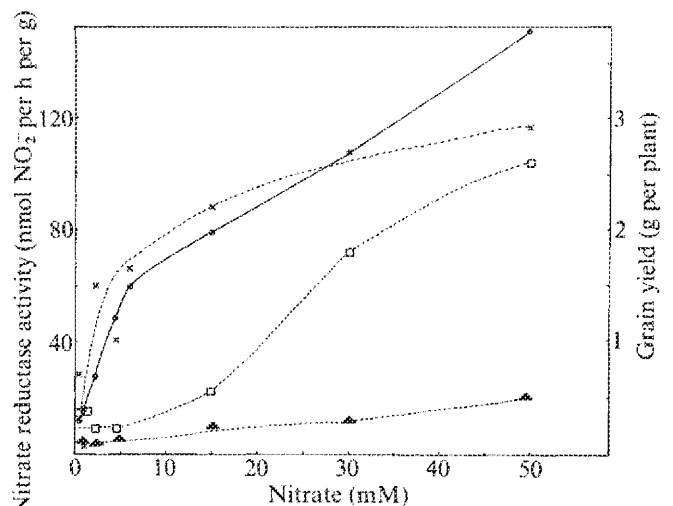


Fig. 1 Nitrate reductase activity as related to nitrate concentration in wheat (*Triticum aestivum* Hope/Chinese Spring, substitution line 7B). The enzyme was extracted from the first fully expanded leaf and assayed according to Filmer<sup>7</sup> (x, 2 weeks; □, 3 weeks; ▲, 4 weeks after sowing). For comparison the final grain weight per plant is shown (●). Plants were grown in sand culture on Long Ashton growth medium<sup>8</sup> adjusted to give the desired NO<sub>3</sub><sup>-</sup> concentration while maintaining constant ionic strength. Day length was 16 h; temperature 25/17 °C and light intensity 35 W m<sup>-2</sup>.

for several hours before nitrate reductase was determined by an *in vivo* assay in the laboratory, later in the day. Storage of intact leaves in this way did not significantly alter the enzyme activity. This is important if the test is to be of any practical use.

The activities of nitrate reductase at the three times of measurements are compared with the final yield in Fig. 2. The data show that, on the earliest date of estimation (3-4 leaf stage), less than maximal nitrate reductase activity is a reliable predictor of suboptimal yield. This is in agreement with the data obtained in the growth room. Amino acid composition was unaffected by the treatments. Once again, there is an increase in yield obtainable at nitrogen levels in excess of those required for maximal nitrate reductase induction. As with the growth room experiments, however, the increase in yield at these high nitrogen levels is far less in relation to added nitrogen than that obtained at lower levels where yield is correlated with nitrate reductase activity.

Although the measurements reported here were carried out in the laboratory, the *in vivo* assay can easily be used in the field. An alternative method which we also investigated,

Fig. 2 Nitrate reductase assayed on three dates (open columns) and final grain yield (hatched) in barley (*Hordeum vulgare*, var. Julia) plants. Enzyme activity was assayed *in vivo* by the method of Stewart *et al.*<sup>9</sup>. Standard errors: enzyme activity,  $\pm 0.155 \mu\text{mol NO}_2^-$  reduced per h per g; yield,  $\pm 238 \text{ kg ha}^{-1}$ .

