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Game theory and the evolution of behaviour

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How far can game theory account for the evolution of contest behaviour in animals? The first qualitative prediction of the theory was that symmetric contests in which escalation is expensive should lead to mixed strategies. As yet it is hard to say how far this is borne out, because of the difficulty of distinguishing a 'mixed evolutionarily stable strategy' maintained by frequency-dependent selection from a 'pure conditional strategy'; the distinction is discussed in relation to several field studies. The second prediction was that if a contest is asymmetric (e.g. in ownership) then the asymmetry will be used as a conventional cue to settle it. This prediction has been well supported by observation. A third important issue is whether or not information about intentions is exchanged during contests. The significance of 'assessment' strategies is discussed.

INTRODUCTION

The theory of games was applied to the evolution of fighting behaviour (Maynard Smith & Price 1973) in the hope of explaining the conventional aspects of this behaviour (Lorenz 1966 and earlier) in terms of individual selection. Before this there had been a tendency to account for such behaviour in terms of the good of the species. This presented an obvious difficulty to a neo-Darwinist, in view of the weakness of group compared with individual selection as an evolutionary force (Williams 1966; Maynard Smith 1964, 1976).

The aim of this paper is to discuss how far the application of game theory, and in particular the concept of an 'evolutionarily stable strategy' is useful in interpreting animal contests. By 'interpreting' I mean giving an account of the selective forces responsible for the evolution of fighting behaviour: the short-term developmental and physiological mechanisms call for a different type of explanation. That is, I am seeking a 'functional' rather than a 'causal' explanation. I am not concerned to show that any particular model – for example the Hawk–Dove game – is an adequate account of any particular case, because clearly it is not and was not intended to be. Rather, I ask whether certain general predictions of the game theory approach are borne out, and whether there are categories of observation that cannot at present be understood.

THE PREDICTIONS OF GAME THEORY

The following three general predictions follow from game theory models of evolution:

- (i) In symmetric contests, we expect to find 'mixed' strategies.
- (ii) In asymmetric contests, we expect the asymmetry to be used as a cue to settle the contest.
- (iii) We do not expect contestants to exchange information about their intentions, although they certainly exchange information about their size and fighting ability.

TABLE 1. PAYOFF MATRIX FOR CONTESTS BETWEEN
HAWK (H) AND DOVE (D)

(The payoffs are to the player adopting the strategy on the left against one adopting the strategy above.)

	H	D
H	-5	+10
D	0	+5

These predictions are now derived and explained in terms of a simple model. Suppose a contest takes place between two individuals over some resource. Individuals can adopt two 'strategies': H (Hawk), i.e. 'fight until victory or defeat', and D (Dove), i.e. 'display, but retreat before being hurt if one's opponent escalates'. The changes in fitness after a contest can then be expressed in a 'payoff matrix', which might be as in table 1. In effect, what this matrix says is that if both contestants adopt H, their expected losses from injury or exhaustion more than outweigh their expected gains; that H always wins against D, but D loses nothing because he retreats before injury; and that D sometimes wins and sometimes loses against another D.

Now imagine a population of individuals playing such a game, and then producing offspring in numbers proportional to their accumulated payoffs, the offspring adopting the same strategy as their parents. The state (or states) to which such a population evolves is called an 'evolutionarily stable strategy' (e.s.s.). In words, to be an e.s.s. a strategy I must have the following property: if almost all the members of a population adopt I , then no mutant strategy M can invade the population. This in turn requires that, for all possible mutants, the expected payoff to M against I must be less than (or at least not greater than) the payoff to I against itself. A mathematical definition is given by Maynard Smith (1974).

With this idea in mind, it is clear that neither H nor D is an e.s.s. for the game in table 1. Thus H is not an e.s.s. because, in a population of Hawks, the expected payoff to H per contest is -5 , and to a D mutant is 0 , which is greater. A similar argument shows that D is not an e.s.s. What then would happen to a population containing both H and D strategists? It can be shown that it would evolve to a

stable mixture of H and D (for the particular numerical values, H and D would be equally frequent). Alternatively, if the strategy *I*, 'play H with probability $\frac{1}{2}$, and D with probability $\frac{1}{2}$ ', could exist and reproduce, then *I* would be an e.s.s.; such a strategy, containing a stochastic element, is called a 'mixed' strategy.

TABLE 2. PAYOFF MATRIX FOR CONTESTS BETWEEN
HAWK (H), DOVE (D) AND BOURGEOIS (B)

	H	D	B
H	-5	+10	+2.5
D	0	+5	+2.5
B	-2.5	+7.5	+5

This, then, is our first prediction, that symmetric games tend to have mixed e.s.s. The exact numbers do not matter, but it is important that the cost of injury outweighed the expected gains of victory. It is an open question whether, in such cases, we should expect a genetically polymorphic population, or a uniform population of phenotypically flexible mixed strategists.

Now suppose that each contest takes place between the 'owner' of a resource and an 'interloper'. A new strategy now becomes possible: *B* (Bourgeois), or 'play H if owner, D if interloper'. The new payoff matrix is shown in table 2. The essential point here is that an escalated fight never takes place between two *B* strategists, because if one is owner the other is not. Clearly, the strategy *B* is an e.s.s. for the matrix; in fact it is the only e.s.s. This is our second prediction, that in asymmetric contests the asymmetry will be used as a cue. The asymmetry need not be of ownership. It could as well be a difference in size or weapons, provided two conditions are satisfied. First, the asymmetry must be unambiguously perceived by both contestants. Secondly, it must not be easy to acquire the 'winning' cue; if it were, every member of the population would acquire it and the asymmetry would disappear.

The third prediction, that information about intentions should not be conveyed, will be explained later when the relevant data are discussed.

ARE THERE MIXED E.S.SS?

Contest behaviour is often very variable, but this does not prove that we are looking at a mixed e.s.s. The difficulty can best be illustrated by an example. Rohwer (1977) studied the behaviour of Harris sparrows in winter flocks. These flocks are temporary, so birds probably do not recognize one another individually. Birds differ strikingly in the amount of black in their plumage. Black birds are more aggressive, and regularly occupy higher positions in the flock hierarchy. These observations raise two questions. The first, relevant here, is why there are individual differences in aggression. The second, relevant to the problem of information transfer, is why these differences are signalled by differences in plumage.

To the first question there are two possible answers. First, the population may be at a mixed e.s.s. Secondly, some sparrows are large and some small (perhaps for chance environmental reasons), and it would not pay a small sparrow to be aggressive. If the latter answer is true, all sparrows adopt the same pure, conditional, strategy: 'if large, play H; if small, play D'; in effect, when small the animal makes the best of a bad job. As others have emphasized (e.g. Parker 1978) there is a crucial difference between a mixed e.s.s. and a pure conditional strategy. But how are they to be distinguished in practice?

I suggest that, to be interpreted as a mixed e.s.s., a strategy must meet two criteria. First, the fitness, over a lifetime, of individuals adopting different strategies must be the same (or, for a true mixed strategist, the payoffs when adopting different policies should be the same). This is a theoretical requirement (Bishop & Cannings 1978) which is easy to see intuitively. Thus suppose mixed strategy *I* plays sometimes H and sometimes D, and does better on the occasions it plays H; clearly, a strategy *J*, playing H more often and D less, would do better, so *I* is not an e.s.s. The second criterion is that if any component of the supposed mixed e.s.s. became more frequent it would have a lower payoff; that is, fitnesses are negatively frequency-dependent. Although hard to prove in the field, it is often easy to see that this would be the case.

Not surprisingly, there are few cases which meet these criteria. Parker (1974*a*) showed that they hold for male dung flies, which have the choice between sticking with a stale cowpat despite the declining rate at which virgin females arrive, or seeking a fresh one. The Harris sparrow may also be an example of a mixed e.s.s., although the situation is not simple. It is difficult to measure individual survival, but the frequencies of light and dark birds are fairly constant through the winter, which fits the e.s.s. hypothesis (S. Rohwer, personal communication). However, there is a rise in the status signalled by individuals between the first and second winters, which makes more sense if it pays to be dominant. Rohwer & Rohwer (1978) have proposed a frequency-dependent mechanism to account for the polymorphism.

More recently, Brockmann *et al.* (1979) have suggested that the criteria are met by the digger wasp, *Sphex ichneumoneus*. Females of this species dig and provision burrows for their eggs. An individual has a choice of digging her own burrow, or entering a burrow already dug by another wasp. The burrow may have been abandoned, in which case entering it is a good policy. Alternatively, the 'owner' may be away hunting. If so, she may find the interloper when she returns, and there is a fight; in these cases 'entering' is a less satisfactory strategy. In one population studied, the average payoffs to the strategies 'enter' and 'dig' were indeed equal. Individual females adopt sometimes one strategy and sometimes the other; they are mixed strategists. It is easy to see that the payoffs would be frequency-dependent in the required way. The only snag is that, although the data are beautifully in accord with the mixed e.s.s. hypothesis in one population (in Maine), they are not so in a population in Michigan.

There are many cases which it is tempting to interpret as mixed e.s.s., but in

which crucial data are missing. It is common to find variability in male mating strategies; e.g. client males in the ruff (Hogan-Warburg 1966; Van Rhijn 1973) or sea-going and precociously mature salmon (Jones 1969). Gadgil (1972) suggested that some such cases may be stable genetic polymorphisms. Others are obviously examples of a pure conditional strategy. For example, in the red deer the strategy 'when adult, hold a harem; when young, try to abduct a hind' is clearly a pure conditional strategy.

In the tree frog, *Hyla cinerea*, most males call, but some satellite males stay close to a calling male and try to intercept and mate with the females he attracts (Perrill *et al.* 1978). Some males employed the satellite strategy from night to night; others changed strategies from night to night, or on the same night. There is no consistent size difference between calling and satellite males. Thirty experiments in which a gravid female was released close to a pair of males resulted in the calling male achieving amplexus on 17 occasions and the satellite on 13. These facts are at least consistent with a mixed e.s.s. interpretation.

An entertaining example is provided by the study by Alcock *et al.* (1977) of the bee *Centris pallida*. Male bees adopt one of two strategies. 'Patrollers' search for sites where buried virgin females are about to emerge, dig for them and attempt mating. Fights over digging sites are common, and are usually won by the larger male. 'Hoverers' wait for females that have not been mated by patrollers, perhaps because a fight was in progress when they emerged. Hoverers are smaller than patrollers. Although measurements of mating success are not available, it seems certain that the larger patrollers are more fit. To a small male, hovering is making the best of a bad job. But the size of a male is determined by the amount of food provided by his mother. Small males are cheaper to produce, both because they need less food and because they are less likely to be parasitized. It is hard to see how producing small males could be forced on a female by circumstances. A possible explanation, pointed out to me by Dr Jane Brockmann, is that females are adopting a mixed e.s.s. and thereby forcing a pure conditional strategy on their sons.

It is early to say how often variation in contest behaviour is properly to be regarded as a mixed e.s.s. At this stage, the important point is that, in a mixed e.s.s., the payoffs to the different components of the strategy should be equal.

ARE ASYMMETRIES TAKEN AS CLUES?

The most contra-intuitive prediction of game theory is that 'ownership' may be taken as a cue to settle contests, even if it does not affect the likelihood of winning an escalated fight or the payoff for winning. To demonstrate that ownership can settle contests irrespective of differences in r.h.p. ('resource-holding power'; Parker 1974*b*), it is sufficient to show three things: (i) contests are won by owners; (ii) a contest between two specific individuals may come out sometimes one way and sometimes the other, according to who is the owner; (iii) if two contestants can both be persuaded that they are the owner of the same resource,

an escalated contest ensues of a kind not normally observed between owner and interloper.

It is not sufficient merely to establish (i), because that would be true if only strong individuals became owners in the first place. All these points were established by Kalmus (1941) for contests between groups of worker bees over food sources; more recently, they have been shown for contests over sun spots (mating territories) in the speckled wood butterfly, *Parage aegeria* (Davies 1978), and for contests over females in the Hamadryas baboon (Kummer 1971). Points (i) and (iii) were established for contests over hilltops (mating territories) in the butterfly *Papilio zelicaon* (L. E. Gilbert, personal communication). Baker (1972) showed that in the peacock butterfly, *Inachis io*, territorial contests are normally won by the owner after a spiral flight. If a second male settles in a territory (e.g. because the owner is absent courting), the contest is still usually settled in favour of the owner, probably because the interloper cannot find his way back to the territory after a spiral flight. However, if the interloper overcomes this difficulty, the contest is settled after further flights in favour of the male able to hold his position above and behind his opponent.

Parker (1978) lists some other cases in which there are strong reasons for thinking that ownership settles contests. It is likely that the phenomenon will prove to be general.

It is more readily accepted that asymmetries in size or weapons can settle a contest without escalation. Theoretical analysis (Maynard Smith & Parker 1976) confirms that acceptance of such asymmetries to settle contests can be an e.s.s., provided that the asymmetry is known unambiguously to both contestants. If recognition of the asymmetry is ambiguous then each contestant might perceive that it was superior (e.g. bigger), leading to an escalated contest. The asymmetry may be unambiguously recognized but a poor guide to the outcome of an escalated fight; in this case, the asymmetry may still be effective in settling contests provided the risks of escalation are high.

To give a recent example, Jakobsson *et al.* (1979) studied fighting in the cichlid fish *Nannacara anomala*. Pairs of males were matched carefully for size, a pair differing by less than 0.2 g in a total of 5 g, yet the heavier fish won in 10 out of 11 fights (Jakobsson, personal communication). The mouth fighting, which is a striking feature of their behaviour, may enable even small differences of weight to be detected, as was suggested for another cichlid by Apfelbach & Leong (1970). It is puzzling, however, that in other species size appears to have little effect on ultimate outcome. For example, Dow *et al.* (1976) claim that there is no correlation between size, coloration or fin area and winning in the fish *Aphysemion striatum* or *A. bivittatum* (although no data are given).

Real difficulties arise when there are asymmetries both of size and ownership in the same contest. Hyatt & Salmon (1978) observed 403 fights in the field between male fiddler crabs, *Uca pugilator*, over burrows. There was no average size difference between owners and interlopers. The owner won in 349 cases and the

interloper in 54. However, in these 54 cases the interloper was larger in 50 cases and smaller only in 1. It seems that ownership is typically taken as the arbiter, but that a sufficiently large size difference can override this. The males have claws strong enough to crush the abdomen of an opponent, but injury has never been observed in these fights.

A different balance is struck in the funnel-web spider, *Agelenopsis aperta* (Riechert 1978). Fights between females over webs were observed in the field. In 81 fights the larger female won in all but 7 cases. However, in 10 cases in which the size difference was less than 10% the owner won on 9 occasions. Thus size is taken as the primary cue, but ownership decides if the size difference is ambiguous. It is worth commenting that shaking a web gives rather reliable information about relative mass.

An even more difficult case is the study by Rand & Rand (1976) of contests between gravid *Iguana* females over egg-laying burrows; 80% of these fights are won by owners. Here, 'owner' means the female temporarily in possession of the burrow. However, since a female cannot build a burrow in a single shift but must take numerous rests, the 'interloper' may be the female who has done most of the digging on the burrow, and hence in a different sense may be the owner. Data on this point are not available, but can hardly be irrelevant. Unless previous work on a burrow in some degree establishes ownership, it is hard to see why a lizard would ever *start* digging a burrow, since only the lizard which finishes a burrow gains any payoff. (In the similar case, discussed above, of the wasp *Sphex ichneumoneus*, the winner of a fight over a burrow is usually the female that has provided the larger number of katydids (Dawkins & Brockman 1979). The length of fights correlates closely with the number of katydids provided by the loser.)

Some theoretical work has been done on contests with both ownership and size (r.h.p.) asymmetries. P. Hammerstein has considered a model in which size asymmetry, if present, can be assessed unambiguously and without cost. He considers two strategies, 'Bourgeois', which ignores r.h.p. asymmetry and considers only ownership, and 'Assessor', which plays H if larger than its opponent, D if smaller, and Bourgeois if there is no detectable size difference (*Agelenopsis* females, described above, adopt the Assessor strategy). If escalation is dangerous, the Assessor strategy is always an e.s.s. The Bourgeois strategy may also be an e.s.s., so that the population may have two alternative stable states.

IS INFORMATION TRANSFERRED DURING CONTESTS?

This question, and the related ones of bluff and lying, are the main problem areas for a game theoretical analysis of contest behaviour. Maynard Smith & Parker (1976) argued that animals would not convey information about their intentions on the following grounds. Suppose that a population existed in which individuals conveyed accurate information about their 'intentions' – i.e. about the level to which they would escalate. If an individual found that an opponent

was announcing a higher intention than its own, it would pay to retreat at once. Therefore a 'lying' mutant which announced a very high (but untrue) intention would be favoured by selection. Before long, everyone would be lying, and it would then pay to ignore the message being transmitted. The argument was put in more mathematical language, but it simply amounts to saying that you should not believe what an opponent at poker tells you.

The difficulty, of course, is that an extensive literature exists to demonstrate that, in some sense, information *is* transmitted during contests (see, for example, Simpson (1968) and Dow *et al.* (1976) on fish; Hazlett (1966, 1972), Hazlett & Bossert (1965) and Dingle (1969) on crustacea; Stokes (1962*a, b*), Dunham (1966) and Andersson (1976) on birds; and Rand & Rand (1976) on lizards). What these papers show is that (i) in the course of a contest animals use not one kind of act but a range of acts indicating different levels of aggression; (ii) an act contains information about the future intentions of the actor, since it is correlated with his future acts; and (iii) the information is transmitted, since the acts of the receiver are influenced by the actor. How is this apparent discrepancy between theory and observation to be reconciled?

No complete answer to this question can yet be given, because the data were often collected with no very clear functional question in mind. Some points are, however, worth making:

(i) Much of the information transmitted concerns 'resource-holding potential' (r.h.p.) (Parker 1974*b*) and not intentions. Briefly, r.h.p. affects the outcome of an escalated contest, and cannot be increased without cost in time or resources; intentions do not affect the outcome of an escalated contest, and can be altered without cost (except via their consequences). It is essential to distinguish between the messages 'I am 6 ft tall' and 'I am going to hit you', because the former cannot easily be a lie and the latter may be (this is not intended to detract from the importance of ruffs, manes, markings, etc. whose function is to make an animal look as large as possible). As stated earlier, an asymmetry in size can be used to settle a contest. If the asymmetry cannot be immediately perceived, an assessment phase of the contest can also be part of an e.s.s.; this holds even if assessment costs something, provided it is cheaper than escalation and yields a reasonably unambiguous result.

No doubt much of the behaviour described by Riechert (1978) in spiders and by Hyatt & Salmon (1978) in fiddler crabs is concerned with r.h.p. assessment, because they have also shown that size differences do influence outcome.

The information used in assessment should be difficult to fake: that is, it should be impossible for an individual by a small expenditure of resources to signal a high r.h.p. In American bighorn sheep, Geist (1966) has shown that differences in horn size can settle contests without a fight. Horns are expensive; they can amount to 10% of body mass. Geist makes the interesting suggestion that the great variability of horn size in these sheep is related to their function in assessment. In red deer, most fights are preceded by roaring contests. Roaring rate in mature stags

correlates with fighting success, and many fights are settled by roaring, without physical contact. Clutton-Brock & Albon (1979), who report these facts, point out that since fighting ability declines as an individual becomes exhausted during the rut, roaring rate may be a more reliable assessor than mere size. Further, roaring rate, like fighting ability, declines with advancing age, whereas size does not. To give one more example of an assessment which is difficult to fake, Davies & Halliday (1978) show that in toads the depth of pitch of calls is related to body size, and is used to decide whether to escalate contests over females.

(ii) Little information about long-term intentions is in fact transmitted. Thus an act may be correlated with an immediately preceding or following act, and yet be a poor guide to whether a contestant will ultimately retreat or attack. Caryl (1979) has reanalysed the data on tits (Stokes 1962*a, b*), grosbeaks (Dunham 1966) and skuas (Andersson 1976) and concludes that the displays are a poor predictor of future attack (although some displays are a good predictor of immediate retreat; I shall return to this point). Thus no one display is followed by attack with high probability; a particular display may be correlated with attack at one time of year but not another; in two of three species, the most aggressive display by one contestant did not correlate with retreat by the other; two different displays may have the same effect on the receiver but predict different things about the actor.

None of this makes much sense if one thinks that the function of these displays is to transmit information about intentions. In fish there is again little reason to think that intentions are signalled. Simpson (1968), in his study of *Betta splendens*, starts by saying that 'a criterion for a successful description of the threat display is the prediction of the outcome of encounters from the differences between the displays of the participants'. He finds one feature, the proportion of time during which the gill covers are raised, which does predict the outcome, but only during the last 2 min of a fight. Earlier in the same fights, winners exceeded losers in this respect in four cases, losers exceeded winners in two cases, and in two cases there was no difference; hardly a successful prediction.

Dow *et al.* (1976) studied the fish *Aphysemion striatum*. The most aggressive act (biting the opponent) was commoner in eventual winners in the *first* quarter of the fight, but there was no difference between contestants subsequently. Now it is inconceivable that it could be selectively advantageous for a fish to tell its opponent at the start of a fight that it intended to retreat, and then to continue the fight; it is as if a trade union negotiator were to say 'I demand a 50% increase for my members; furthermore, I will settle for 5%'. The explanation must lie in the artificiality of the experimental procedure (the fight was initiated by the sudden removal of an opaque barrier separating the fish), a point which is recognized by the authors.

Jakobsson *et al.* (1979) observed fights in the cichlid fish *Nannacara anomala*, also in the laboratory. Both the frequencies of acts, and the reaction pattern to each act from the other fish, were very similar in ultimate winners and losers,

differences appearing mainly towards the end of a fight. However, after receiving a bite (the only act likely to cause injury) a fish often retaliated by biting back. This illustrates the point that there may be a correlation between successive acts, so that 'information' is in a sense being transferred, yet an act may convey little information about long-term intentions to retreat or continue. As mentioned earlier, these fights are probably settled by size assessment during mouth wrestling.

(iii) 'Lying' may be impossible, or may be punished. The theoretical case against information transfer rested essentially on the argument that accurate information transfer would not be proof against invasion by a lying mutant. The concept of lying in an animal requires more careful definition. If in most members of a species the signal A is usually followed by the act X, then the signal A may be said to 'mean' X, and a mutant who performs signal A but *not* act X may be said to be lying. Rohwer's (1977) experiments on Harris sparrows are suggestive here. Typically, dark birds are aggressive and pale ones timid. To be dark can be interpreted as a signal, because all birds are capable of developing dark plumage, and do so in the spring. By painting dark birds light, and light ones dark, Rohwer constructed artificial 'liars'. These liars, of both kinds, received more than their fair share of attacks from other birds. More recently (Rohwer, personal communication) it has been shown that pale birds injected with testosterone were also persecuted, but if at the same time they were painted dark (bringing behaviour and signal into line) they could succeed as dominants.

Now if it were part of the behavioural strategy of normal individuals to 'punish' lying, this could stabilize accurate information transfer, rather as 'retaliation' can stabilize conventional as opposed to escalated behaviour. The difficulty, of course, is to explain why 'punishing' should be typical behaviour; it is easy to see that punishing would be good for the species, but less clear what could be the advantage to the individual.

(iv) The advantage of a 'surrender' signal. The most striking feature of Caryl's reanalysis of bird contest data was to show that although there are no good predictors of attack, there *are* good predictors of retreat – for example, erecting the crest in the blue tit. Similarly Dow *et al.* (1976) found in *Aphysemion* that a particular act, 'fin clamp', although generally rare, was the last act of the loser in 18 out of 21 fights. This was not a prediction of any game theory model, but it does make sense. It pays the sender to give the signal, because it prevents a damaging attack by the winner; it pays the winner to observe it (i.e. not to launch a damaging attack), because an attack would gain nothing and would risk retaliation; there would be no point in lying, because a bird which signals 'surrender' and then does not is no better off than a bird which gave no signal.

(v) Communication is useful if resources are divisible. The obvious divisible resource is space, e.g. in territorial behaviour. There are theoretical grounds for thinking that in a contest over a divisible resource, communication by graded signals could evolve. There is need for further work on this possibility.

DISCUSSION

Evolutionary game theory is, I believe, the appropriate framework for a functional interpretation of contest behaviour. There is no shortage of problems, but progress has been rapid. There are, however, some general criticisms of the approach that should be discussed.

First, there has been criticism of the basic model itself. The model assumes parthenogenetic inheritance; that is, it assumes that like begets like but does not allow for the complexities of sexual reproduction. Auslander *et al.* (1978) describe a two-species system with sexual reproduction and density-dependent population regulation, and show that although a static e.s.s. exists the populations may not reach this e.s.s. when genetic and population dynamics are included. Their results are of considerable interest, but do not seriously undermine the use of e.s.s. theory for the analysis of phenotypic evolution in single species. Further justification for the belief that, given sufficient genetic flexibility, selection will equalize fitnesses of different phenotypes at an e.s.s. is provided by Slatkin (1978).

The e.s.s. model also assumes an infinite and randomly mixing population. Riley (1978) has shown that the stability criteria for a finite population are different. Both criticisms are formally correct. It is certainly possible to construct cases in which sex or finite population size will alter the outcome. This should be borne in mind, but to introduce these complexities into the model at this stage would in my view be a mistake. It would be to abandon the simplicity and predictive power of the model in a fruitless pursuit of precision. There is, however, one extension of the basic model which is worth pursuing. Actual populations are viscous, so that relatives live close to one another. Contests are therefore often between relatives. Extensions of the model to allow for this have been proposed by Mirmirani & Oster (1978) and Treisman (1977), and, from a different standpoint, by Grafen (1979) and Hines & Maynard Smith (1979).

From an observational standpoint, the main criticism has been by Geist (1974). His main complaints were that we wrongly supposed that there is a distinction between 'dangerous' and 'conventional' behaviour in animal contests, and that we failed to do justice to earlier explanations of contest behaviour in terms of individual selection. There is, I think, some justice in these complaints. Geist is surely correct in emphasizing that animals do injure and even kill one another, and that their behaviour and weapons can be interpreted in terms of efficiency in defence and attack (Geist 1966). In fact, we were not concerned to deny this; indeed, our interpretations would be meaningless unless escalation and injury do sometimes occur. Nevertheless, there are phenomena, such as the acceptance of ownership discussed in § 4, or the 'deliberate' aiming at the best-protected part of an opponent, (see, for example, Dingle & Caldwell (1969) on stomatopods) which can reasonably be called 'conventional' and which demand explanation.

In fact, the disagreement between Geist (1974) and Maynard Smith & Price (1973) was more apparent than real. Part of the difficulty arose because of our

failure to notice that Geist had earlier put forward part of our argument. In addition to attempting a general formulation for the analysis of contests, we proposed that a specific strategy, namely 'retaliation', was likely to be a component of evolutionarily stable behaviour. I think that this conclusion is correct (despite some mathematical difficulties; see Gale & Eaves 1975), but it had been stated quite explicitly by Geist (1966). In a later analysis of contest behaviour in ungulates, V. Geist has given the concept of retaliation a more central position and has extended his earlier argument in an attempt to relate the types of weapons and behaviour to the ecology of different species. Had there been space, the role of retaliation would have been treated here as a fourth prediction of game theory; it was omitted only because it is observationally less controversial.

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