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Evolution and the Theory of Games: In situations characterized by conflict of interest, the best strategy to adopt depends on what others are doing

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*In situations characterized by conflict of interest, the best strategy to adopt depends on what others are doing*

I want in this article to trace the history of an idea. It is beginning to become clear that a range of problems in evolution theory can most appropriately be attacked by a modification of the theory of games, a branch of mathematics first formulated by Von Neumann and Morgenstern (1944) for the analysis of human conflicts. The problems are diverse and include not only the behavior of animals in contest situations but also some problems in the evolution of genetic mechanisms and in the evolution of ecosystems. It is not, however, sufficient to take over the theory as it has been developed in sociology and apply it to evolution. In sociology, and in economics, it is supposed that each contestant works out by reasoning the best strategy to adopt, assuming that his opponents are equally guided by reason. This leads to the concept of a "minimax" strategy, in which a contestant behaves in such a way as to minimize his losses on the assumption that his opponent behaves so as to maximize them. Clearly, this would not be a valid approach to animal conflicts. A new concept has to be in-

troduced, the concept of an "evolutionarily stable strategy." It is the history of this concept I want to discuss.

### Evolution of the sex ratio

Consider first the evolution of the sex ratio. In most animals and plants with separate sexes, approximately equal numbers of males and females are produced. Why should this be so? Two main kinds of answer have been offered. One is couched in terms of advantage to the population. It is argued that the sex ratio will evolve so as to maximize the number of meetings between individuals of opposite sex. This is essentially a "group selection" argument. The other, and in my view certainly correct, type of answer was first put forward by Fisher (1930). It starts from the assumption that genes can influence the relative numbers of male and female offspring produced by an individual carrying the genes. That sex ratio will be favored which maximizes the number of descendants the individual will have and hence the number of gene copies transmitted. Suppose that the population consisted mostly of females: then an individual which produced only sons would have more grandchildren. In contrast, if the population consisted mostly of males, it would pay to have daughters. If, however, the population consisted of equal numbers of males and females, sons and daughters would be equally valuable. Thus a 1:1 sex ratio is the only stable ratio; it is an "evolutionarily stable strategy."

Fisher allowed for the fact that the cost of sons and daughters may be different, so that a parent might

have a choice, say, between having one daughter or two sons. He concluded that a parent should allocate equal resources to sons and daughters. Although Fisher wrote before the theory of games had been developed, his theory does incorporate the essential feature of a game—that the best strategy to adopt depends on what others are doing. Since that time, it has been realized that genes can sometimes influence the chromosome or gamete in which they find themselves, so as to make that gamete more likely to participate in fertilization. If such a gene occurs on a sex-determining (X or Y) chromosome, then highly aberrant sex ratios can evolve.

More immediately relevant are the strange sex ratios in certain parasitic hymenoptera (wasps and ichneumonids). In this group of insects, fertilized eggs develop into females and unfertilized eggs into males. A female stores sperm and can determine the sex of each egg she lays by fertilizing it or leaving it unfertilized. By Fisher's argument, it should still pay a female to produce equal numbers of sons and daughters. More precisely, it can be shown that if genes affect the strategy adopted by the female, then a 1:1 sex ratio will evolve. Some parasitic wasps lay their eggs in the larvae of other insects, and the eggs develop within their host. When adult wasps emerge, they mate immediately before dispersal. Such species often have a big excess of females. This situation was analyzed by Hamilton (1967). Clearly, if only one female lays eggs in any given larva, it would pay her to produce one male only, since this one male could fertilize all his sisters on emergence. Things get more com-

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plicated if a single host larva is found by two parasitic females, but the details of the analysis do not concern us. The important point is that Hamilton looked for an “unbeatable strategy”—that is, a sex ratio which would be evolutionarily stable. In effect, he used Fisher’s approach but went a step farther in recognizing that he was looking for a “strategy” in the sense in which that word is used by game theorists.

## Animal contests and game theory

A very similar idea was used by the late G. R. Price in an analysis of animal behavior. Price was puzzled by the evolution of ritualized behavior in animal contests—that is, by the fact that an animal engaged in a contest for some valuable resource does not always use its weapons in the most effective way. Examples of such behavior have been discussed by Lorenz (1966), Huxley (1966), and others. It seems likely that ethologists have underestimated the frequency and importance of escalated, all-out contests between animals (see particularly Geist 1966). Yet display and convention are a common enough feature of animal contests to call for some explanation. Both Lorenz and Huxley accepted group selectionist explanations: Huxley, for example, argued that escalated contests would result in many animals being seriously injured, and “this would militate against the survival of the species.” Similar assumptions are widespread in ethology, although not often so clearly expressed.

Price was reluctant to accept a group selection explanation. It occurred to him that if animals adopted a strategy of “retaliation,” in which an animal normally adopts conventional tactics but responds to an escalated attack by escalating in return, this might be favored by selection at the individual level. He submitted a paper to *Nature* arguing this point, which was sent to me to referee. Unfortunately the paper was some fifty pages in length and hence quite unsuitable for *Nature*. I wrote a report saying that the paper contained an interesting idea, and that the author should be urged to submit a short account of it to *Nature* and/or to submit the existing manuscript to a more suitable

journal. I then thought no more of the matter until, about a year later, I spent three months visiting the department of theoretical biology at Chicago. I decided to spend the visit learning something about the theory of games, with a view to developing Price’s idea in a more general form and applying it to certain other problems. I was at that time familiar with Hamilton’s work on the sex ratio (indeed, the work formed part of his Ph.D. thesis, of which I was the external examiner), but I had not seen its relevance to Price’s problem.

While at Chicago, I developed the formal definition of an evolutionarily stable strategy which I will give in a moment and applied it to the “Dove–Hawk–Retaliator” and “War of Attrition” games. I also realized the similarity between these ideas and the work of Hamilton (and also MacArthur 1965) on the sex ratio. When I came to write up this work, it was clearly necessary to quote Price. I was somewhat taken aback to discover that he had never published his idea and was now working on something else. When I returned to London I contacted him, and ultimately we published a joint paper (Maynard Smith and Price 1973) in which the concept of an evolutionarily stable strategy was applied to animal contests.

At this point it will be convenient to describe some ideas from the theory of games. By “game” or “contest” is meant an encounter between two individuals (I am not concerned with  $n$ -person games) in which the various possible outcomes would not be placed in the same order of preference by the two participants: there is a conflict of interest. By “strategy” is meant a complete specification of what a contestant will do in every situation in which he might find himself. A strategy may be “pure” or “mixed”; a pure strategy states “in situation A, always do X”; a mixed strategy states “in situation A, do X with probability  $P$  and Y with probability  $Q$ .” Suppose that there are three possible strategies, A, B, and C. A “payoff matrix” is then a  $3 \times 3$  matrix listing the expected gains to a contestant adopting these three strategies, given that his opponent adopts one of the other strategies.

These ideas will be made clearer by an example. Consider the children’s game “Rock–Scissors–Paper.” In each contest, a player must adopt one of these “strategies” in advance: then Rock blunts Scissors, Scissors cuts Paper, and Paper wraps Rock. Suppose that the winner of each contest receives one dollar from the loser; if both adopt the same strategy, no money changes hands. The payoff matrix is

	R	S	P
R	0	+1	−1
S	−1	0	+1
P	+1	−1	0

The payoffs are to the player on the left. This particular game is a “zero-sum” game, in the sense that what one player wins the other loses; in general the games considered below are not of this kind. Clearly, a player adopting the pure strategy “Rock” will lose in the long run, because his opponent will catch on and play “Paper.” A player adopting the mixed strategy “ $\frac{1}{3}$  Rock,  $\frac{1}{3}$  Scissors,  $\frac{1}{3}$  Paper” will break even.

How are these ideas to be applied to animal contests? A genotype determines the strategy, pure or mixed, that an animal will adopt. Suppose an animal adopts strategy  $I$  and his opponent strategy  $J$ ; then the payoff to  $I$  will be written  $E_J(I)$ , where  $E$  stands for “expected gain.” This payoff is the change in  $I$ ’s fitness as a result of the contest, fitness being the contribution to future generations.

## Evolutionarily stable strategy

We are now in a position to define an evolutionarily stable strategy, or ESS for short. Suppose that a population consists of individuals adopting strategies  $I$  or  $J$  with frequencies  $p$  and  $q$ , where  $p + q = 1$ . What is the fitness of an individual adopting strategy  $I$ ?

$$\text{Fitness of } I = p \cdot E_I(I) + q \cdot E_J(I)$$

$$\text{Fitness of } J = p \cdot E_I(J) + q \cdot E_J(J)$$

If a particular strategy, say  $I$ , is to be an ESS, it must have the following property. A population of individuals playing  $I$  must be “protected” against invasion by any mu-

tant strategy, say  $J$ . That is, when  $I$  is common, it must be fitter than any mutant. That is,  $I$  is an ESS if, for all  $J \neq I$ ,

$$\begin{aligned} &\text{either } E_I(I) > E_I(J) \\ &\text{or } E_I(I) = E_I(J) \\ &\text{and } E_J(I) > E_J(J) \end{aligned} \quad (1)$$

If these conditions are satisfied, then a population of individuals playing  $I$  is stable; no mutant can establish itself in such a population. This follows from the fact that when  $q$  is small, the fitness of  $I$  is greater than the fitness of  $J$ .

It is important to emphasize at this point that the ESS is not necessarily the same as the strategy prescribed by game theorists for human players. There the assumption is that a player will adopt that strategy which minimizes his losses, given that his opponent plays so as to maximize them. Lewontin (1961) applied such "minimax" strategies to evolution. He was concerned with a contest not between individuals but between a species and "nature." The objective of a species is to survive as a species—to avoid extinction. It should therefore adopt that strategy which minimizes its chances of extinction, even if nature does its worst. That is, the species must adopt the minimax strategy. For example, a species should retain sexual reproduction rather than parthenogenesis, because this will enable it to evolve to meet environmental change. This is clearly a group selectionist approach; the advantage is to the species and not to the individual female. In contrast, the concept of an evolutionarily stable strategy is relevant to contests between individuals, not between a species and nature, and is concerned solely with individual advantage.

Let us now apply these ideas to a particular problem. Suppose that two animals are engaged in a contest for some indivisible resource which is worth  $+V$  to the victor. An animal can "display," it can "escalate"—in which case it may seriously injure its opponent—or it can retreat, leaving its opponent the victor. Serious injury reduces fitness by  $-W$  (a "wound") and forces an animal to retreat. Finally, a long contest costs both animals  $-T$ . The two simplest strategies are

*Hawk.* Escalate, and continue to do so until injured or until opponent retreats.

*Dove.* Display. Retreat if opponent escalates, before getting injured.

We suppose that two Hawks are equally likely to be injured or to win. We also suppose that two Doves are equally likely to win, but only after a long contest costing both of them  $-T$ . The payoff matrix is then

	H	D
H	$\frac{1}{2}(V - W)$	$V$
D	$0$	$\frac{1}{2}V - T$

If  $W > V$ , then there is no pure ESS. Thus  $H$  is not an ESS, because  $E_H(H) < E_H(D)$ , and  $D$  is not an ESS, because  $E_D(D) < E_D(H)$ . The only ESS is

$$\begin{aligned} &H \text{ with probability } (2T + V)/ \\ &\hspace{15em} (2T + W) \\ &D \text{ with probability } 1 - (2T + V)/ \\ &\hspace{15em} (2T + W) \end{aligned}$$

Thus at an evolutionary equilibrium the population will consist of a mixture of Hawks and Doves. Price's suggestion was that a third strategy, "Retaliator,"  $R$ , might be an ESS;  $R$  plays  $D$  against  $D$  and  $H$  against  $H$ . The payoff matrix is

	H	D	R
H	$\frac{1}{2}(V - W)$	$V$	$\frac{1}{2}(V - W)$
D	$0$	$\frac{1}{2}V - T$	$\frac{1}{2}V - T$
R	$\frac{1}{2}(V - W)$	$\frac{1}{2}V - T$	$\frac{1}{2}V - T$

It turns out that Price was right. Thus a population of  $R$  is stable against invasion by mutant  $H$ , because  $E_R(R) > E_R(H)$ .  $R$  is not stable against  $D$ , because in the absence of  $H$  they are identical. But a population consisting initially of a mixture of  $R$ ,  $D$ , and  $H$  will evolve to  $R$ . This game is analyzed further in Maynard Smith and Price (1973) and by Gale and Eaves (1975).

This analysis suggests that we would expect to find retaliation a feature of actual behavior. One example must suffice: a rhesus monkey which loses a fight will passively accept incisor bites but will retaliate viciously if the winner uses its canines (Bernstein and Gordon 1974).

One assumption made above—that two Doves can settle a contest—needs some justification. Why don't they go on forever? Consider the following game. Two players,  $A$  and  $B$ , can only display. The winner is the one who goes on for longer; the only choice of strategy is how long to go on for.  $A$  selects time  $T_A$  and  $B$  selects  $T_B$ . The longer the contest actually continues, the more it costs the players; the costs associated with these times are  $m_A$  and  $m_B$ . If  $T_A > T_B$ , then we have

$$\begin{aligned} \text{payoff to } A &= V - m_B \\ \text{payoff to } B &= -m_B \end{aligned}$$

The cost of  $m_A$  which  $A$  was prepared to pay is irrelevant, provided that it is greater than  $m_B$ . Our problem then is: How should a player choose a time, and a corresponding value of  $m$ ? More precisely, what choice of  $m$  is an ESS? For obvious reasons, I have called this the "War of Attrition." Clearly, no pure strategy can be an ESS. Any population playing  $m$ , say, could be invaded by a mutant playing  $M$ , where  $M > m$ ; if  $m > V/2$ , it could also be invaded by a mutant playing  $0$ . It can be shown that there is a mixed ESS given by

$$p(x) = \frac{1}{V} e^{-x/V} \quad (2)$$

where  $p(x)\delta x$  is the probability of playing  $m$  between  $x$  and  $x + \delta x$ .

What does this mean? There are two possible ways in which an ESS of this kind could be realized. First, all members of the population might be genetically identical and have a behavior pattern which varied from contest to contest according to Eq. 2. Second, the population might be genetically variable, with each individual having a fixed behavior, the frequencies of different kinds of individuals being given by Eq. 2. In either case, the population would be at an ESS.

G. A. Parker (1970) has described a situation which agrees rather well with Eq. 2. Female dung flies of the genus *Scatophaga* lay their eggs in cow pats. The males stay close to the cow pats, mating with females as they arrive to lay their eggs. What strategy should a male adopt? Should he stay with a pat once he has found one, or should he move



on in search of a fresh pat as soon as the first one begins to grow stale? This is comparable to the choice of a value of  $m$  in the War of Attrition. His choice will be influenced by the fact that females arrive less frequently as a pat becomes staler. His best strategy will depend on what other males are doing. Thus if other males leave a pat quickly, it would pay him to stay on, because he would be certain of mating any females which do come. If other males stay on, it would pay him to move.

Parker found that the actual length of time males stayed was given by a distribution resembling Eq. 2. By itself this means little, because it is the distribution one would expect if every male had the same constant probability of leaving per unit time. It is the typical negative exponential distribution expected for the "survivors" of a population suffering a constant "force of mortality." What is significant is that Parker was able to show that the expected number of matings was the same for males which left early as for those which stayed on. This means that the males are adopting an ESS; natural selection has adjusted the probability of leaving per unit time to bring this about.

It is not known whether contests between pairs of animals, in which only display is employed, show the appropriate variation in length. It will be interesting to find out.

A major complication in applying these ideas in practice arises because most contests are asymmetrical (Parker 1974; Maynard Smith and Parker, in press), either in the fighting ability of the contestants (i.e. in what Parker has called "resource-holding potential," or RHP), or in the value of the resource to the contestants (i.e. in payoff). Clearly, these asymmetries can only affect the strategies adopted if they are known to the contestants. Thus suppose two animals differ in size, and hence in RHP, but have no way short of escalation of detecting the difference. Then the difference cannot alter their willingness to escalate (i.e. their strategy), although it would affect the outcome of an escalated contest.

In some cases an asymmetry may be clearly perceived by both contestants

but have relatively little effect on RHP or on payoff. The obvious example is the asymmetry between the "owner" of a resource (e.g. a territory, a female, an item of food) and a "latecomer." There is no general reason why an owner should have a higher RHP than a latecomer. The value of a resource will often be greater to the owner, but, as I shall show in a moment, no such difference is necessary before an asymmetry can be used to settle a contest conventionally.

To fix ideas, consider the game of Hawks and Doves discussed above, with the arbitrary values  $V = 60$ ,  $W = 100$ , and  $T = 10$ . The payoff matrix for the symmetrical case is then

	H	D
H	-20	+50
D	0	+20

Suppose that an animal may be either the owner of the resource or a latecomer, for a particular animal is equally likely to find himself playing either role. Consider now the strategy  $I$ : "Play  $H$  if you are owner; play  $D$  if you are latecomer." Then, since an animal is owner and latecomer with equal frequency,

$$E_I(I) = \frac{1}{2} \times 50 + \frac{1}{2} \times 0 = +25$$

Now let  $J$  be a strategy which ignores the asymmetry and plays  $H$  with probability  $p$  and  $D$  with probability  $(1 - p)$ . Then

$$E_I(J) = \frac{1}{2}[50p + 20(1 - p)] + \frac{1}{2}[-20p] = 5p + 10$$

For any value of  $p$ ,  $E_I(I) > E_I(J)$ . Thus the strategy  $I$ , which amounts to the conventional acceptance of ownership, is an ESS against any strategy which ignores ownership. (Notice that the game permits the alternative ESS, "play  $H$  if you are latecomer; play  $D$  if you are owner." This raises difficulties which are discussed by Maynard Smith and Parker, in press.)

It follows that conventional acceptance of ownership can be used to settle contests even when there is no asymmetry in payoff or RHP, provided that ownership is unambiguous. Some actual examples will help to illustrate this point.

### The ESS in practice

The hamadryas baboon, *Papio hamadryas*, lives in troops composed of a number of "one-male groups," each consisting of an adult male, one or more females, and their babies. The male, who is substantially larger than the females, prevents "his" females from wandering away from his immediate vicinity; a female rapidly comes to recognize this "ownership." It is rare for an owning male to be challenged by another. How is this state of affairs maintained?

Kummer (1971) describes the following experiment. Two males, previously unknown to each other, were placed in an enclosure; male  $A$  was free to move about the enclosure whereas male  $B$  was shut in a cage from which he could see what was happening but not interfere. A female strange to both males was then loosed into the enclosure. Within 20 minutes male  $A$  had convinced the female of his ownership, so that she followed him about. Male  $B$  was then released into the enclosure. He did not challenge male  $A$ , but kept well away from him, accepting  $A$ 's ownership.

These observations can be explained in two ways. First, male  $B$  may have been able to detect that male  $A$  would win an escalated contest if challenged; second, there may be a conventional acceptance of ownership, for the reasons outlined above. Kummer was able to show that the second explanation is correct. Two weeks later, he repeated the experiment with the same two males but with a different female, but on this occasion male  $B$  was loose in the enclosure and male  $A$  confined. Male  $B$  established ownership of the female and was not challenged by  $A$ .

One last observation is relevant. If a male is removed from a troop, his females will be taken over by other males. If after some weeks the original male is reintroduced, an escalated fight occurs; both males now behave as "owners."

It could be argued that in the hamadryas baboon there is a difference in payoff, because when a male first takes over a new female he has to invest time and energy in per-

suading her to accept his ownership. This is probably correct, although the theoretical analysis shows that no such difference is required for the establishment of an ESS based on conventional acceptance of ownership. An asymmetry in payoff is less likely in the anubis baboon (Packer 1975). In this species, there is a fairly stable male dominance hierarchy for food but not for females. Females are not the permanent property of particular males; instead, a male "owns" a female only for a single day—or for several days if he can prevent her from moving away during the night. Once in temporary possession of a female, a male is not challenged, even by those above him in the dominance hierarchy. Why should contests about food and females be settled differently? One possible explanation is that the ownership principle could not be used to settle contests over food, because it must often be the case that two animals see a food item almost simultaneously. Ownership would be ambiguous; two animals would both regard themselves as owners of the same item, and escalated contests would ensue.

This last possibility is beautifully illustrated by the work of L. Gilbert (pers. comm.) on the swallowtail butterfly, *Papilio zelicaon*. Because this is a relatively rare butterfly, the finding of a sexual partner presents a problem. This problem is solved by "hilltopping." Males establish territories at or near the tops of hills, and virgin females fly uphill to mate. There are, however, more males than hilltops, so most males must accept territories lower down the slopes. They attempt to waylay females on their way up and, although they sometimes succeed, the evidence suggests that the male actually at the hilltop mates most often. Gilbert marked individual males and observed that a strange male did occasionally arrive at a hilltop and challenge the owner, but the stranger invariably retreated after a brief "contest."

As in Kummer's experiments with baboons, we have to choose between two explanations. Either the owner of a hilltop is a particularly strong butterfly, and this fact is perceived by the challenger during a brief contest, or there is again an ESS

based on conventional acceptance of ownership. Gilbert showed that the latter explanation is correct by an experiment analogous to that of removing a male hamadryas baboon from a troop and then restoring it. He allowed two male butterflies to occupy a hilltop on alternate days, keeping each in the dark on their off days. After two weeks, when both males had come to regard themselves as owners of the same hilltop, he released them on the same day. A contest lasting many minutes and causing damage to the contestants ensued.

Much has been left out of these simple models. Contests in which only partial information about asymmetries is available to the contestants, or in which information is acquired in the course of a contest, are discussed by Maynard Smith and Parker (in press). The same paper discusses the possibility of "bluff"—that is, the possession of structures such as manes, ruffs, or crests, which increase apparent RHP without an equivalent increase in actual fighting ability.

I suggested at the beginning of this article that the concept of an ESS is also relevant to the evolution of ecosystems; this idea is developed by Maynard Smith and Lawlor (in press). It is impossible to do more here than indicate the nature of the problem. In nature, animals and plants compete for resources—food, space, light, etc. Genetic changes in an individual can alter its "choice" of resources: for example, the food items taken by an animal, or the time of year a plant puts out its leaves. Individuals will choose their resources so as to maximize their fitness. The best choice will depend on what other individuals, of the same and other species, are doing. If everyone else is eating spinach it will pay to concentrate on cabbage; since most forest trees put out their leaves late in spring, it pays forest herbs to put out leaves early.

Since the appropriate strategy for an individual depends on what others are doing, we are again concerned with the search for an ESS. Lawlor and I conclude that two competing species will tend to become specialists on different resources, even though in isolation each species would be a generalist.

This conclusion is not a new one: it accords with a good deal of observational data and has received several previous theoretical treatments. We would claim, however, that we have clarified a familiar idea and set it in a wider context. That wider context is simply this: whenever the best strategy for an individual depends on what others are doing, the strategy actually adopted will be an ESS.

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