

established priority of access to a female is generally not challenged by another male; however, when two males both perceive themselves as having access to the same female, an escalated fight occurs (Maynard Smith 1982).

A recent study by Sigg and Falett (1985) extended that of Hammerstein et al. to demonstrate that hamadryas baboons would show respect for ownership of food items and feeding areas. Although the authors did not themselves mention game theory, their results can shed considerable light on the issue of whether respect for ownership can, by itself, be used to settle disputes. Sigg and Falett (1985) found that a dominant partner would not take a food container or fruits from a subordinate who had previously established possession. However, in dominance tests, where pieces of food were placed in between the two animals, the dominant one would not allow the subordinate to gain possession. Two choice experiments indicated that the important feature was who had used a feeding place or food container, rather than a general preference for familiarity. This suggests that a convention concerning acceptance of ownership (rather than fighting over each resource item) is operating, as Maynard Smith suggested.

Instead of relating their results to the game theoretic approach, Sigg and Falett emphasised the functional advantage of avoiding a costly fight, a speculation that was supported by the greater respect for ownership found in male-male pairs than in male-female or female-female pairs.

The cost involved in a damaging fight is an important component of game theoretic models such as the hawk-dove-bourgeois game, which is the one concerned with ownership (Maynard Smith 1974; 1976a; 1982). This involves two pure strategies, hawk and dove, and a conditional strategy, bourgeois, which responds like a hawk (attacks) when it is the owner of a resource, and like a dove (displays, but retreats if attacked) when it is the intruder. Maynard Smith showed that in a population consisting of three strategies, bourgeois was an evolutionarily stable strategy, indicating that conventional acceptance of ownership can be used to settle disputes even when there is no correlated asymmetry (RHP difference) or differences in payoff.

The cost incurred by a damaging fight is also an important component of Hammerstein's (1981) model, which considered cases where there was an asymmetry in RHP as well as ownership, in an analysis again based on the original hawk-dove game. He concluded that if the risk of injury through escalation was considerable compared to the value of the resource, contests could be settled by an uncorrelated asymmetry such as ownership (i.e., the bourgeois strategy), even if a correlated asymmetry (RHP difference) existed. However, if the RHP difference exceeded a critical value, it could be used to settle contests.

Of the examples cited by Hammerstein (1981) and Maynard Smith (1982) to support these predictions, one (concerning hermit crabs: Hyatt & Salmon 1979) could have involved unequal payoffs (see above) instead of a conventional acceptance of ownership, and in the other (on funnel-web spiders: Riechert 1979) size was the most important factor in settling the contests. In a further example where the resident shows an advantage (the bowl and doily spider: Suter & Keiley 1984), equal payoff has also been demonstrated, the resource being of greater value to the resident. In other cases, size (a correlated asymmetry) overrides ownership in determining the outcome of a contest (e.g., Hildrew & Townsend 1980; Petrie 1984).

There is apparently not one unambiguous illustrative example of Hammerstein's predictions in the literature, and hence it appears that models based on the war of attrition game (e.g., Maynard Smith & Parker 1976; Parker & Rubenstein 1981) are more appropriate for examining cases of ownership where there are other asymmetries. However, the circumstances in Sigg and Falett's study of respect for ownership in hamadryas baboons do fit the conditions of Hammerstein's model, and their results support the model's predictions for these circumstances.

Since the baboons differed in dominance, their encounters were asymmetric, both in RHP and ownership. For a male baboon, the risk of injury in an intermale fight is high, and the value of a specific food item relatively low, thus fulfilling the conditions under which Hammerstein predicted that an uncorrelated asymmetry could override a correlated asymmetry such as dominance. It is also interesting to note that when ownership had not been established, disputes were settled on the basis of the correlated asymmetry, i.e., dominance. The observation that among females (where the risk of injury is smaller) the dominant member of the pair is more likely to ignore ownership and take the object is also consistent with Hammerstein's predictions.

It is therefore likely that Hammerstein's model, which on previous evidence appeared unpromising, may be particularly relevant to ownership possession of discrete items which make a relatively low contribution to fitness, rather than in relation to territories and resources essential for reproduction. It would be interesting to look for other examples of respect for ownership under the conditions predicted by this model, especially in view of the relevance of the evolution of respect for ownership to the ultimate origins of human ownership conventions.

Reliability in signalling motivation

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In the beginning of his article Maynard Smith (1984) suggests that "evolutionary game theory has been developed to analyse the evolution of behaviour, or of other aspects of the phenotype, when fitnesses are frequency dependent." He illustrates the approach with the classical model of Fisher (1930), which explained the 1:1 sex ratio: "If there are more males in the population than females, then a female will have most grandchildren if she produces only daughters, and vice versa." If the behaviour of individuals could in fact be explained by the frequency of the behaviour of individuals in the population then evolutionary game theory could contribute new aspects to the understanding of behavioural adaptations, because previous to that suggestion, behavioural adaptations have been studied mainly by observations of pairwise interactions. But later in the article Maynard Smith develops models, based on asymmetries in resource holding power (RHP) between rivals. He suggests that "most pairwise contests, however, are complicated by the fact that there are differences not only of ownership but also of size and strength. The strategy 'assessor,' whereby an animal engages in an initial exchange of signals and continues to contest only if it estimates that it is at least as large as its opponent, is an ESS against strategies that ignore assessment" (p. 98). It is obvious that once an animal develops the strategy of assessor, its behaviour is to a large extent frequency independent. It is common knowledge that animals differ not only in their RHP, which is a consequence of their advantage in size, strength, and so on, but also in their motivation to fight. One animal may be hungry while the other is satiated. One animal has already copulated many times and exhausted itself while its rival is still fresh. One may have a brood to defend while the other is just starting to claim a territory. We also know from everyday experience that such asymmetries determine to a large extent which of two rivals is likely to win the conflict. For example, an animal who is hungry is more ready to invest in a conflict about food than a rival who is satiated and consequently has a smaller chance to gain from the conflict. Differences in motivation provide real advantages. It is reasonable for a hungry individual to invest more in fighting, that is, not necessarily to stop fighting even if it is wounded, if determination in fighting increases its

chances to win the food. On the other hand, it does not pay a satiated individual to have high motivation to fight over food because it may be wounded for the sake of food, which is marginal for it at that particular time.

If there were a way to signal differences in motivation in a reliable way these asymmetries could be used to resolve conflicts to the best interest of the two rivals by the exchange of signals. But Maynard Smith does not believe there is a reliable way to signal motivation, stating that "the classical ethological explanation, that animals exchange information about their 'motivation,' or 'intentions,' makes little sense from an evolutionary point of view, because honest signalling about motivation would not be evolutionarily stable, it would always pay to misinform, and therefore it would pay to disbelieve." Although he agrees that RHP may be signalled in a reliable way, he assumes that "motivation can be altered without cost." He suggests that "this distinction has not in general been recognized by ethologists." This seems to ignore the experience of ethologists who claim that they can often predict the future behaviour of an animal from its signals, which seem to display its motivation.

In 1977 I suggested a model that explains how the signalling of motivation may be reliable. An individual who displays higher motivation (to win a conflict or to attract collaborators) is demanded, by the pattern of the signal, to invest in signalling more than an individual who displays lower motivation. For example, animals signal greater motivation to attack by leaving cover, coming closer to their rivals, and even assuming postures near their rivals that are less efficient for attacking, such as relaxed muscles or the exposure of a vulnerable part of their body. The higher cost, in terms of risk, demanded of an individual who signals a higher motivation to attack, inhibits individuals with a lower motivation from signalling as if they had higher motivation. I termed the risk involved in signalling a "handicap," like the handicaps taken on by the superior contestant in races, chess, or golf, which advertize the claim of superiority. It is important to notice that such handicaps, which confer reliability on signals, may be assumed by individuals with a similar genotype but different in their momentary motivation. The differences of opinion I have had with Maynard Smith (1976b) concerning the application of the handicap principle to explain sexually selected characters (Zahavi 1975) are irrelevant to the possibility of using the model of the handicap for the advertisement of phenotypic differences. The evolution of cooperation is presented by Maynard Smith as a problem distinct from that of antagonistic interactions. But the mere exchange of signals requires cooperation (Zahavi 1977; 1981). Hence there is an element of cooperation in all cases in which rivals exchange signals. Also, all cooperative interactions have an element of rivalry. The conflict of interest between sexual partners (Williams 1966), parents and their offspring (Trivers 1974), and between group living animals (Emlen 1978; Zahavi 1976) is well known. [See also *BBS* multiple book review of Symons: *The Evolution of Human Sexuality* *BBS* 3(2) 1980.] Hence there should not be much difference between the analysis of antagonistic and collaborative interactions; both require reliable signals and both use the same evolutionary strategies to develop reliable signalling systems. That is probably why the signals used in male-male conflict are often so similar to those used to attract a sexual mate.

To summarize: I suggest that the observations of ethologists that animals display their motivation is supported by logical models. If animals signal their motivation and RHP and their rivals and collaborators can assess these signals, then the frequency of a behavioural strategy in a population is a consequence of all the pairwise interactions within a particular environment. This view is very different from that of "evolutionary game theory," which attempts to explain the adaptive significance of a behavioural strategy by its frequency in the population.

ACKNOWLEDGMENTS

I wish to thank Dina Ralt, Ilan Eshel, and my wife, Avishag Kahan, Zahavi, for their suggestions to the comment.

Author's Response

Ownership and honesty in competitive interaction

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Archer. Archer discusses whether ownership can be used to settle a contest in the absence of any difference between owner and intruder either in fighting ability or in the value of the resource. He points out that in most carefully investigated cases some difference has been found in one or the other of these respects. This is true but not relevant. If I asserted that motorcars can run without headlights, I would not change my opinion if someone pointed out that almost all cars do as a matter of fact have headlights. Of course, in most real contests there are differences in size or resource value between the contestants. My point is that such differences are not necessary for the evolutionary stability of what I have called the Bourgeois strategy. The work of Sigg & Faler (1985) that Archer cites to show that contests between baboons over food are settled by ownership, and not by fighting ability, confirms this.

Archer is quite right to say that the Bourgeois strategy is stable only if the value of the resource is less than the risk of injury (both measured as changes in fitness). This follows at once from an analysis of the Hawk-Dove game. However, it does not follow that ownership will only be relevant in trivial contests. For example, male lions jointly holding a pride respect ownership of oestrous females (Packer & Pusey 1982). This is not a trivial resource, but the gain in fitness involved is small compared to the cost of an escalated fight.

Archer suggests that the war of attrition game might be more appropriate for examining cases of ownership when there are other asymmetries. I think this is a misunderstanding. The essential difference between the war of attrition and the Hawk-Dove game is that in the former the contestant can choose any level of expenditure from a continuous distribution (e.g., length of time for which it will display), whereas in the Hawk-Dove game the choice is between discrete alternatives, with different potential costs (e.g., fighting or displaying at a distance). Which model is appropriate in any particular case depends on which of the two assumptions is nearer the truth. However, the choice of model does have an important impact on whether ownership can settle contests in the absence of any other asymmetries. The conclusion that it can (stated above) holds only for the Hawk-Dove game. A war of attrition between an owner and an intruder can be settled conventionally in favour of the owner only if there is some difference (which can be very small) either in average

igning ability, or in average payoff, in favour of owners. This does provide some theoretical justification for the belief that such differences are necessary. What is required, however, is that there be some average difference between owners and intruders. It is not necessary that this difference be perceptible in particular cases: Indeed, it can be reversed in some cases, and ownership will continue to settle contests.

Some of the conceptual difficulties people have over the idea of "ownership," and the "Bourgeois" strategy, should disappear if we consider plausible behavioural mechanisms. I do not suppose that animals have a concept of ownership. The Bourgeois strategy would be realised if an animal makes a large effort to hold a resource when it has been in undisputed possession of it for some time, but only a small effort if it has only just encountered the resource. This raises the interesting question of the time scale during which we can expect an animal in possession of a resource to change from making an effort to defend it to making a great effort. What is T , the time for which one must hold a resource before one is prepared to fight for it? Empirically, the answer varies from a few seconds in the speckled wood butterfly to many hours in the great tit. I suggest that the reason is as follows. T will be greater, but not too much greater, than the time for which an owner of a resource may be temporarily absent: If T were less than this, intruders could be frequently engaged in escalated fights. This explains the difference between butterflies and tits: It also explains why wagtails revisit their territories occasionally on days on which it does not pay them to feed in the territory (Davies & Houston 1984) – it would not pay to give another bird a conviction of ownership.

Zahavi. The question raised by Zahavi is perhaps the most interesting in current evolutionary game theory. How can signals made during contests be "honest," in the sense of correctly predicting what an animal will do next? The difficulty is clear. Suppose that in some population contests take place over items of food and that some signal is made by animals who are hungry and will attack an opponent physically if it does not withdraw. An opponent, receiving signal X, would do best to withdraw, unless it is so hungry that it is willing to risk an escalated fight. But if that is true, then it would pay animals who are moderately hungry, and not about to make an escalated attack, to signal X, because by so doing they will persuade most opponents to withdraw. In time, the relation between signal and future action will disappear, and then it will no longer pay to take notice of the signal. How, then, can honesty be maintained?

One answer, discussed in my target article, is that the best signals reflect, not a motivation like hunger, but a property like size or strength that cannot be faked. A second possibility is that hunger itself can be signalled in an unfakeable manner. A. Hansen (personal communication) reports that bald eagles, competing for food, display empty crops: A bird with an empty crop usually wins without further escalation. One cannot fake an empty crop. Zahavi (1977) proposed an alternative explanation. He proposed that signal X is intrinsically dangerous: For example, it consists of approaching close to an opponent, so that if the opponent attacks, the signaller cannot avoid physical contact. Then it would not pay any individual to

do X unless it really was hungry. The signal would remain honest.

I think I have in the past given too little credit to this suggestion of Zahavi's. My excuse is that he has never offered any formal proof that his suggestion will work. This is important, because an earlier application of his "hardship" idea (Zahavi 1975) to sexual selection fairly certainly cannot work (Maynard Smith 1976b; in press; Kirkpatrick 1986). What is required (in my opinion – I am sure Zahavi does not agree) is a formal model, in which the possible options, and their payoffs in fitness terms, are clearly defined, and in which it can be shown that to perform an action X when the payoff for winning is high, but not otherwise, is evolutionarily stable. In the absence of such a model, I do not see how one can evaluate the suggestion.

I have made several attempts to produce such a model. None were successful, but none were of a kind to persuade me that no model is possible. Recently, Enquist (1984) produced a model that does have the required properties, and some empirical evidence to support it. The model would take too long to describe, but the empirical evidence is easily summarised. He shows that when fulmars fight over food items those signals that are most risky, in the sense of most often leading to physical fights, are also the signals most likely to cause an opponent to withdraw.

Thus I now accept the idea, suggested by Zahavi (1977), that risky signals can honestly reflect motivation. More work is needed before we can judge how important this has been in generating the great variety of signals made during contests.

Finally, I do not understand why Zahavi thinks that what he is saying is in some way contrary to evolutionary game theory. My own view is that a game theoretic analysis is the only way of deciding whether his proposed explanation of honest signals is logically tenable.

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