The Logic of Animal Conflict

J. MAYNARD SMITH
School of Biological Sciences, University of Sussex, Falmer, Sussex BN1 9QG

G. R. PRICE
Galton Laboratory, University College London, 4 Stephenson Way, London NW1 2HE

Conflicts between animals of the same species usually are of "limited war" type, not causing serious injury. This is often explained as due to group or species selection for behaviour benefiting the species rather than individuals. Game theory and computer simulation analyses show, however, that a "limited war" strategy benefits individual animals as well as the species.

IN a typical combat between two male animals of the same species, the winner gains mates, dominance rights, desirable territory, or other advantages that will tend toward transmitting its genes to future generations at higher frequencies than the loser's genes. Consequently, one might expect that natural selection would develop maximally effective weapons and fighting styles for a "total war" strategy of battles between males to the death. But instead, intraspecific conflicts are usually of a "limited war" type, involving inefficient weapons or ritualized tactics that seldom cause serious injury to either contestant. For example, in many snake species the males fight each other by wrestling without using their fangs[1,2]. In mule deer (*Odocoileus hemionus*) the bucks fight furiously but harmlessly by crashing or pushing antlers against antlers, while they refrain from attacking when an opponent turns away, exposing the unprotected side of its body[3]. And in the Arabian oryx (*Oryx leucoryx*) the extremely long, backward pointing horns are so inefficient for combat that in order for two males to fight they are forced to kneel down with their heads between their knees to direct their horns forward[4]. (For additional examples, see Collins[5], Darwin[4], Hingston[6], Huxley *et al.*[7], Lorenz[8] and Wynne-Edwards[9].)

How can one explain such oddities as snakes that wrestle with each other, deer that refuse to strike "foul blows", and antelope that kneel down to fight?

The accepted explanation for the conventional nature of contests is that if no conventional methods existed, many individuals would be injured, and this would militate against the survival of the species (see, for example, Huxley[7]). The difficulty with this type of explanation is that it appears to assume the operation of "group selection". Although one cannot rule out group selection as an agent producing adaptations, it is only likely to be effective in rather special circumstances[10–12]. Consequently it seems to us that group selection cannot by itself account for the complex anatomical and behavioural adaptations for limited conflict found in so many species, but there must also be individual selection for these, which means that a "limited war" strategy must be differentially advantageous for individuals.

We consider simple formal models of conflict situations, and ask what strategy will be favoured under individual selection. We first consider conflict in species possessing offensive weapons capable of inflicting serious injury on other members of the species. Then we consider conflict in species where serious injury is impossible, so that victory goes to the contestant who fights longest. For each model, we seek a strategy that will be stable under natural selection; that is, we seek an "evolutionarily stable strategy" or ESS. The concept of an ESS is fundamental to our argument; it has been derived in part from the theory of games, and in part from the work of MacArthur[13] and of Hamilton[14] on the evolution of the sex ratio. Roughly, an ESS is a strategy such that, if most of the members of a population adopt it, there is no "mutant" strategy that would give higher reproductive fitness.

A Computer Model

A main reason for using computer simulation was to test whether it is possible even in theory for individual selection to account for "limited war" behaviour.

We consider a species that possesses offensive weapons capable of inflicting serious injuries. We assume that there are two categories of conflict tactics: "conventional" tactics, C, which are unlikely to cause serious injury, and "dangerous" tactics, D, which are likely to injure the opponent seriously if they are employed for long. (Thus in the snake example, wrestling involves C tactics and use of fangs would be D tactics. In many species, C tactics are limited to threat displays at a distance, without any physical fighting. We consider a conflict between two individuals to consist of a series of alternate "moves". At each move, a contestant can employ C or D tactics, or retreat, R. If a contestant employs D tactics, there is a fixed probability that his opponent will be seriously injured: a contestant who is seriously injured always retreats. If a contestant retreats, the contest is at an end and his opponent is the winner. A possible conflict between contestants A and B can be represented in this way:

A's move C C C C C C C C C C C C D C C C C C C C D

B's move C C C C C C C C C C C D C C C C C C C R

If a contestant plays D on the first move of a contest, or plays D in response to C by his opponent, this is called a "probe" or a "provocation". A probe made after the opening move is said to "escalate" a contest from C to D level. A contestant who plays D in reply to a probe is said to "retaliate". In the example shown above, A probes on his twelfth and twentieth moves; B retaliates after the first probe, but retreats after the second, leaving A the winner. At the end of a contest there are "pay-offs" to each contestant. The pay-offs are taken as measures of the contribution the contest has made to the reproductive success of the individual. They take account of three factors: the advantages of winning as compared with losing, the disadvantage of being seriously injured, and the disadvantage of wasting time and energy in the contest.

A "strategy" for a contestant is a set of rules which ascribe probabilities to the C, D, and R plays, as functions of what has previously happened in the course of the current contest. (No memory of what has happened in previous contests with the same or other opponents is assumed.) For computer simulation we programmed five possible strategies, each of which might be thought on *a priori* grounds to be optimal in certain circumstances. The strategies considered were as follows:

(1) "Mouse". Never plays D. If receives D, retreats at once before there is any possibility of receiving a serious injury. Otherwise plays C until the contest has lasted a preassigned number of moves.

(2) "Hawk". Always plays D. Continues the contest until he is seriously injured or his opponent retreats.

(3) "Bully". Plays D if making the first move. Plays D in response to C. Plays C in response to D. Retreats if opponent plays D a second time.

(4) "Retaliator". Plays C if making the first move. If opponent plays C, plays C (but plays R if contest has lasted a preassigned number of moves). If opponent plays D, with a high probability retaliates by playing D.

(5) "Prober-Retaliator". If making the first move, or after opponent has played C, with high probability plays C and with low probability plays D (but plays R if contest has lasted a preassigned number of moves). After giving a probe, reverts to C if opponent retaliates, but "takes advantage" by continuing to play D if opponent plays C. After receiving a probe, with high probability plays D.

The contestants were programmed as having identical fighting prowess, so that they differed only in the strategies they followed. The five strategies represent extremes, but from results with these it is possible to estimate the results likely to be found with intermediate types. The Hawk strategy is a "total war" strategy; Mouse, Retaliator, and Prober-Retaliator are "limited war" strategies. The question of main interest is whether individual selection will favour the former or one of the latter types.

The Simulation Test

The five strategies determine fifteen types of two-opponent contests. Two thousand contests of each type were simulated by computer, using pseudo-random numbers generated by an algorithm to vary the contests. The following probabilities were used: Probability of serious injury from a single D play=0.10. Probability that a Prober-Retaliator will probe on the opening move or after opponent has played C=0.05. Probability that Retaliator or Prober-Retaliator will retaliate against a probe (if not injured) by opponent=1.0. Pay-offs were calculated as follows: Pay-off for winning=+60. Pay-off for receiving serious injury= −100. Pay-off for each D received that does not cause serious injury (a "scratch")= −2. Pay-off for saving time and energy (awarded to each contestant not seriously injured) varied from 0 for a contest of maximum length, to +20 for a very short contest. The contest example shown earlier was one of the 2,000 Prober-Retaliator versus Prober-Retaliator contests.

Table 1 shows the average pay-off to each contestant in each type of contest. The number in a given row and column is the pay-off gained by the row strategy when the opponent uses the column strategy. For example, in contests between Mouse and Hawk, the average pay-offs are 19.5 to Mouse and 80.0 to Hawk.

To tell whether a strategy is evolutionarily stable against the other four strategies, we examine the corresponding column in Table 1. For example, for Hawk to be an ESS, it is necessary that it be the most profitable strategy in a population almost entirely of Hawks. In such a population, a given animal of any type will almost always have a Hawk as opponent. Therefore the pay-offs in the "Hawk" column apply. These show that Mouse and Bully are both more successful than Hawk. Therefore natural selection will cause alleles for Mouse and Bully behaviour to increase in frequency, and alleles giving Hawk behaviour to decrease. Thus Hawk is not an ESS.

Examining the other columns, we see that Mouse is not an ESS because Hawk, Bully, and Prober-Retaliator average higher pay-offs in a population almost entirely of Mouse. Nor is Bully an ESS. However, Retaliator is an ESS since no other strategy does better, though Mouse does equally well. And the last column shows that Prober-Retaliator is almost an ESS.

How would we expect such a population to evolve? It will come to consist mainly of Retaliators or Prober-Retaliators, with the other strategies maintained at a low frequency by mutation. The balance between the two main types will depend on the frequency of Mouse, since the habit of probing is only an advantage against Mouse. For the particular values in Table 1, it can be shown that if the frequency of Mouse is greater than 7%, Prober-Retaliator will replace Retaliator as the predominant type. It is worth noting that a real population would contain young, senile, diseased and injured individuals adopting the strategy Mouse for non-genetic reasons.

Thus the simulation shows emphatically the superiority, under individual selection, of "limited war" strategies in comparison with the Hawk strategy.

Briefly, the reason that conflict limitation increases individual fitness is that retaliation behaviour decreases the fitness of Hawks, while the existence of possible future mating opportunities reduces the loss from retreating uninjured.

This general result will not be altered by moderate changes in the program parameters, though very large changes will alter it. One way would be by changing the probability of serious injury from a single D from 0.10 to 0.90. This would give advantage to "Pre-emptive Strike" policies, making Hawk an ESS. (Such species are probably rare, because excessively dangerous weapons or tactics would be opposed by kin selection.) Another way to make selection favour "total war" behaviour would be by giving the same pay-off penalty for retreating uninjured as for serious injury. This would correspond to a species where an individual fights only a single battle in its lifetime, on which its reproductive success entirely depends. Our choice of +60 for winning, 0 for retreating uninjured, and −100 for serious injury represents a species where males have more than one opportunity to gain a mate. Changing these values to +60, −100, and −100 respectively, would make Hawk the optimal strategy. Conversely, +60, 0,

Table 1 Average Pay-offs in Simulated Intraspecific Contests for Five Different Strategies

| | | Opponent | | | | |
		"Mouse"	"Hawk"	"Bully"	"Retaliator"	"Prober-Retaliator"
Contestant receiving the pay-off	"Mouse"	29.0	19.5	19.5	29.0	17.2
	"Hawk"	80.0	−19.5	74.6	−18.1	−18.9
	"Bully"	80.0	4.9	41.5	11.9	11.2
	"Retaliator"	29.0	−22.3	57.1	29.0	23.1
	"Prober-Retaliator"	56.7	−20.1	59.4	26.9	21.9

−500 would represent a long-lived species with numerous opportunities to gain mates, where individual selection would still more strongly favour cautious strategies.

Real Animals

Real animal conflicts are vastly more complex than our simulated conflicts. (An interesting study by Dingle[15] shows that this holds true even at the lowly level of the mantis shrimp.) Probably our models are true to nature in emphasising a category distinction rather than an intensity distinction between "conventional" and "dangerous" tactics. In real animals, however, there exist not only the category distinction, but also individual differences in the intensity and skill with which each kind of tactic is employed. Also, in many species there are several categories of increasingly dangerous tactics, instead of only one.

The advantage from making a category distinction is that this simplifies behavioural requirements for limited conflict. It is probably easier for genetics to program a snake not to use fangs at all in certain situations than to program it to use fangs as intensively as possible up to intensity k, but not at intensities greater than k. Similarly, fair and foul blows are distinguished in boxing, and conventional and nuclear weapons in war.

Under the condition that any act of physical aggression is treated as a D act, the theoretical model will result in symbolic fighting by threat from a distance. This would be advantageous for a species that has an inherent difficulty in fighting physically at a safe level. For example, domestic and wild cattle, which have very dangerous horns and are somewhat clumsy in their charges, make much use of threat displays (stomping, pawing, bellowing). The model will not, however, give rise to conflict behaviour that is wholly symbolic and never backed up by physical aggression or other sanctions, since such behaviour would not be evolutionarily stable without some mechanism reducing the reproductive success of mutant individuals deficient in responding to the symbols. An interesting problem is how the felids, with their dangerous teeth and claws, limit their physical combats to non-fatal levels. Probably the explanation is that they have a hierarchy of many conflict categories and limit their probing to small escalations. Consequently, it takes repeated escalations to raise the conflict to the most dangerous level.

In most animal species there is probably a high correlation between prowess in C tactics and in D tactics. This means that C level conflict provides information to each animal about how its opponent is likely to perform if the conflict is escalated. This permits improvement in strategies over those used in the computer model. Instead of probing at random, an animal will be more likely to probe if its opponent is inferior in conventional fighting. On the other hand, if its opponent is very superior in conventional tactics, an animal will frequently retreat without waiting for its opponent to try a probe. Thus actual animals may combine Prober-Retaliator and Mouse capabilities.

If animals can adopt different strategies according to the opponent that confronts them, then an interesting possibility appears. The "Hawk" column of Table 1 shows that the best strategy against a Hawk is Mouse: that is, retreat immediately. If a species includes deviant individuals who follow the Hawk strategy and fight recklessly against every opponent, then it will be advantageous for ordinary members of the species to be able to estimate recklessness and avoid combat with Hawks. But if this happens, then it will be advantageous to simulate wild, incontrollable rage. And in fact the threat displays of some species do have an appearance of maniacal fury, hence there probably is some advantage in acting this way. However, if most species members simulate insane rage when actually their fighting is limited and controlled, then selection will favour indi-

viduals who partly discount the threat displays, and "call the bluff" of the pseudo-Hawks.

This leads to the suggestion that it might be advantageous for an individual animal to be maniacal in an easily recognisable way that could not be counterfeited. A possible instance of this is the phenomenon of going "on musth", which occurs periodically in adult male elephants[16,17]. The temporal glands secrete a dark brown fluid that runs down the face, giving a visual and olfactory sign that cannot be counterfeited. The madness of the animal "on musth" causes other elephants to avoid him, and this may give an increase in dominance status that persists for a time after the musth period is over.

Conflict in which Injury is Impossible

The previous section offers an explanation of why, in a species with offensive weapons capable of inflicting serious injury, escalated fighting may be rare or absent. In doing so, it raises a second problem. In a contest between opponents who are unable to inflict serious injury, victory goes to the one who is prepared to continue for a longer time. How are such contests decided?

Suppose that the pay-off to the victor is v. If a contest is ever to be settled, there must also be some disadvantage to the contestants in a long contest. If so, the only choice of strategy open to a contestant is of the period for which he is prepared to continue, and hence of the pay-off, say $-m$, he is prepared to accept. Thus if two contestants adopt strategies m_1 and m_2, where $m_1 > m_2$, the pay-off to the first is $v - m_2$ and to the second is $-m_2$. Our problem then is how a contestant should choose a value of m, or, more precisely, whether there is a method of choosing m which is an ESS.

To answer this question, we need a more precise definition of an ESS. We define $E_J(I)$ as the expected pay-off to I played against J. Then I is an ESS if, for all J, $E_I(I) > E_I(J)$; if for any strategy J, $E_I(I) = E_I(J)$, then evolutionary stability requires that $E_J(I) > E_J(J)$. The relevance of the latter condition is as follows. If in a population adopting strategy I a mutant J arises whose expectation against I is the same as I's expectation against itself, then J will increase by genetic drift until meetings between two J's becomes a common event.

It is easy to show that no "pure" strategy (that is, no fixed value of m) is an ESS. Thus in a population adopting strategy m, a mutant adopting $m + \epsilon$ would always do better (and if $m > v$, a mutant adopting a zero strategy would also do better). It is, however, possible to find a mixed strategy which is an ESS. Let strategy I be a mixed strategy which selects a value of m between x and $x + \delta x$ with probability $p(x)\delta x$.

Then if

$$p(x) = (1/v)\exp(-x/v) \tag{1}$$

it can be shown that I is an ESS.

We conclude that an evolutionary stable population is either genetically polymorphic, the strategies of individuals being distributed as in equation (1), or that it consists of individuals whose behaviour differs from contest to contest as in (1). There is no stable pure strategy, and hence no behaviourally uniform population can be stable.

Conclusions

There are many complications left out of these simple models. The analysis is, however, sufficient to show that individual selection can explain why potentially dangerous offensive weapons are rarely used in intraspecific contests; a stable strategy does, however, require that contestants should respond to an "escalated" attack by escalating in return. Also, if contests are settled by a process of attrition, then evolutionary stability requires that the popula-

tion be genetically polymorphic, or that individuals vary their behaviour from contest to contest.

A more detailed analysis will be published elsewhere.

Ideas similar to those described here have been applied to human neurotic behaviour by J. S. Price[18].

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Lithospheric Plate Motion, Sea Level Changes and Climatic and Ecological Consequences

JAMES D. HAYS & WALTER C. PITMAN III

Lamont-Doherty Geological Observatory of Columbia University

We demonstrate quantitatively that the world-wide Mid to Upper Cretaceous transgression and subsequent regression may have been caused by a contemporaneous pulse of rapid spreading at most of the mid-oceanic ridges between −110 to −85 m.y. The rapid spreading caused the ridges to expand and hence reduced the volumetric capacity of the basins. The subsequent regression was caused by a reduction in spreading rates beginning at −85 m.y.

THE global nature of the great marine transgressions and regressions such as occurred in the Upper Cretaceous has been recognised for nearly a century[1]. These fluctuations of sea level have been variously attributed to gradual filling of ocean basins by detritus displacing water onto the continents, down faulting of ocean basins to cause regressions[1] and simultaneous vertical movements of both continents and ocean basins[2,3]. The transgressions and regressions have been linked to orogenic cycles; it has been argued[2] that during intervals of low orogenic activity reduced horizontal compression caused continental subsidence relative to sea level, hence transgressions, and that conversely orogenic episodes produced increased horizontal compression, increased continental elevation and marine regression[4]. Late Cainozoic sea level changes are certainly attributable to glaciation, but this cause is not applicable to the Upper Mesozoic.

Changes in the volume of ocean basins could explain flooding of portions of continental surfaces. It has been proposed[5-7] that such changes occur due to alterations in the volume of the mid-oceanic ridges. Valentine and Moores[5] linked these volumetric changes to the assembly and breakup of super continents. Hallam[8] speculated that the Upper Cretaceous transgression and regression may have been caused by a contemporaneous pulse of rapid spreading which substantially increased the volume of the world ridge system. We show that this latter proposal is correct.

Cause of Upper Cretaceous Transgression

The lithosphere formed at a spreading ridge axis is initially hot and therefore elevated; as it moves away from the axis, it cools and subsides[9,10]. This cooling and subsidence is time dependent[11]; the depth to which any portion of flanking crust has subsided is essentially a function of age only. So one empirical age–depth relation fits most ridges regardless of spreading rate[11] (Table 1). Therefore, the volume of any ridge is a function of its spreading rate history and changes in the spreading rate cause, in time, changes in ridge volume. (It has been suggested that the axial portion of fast spreading ridges is deeper than that of slow spreading ridges[11]; however, subsequent analysis has shown that this is not systematically true[12].) Larson and Pitman[13] correlated anomaly lineations of Middle and Upper Mesozoic age in the Atlantic and Pacific. They calibrated these lineations with Deep-Sea Drilling Project data, thereby extending the magnetic polarity time scale to −160 m.y. From the geometry of these lineations they showed that during the Upper Cretaceous (−110 m.y. to −85 m.y.) there was an episode of rapid spreading in the central and south Atlantic and the Pacific. The geological evidence suggests an initial rise of sea level that began at or before the boundary between Upper and Lower Cretaceous (−100 m.y.), the cresting of this rise some time between the Turonian and Lower Maastrichtian (−90 and −70 m.y.) and a withdrawal that was most pronounced in the Maastrichtian but continued into the Cainozoic[14-17].