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Being Honest About One's Intentions: An Evolutionary Stable Strategy for Animal Conflicts

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In several vertebrate species it has been demonstrated that individuals recognize each other, and in many other species (even invertebrates) the conditions for it seem to be fulfilled. Individual recognition might therefore be a wide-spread phenomenon in the animal kingdom. This has consequences for the settlement of conflicts between animals: individuals may use information about the outcome of earlier conflicts even if the individuals do not differ in fighting ability. Conflicts will then be asymmetric, and bluff is very unlikely. Possible consequences of individual recognition for the settlement of conflicts are studied by means of simulation. Four strategies will be considered: (1) "Retaliator" (based on Maynard Smith's models and used as a control condition, (2) "Threat-right" (threatens towards a submissive and will follow with attack if the submissive does not retreat; retreats from a threatening or attacking dominant), (3) "Attack-right" [as (2), but without threatening], and (4) "Threat-dominance" [as (2), but with a low probability of threatening and attacking a dominant]. If the knowledge about strength or dominance of the other individuals is perfect, the "Threat-right" strategy (thus a warning before a real attack) turns out to be most successful under a wide variety of conditions. If that knowledge is not perfect (during the learning phase), other strategies can yield better results. The effects of a number of possibilities to settle dominance will be considered (outcome first escalated conflict, last escalated conflict, etcetera). These possibilities will be related to the strategies of settling conflicts, to the expected number of conflicts within the pair of individuals, and to variations in the strength of an individual.

1. Introduction

Most animals live in groups, which are often small. Then an individual meets only a limited number of conspecifics during its lifetime. In fact, the probability of an encounter between two individuals which have never met before is very low in most species. Most encounters occur between individuals which daily cross each other's path.

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Encounters do not necessarily influence the behaviour of the individuals concerned; an animal may continue its business after a meeting, unaffected by the presence of the other. In many instances, however, encounters strongly effect the behaviour of both parties involved. Encounters often give rise to conflicts: one animal has to give way to the other, one animal has to leave a newly discovered food resource, or one animal (a male) has to dismount from a female which was just ready for copulation.

We may question how, within these small groups of animals, conflicts are settled. Is it possible to apply the theories developed in the last few years (Maynard Smith, 1972; Maynard Smith & Price, 1973; Maynard Smith, 1974; Parker, 1974; Maynard Smith & Parker, 1976), or are their assumptions too simple? We are of the opinion that although these theories are very stimulating in discussions about animal conflicts, at least one essential factor has been neglected: experience from earlier conflicts with the same individual.

To trace the importance of this factor one has to realize that animals never live randomly amongst each other. For instance, during the spring male ruffs may spend most of their time on communal display grounds (Hogan-Warburg, 1966; van Rhijn, 1973). About seven (2–40) males, individually recognizable by humans, stay together for approximately 40 days on the same arena of about 15 m^2. The high degree of plumage diversity among these males seems to be evolved for individual recognition. On the arena the positions of the different males are very constant, and most aggressive encounters occur between neighbouring males. In jackdaws (Röell, 1978) most birds breeding in the same colony remain together for the whole year. They feed in the same flocks and roost communally. Most aggressive encounters occur between colony members, among which a fairly stable dominance hierarchy exists. Most threatening and fighting of a territorial male stickleback (van den Assem, 1967) occurs with a very limited number of individuals on neighbouring territories. Even in huge groups of wintering geese, individuals are not randomly distributed: it has been discovered that families (mates with the offspring of the last summer) remain together in winter flocks, and that the spatial distribution of families is also patterned (e.g. Raveling, 1970).

To summarize these data, for most vertebrates the conditions necessary for the establishment of personal relationships, and thus for individual recognition, seem to be fulfilled. We shall now consider to what extent individual recognition does in fact occur between animals. Cases of parents being acquainted with their offspring, and of mates recognizing each other, have been reported by a number of authors (e.g. Beer, 1975). Individual recognition also occurs between (potential) rivals. The existence of stable dominance hierarchies is a strong indication for it. Experimental evidence for recognition between rivals is available for a large variety of animals. For instance, in mammals it has been demonstrated in mice (Bowers & Alexander, 1967) and gerbils (Halpin, 1976). In birds; white-throated sparrows (Brooks & Falls, 1975*a*,*b*; Falls & Brooks, 1975), field sparrows (Goldman, 1973) and indigo buntings (Emlen, 1971). In fish; swordtails (Zayan, 1974, 1975) and even in invertebrates (hermit crabs, Hazlett, 1969; shrimps; Johnson, 1977). With respect to its mechanism, the roles of sound (Emlen, 1971; Goldman, 1973; Brooks & Falls, 1975*a*,*b*; Falls & Brooks, 1975), and smell (Bowers & Alexander, 1967; Gorman, 1976; Halpin, 1976) have clearly been established.

It is thus likely that individual recognition is a wide-spread phenomenon. Consequently, we may expect that, to settle a conflict with a certain opponent, an individual uses information about earlier conflicts with the same opponent. The contestant's estimate of winning an escalated conflict with a known opponent will therefore seldom be equal to the estimate of losing ($P \neq 0{\cdot}5$), and thus, symmetric conflicts must be extremely rare, but we are not the first to claim that (see e.g. Maynard Smith & Parker, 1976).

Asymmetric conflicts can easily be settled by using the asymmetry as a clue, provided that the asymmetry is unambiguously to both contestants (Maynard Smith & Parker, 1976; Maynard Smith, in press). In the case of individual recognition the result of earlier conflicts is sufficient as a clue. Information about this asymmetry needs not to be transferred during each new contest. This kind of information concerning the "resource-holding potential" or "RHP" (Parker, 1974) of the individuals, was distinguished by Maynard Smith (1980) from information about intentions. He argued that most information transmitted during contests concerns RHP, because it affects the outcome of an escalated contest, while intentions do not. We are of the opinion that signalling about intentions may be sensible, because it could determine whether a conflict will occur. A dominant individual may signal for instance: "I want to eat now, if you do not go away I shall hit you", or as an alternative: "I am not hungry, do not worry". In the case of individual recognition we therefore expect information about intentions to be the most important part of threat signals.

Several predictions about fighting and threat have been deduced from a model for symmetric conflicts ("the War of Attrition": Maynard Smith, 1974). One of these predictions implies that, during a conflict, an animal will not convey information about its intentions (duration of threat, attack probability, etc. Maynard Smith, 1974, in press; Maynard Smith & Parker, 1976). Support for this prediction was given in a stimulating paper by Caryl (1979), who re-analysed material which was originally presented as a plea for the opposite view (communication about intentions: Stokes, 1962*a*, *b*; Dunham, 1966; Andersson, 1976). This prediction is neither compatible with our expectation for a situation with individual recognition, nor with the traditional view of ethologists, who assumed that threat displays are designed for communication about intentions (e.g. Moynihan, 1955; Cullen, 1966; Smith, 1977). Some comments on Caryl's conclusions will be published elsewhere (van Rhijn, 1980).

2. The Rules of our Simulation

In order to support the verbal arguments for the importance of individual recognition in the settlement of conflicts, we decided to simulate conflicts in a group of a limited number of individuals with unequal fighting abilities. In addition we expected that by means of these simulations we would obtain a better insight into the conditions under which conflicts could be settled in the proposed way. To make our simulations comparable to earlier work, we used about the same principles as Maynard Smith & Price (1973). We also assumed that an animal could use two categories of conflict-tactics: conventional tactics (C) or threat, and dangerous tactics (D) or fighting. We also considered a conflict between two individuals to consist of a series of alternate "moves" of threat (C), fighting (D), or retreat (R). We considered four different stategies:

(1) "Retaliator" (used as a control condition). Plays C if initiating the contest. Plays C if opponent plays C, but plays R if the conflict has lasted a pre-assigned number of moves. If opponent plays D, retaliates by playing D, but plays R if injured during the fight.

(2) "Threat-right". Plays C if making its first move against a submissive or unknown conspecific. In the following moves plays D if submissive or unknown opponent plays C or D, but plays R if injured. Never takes an initiative against a dominant individual. If dominant plays C or D, play R.

(3) "Attack-right". Plays D if making its first move against a submissive or unknown conspecific. In the following moves plays D if submissive or unknown opponent plays C or D, but plays R if injured. Never takes an initiative against a dominant individual. If dominant initiates with C or D, plays R.

(4) "Threat-dominance". Plays C if making its first move against a submissive or unknown conspecific. In the following moves plays D if submissive or unknown opponent plays C or D, but plays R if injured. Takes no initiatives in most encounters with dominant individuals: if dominant initiates with C or D, plays R. With a low probability, however, plays against dominants as if they were submissive or unknown conspecifics.

Our control strategy (1) represents Maynard Smith & Price's (1973) "Retaliator" strategy. The pre-assigned number of moves was determined by means of formula (4) of "the War of Attrition" model (Maynard Smith, 1974, p. 214). Consequently it is an example of an Evolutionary Stable Strategy for symmetric conflicts. Individual recognition is irrelevant for this strategy. The other three strategies (2, 3 and 4) strongly depend on individual recognition: they are representations of dominance hierarchies of the peck-right or peck-dominance type (Schjelderup-Ebbe, 1935). The "Threat-right" (2) is characterized by a one-way traffic of initiatives from dominant towards submissive, starting with a warning (C), and escalating into a real fight (D) if that warning is ignored by the opponent. The "Attack-right" (3) can be distinguished from strategy (2) by the lack of a warning. Finally, in the "Threat-dominance" strategy (4) the one-way traffic of strategy (2) sometimes becomes bidirectional.

All our simulations were based on interactions in a group of ten individuals with different "fighting abilities". To these individuals we awarded strengths of respectively: 47, 52, 55, 57, 59, 61, 63, 65, 68 and 73, corresponding with a normal distribution with a mean of 60 and a s.d. of 7·75. All possible types of encounters between two strategies were considered. Taking account of initiative and combination of individuals, we got 90 different types of encounters if both contestants adopted the same strategy, and 180 if they accepted different strategies. In the cases that a submissive animal took no (or a restricted number of) initiatives against a dominant (strategies 2, 3 and 4) the dominant could take over the initiative.

The pay-offs we used were largely similar to those used by Maynard Smith & Price (1973). For winning we used a pay-off = +60, for receiving serious injury = −100, and for each single C-play = −1. The pay-off for each single D-play was varied to study the conditions under which the "Attack-right" strategy was successful. The probability of receiving serious injury was also varied in different simulations. Finally, the probability that "Threat-dominance" (4) plays against dominants as if they were submissive or unknown conspecifics was set = 0·10.

3. Perfect Knowledge about Strengths

In our first series of simulations we assumed that individuals adopting strategies (2), (3) or (4) had a perfect knowledge about the strengths of all individuals in the group. In this series the term "dominant" is equivalent to stronger, and the term "submissive" to weaker. The term "unknown" is not relevant for this series.

The suppositions for the first simulation were very simple. We used a pay-off for each single D-play $= -5$. With this figure we wanted to indicate that (independent of the risk of injury) fighting is more expensive than threatening (pay-off for each single C-play $= -1$). We further supposed that the stronger individual never becomes seriously injured and thus always wins the conflict. Finally, we set the probability of serious injury for the

TABLE 1

Average pay-offs

Contestant		Opponent (1)	(2)	(3)	(4)
Retaliator	(1)	+4	−33	−29	−35
Threat-right	(2)	+15	+30	+21	+28
Attack-right	(3)	+20	+28	+16	+27
Threat-dominance	(4)	+9	+25	+15	+24

Perfect knowledge about strengths; D-play $= -5$; P(injury/play) $= 0{\cdot}00$ (stronger), and $= 0{\cdot}20$ (weaker).

weaker individual per D-play received $= 0{\cdot}20$. The average pay-off ($n = 180$ for each figure) to each contestant is given in Table 1. It turns out that, for each opponent, strategy (1) is least successful, and strategy (2) most successful (except in confrontations with strategy (1), strategy (3) seems to be most successful).

It may be questioned whether the supposition that the stronger always wins and never becomes injured is very realistic. We therefore also considered another extreme, namely that for an individual the probability of winning an escalated conflict equals the ratio between its own strength and the sum of the strengths of itself and its opponent, or in a formula:

$$P(\text{winning}) = S(\text{own})/[S(\text{own}) + S(\text{opp})].$$

The probability of becoming seriously injured (loosing) is given by:

$$P(\text{injury}) = 1 - S(\text{own})/[S(\text{own}) + S(\text{opp})]$$
$$= S(\text{opp})/[S(\text{own}) + S(\text{opp})].$$

To make the results of this simulation comparable to the previous one, the mean number of serious injuries per pair of D-plays (one D of the one individual and one D of its opponent) was set $= 0{\cdot}20$. Consequently:

$$P(\text{injury/play}) = S(\text{opp})/5[S(\text{own}) + S(\text{opp})].$$

The pay-offs ($n = 180$ for each figure) are given in Table 2. It turns out that in conflicts with opponents adopting strategy (2), (3) or (4) (columns) strategy (1) is still least successful, and strategy (2) most successful. In conflicts with opponents adopting strategy (1), however, strategy (1) is most successful, and strategy (2) the least.

With a mean number of 0·20 serious injuries per pair of D-plays, the average pay-offs are strongly influenced by the cost of D-plays. Escalated

TABLE 2

Average pay-offs

Contestant		Opponent (1)	(2)	(3)	(4)
Retaliator	(1)	+2	+2	−1	−6
Threat-right	(2)	−21	+30	+25	+25
Attack-right	(3)	−15	+28	+22	+21
Threat-dominance	(4)	−12	+27	+21	+20

Perfect knowledge about strengths; D-play = −5; P(injury/play) = S(opp)/5[S(own) + S(opp)].

conflicts last on an average five pairs of D-plays, which is equivalent to a contribution of −25 to the pay-offs to each of the two contestants. We therefore investigated what happened when the mean number of serious injuries per pair of D-plays was set to a considerably higher value, namely 1·00. In that case escalated conflicts last on an average only one pair of D-plays, which is equivalent to a contribution of −5 to the pay-offs to each of the two contestants. An example is shown in Table 3 ($n = 180$ for each figure). Apart from the mean number of 1·00 serious injuries per pair of D-plays, all parameters for this simulation were equal to those underlying Table 2. It appears that (on the whole) strategy (2) is again most successful, and strategy (1) least. Further, in conflicts with opponents adopting strategy (1), the pay-offs to strategies (2), (3) and (4) become considerably higher than in Table 2. This is certainly due to the low number of D-plays in escalated conflicts. Finally, in conflicts with opponents adopting strategy (3) the pay-offs to all strategies [except (1)] become considerably lower than in Table 2. This last phenomenon is due to the fact that a submissive is unable to retreat before a dominant adopting strategy (3) performs its first D-play. Consequently the risk of injury is rather high if (3) is the opponent strategy. All peculiarities of Table 3 were also found in other simulations with a mean number of 1·00 serious injuries per pair of D-plays.

TABLE 3

Average pay-offs

Contestant		Opponent (1)	(2)	(3)	(4)
Retaliator	(1)	+2	-2	+3	-7
Threat-right	(2)	+8	+30	+3	+26
Attack-right	(3)	+2	+28	-4	+26
Threat-dominance	(4)	+6	+27	+3	+24

Perfect knowledge about strengths; D-play $= -5$; $P(\text{injury/play}) = S(\text{opp})/[S(\text{own}) + S(\text{opp})]$.

In most cases the success of the "Attack-right" strategy (3) is somewhat lower than the "Threat-right" strategy (2). This difference is closely bound up with the high cost of a D-play (-5; the first move of the "Attack-right" strategy) compared with the cost of a C-play (-1; the first move of the "Threat-right" strategy). One may wonder whether the cost of a D-play is the main cause of the lower success of the "Attack-right" strategy. To answer this question, we simulated conflicts where for each single D-play the pay-off was set to $= -1$ (equal to the pay-off for each single C-play). An

TABLE 4

Average pay-offs

Contestant		Opponent (1)	(2)	(3)	(4)
Retaliator	(1)	+2	+12	+9	+3
Threat-right	(2)	-9	+30	+25	+26
Attack-right	(3)	-4	+30	+24	+24
Threat-dominance	(4)	-2	+28	+23	+22

Perfect knowledge about strengths: D-play$=-1$; $P(\text{injury/play}) = S(\text{opp})/5[S(\text{own}) + S(\text{opp})]$.

example is given in Table 4 ($n = 180$ for each figure). Apart from the pay-off for a D-play $= -1$, this simulation is equivalent to that underlying Table 2. It turns out that both strategies [(2) and (3)] are almost equally successful. This conclusion was also attained in other simulations with a pay-off for a D-play $= -1$. Consequently, it seems that the differences in success between the "Threat-right" and "Attack-right" strategy are mainly due to differences in pay-offs for D-plays and C-plays.

Examining the results of these different simulations, one might become curious to the extent by which dominant and submissive individuals profit by the different strategies. We therefore separately analysed the pay-offs for the dominant and submissive individuals in each conflict. An example is given in Table 5 ($n = 90$ for each figure). This example is based on the same

TABLE 5

Average pay-offs to dominant and submissive individuals

Contestant		Dominant opponent (1)	(2)	(3)	(4)
Submissive					
Retaliator	(1)	−1	−56	−60	−53
Threat-right	(2)	0	0	−9	0
Attack-right	(3)	+1	0	−11	0
Threat-dominance	(4)	+2	−5	−16	−8

Contestant		Submissive opponent (1)	(2)	(3)	(4)
Dominant					
Retaliator	(1)	+6	+59	+58	+40
Threat-right	(2)	−41	+59	+59	+50
Attack-right	(3)	−32	+55	+55	+41
Threat-dominance	(4)	−26	+59	+59	+48

Perfect knowledge about strengths; D-play$=-5$; $P(\text{injury/play}) = S(\text{opp})/5[S(\text{own}) + S(\text{opp})]$.

simulations as Table 2. It turns out that for submissive individuals the "Retaliator" strategy (1) is very, and the "Threat-dominance" strategy (4) somewhat disadvantageous if the opponent adopts strategy (2), (3) or (4). For dominant individuals the "Attack-right" strategy (3) is disadvantageous (because of the cost of a D-play) if the opponent adopts strategy (2), (3) or (4). In other simulations the same conclusions could be drawn.

4. Learning Each Other's Strengths

It is seldom possible to determine the strength of an opponent only by looking at that individual. It is therefore plausible that, at least for the first encounter between two individuals, knowledge about each other's strengths is not perfect. In this section we want to consider how the knowledge about the strengths of other individuals can be obtained, and how (for each combination of strategies) the outcome of conflicts alter during this learning process.

For the first simulation in this series the suppositions were very simple again. The pay-off for each single D-play was set $= -5$, as in the simulations underlying Tables 1, 2 and 3. The mean number of serious injuries per pair of D-plays was set $= 0{\cdot}50$, which is intermediate to the values of $0{\cdot}20$ and $1{\cdot}00$, used in the previous simulations. We further assumed that the stronger individual always wins the conflict, and thus that the probability of serious injury for the weaker individual per D-play received $= 0{\cdot}50$. The dominance between two individuals was supposed to be settled after one escalated fight. It is easy to see that in this particular case (the stronger always wins) perfect knowledge about each other's strengths can be obtained after this single fight. For each pair of individuals we simulated five subsequent encounters (rounds). The average pay-off to each contestant in these five rounds ($n = 180$ for each round) is given in Fig. 1. It turns out that generally after the first round strategy (1) is least successful, and strategy (2) most successful. This result is not surprising, since (after this first round) the simulation is completely analogous to the previous series with perfect knowledge about strengths.

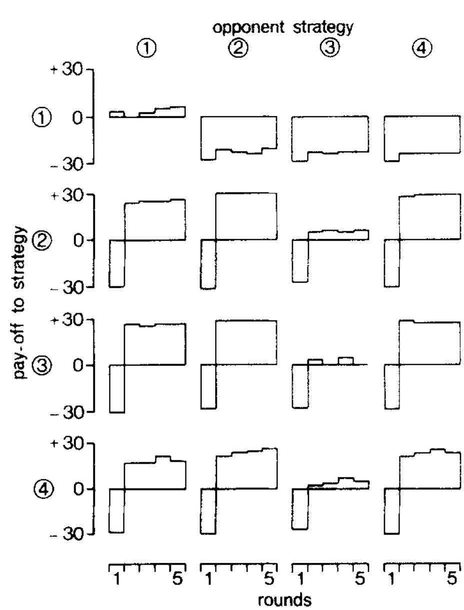

FIG. 1. Average pay-offs per round. P(injury/play) $= 0{\cdot}00$ (stronger), and $= 0{\cdot}50$ (weaker); dominance settlement based on the outcome of the first escalated conflict.

One might question what happens when perfect knowledge cannot be acquired. For that reason we changed one supposition in the previous simulation: the probability of winning an escalated conflict was set to:

$$P(\text{winning}) = S(\text{own})/[S(\text{own}) + S(\text{opp})],$$

and thus the probability of serious injury per D-play received to:

$$P(\text{injury/play}) = S(\text{opp})/2[S(\text{own}) + S(\text{opp})].$$

The dominance between two individuals was settled after one escalated conflict. The outcomes of subsequent escalated conflicts did not alter this dominance relation. The results are shown in Fig. 2. It appears that in conflicts with opponents adopting strategy (2), (3) or (4), strategy (1) is still least successful (although some improvement can be observed in comparison to Fig. 1), but strategy (2) is no longer the most successful: it is surpassed by strategy (3). It conflicts with strategy (1) as an opponent, strategy (1) is most successful.

In Figs 1 and 2 the average pay-offs remain almost constant after the first round. This is due to the fact that a dominance relation is settled for ever

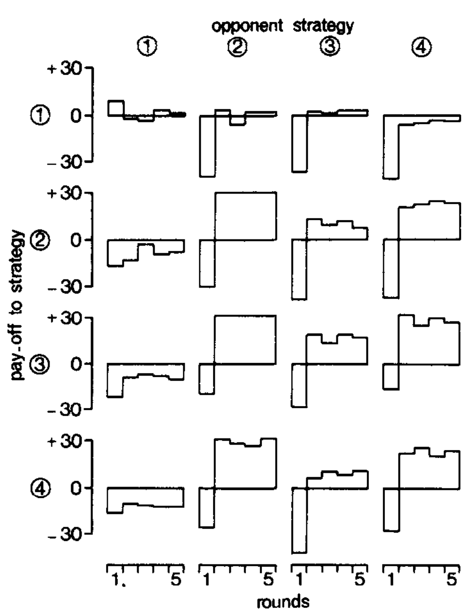

FIG. 2. Average pay-offs per round. $P(\text{injury/play}) = S(\text{opp})/2[S(\text{own}) + S(\text{opp})]$; dominance settlement based on the outcome of the first escalated conflict.

during the first escalated conflict, which normally occurs in the first round. We also studied the effect of variable dominance relations. This was done by changing one supposition in the previous simulation, namely the one concerning the settlement of dominance relations. We analysed three possibilities:

(a) the dominance is determined by the outcome of the last escalated conflict (Fig. 3),
(b) the dominance is settled if one of the contestants won at least one more escalated conflicts in encounters of that pair, than the other contestant (Fig. 4), and
(c) the dominance is settled if one of the contestants won at least three more escalated conflicts in encounters of that pair, than the other contestant (Fig. 5).

In Figs 3 and 4 we simulated five subsequent rounds again for each pair of individuals ($n = 180$ for each round or column). In Fig. 5, 25 subsequent rounds were simulated; averages were determined for each group of five rounds ($n = 900$ for each group or column). In Figs 3 and 4 a gradual increase of the success of strategy (1) can be observed. In Fig. 3 strategy (1)

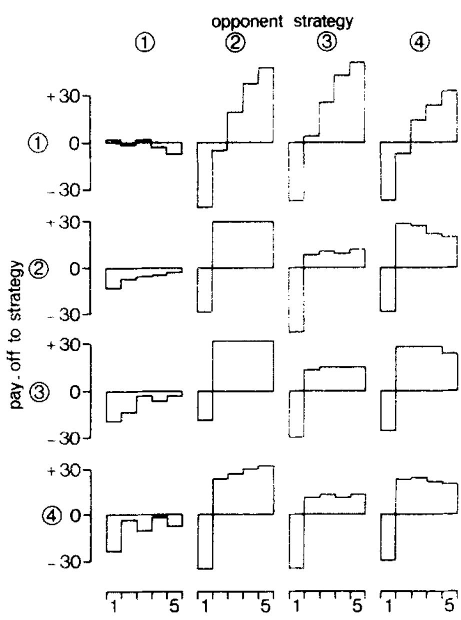

FIG. 3. Average pay-offs per round. $P(\text{injury/play}) = S(\text{opp})/2[S(\text{own}) + S(\text{opp})]$; dominance settlement based on the outcome of the last escalated conflict.

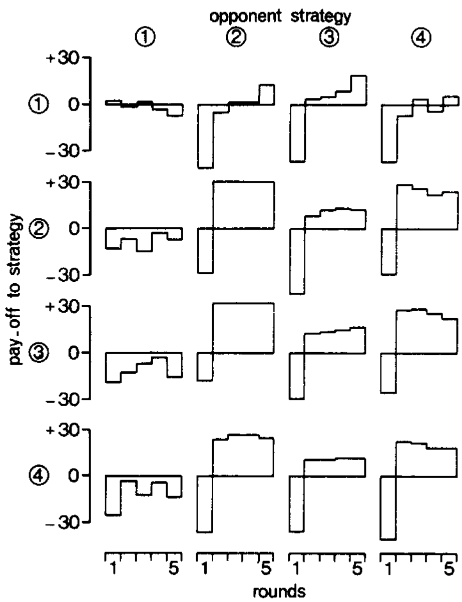

FIG. 4. Average pay-offs per round. $P(\text{injury/play}) = S(\text{opp})/2[S(\text{own}) + S(\text{opp})]$; dominance is settled in a pair if one of the contestants won at least one more escalated conflict than the other contestant.

even becomes the most successful strategy. In Fig. 5 the success of all strategies increase. In Figs 4 and 5 strategy (3) is most successful, at least in conflicts with opponents adopting strategy (2), (3) or (4). In conflicts with strategy (1) as an opponent, strategy (1) remains most successful.

The strong increase of the success of strategy (1) in Fig. 3, and to a smaller extent in Fig. 4, is due to the fact that strategy (1) retaliates against dominant individuals adopting strategy (2), (3) or (4). Escalation occurs and the dominant is not necessarily the winner. Consequently a change in the dominance relation may occur in favour of strategy (1). A change in the opposite direction will never occur with respect to strategies (2) and (3), and seldom with respect to strategy (4) (escalates with a low probability in conflicts with dominants). Thus, the animal using strategy (1) gradually rises in the dominance hierarchy, and reaches a much higher position than can be expected on the basis of strength. The same phenomenon (but less strongly) can be observed by strategy (4).

We were surprised by the low success of strategy (2) in the simulations underlying Figs 2, 3, 4 and 5. In confrontations with strategies (2), (3) and (4), strategy (2) appeared to be less successful than strategy (3). In other

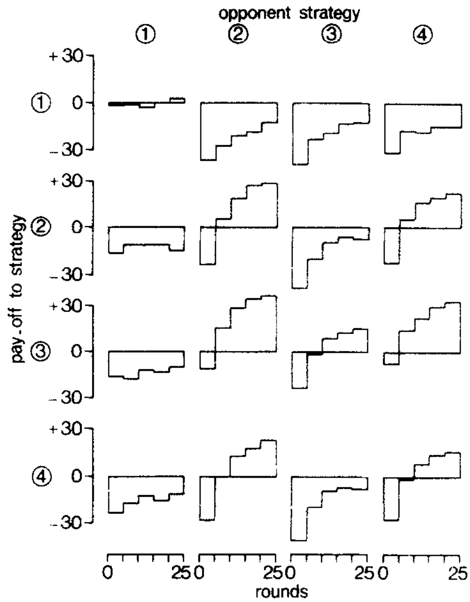

FIG. 5. Average pay-offs per five rounds. $P(\text{injury/play}) = S(\text{opp})/2[S(\text{own}) + S(\text{opp})]$; dominance is settled in a pair if one of the contestants won at least three more escalated conflicts than the other contestant. Note the deviating scale on the x-coordinate.

words, "being honest about intentions" is not an Evolutionary Stable Strategy under the given assumptions. One may wonder why. We are of the opinion that the high mean number of serious injuries per pair of D-plays (0·50) is the most important factor causing the success of strategy (3). The "Attack-right" strategy (3) always initiates escalation, and is thus less likely to receive injury than the opponent strategy. If the number of injuries per pair of D-plays was lower, the advantage of taking the initiative for escalation must be smaller. We therefore give an example of one case in which the mean number of serious injuries per pair of D-plays was set = 0·10. All other suppositions were similar to the simulations underlying Fig. 4. Thus:

$$P(\text{injury/play}) = S(\text{opp})/10[S(\text{own}) + S(\text{opp})], \quad \text{and}$$

the dominance is settled in a pair of individuals if one of the contestants won at least one more escalated conflict in encounters of that pair, than the other contestant. The results are shown in Fig. 6. It turns out that in confrontations with strategies (2) and (3), strategy (2) is most successful, as we expected; in confrontations with strategy (1), strategy (1) remains the best.

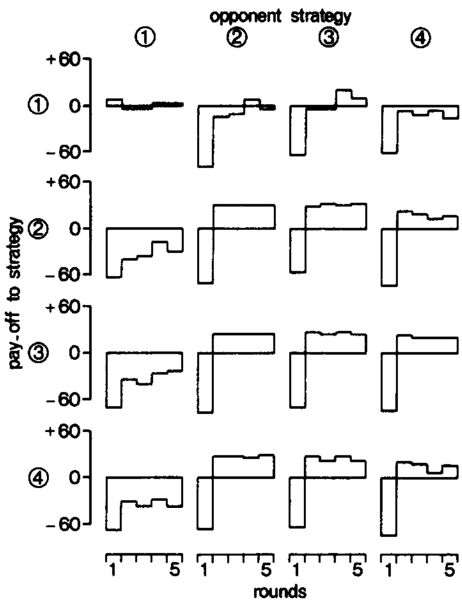

FIG. 6. Average pay-offs per round. $P(\text{injury/play}) = S(\text{opp})/10[S(\text{own}) + S(\text{opp})]$; dominance is settled in a pair if one of the contestants won at least one more escalated conflict than the other contestant. Note the deviating scale on the x-co-ordinate.

5. Discussion

After reading the previous sections one might still wonder which strategy is most successful if animals are able to recognize each other. Our simulations do not give a simple answer to this question; they only predict how nature should work under certain preassigned conditions. One has to realize that the conditions are chosen by the theoretician and not by nature. Nevertheless we are of the opinion that simulation is a fruitful technique. It helps to formulate the right questions and to perform the right experiments in the study of conflicts between real animals. Further, by changing the conditions in the simulation one can obtain a better insight into the relation between assessment strategy for conflicts and the conditions in real animals. We shall therefore try to evaluate the results of the four strategies used in our simulations.

The average pay-off to the "Retaliator" strategy is low in most contests. In confrontations with strategies (2), (3) and (4), the "Retaliator" strategy is less successful in most cases than the other strategies, except when strategy (1) is strongly favoured by the settlement of dominance (e.g. Fig. 3). In confrontations with strategy (1), the "Retaliator" strategy seems to be more successful in most cases than the other strategies. This is particularly the case when for the weaker contestant the probability of winning an escalated conflict is not far below 0·5, e.g.

$$P(\text{winning}) = S(\text{own})/[S(\text{own}) + S(\text{opp})].$$

When the weaker contestant almost always loses an escalated conflict, the "Retaliator" strategy is less successful than the other strategies if the opponent adopts strategy (1) (e.g. Fig. 1). It is therefore likely, that, if individual recognition is possible in a population in which all individuals adopt the "Retaliator" strategy, no other strategies will evolve, unless the probability of winning an escalated conflict is very low for the weaker contestant. On the other hand, if a population consists of individuals adopting strategy (2), (3) or (4), it is very unlikely that mutants adopting the "Retaliator" strategy will increase in frequency.

In most situations with perfect knowledge about strengths, the "Threat-right" strategy is more successful than the other strategies if the opponent strategy is (2), (3) or (4) (Tables 1–4 and Fig. 1). It is easy to see that if the knowledge about dominance (not necessarily based on strength) is perfect, the "Threat-right" strategy is also more successful than the other strategies. In that case the dominance hierarchy is an imperfect indicator of victory in an escalated fight, but the outcome of—for instance—the first escalated conflict between two individuals (Figs 1 and 2) is a perfect indicator of the dominance relation between these individuals. Similar cases have been analysed by Maynard Smith & Parker (1976). They demonstrated that if some kind of cue (in our case: outcome of the first escalated conflict) can be estimated accurately, this cue will be used as a conventional means (threat) of settling conflicts. Only in situations with imperfect knowledge about both strengths and dominance, is strategy (2) not necessarily more successful than the other strategies. For that reason the supposition that unknown conspecifics are treated in the same way as submissive individuals [strategies (2), (3) and (4)], seems to be rather unrealistic and needs further research in real animals.

The success of the "Attack-right" strategy in a situation with perfect knowledge about strengths was mainly reduced by the high cost of a D-play in comparison to a C-play (Table 2 and 4). In the learning situation, however, the "Attack-right" strategy could be very successful if the risk of injury per D-play received was high (Figs 2–5), because the probability of winning was high for the initiator of escalation. Thus, individuals adopting strategy (3) are able to reach high positions in the dominance hierarchy. The advantage of strategy (3) in learning situations disappears when the risk of injury per D-play received is low (Fig. 6), thus if escalation continues for a long period.

The "Threat-dominance" strategy was never most successful in our simulations. This is not very surprising. In the case of perfect knowledge only pure strategies (Maynard Smith & Parker, 1976) are evolutionary stable. Strategy (4) is not pure because of the chance of escalation against dominants. In the learning situation escalation against dominants can improve the position in the dominance hierarchy. Strategy (1), however, which always escalates against dominants profits much more by this phenomenon. Nevertheless, we do not believe that strategy (4) is a nonsense strategy. Its low success is closely linked with the simplicity of the conditions used in our simulations. For instance, if the strength of an individual is not constant over time, and if the dominance hierarchy can be adapted in the course of time, the "Threat-dominance" strategy may be the most successful under certain conditions.

In fact the settlement of dominance relations is part of a strategy. We considered four different ways of dominance settlement:

(a) the outcome of the first escalated conflict counts (Figs 1 and 2),
(b) the outcome of the last escalated conflict counts (Fig. 3),
(c) in a pair one contestant won at least one more escalated conflict than the other contestant (Figs 4 and 6), and
(d) in a pair one contestant won at least three more escalated conflicts than the other contestant (Fig. 5).

To reduce the possibility that mutants adopting other strategies will increase in number in a population with individuals playing the "Threat-right" or the "Attack-right" strategy, the outcome of the first escalated conflict (a) is a safe and cheap expedient to settle the dominance. In populations with individuals playing the "Threat-dominance" strategy, the outcome of the last escalated conflict (b) is an expedient to maintain a high position in the dominance hierarchy, if mutants adopting strategy (2) or (3) arise. Both other ways of settling a dominance relation [(c) and (d)] can be important in situations where the strength of an individual is not constant over time. If encounters within pairs of individuals are very common, the considerable investment of a dominance settlement on the basis of a difference of at least a number of winnings of escalated conflicts (d) may be necessary. If encounters are not so common, a difference of one (c) winning of an escalated conflict can be sufficient.

To conclude this paper a few things have to be said about the trustworthiness of signals in conflicts between animals and the evolution of bluff. One of the predictions of the "War of Attrition" model (Maynard Smith, 1974) was that information about the probability to attack should not be conveyed (information about intentions). This model refers to symmetric conflicts so that its predictions may be relevant for conflicts between individuals which are unknown to each other. Maynard Smith & Parker (1976) also considered the possibility of bluff in asymmetric conflicts. They reasoned that "if contests are settled by asymmetric cues", "the evolution of features which exaggerate apparent size (or whatever feature is used as a cue)" may be important (p. 174). We want to stress that if individual recognition plays a role in the evaluation of that asymmetric cue, bluff (about intentions and RHP) can hardly evolve, because bluffers shall mostly be recognized.

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