



Group on Measuring Fitness in Social Systems - Seated, left to right: Jerram Brown, Mildred Dickemann, Donald Sade, John Bonner. Standing: Frank McKinney, Bob Metcalf, Ulli Reyer, Eric Charnov, John Krebs, Tom Olivier.

Measuring Fitness in Social Systems Group Report

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INTRODUCTION

The aim of this report is to discuss a number of problems which relate to field tests of ideas about the evolution of social behavior. After a very brief introductory discussion of the notion of inclusive fitness, the report deals with the following topics: studies of aid-giving in birds and social insects, some alternative biological systems for studying the evolution of cooperation and conflict, the comparative method for studying adaptation, and some problems which arise in trying to use the idea of evolutionarily stable strategies in field studies.

SOME COMMENTS ON INCLUSIVE FITNESS

Direct and Indirect Fitness

Many field studies of sociobiological ideas involve making some kind of estimate of fitness. The idea that individuals can propagate their genes via relatives other than direct descendants (embodied in Hamilton's concept of inclusive fitness) is central to studies of the evolution of social behavior. It is sometimes useful to think of inclusive fitness as being made up of two major components, 'direct' (measured in terms of genes in direct descendants) and 'indirect' (measured as genes propagated through other relatives), and some field studies have attempted to assess the relative importance of these two components.

The value of the distinction between direct and indirect fitness is still controversial. Some members of the group argued that it is valuable because it allows one to ask questions about the difference made by the indirect component in explaining observed behavior (Brown). Brown also argues that the term 'direct' is appropriate for the component of fitness dependent on production of offspring because the genetic path linking parent to offspring is shorter than that linking sibling to sibling, even though the end result in terms of relatedness is usually identical. In the case of a mother in a species with internal fertilization, the relationship with offspring is more certain than that with siblings, but this is not necessarily true for males, or females with external fertilization.

The distinction between direct and indirect fitness was criticized on two grounds (Krebs). First it is somewhat arbitrary from the genetical standpoint. Since full siblings are just as closely related to one another as are parents and offspring, there is no genetic reason for treating parents and offspring as a special case. It is true that parental care is much more common and in historical perspective better known, than sibling care. But the answer to the question of why parental care is much more common is more likely to be related to ecological constraints than to genetic mechanisms. Second, the terms direct and indirect are sometimes taken to imply that direct fitness is in some way a more straightforward mechanism of evolutionary change. People talk of "resorting to indirect fitness if classical (direct) explanations won't do." As explained above, the distinction is meant to refer to the number of steps in the pathways linking two individuals genetically and not to the effectiveness of the two routes in bringing about evolutionary change.

Relatedness

The extent to which an aid-giver gains a contribution to its indirect fitness depends partly on the coefficient of a relationship (r) between donor and recipient. Occasionally a confusion

has arisen about the use of r . It is sometimes said, for example, that if all the members of a species share about 90% of their genes, they should all be altruistic to one another. The fallacy of this argument can be illustrated as follows. If an aid-giver donates benefit at random to other members of the population, there is on average an equal increment in fitness to all genotypes, so that no evolutionary change occurs. Only as a result of differential increments in fitness will gene frequencies change. Therefore, regardless of the overall degree of genetic similarity between members of a population, an altruistic trait will spread only if altruism is dispensed preferentially to close relatives.

Measuring Fitness and Relatedness

Although theoretical discussions of fitness usually refer to differential survival of genes or genotypes, most field workers measure survival and reproduction of individuals. There are many problems inherent in using approximate estimates of fitness (8), one of which is that of how to combine different components such as survival and reproductive success into an aggregate measure of inclusive fitness. Usually the measure adopted in a study is constrained more by practical problems than by theoretical considerations. This raises the general question of whether sociobiologists should focus their attention exclusively on systems which are tractable for measuring fitness.

Two main methods have been used in assessing coefficients of relatedness: direct studies of family pedigrees and genetic markers identified by electrophoresis. The latter method has the advantage of being quicker, but its accuracy may be limited if only a few polymorphisms can be identified. The pedigree method may give misleading results if paternity is unknown (see Harvey et al., this volume).

FIELD STUDIES OF COOPERATIVE BEHAVIOR IN BIRDS AND INSECTS

Among the classical case histories of sociobiological field studies are numerous investigations of cooperative behavior in

Hymenoptera and birds. Some of the disagreements which have arisen as a result of these studies have stemmed from a confusion between the different types of questions which have been addressed. The aim of such studies is not to 'test the theory of kin selection' or distinguish between the theories of 'kin selection' and 'individual selection.' Individual selection is the special case of kin selection in which the kin are offspring, so the two hypotheses are not mutually exclusive alternatives.

So what are the aims of studies of cooperative behavior in birds and insects? Four closely related but distinct aims are often confused: (a) to determine the relative importance of direct and indirect contributions to inclusive fitness, (b) to ask ecological questions about the selection pressures which have determined the importance of direct and indirect components of fitness, (c) to speculate about the evolutionary origin of cooperative sociality, and (d) to identify alternative strategies or decisions open to an individual in a social group. While it is clear that most published studies have at least touched on more than one of these questions, for the purposes of discussion it will be helpful to consider them separately.

Determining the Relative Importance of Direct and Indirect Components of Fitness

Consider a bird such as the Florida Scrub Jay, in which a male may spend the first part of his life helping his parents to rear young (i.e., rear his younger siblings) and later on acquire his own territory and become a breeder (5).

One can ask how much genetic profit such a male gains as a result of helping collateral relatives (usually siblings) and as a result of rearing direct descendants. The question can be posed as a 'decision' facing a young male at the beginning of a breeding season, in which case it is necessary to estimate the following quantities in order to calculate the solution. If the individual decides to help, it expects to make an immediate gain of indirect fitness (production of siblings) and a future

gain, of indirect fitness (e.g., increase in skill at helping in the future). If the male chooses to breed, it expects to make an immediate direct gain in terms of offspring and a future direct gain which might, for example, reflect an increase in future breeding success as a consequence of experience. Some future direct gain might also accrue to a helper if, for example, the probability of gaining a territory in the future is greater when surrounded by more younger siblings, or if experience gained by helping improves future skill as a parent. The aim of many studies of helping in birds has been to ask whether helpers gain more from future direct or immediate indirect fitness. The relative importance of these two components may determine whether one characterizes the helping as 'altruistic' (indirect gain is the major factor) or mutualistic/selfish (future direct gain is the major factor) (Brown, this volume). In some birds it may be possible to completely separate the two components. For example, in the Pied Kingfisher (16) some helpers are kin and others are unrelated to the breeding pair.

Metcalf's work on *Polistes* wasps (10,11) provides a good example of how components of fitness have been measured in a social insect. *Polistes* wasps may found nests as solitary individuals or as pairs of sisters. In a pair, one individual (the α or dominant) does all, or virtually all, the reproduction, but the second or β female contributes to nest building and maintenance. Metcalf estimated fitness by measuring the relative success in passing on genes of β , α , and solitary foundresses. His results showed that an α foundress has a significantly higher expected success than a β female, but that the β and solitary females do about equally well. The measure of fitness involved estimates of the coefficients of relatedness (using isozyme techniques) between members of a foundress pair and the number of offspring produced by pair and solitary foundresses. Pairs of females sharing the same nest are related on the average by 0.63, and the calculations show that a β female's gene contribution to the next generation is about 90% as a result of helping her sister and 10% the result of direct production of offspring. The study allows us to draw two conclusions. For β females

indirect fitness is a major component of inclusive fitness, and β females would do no better by founding nests as solitary individuals, given that they are condemned to be β s.

The study of Metcalf was done in Illinois, and a parallel study in Kansas revealed slight differences. In Illinois, pair nests produced about twice as many offspring as solitary nests and had a higher survival rate up to the time of reproduction. In Kansas, however, group nests produced no more offspring than those of solitary females, but the young emerging from group nests matured earlier. It is not yet possible to say whether the general conclusions from Metcalf's study also apply to the Kansas population (Michener, personal communication).

Ecological Questions about Helping

One of the conclusions drawn from studies of helpers in territorial birds has been that helping tends to occur in saturated habitats where young males have little chance to establish a territory. This is an answer to a question about ecological pressures which might lead to the evolution of helping and is to some extent distinct from the type of question discussed in the previous section. The distinction can perhaps be illustrated by referring back to Metcalf's study of *Polistes* wasps. While Metcalf addressed the question of how different kinds of foundresses pass on their genes to the next generation, he did not consider the question of why some females are solitary and others are pair foundresses. One answer might be in terms of habitat quality. If all suitable nest sites are occupied by females, a newly arriving queen may have no choice but to join another. This hypothesis, which might for example be tested by removal of nests from occupied sites, refers to the ecological conditions which favor joining as opposed to solitary nesting. Ecological questions about helping have been more often posed in bird studies than in studies of social insects.

The Evolutionary Origins of Cooperation

By its very nature this is a rather intractable question. There has been more discussion of this problem in relation to the

eusocial Hymenoptera than for birds. One argument sometimes used to favor the idea that eusociality in insects arose as a result of parental manipulation is that many of the proximate mechanisms of social communication in hymenopteran colonies are such that the queen appears to be in control. For example, worker reproduction can be suppressed by chemical cues from the queen. Another line of argument is that the queen in primitively social bees and wasps is clearly more different from a typical solitary hymenopteran than are the workers. The queen has relatively larger ovaries, has specialized behavior and lives longer than solitary female hymenopterans, perhaps suggesting that she has evolved specifically in the direction of parental manipulation.

A more fundamental approach to the problem is to make a genetic model of the evolution of parent-offspring conflict and ask whether there are any particular reasons for supposing that either parents or offspring will 'win' in an evolutionary race.

The answer seems to be that there is usually no particular genetic asymmetry which would favor the evolution of either parental or offspring dominance. Genetic models suggest that the evolutionarily stable state will usually be a compromise (14,16). Such models also underline the fact that 'parental manipulation' and 'kin selection' should not be considered as alternative hypotheses. As mentioned earlier, kin selection is a general statement about routes of gene propagation, and parental manipulation is a special case within this framework. However practical considerations might often play an overriding role in determining the outcome of parent-offspring conflict. Sexual incompatibility mechanisms in plants (9) can be viewed as examples of parental manipulation; parent plants prevent pollen grains from fertilizing their sisters. Presumably there is an asymmetry in practical power which enables parental domination in this case. As an example of offspring domination Williams (18) cites the fact that parents appear to be unable to control the sex ratio of their offspring in ways which would be adaptive to the parent.

Charnov (3) has pointed out that there may be a special kind of asymmetry in the evolutionary origin of sociality in wasps. Imagine a hypothetical queen which manipulates her daughters to stay at home and rear younger siblings. The daughters are equally related to their own offspring and their full siblings (assuming a 50:50 sex ratio) so that there is no penalty to the daughters for looking after younger siblings. This holds as long as the queen can provide each daughter with as many eggs as she herself could produce, and the 'willingness' of daughters to be manipulated may increase if good nest sites are in short supply. The queen, however, gains a genetic advantage from persuading daughters to help, because she exchanges grandchildren ($r = 0.25$) for children ($r = 0.5$). Thus at the point of origin of eusocial behavior there could be selection for parental domination with no selection for offspring resistance to manipulation. This does not in any way contradict Trivers' and Hare's (17) suggestion that after the establishment of eusociality workers might successfully retaliate and manipulate the sex ratio in their favor.

Identifying Alternative Strategies

This question is discussed in more detail in the section on ESSs. The point can be illustrated with reference to Metcalf's wasps. In the earlier discussions it was assumed that the alternative strategies open to an individual are solitary α and β . It is possible, however, that the alternatives are 'found a nest' and 'take over a nest.' Individuals adopting the second strategy might sometimes end up as β females and sometimes as solitary females. Although it seems very unlikely that this interpretation is correct for *Polistes*, a similar argument has been used to account for shared nesting in the great golden digger wasp (*Sphex ichneumoneus*) (2). The general point is that any study of the costs and benefits of cooperative behavior has to make assumptions about the strategies available to an individual.

ALTERNATIVE SYSTEMS FOR STUDYING THE EVOLUTION OF COOPERATION AND CONFLICT

The principles of Hamilton's kin selection theory can be applied outside the conventional contexts of helping and cooperation in animals. Two possible systems which might be rewarding to study from this perspective are the endosperm and embryo sac of higher plants and the slime molds.

Embryo Sacs

The triploid endosperm of higher plants is usually formed by the fusion of two meiotic products of the female and a sperm. The zygote is as usual formed by the fusion of one female meiotic product (the egg) and a sperm. The egg and the female contribution to the endosperm are often genetically identical because all three cells arise by mitosis from one cell formed through meiosis. The male's contribution to the endosperm is genetically identical to the sperm which fertilizes the egg. The role of the endosperm is to 'feed' the developing zygote. While it has the potential to develop into a whole plant itself, the endosperm so to speak altruistically sacrifices itself for the zygote, to which it is very closely related. However, sometimes the female gene contribution to the endosperm is not identical to that of the ovum, and it might be interesting to compare plants with different degrees of relatedness between endosperm and zygote. The phenomenon could also perhaps be viewed as an example of parent-offspring conflict. Perhaps the parent plant sets up an initial asymmetry such that the endosperm is condemned not to grow into an adult plant and can only increase its inclusive fitness by feeding the zygote. These are outrageous speculations, but the point is that questions about conflict and cooperation between close relatives might profitably be studied in the system (4).

Slime Molds

Slime molds show apparent sacrifice when a group of cells aggregates to form a fruiting body. Some individuals (about 25% of cells) form the stalk of a fruiting body and die, while others

form the spores and perpetuate their genes. Each cell has the potential to become a stalk or a spore up to the moment of fruiting body formation. Little is known about the genetic relatedness of slime mold aggregations in the field, but in the laboratory, they may be members of the same clone or genetically mixed. In one study (1,6), a mutant which tended to get itself in a position to form spores was identified. The mutant did not, surprisingly, increase in frequency in the population, presumably because it did less well at another stage in its life cycle. Slime molds may provide in many respects an ideal model system for studying aid-giving and indirect fitness (13).

COMPARISON BETWEEN SPECIES

Comparative studies of closely related species provided the first clear indication of how social groups might be influenced by ecological pressures. Among the advantages of comparative studies are the following. They may help to identify possible strategies. If species B, a close relative of A, has a particular trait (e.g., living in groups), it might be reasonable to propose that the trait is an evolutionary option that has been open to A. A second contribution of comparative studies has been to generate hypotheses and identify questions. Much of the experimental work attempting to relate group living to dispersion of food and the influence of predators uses ideas generated by comparative studies. Questions such as why apes have abnormally large home ranges for their body size, or why terrestrial monkeys have exceptionally small home ranges in relation to their daily metabolic needs would not have been recognized without comparative surveys of home range size, body size, and metabolic requirements of primates. Among the limitations of comparative studies are the problems of disentangling cause and effect, the choice of taxonomic units for comparison, and the fact that most of the interpretations and hypotheses tested are qualitative rather than quantitative.

EVOLUTIONARILY STABLE STRATEGIES (ESS) IN THE FIELD

One of the most important theoretical developments in sociobiology during the last few years has been the realization that the

costs and benefits of alternative behavior patterns may be frequency dependent. When two or more ways of achieving the same end are observed, we have to consider the possibility that the two strategies coexist in stable equilibrium because of frequency dependent benefits. For example, if males of particular species could obtain matings either by defence of a mating territory or by sneaking, it is possible that the payoffs for the two strategies are equal at an equilibrium mixture (too many sneakers favors defense, with too many defenders, sneaking is favored). Without going into the intricacies of the theory it is worth making three points about the attempts to test ESS ideas in the field. The first is that such exercises should not be viewed as attempts to test ESS theory. The theory is used as a tool to generate ideas about the frequency dependent costs and benefits associated with alternative strategies. The second point is a methodological one. If the prediction of an ESS model is that the net payoff for two or more alternative strategies is equal, the investigator is faced with the difficult task of trying to demonstrate that there is no difference between a number of sets of measurements (e.g., the number of matings achieved by sneakers and guarders). Since the null hypothesis is usually that there is no difference between the groups of measurements, it may be difficult to convince a skeptic that one has actually demonstrated equal payoffs. An alternative, and more powerful test of an ESS hypothesis might be to perturb the frequencies of the alternative strategies away from the hypothesized equilibrium and predict that the payoffs should be frequency dependent. In this connection it is perhaps worth emphasizing the distinction between cases in which the two strategies coexist in equilibrium (mixed ESS) and the case where one strategy has a higher payoff, and the other can be viewed as making the best of a bad job. Thus sneakers could in some species be young males with no chance of setting up their own territories but an occasional chance of stealing a copulation. One of the tasks facing field workers is to distinguish between this case and that of a mixed ESS.

The third problem is one of correctly identifying the strategies. This point can be illustrated by referring to the bluegill sunfish (Gross, in preparation). There are three kinds of breeding male sunfish within a population, small (sneakers), medium (satellites), and large (territorial) males. However, an analysis of the life history reveals that the three behavior types result from two strategies. One strategy is to postpone breeding until the age of about seven years and then become a large breeder. The alternative is to start breeding at the age of two and pass through the small and middle sizes before dying at the age of about five years. The decision point is at the age of two, and the strategies are to postpone reproduction and grow, or to reproduce early and grow less. Calculations suggest that the two strategies coexist as an ESS.

Conclusions

This report has described some of the problems which have arisen in trying to carry out field tests of sociobiological hypotheses. There are a number of further points which are important but have not been discussed, for example the question of whether technical limitations in the ability of field workers to measure fitness will set limits on testing hypotheses. The discussion has not referred to trait group selection as a mechanism for the evolution of aid-giving behavior (19). In one case, trait group selection might have been important in the evolution of sex ratios (8) and recent studies of migration between rhesus monkey groups suggest that genetic isolation of groups may be greater than previously thought (12).

Finally, a comment about applying sociobiological arguments to human populations. At the moment most tests of sociobiological theories with animals have been qualitative, and the same applies with even greater force to human studies. However, there is often a superficial concordance between qualitative predictions of sociobiological theories and observations of human behavior. This might suggest a hint of cautious optimism for the future studies of human behavior using the neo-Darwinian framework.

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