THE EVOLUTION OF SOCIAL DOMINANCE
I: TWO-PLAYER MODELS

by

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(Acc. 26-V-2003)

Summary

A difference in dominance rank is an often-used cue to resolve conflicts between two animals without escalated fights. At the group level, adherence to a dominance convention efficiently reduces the costs associated with conflicts, but from an individual's point of view, it is difficult to explain why a low ranking individual should accept its subordinate status. This is especially true if, as suggested by several authors, dominance not necessarily reflects differences in fighting ability but rather results from arbitrary historical asymmetries. According to this idea, rank differentiation emerges from behavioural strategies, referred to as winner and loser effects, in which winners of previous conflicts are more likely to win the current conflict, whereas the losers of previous conflicts are less likely to do so. In order to investigate whether dominance, based on such winner and loser effects, can be evolutionarily stable, we analyse a game theoretical model. The model focuses on an extreme case in which there are no differences in fighting ability between individuals at all. The only asymmetries that may arise between individuals are generated by the outcome of previous conflicts. By means of numerical analysis, we find alternative evolutionarily stable strategies, which all utilize these asymmetries for conventional conflict resolution. One class of these strategies is based on winner and loser effects, thus generating evolutionarily stable dominance relations even in the absence of differences in resource holding potential.

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[2] The authors wish to thank Charlotte Hemelrijk, Bernard Thierry and an anonymous referee for their useful suggestions to improve the quality of the manuscript.

Behaviour 140, 1305-1332

Introduction

An efficient way to reduce the disadvantages associated with group living is to decide the inevitable conflicts of interests between group members by means of ritualised conflict resolution strategies (Maynard Smith, 1982), rather than by physical fighting. Such strategies make use of some asymmetry between individuals other than the outcome of an escalated fight to resolve conflicts (Maynard Smith & Parker, 1976; Hammerstein, 1981). An often-used asymmetry is a difference in dominance rank (Schjelderup-Ebbe, 1922).

Although the establishment of dominance relations takes away the need to engage in costly fights in every small quarrel, this ‘solution’ has merely moved the problem to another level. Instead of having to resolve many small conflicts over resources, individuals now have to resolve one large conflict, that is, they must decide on the issue which of them will obtain the dominant status.

This decision could be based on some underlying asymmetry between individuals (Landau, 1951a), such as a difference in size or another aspect of their resource holding potential (RHP). When dominance status is always determined by the outcome of escalated fights, and when these fights are always won by the largest individuals, these individuals might automatically become dominant. Theoretical considerations indicate, however, that such *direct* determination of dominance by RHP asymmetries cannot account for the ordered structure of social hierarchies observed empirically (*e.g.* Schjelderup-Ebbe, 1922), unless the RHP asymmetries between individuals are unrealistically large (Landau, 1951a; Mesterton-Gibbons & Dugatkin, 1995).

Yet, when there are relatively small RHP differences between individuals, social ranks could still be *indirectly* determined by RHP asymmetries. This requires that individuals can accurately observe the small RHP differences and, most importantly, that all individuals adhere to a convention, such as ‘the larger one is allowed to be dominant’ (Parker, 1974; Maynard Smith & Parker, 1976; Hammerstein, 1981). Now, rank differentiation between large and small individuals does not arise because the smaller individual is unable to win, but rather because the smaller individual submits to a convention that assigns it the subordinate status. Such conventions can be used even when the size differences between individuals are only small, or when size differences do not accurately reflect actual RHP differences

(Hammerstein, 1981). However, since the asymmetries between individuals are usually based on fixed individual characteristics, this mechanism cannot explain a number of experimental results. For example, experiments using cockroaches (Dugatkin *et al.*, 1994) and cichlid fish (Chase *et al.*, 2002) have shown that repeatedly reconstituting groups of individuals may result in completely different dominance hierarchies, indicating that dominance status need not at all be determined by fixed asymmetries between individuals.

Indeed, several authors have argued that dominance may be based on random historical or social asymmetries generated by the interactions between individuals (Landau, 1951b; Hogeweg & Hesper, 1983; Bonabeau *et al.*, 1996; but see Bonabeau *et al.*, 1999). For example, individuals that have previously won conflicts may have a higher tendency to behave aggressively in the current conflict, while losers in previous conflicts may act more submissively. These two effects — in the literature known as winner and loser effects (Chase *et al.*, 1994), respectively — result in a positive feedback between past performance and future probabilities of winning, from which rank differentiation may emerge (Hogeweg & Hesper, 1983). Winner and loser effects based on various proximate mechanisms have been described for a variety of species in the literature (see Chase *et al.*, 1994, and references therein). Moreover, theoretical models have shown that winner and loser effects give rise to rank differentiation within pairs of individuals and, as an emergent property at the group level, a stable linear dominance hierarchy, even without underlying asymmetries between individuals (Landau, 1951b; Hogeweg & Hesper, 1983; Hemelrijk, 1999).

At the very least, these lines of evidence suggest that dominance is not completely determined by individual characteristics such as RHP asymmetries. Yet, the implication that dominance is — to some extent — based on random historical asymmetries leads one to ask why the subordinate individual should accept its subordinate status. Why should a low-ranking individual not fight, when its status was assigned arbitrarily and when, consequently, its chances of winning are fair? Winning would entitle it to the long-term benefits of the dominant status, and it would seem that these benefits should certainly outweigh the costs of a few extra fights, especially when one takes into consideration that dominance relations can persist for very long times.

These considerations indicate that the evolutionary stability (Maynard Smith & Price, 1973) of dominance based on winner and loser effects is far from obvious. One can rightfully ask whether winner and loser effects can evolve when the outcome of a previous interaction is arbitrary, that is, when the conflict outcomes hold no information about underlying RHP asymmetries. One can also question whether winner and loser effects may function as evolutionarily stable mechanisms to obtain information about hidden RHP asymmetries. To be sure, the history of winning and losing fights provides indirect information about differences in fighting ability. It is, however, not at all clear how large these asymmetries have to be in order to support evolutionarily stable winner and loser effects.

In this paper, we attempt to approach these questions by means of game-theoretical methods. We will develop an idealized model of repeated animal conflicts, and analyse the conditions under which a dominance convention based on winner and loser effects may evolve. For the sake of our argument, we concentrate initially on an extreme case in which there are no RHP differences at all between individuals. This allows us to investigate whether winner and loser effects can exist without such asymmetries. Moreover, we focus our attention in this paper on rank differentiation within pairs of individuals. Therefore, we restrict ourselves to the analysis of a two-player model. In a companion paper (Van Doorn *et al.*, this issue), we extend our model to more than two players, allowing us to investigate the formation of social hierarchies.

Model description

Game theory is well suited to analyse evolutionary problems where the success of a given strategy depends strongly on the strategies of other players, as in the case of conflict resolution strategies (Maynard Smith, 1982). However, the game-theoretical approach has a severe limitation in that it allows for the analysis of highly idealised models only. Models that attempt to give right to the biological complexity often run into the problem of delimiting the strategy space in such a way that mathematical analysis is still tractable.

In our case, the same problem occurs, since conflict resolution strategies may depend in a complicated way on the outcome of past conflicts (not only between the focal individual and its opponent, but also between the focal and other opponents, or between the opponent and the other individuals in the group). Moreover, individuals may behave differently depending on whether previous conflicts were resolved by means of ritualised or escalated fights.

To cope with this problem, we will develop a number of idealised models, rather than a single more realistic model. This allows for an exploration of the biological complexities in several directions, without losing the tractability of the individual models.

Our first abstraction is that we describe conflicts between two individuals as a (slightly modified) Hawk-Dove game (Maynard Smith, 1982). That is to say, we assume that, whenever a conflict over some resource arises, individuals independently choose between two actions, designated Hawk and Dove. An individual playing Hawk is willing to escalate the conflict if the opponent does not retreat. An individual playing Dove retreats if the opponent escalates. Hence, if a Hawk meets a Dove the conflict is resolved without an escalated fight, and the Hawk obtains the resource. We will interpret Hawk-Dove interactions as ‘dominance interactions’. If two Doves meet, the conflict is resolved without aggression, and either one of the players obtains the resource with equal probability, or they equally split the resource (we consider these two cases separately). Finally, if two Hawks meet, the conflict escalates, until one of them is injured and the other gets the resource. For the moment, we restrict ourselves to the special case where both players have an equal probability of winning the escalated conflict. This assumption allows us to investigate whether dominance, based on winner and loser effects, can be evolutionarily stable without any underlying RHP asymmetries. According to these rules, the payoffs for a focal individual are as follows

Focal	Opponent	
	Hawk	Dove
Hawk	$\begin{cases} V - D, & \text{if the focal wins} \\ -C - D, & \text{if the focal loses} \end{cases}$	$V - D$
Dove	0	$\begin{cases} \frac{1}{2}V, & \text{if the resource is equally divided} \\ V, & \text{if the focal obtains the resource} \\ 0, & \text{if the opponent obtains the resource} \end{cases}$

The parameter V denotes the value of the resource, and C denotes the cost of losing an escalated fight. Note that our payoffs differ slightly from those of the classical Hawk-Dove game: we included a small cost D associated with playing Hawk. In the case that two players play a single round of this modified Hawk-Dove game, the evolutionarily stable probability of playing Hawk, denoted p, can be calculated as

$$p = \frac{V - 2D}{C}. \tag{1}$$

For $D = 0$ one recovers the well-known mixed evolutionarily stable strategy (ESS) of the classical Hawk-Dove game (Maynard Smith, 1982).

We assume that individuals have a large number of conflicts. To be precise, the probability that two individuals will not interact again is taken to be $1/T$, such that, on average, individuals interact T times. Our next idealisation is to assume that individuals can only remember the outcome of the preceding conflict and have no information about earlier conflicts. This restricts the strategy space to a class of simple memory-dependent strategies. In order to delimit the strategy space further, one needs to make assumptions about the information that is actually available to individuals.

In this paper, it is assumed that, whenever an individual meets an opponent, the individual will use information about the previous conflict with this particular opponent only. So, individuals do not take into consideration any information that relates to either their own or their opponent's relation with other individuals. The effect of the use of such social information in conflict resolution strategies is discussed in the companion paper (Van Doorn *et al.*, this issue). The restrictions imposed in the present paper allow us to describe all interactions between individuals in a group (whatever its size) as repeated pairwise conflicts between 'isolated' pairs of players. Under these assumptions, an individual may find itself in six different situations: it may have won or lost the previous conflict after an escalated fight, it may have won or lost after a dominance interaction or, it may have obtained the resource or not after an interaction without aggression. A conflict resolution strategy $\vec{p}$ is now defined as a vector of six strategic parameters

$$\vec{p} = (p_{hhw}\ p_{hhl}\ p_{hd}\ p_{dh}\ p_{ddw}\ p_{ddl}), \tag{2}$$

which prescribe the probability to play Hawk when an individual finds itself in either one of these six situations. The first two letters of the subscripts denote the actions of the focal and its opponent, respectively, in the previous conflict (h for Hawk, d for Dove). The third letter of the subscript, where necessary, denotes the outcome of the previous conflict (w for 'win', *i.e.* when the resource was obtained, l for 'lose' otherwise). The six strategic parameters are allowed to vary between δ and $1 - \delta$, where δ is a small number (see Appendix). This 'trembling hand' approach (Selten, 1975) is used to introduce occasional errors in decision-making, preventing the evolution of equilibrium solutions that are sensitive to such errors.

Information levels

The fact that we distinguish between the strategic variables p_{ddw} and p_{ddl} implies that an individual is assumed to be able to discriminate between Dove-Dove interactions in which it obtained the resource and Dove-Dove interactions in which it did not. This presupposes that the resource is not equally divided when both players play Dove. Otherwise, it would be impossible to designate a winner and a loser of the interaction. Nevertheless, we may still account for the case that the resource is equally divided, without resulting in any asymmetry between individuals, by imposing the constraint $p_{ddw} = p_{ddl}$. In fact, one may consider other constraints too, reflecting for instance limited mental capacities. These constraints result in what we will refer to as models of different 'information levels'.

At the lowest information level (which we will refer to as information level NONE), individuals use no information whatsoever regarding the outcome of the previous conflict. At level NONE, individuals may only vary their overall tendency to play Hawk, as implied by the constraint $p_{hhw} = p_{hhd} = p_{hd} = p_{dh} = p_{ddw} = p_{ddl}$. At the highest information level (level ALL), no restrictions on the strategic parameters are imposed (with the exception of $p_{ddw} = p_{ddl}$ for the scenario where the resource is divided), corresponding to the case where individuals are able to distinguish all possible conflict outcomes and may behave differently in each of the six possible conflict situations. Intermediate information levels correspond to situations where individuals may only distinguish victories (cases in which the resource was obtained) from defeats (cases in which the resource was not obtained) (level DVD), or situations where individuals discriminate between victories and defeats and, in addition, behave differently after escalated fights (level DVD-HH) or Dove-Dove interactions (level DVD-DD). Table 1 shows the restrictions imposed on the strategic parameters for each of these information levels.

Equilibria of the model

The model was analysed by a combination of analytical and numerical techniques (see the Appendix for details). We first calculated the expected payoff, $W(\vec{q}, \vec{p})$, of a rare mutant playing strategy $\vec{q}$ in a resident population where all individuals play strategy $\vec{p}$. From the payoff function, one obtains fitness gradients, which, under suitable assumptions (Hofbauer & Sigmund, 1998, Chapter 9: adaptive dynamics), determine the direction and rate of evolution of the strategy $\vec{p}$.

The results presented throughout this paper were obtained by simulations for one particular choice of parameters ($V = 0.3$, $C = 1$, $D = 0.025$, $T = 100$). Under these parameter conditions, the evolutionarily stable probability of playing Hawk for a single round of the Hawk-Dove game is given by $p = 0.25$ (equation (1)). We checked other parameter conditions and found qualitatively similar results, at least as long as individuals have a large number of interactions ($T \gg 1$) and as long as fighting is costly and the cost of playing hawk is low relative to the value of the resource ($0 < D < V < C$).

In order to determine what kind of strategies evolve in the model, we ran a large number of simulations using the fitness gradient approach explained in the Appendix. Each simulation was started from random initial conditions and continued until convergence to an equilibrium. For most information levels (Table 1), multiple stable equilibria exist. The equilibria can be classified into five clearly distinguishable categories (Fig. 1): mixed (M), dominance (D), alternating (A), peaceful (P) and strange (S). Most categories contain a number of different equilibria, which all share the defining properties of the particular class of equilibria. Below we will describe the defining properties of the equilibrium categories. An overview is presented in Fig. 2 and Table 2.

The simplest equilibrium type is the 'mixed' equilibrium. It occurs only when individuals have no memory and use no information whatsoever about the previous conflict (information level NONE). In this case, the game is identical to a simple Hawk-Dove game. Indeed, for the mixed equilibrium of information level NONE, the values of all strategic parameters are identical and equal to the mixed ESS of a single Hawk-Dove game (equation (1)).

The 'dominance' equilibria are characterized by a winner and loser effect: the winner of the previous fight is willing to escalate, whereas the loser is less likely to do so, which results in a positive correlation between the outcomes of past and future conflicts. This can most easily be seen from a time series of decisions that we generated for these strategies. For example, a typical time series of the decisions of two players playing the dominance strategy D_3 (Table 2) against each other would be

$$\begin{array}{l} \text{player 1: } d \\ \text{player 2: } d \end{array} \begin{pmatrix} d \\ h \end{pmatrix}_3 \begin{array}{c} h \\ h \end{array} \begin{pmatrix} d \\ h \end{pmatrix}_3 \begin{array}{c} h \\ h \end{array} \begin{pmatrix} h \\ d \end{pmatrix}_8 \begin{array}{c} h \\ h \end{array} \begin{pmatrix} d \\ h \end{pmatrix}_4 \begin{array}{l} h \ldots \\ h \ldots \end{array},$$

TABLE 1. *The different information levels of the two-player model*

Model variant 1: undividable resource
one of the players obtains the resource after a Dove-Dove interaction

Level	Interpretation	Constraints
NONE	Use no information	$p_{hhw} = p_{hhl} = p_{hd} = p_{dh} = p_{ddw} = p_{ddl}$
DVD	Discriminate cases in which the resource was won (Victories) from cases in which it was not (Defeats)	$p_{hhw} = p_{hd} = p_{ddw}$ $p_{hhl} = p_{dh} = p_{ddl}$
DVD-HH	As level DVD, but, in addition, remember whether the previous conflict was resolved by Hawk-Hawk interaction or otherwise	$p_{hd} = p_{ddw}$ $p_{dh} = p_{ddl}$
DVD-DD	As level DVD, but, in addition, remember whether the previous conflict was resolved by Dove-Dove interaction or otherwise	$p_{hhw} = p_{hd}$ $p_{hhl} = p_{dh}$
ALL	Use all available information	none

Model variant 2: dividable resource
the resource is split equally after a Dove-Dove interaction

Level	Interpretation	Constraints
NONE	Use no information	$p_{hhw} = p_{hhl} = p_{hd} = p_{dh} = p_{ddw} = p_{ddl}$
DVD	Discriminate Victories from Defeats	$p_{hhw} = p_{hd}$, $p_{hhl} = p_{dh}$ $p_{ddw} = p_{ddl}$
ALL	Use all available information	$p_{ddw} = p_{ddl}$

where the brackets are used to abbreviate repeated (series of) decisions, h is shorthand for the decision 'play Hawk' and d for 'play Dove'. We assume that all players play 'Dove' in their first interaction with a new opponent. As this time series shows, there are periods in which one individual plays Hawk in every interaction and the other individual plays Dove. During these periods, the individual that plays Hawk can be interpreted to dominate the other individual, resulting in an unequal division of the resource between the players. A period of dominance asymmetry ends with an escalated fight, after which the dominance relation between the players may either be reversed or not.

Another dominance strategy, D_4, is characterised by prolonged series of escalated conflicts followed by a long lasting dominance relation:

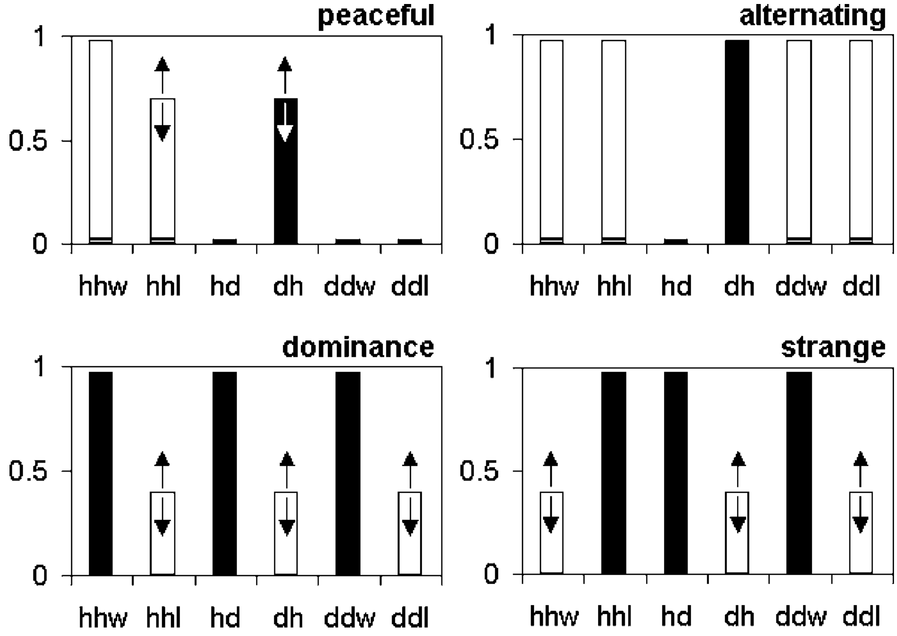

Fig. 1. Characteristics of the different types of equilibria. Except for the mixed equilibrium, which is described in the text, the four plots show for every category of equilibria the probabilities of playing Hawk in each of the six different situations in which an individual may find itself. Each equilibrium category has distinguishing features, which are indicated by black bars. The other strategic parameters are of lesser importance (indicated by white bars). Strategic parameters may vary between different equilibria belonging to the same category (as indicated by arrows, or by showing alternative high/low values). Upper left: Peaceful strategies satisfy two conditions. Individuals do not fight after Dove-Dove (*ddw* or *ddl*) or Hawk-Dove (*hd*) interactions and individuals do not always fight after a Dove-Hawk (*dh*) interaction. The different peaceful equilibria differ in their behaviour after Hawk-Hawk (*hhw* or *hhl*) interactions, which, however, hardly ever occur. Upper right: In alternating equilibria, all strategic parameters approach pure strategies. Most importantly the strategic parameters p_{hd} and p_{dh} approach 0 and 1, respectively. Consequently, individuals alternate between two roles. Lower left: Dominance equilibria are characterized by the property that individuals that won the previous conflict will always play Hawk (black bars). Lower right: Strange equilibria are similar to dominance equilibria, except that the loser of an escalated fight, rather than the winner, continues to play Hawk.

$$\begin{array}{ll} \text{player 1:} & d \\ \text{player 2:} & d \end{array} \begin{pmatrix} h \\ h \end{pmatrix}_7 \begin{pmatrix} h \\ d \end{pmatrix}_{24} \begin{pmatrix} h \\ h \end{pmatrix}_5 \begin{pmatrix} d \\ h \end{pmatrix}_{19} \begin{array}{l} \ldots \\ \ldots \end{array}$$

‘Alternating’ equilibria are conventions in which the resources are equally divided over the players. In these equilibria, individuals alternate between

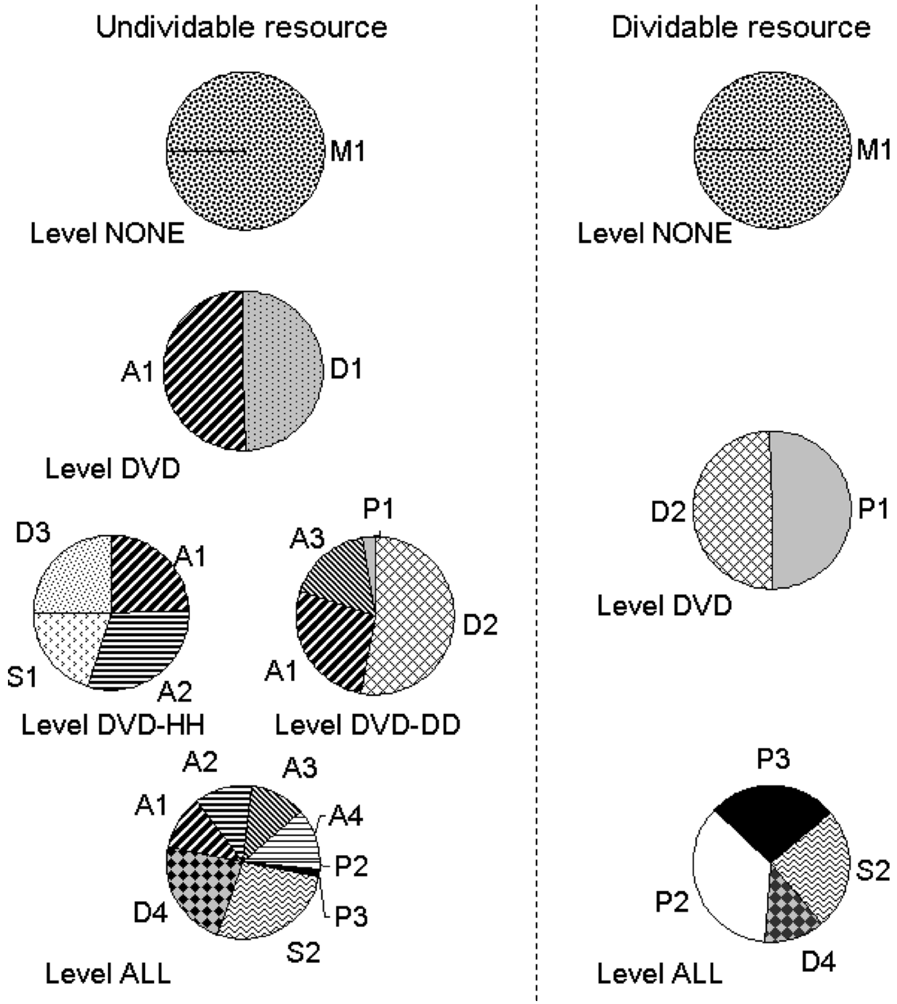

Fig. 2. Equilibria of the two-player model. For every information level, 400 simulations were run, starting from random initial conditions, until convergence to an equilibrium. The pie diagrams show the different equilibria that were found at the given information level as well as the proportion of simulations in which they were reached by evolution. As explained in Fig. 1, unique labels (M, D, A, P or S, shown next to the pie slices) could be assigned to every equilibrium. These labels can also be found in Table 2, which show the values of the six strategic parameters for every equilibrium. Parameters as in Table 2.

an aggressive and a subordinate role. As a result, the players take turns in claiming the resource, and both obtain an equal share:

TABLE 2. *Equilibria of the two-player model*

Type[1]	Label[2]	Level[3]	Values of strategic parameters[4]					
			p_{hhw}	p_{hhl}	p_{hd}	p_{dh}	p_{ddw}	p_{ddl}
M	M_1	NONE	0.25	0.25	0.25	0.25	0.25	0.25
D	D_1	DVD	1	0.24	1	0.24	1	0.24
	D_2	DVD, DVD-DD	1	0.25	1	0.25	1	1
	D_3	DVD-HH	1	0	1	0.32	1	0.32
	D_4	ALL	1	0.86	1	0	1	1
A	A_1	DVD, DVD-HH, DVD-DD, ALL	0	1	0	1	0	1
	A_2	DVD-HH, ALL	1	0	0	1	0	1
	A_3	DVD-DD, ALL	0	1	0	1	1	0
	A_4	ALL	1	0	0	1	1	0
P	P_1	DVD, DVD-DD	0	0.74	0	0.74	0	0
	P_2	ALL	0	1	0	0.73	0	0
	P_3	ALL	1	0	0	0.73	0	0
S	S_1	DVD-HH	0	1	1	0.32	1	0.32
	S_2	ALL	0.86	1	1	0	1	1

1) Equilibria were classified into five categories: M (mixed), D (dominance), A (alternating), P (peaceful) and S (strange).

2) Label used in Figs 2 and 3 and text.

3) See Table 1 for a description of the information levels.

4) 400 simulations were started for every level from random initial conditions and continued until convergence to an equilibrium. The values of the strategic parameters were kept between 0.025 and 0.975 (see the Appendix). For convenience, the values 0 and 1 are used to represent these extreme values. Parameters were: $V = 0.3$, $C = 1.0$, $D = 0.025$, $T = 100$.

$$\begin{array}{l} \text{player 1: } d \\ \text{player 2: } d \end{array} \begin{pmatrix} hd \\ dh \end{pmatrix}_{11} \begin{array}{c} hd \\ dd \end{array} \begin{pmatrix} hd \\ dh \end{pmatrix}_{16} \begin{array}{c} \ldots \\ \ldots \end{array}$$

The different alternating strategies differ only in the resolution of Hawk-Hawk and Dove-Dove situations, which occur with a low probability only (when one of the player has made a mistake). Because of the low frequency of escalated fights, mean population fitness is higher for alternating strategies than for dominance strategies.

Moreover, individuals may also equally divide the resources without aggression at all (*i.e.* without playing Hawk). This results in a 'peaceful' strategy for which mean population fitness is even higher than for alternating strategies:

$$\begin{matrix} \text{player 1:} \\ \text{player 2:} \end{matrix} \begin{pmatrix} d \\ d \end{pmatrix}_{19} \begin{pmatrix} hd \\ dh \end{pmatrix}_{3} \begin{pmatrix} d \\ d \end{pmatrix}_{25} \begin{pmatrix} hd \\ dh \end{pmatrix}_{4} \begin{matrix} h \\ d \end{matrix} \begin{pmatrix} d \\ d \end{pmatrix}_{54}$$

Peaceful strategies evolve when the resource is equally split after a Dove-Dove interaction but they also have a small range of attraction when this is not the case. This indicates that the peaceful strategies are sensitive to deviations from an exactly symmetric resolution of Dove-Dove interactions. The difference in mean population fitness between peaceful and alternating strategies is caused by the small cost of playing Hawk, as determined by the parameter D. When there is no cost associated with playing Hawk ($D = 0$), peaceful strategies can be invaded and replaced by alternating strategies.

The final category of equilibria comprises of ‘strange’ strategies. They are the paradoxical counterparts of dominance strategies, where the loser instead of the winner of escalated fights is allowed the dominant status. Although this class of equilibria does not seem to make sense from a biological point of view, similar solutions have been found in other game theoretical models. They occur because any asymmetry between individuals (in our case, the outcome of escalated fights) can be used to settle a conflict in both a common sense (D strategy) and a paradoxical manner (S strategy) (Maynard Smith, 1982). Both common sense and paradoxical solutions are evolutionarily stable. However, paradoxical solutions will only evolve from a situation where the asymmetry is ignored, when the asymmetry between individuals is completely payoff-irrelevant (*i.e.* irrelevant with respect to the expected costs and benefits of the current conflict) (Hammerstein, 1981). For our model, this means that S strategies will no longer evolve from biologically reasonable initial conditions as soon as RHP asymmetries between individuals are included (see below).

Evolutionary pathways

It is likely that conflict resolution strategies tend to become more complex during the course of evolution, as selection sequentially removes some or all of the constraints imposed in our models. For example, the ability to remember whether the previous conflict was won or lost could evolve first (corresponding to a transition from level NONE to level DVD). This could then be followed by a further elaboration of mental abilities such that escalated fights are discriminated from other interactions (transition to level DVD-HH) and finally that all aspects of the previous interaction are taken into account (level ALL). In fact, evolution could proceed along a number of possible pathways in the following manner:

dividable resource: NONE → DVD → ALL

undividable resource:

$$\begin{tikzcd}
 & & \text{DVD-HH} \arrow[dr] & \\
\text{NONE} \arrow[r] & \text{DVD} \arrow[ur] \arrow[dr] & & \text{ALL} \\
 & & \text{DVD-DD} \arrow[ur] &
\end{tikzcd}$$

We simulated the different routes along which strategies can become more complex (Fig. 3). After leaving the mixed strategy equilibrium of information level NONE, the equilibrium strategies attained in level DVD remain in the same category (dominance, alternating, peaceful or strange) during further transitions to higher information levels. If changes occur, they are quantitative only (*e.g.* a population playing strategy D_1 at level DVD evolves to strategy D_3 at level DVD-HH), meaning that the type of strategy is always preserved during transitions between information levels.

This implies that the transition from information level NONE, where no information is used, to level DVD, where individuals discriminate between different conflict outcomes in the simplest possible way, determines the outcome of long-term evolution. Further analysis of these transitions is facilitated by the fact that the strategies at information levels NONE and DVD contain only a small number of independent variables, allowing the application of qualitative and graphical methods.

Figure 4 shows a projection of the strategy space corresponding to information level DVD of the model. The data in Fig. 4 are based on the dividable resource scenario, but the following results are also valid for the undividable resource scenario. On the axes are two strategic variables: $p_{\mathrm{win}} (= p_{hhw} = p_{hd})$ and $p_{\mathrm{lose}} (= p_{hhl} = p_{dh})$. Information about the third strategic variable, $p_{\mathrm{equal}} (= p_{ddw} = p_{ddl})$, is lost in this projection, but, as it turns out, this variable does not influence the dynamics qualitatively with respect to the aspects we wish to discuss here. The strategy space corresponding to information level DVD contains the strategies of information level NONE as a subset. Strategies at information level NONE are characterised by $p_{\mathrm{win}} = p_{\mathrm{lose}} = p_{\mathrm{equal}}$ and, therefore, evolution at information level NONE is constrained to the diagonal. As Fig. 2 showed, there

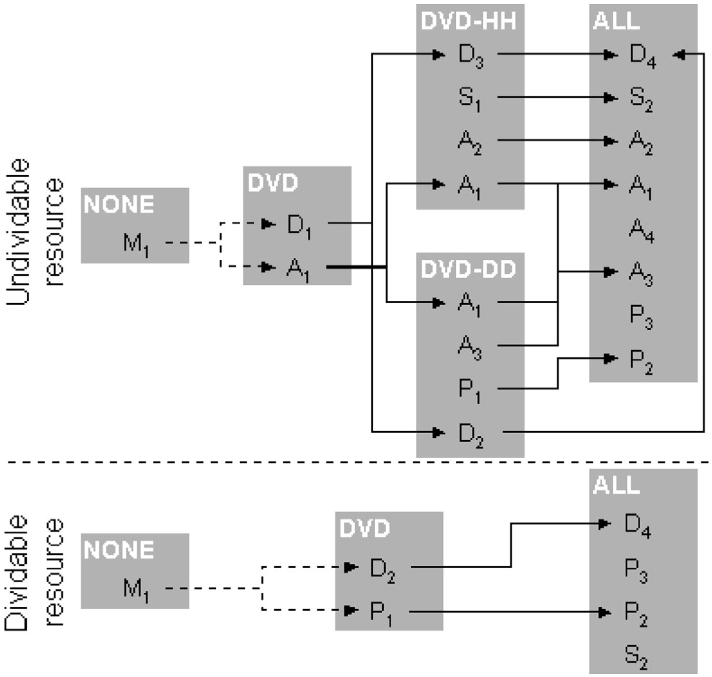

Fig. 3. Transitions between information levels. In the course of evolution, species may shift from lower to higher information levels (grey rectangles), as increasingly detailed information is processed. To investigate the effect of a transition between two information levels (say a transition from level x to level y), we ran 200 simulations with initial conditions slightly perturbed from an equilibrium of information level x, until convergence to an equilibrium of level y. In most cases, all simulations started from a particular equilibrium converged to a single equilibrium at the higher information level (as indicated by the solid arrows). Only from the mixed equilibrium of level NONE two equilibria can be reached with about equal probability at the higher information level DVD (dashed arrows). Parameters as in Table 2.

is only one evolutionary equilibrium at level NONE. For our choice of parameters, the values of the three strategic variables at this equilibrium are $p_{\text{win}} = p_{\text{lose}} = p_{\text{equal}} = 0.25$. Indeed, Fig. 4 shows that individual based simulations (see the Appendix) converge to this equilibrium along the diagonal from different initial conditions, as long as individual strategies are constrained to information level NONE. As soon as evolution away from the diagonal is allowed, corresponding to a transition from level NONE to level DVD, the simulations diverge and approach either the dominance equilibrium of level DVD in the lower right corner of the strategy space, or the

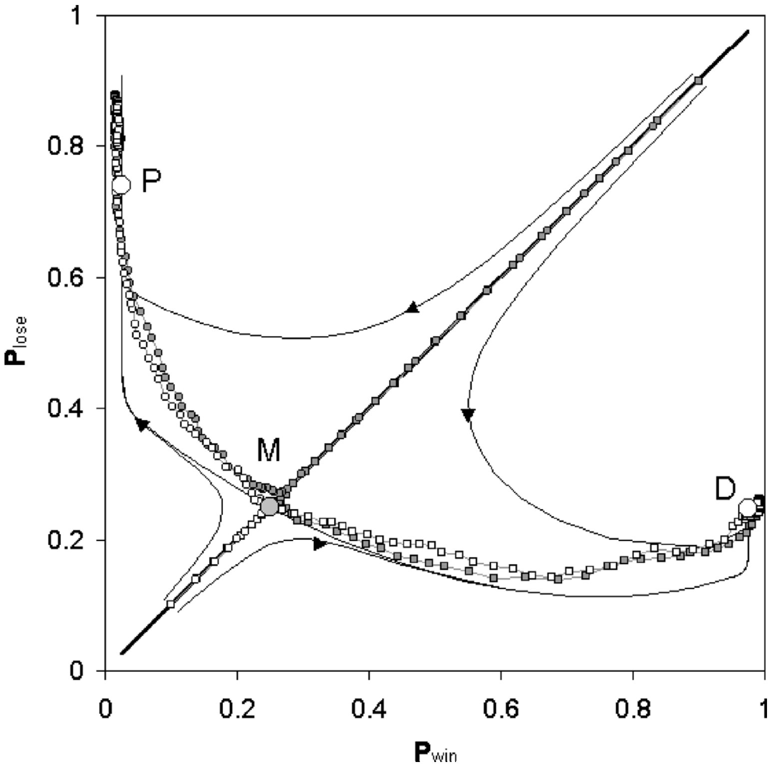

Fig. 4. The dichotomy between dominance strategies and other conventions. In the dividable resource scenario, there are three strategic variables at information level DVD (defined in the text as p_{win}, p_{lose} and p_{equal}). We show here a two-dimensional projection of the strategy space, since p_{equal} does not influence the dynamics. We studied the evolution of conflict resolution strategies after a transition from level NONE to level DVD, by means of individual based simulations (details are given in the Appendix). The figure shows four different simulations, started from two initial conditions: the simulations denoted by white circles and squares were started from the initial condition $p_{\mathrm{win}} = p_{\mathrm{lose}} = p_{\mathrm{equal}} = 0.1$, the simulations denoted by grey symbols were started at $p_{\mathrm{win}} = p_{\mathrm{lose}} = p_{\mathrm{equal}} = 0.9$. In the first 10,000 generations of the simulations, strategic parameters were constrained to information level NONE. Evolution then proceeds along the diagonal towards the mixed strategy equilibrium of level NONE (big grey circle). Data is plotted every 500 generations. After 10,000 generations, the constraint on the strategic parameters was removed, corresponding to a transition to information level DVD. The individual based simulations then diverged, with equal probability, to either the dominance equilibrium (lower right, grey and white squares) or the peaceful equilibrium (upper left, grey and white circles). The mixed strategy equilibrium is exactly on the boundary line (thick black line) between the domains of attraction of the stable equilibria of information level DVD (big white circles). The thin black lines with arrows represent deterministic evolutionary trajectories of the model at information level DVD. Parameters as in Table 2.

peaceful equilibrium in the upper left corner. In the undividable resource scenario, the latter equilibrium is an alternating equilibrium.

Closer inspection reveals that there are three evolutionary equilibria at information level DVD. Two of them are stable (the dominance and peaceful equilibrium) and the third one is unstable. The unstable equilibrium coincides exactly with the mixed equilibrium of information level NONE (equilibrium M_1 of Table 2). This equilibrium is stable with respect to movement along the diagonal, hence the convergence to this equilibrium at level NONE, but unstable in the direction perpendicular to the diagonal. The diagonal serves as the boundary line (separatrix) between the regions of attraction of the two stable equilibria. Specifically, the mixed equilibrium is exactly on this boundary line. This explains why both peaceful and dominance equilibrium can be reached from the mixed equilibrium M_1 with about equal probability during the transition between information levels NONE and DVD.

A phase space analysis of the model for undividable resource shows a very similar topology of equilibrium points.

Asymmetries in resource holding potential

We have deliberately made the strong assumption that there are no observable or hidden RHP differences between the players. This allowed us to demonstrate that evolutionarily stable dominance relations based on winner and loser effects are possible without such underlying asymmetries. We are, of course, aware of the fact that in many biological systems RHP asymmetries are present. In order to check to what extent our conclusions are affected by the presence of RHP asymmetries, we analysed an extended version of our model. In this model, we assumed that there are two RHP classes, representing individuals with high and low fighting ability. If two individuals, belonging to the same RHP class, engage in a Hawk-Hawk interaction, each of them has an equal probability of winning, as before. However, when two individuals belonging to different RHP classes engage in an escalated fight, the individual with the low fighting ability has a considerably lower probability of winning (for the sake of concreteness, we will assume it wins only one out of eight fights).

In order to study the effects of RHP asymmetries, we again considered the transition between information level NONE and DVD. As shown in Fig. 5,

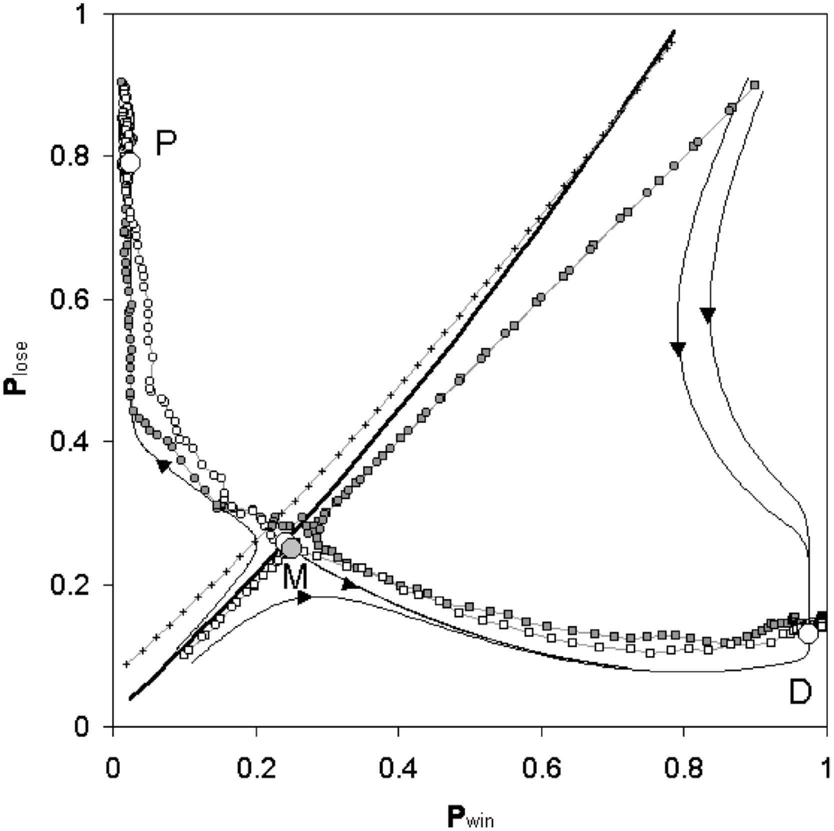

Fig. 5. Effects of RHP differences and errors in individual recognition. As in Fig. 4, we performed individual based simulations corresponding to a transition between information levels NONE and DVD (dividable resource scenario), this time including hidden RHP differences between individuals as explained in the text. Due to these RHP asymmetries, the boundary line or separatrix (thick black line) between the domains of attraction of the equilibria of information level DVD (big white circles) has shifted slightly away from the diagonal. Therefore, the mixed equilibrium of information level NONE (big grey circle) no longer coincides with the unstable equilibrium of level DVD. Formally, this implies that further evolution from the equilibrium of information level NONE will always converge to the dominance equilibrium, as shown by the deterministic trajectory (thin black lines with arrows) leading from the mixed equilibrium (M) to the dominance equilibrium (D). The individual based simulations, however, show that, due to stochastic effects, convergence to the peaceful equilibrium is still possible, although the probability of reaching this equilibrium is now smaller than 50% (for this level of RHP asymmetry approximately 20% of the simulations converged to the peaceful equilibrium). When individuals not only differ in RHP, but also make occasional errors in individual recognition, the separatrix will shift even further away from the diagonal: the grey line with crosses represents the separatrix when individuals make errors in 50% of their interactions.

RHP asymmetries result in one important qualitative change. The boundary line between the domains of attraction of the dominance and peaceful equilibrium has shifted slightly. Because of this, the mixed equilibrium M_1 no longer coincides exactly with the unstable equilibrium of level DVD. In fact, the equilibrium M_1 is now in the domain of attraction of the dominance equilibrium, and formally speaking, evolution from the mixed equilibrium M_1 will now always lead to the dominance equilibrium. However, even with this large RHP asymmetry, the mixed equilibrium is still very close to the separatrix. Therefore, the peaceful equilibrium can still be reached if the evolutionary dynamics is subject to small perturbations. Indeed, individual based simulations, which naturally include such small perturbations, show that the peaceful equilibrium is still attained, be it with a lower probability than the dominance equilibrium.

At higher information levels, RHP differences influenced the precise location of the equilibria (particularly for the dominance and strange equilibria), as well as the probability with which equilibria were reached from random initial conditions. However, RHP differences did not affect the transitions between higher information levels along the evolutionary pathways as shown in Fig. 3.

The effect of errors in individual recognition

Another assumption that we made is that individuals have complete information about their situation. In other words, players always accurately remember the outcome of the previous conflict with their opponent. In order to check the robustness of our model with respect to this assumption, we again ran simulations for the transition from level NONE to level DVD, this time varying the quality of individual memory. That is to say, players made occasional errors in that they sometimes based their decision on a previous conflict with an arbitrary other opponent. These errors in individual recognition did not influence the results as long as there were no RHP asymmetries included. This is explained by the fact that the quality of individual memory is irrelevant when no information about the outcome of the previous conflict is used. The fitness of mutant strategies $p_{\text{win}} \approx p_{\text{lose}} \approx p_{\text{equal}}$ that are close to the strategies of information level NONE is therefore not at all affected by the quality of individual memory. Consequently, the boundary separating the domains of attraction of the dominance and peaceful equilibrium will remain on the diagonal and the unstable equilibrium of level DVD will continue to coincide with the mixed equilibrium of level NONE, as in Fig. 4, regardless of the likelihood of errors in individual recognition.

However, when hidden RHP differences are included, errors in individual recognition enlarge the effect of the presence of RHP differences (Fig. 5). The separatrix shifts farther away from the diagonal, and, consequently, the unstable equilibrium of level DVD moves farther away from the mixed equilibrium of level NONE. Still, the effects are not large and the behaviour of the model with RHP differences and errors in individual recognition is comparable to the original model, which assumed complete information and absence of RHP asymmetries.

The interaction effect between RHP differences and errors in individual recognition results from the fact that the RHP differences between individuals generate a positive correlation between the outcomes of interactions between opponents and through time. There will be individuals that consistently win a large fraction of their escalated conflicts (those with high RHP) and others that consistently lose a large fraction of their conflicts (those with low RHP). If the population plays a peaceful or alternating strategy, mistakes in individual recognition will often lead to unintended escalated fights. In a population playing the dominance strategy, however, mistakes will be less likely to have unintended effects. For example, an individual may mistake its current opponent for another opponent it encountered previously. However, due to the correlation between the outcomes of the previous interactions with these two opponents, the mistake will often not have an effect at all, since the intended behaviour for the one opponent is equal to the intended behaviour for the other opponent. In short, if the population plays the dominance strategy, individuals can generalize to some extent from the outcome of previous interactions with arbitrary opponents. This makes individuals playing the dominance strategy less vulnerable to mistakes in individual recognition than individuals playing the alternating or peaceful strategy. This explains why the interaction between RHP differences and quality of individual recognition favours evolution of a dominance strategy.

Discussion

Our results show that the historical asymmetry generated by the outcome of a previous interaction can be used as the deciding asymmetry in a conflict resolution strategy, even when this asymmetry is completely arbitrary and holds no information about differences in RHP. This conclusion is in line with well-established results from game theory, which state that any asymmetry, regardless of whether or not it accompanies a difference in RHP or expected payoff between the players, must be used for conventional conflict settlement. In other words, any strategy that ignores the asymmetry cannot be an ESS. This result was first shown by Maynard Smith & Parker (1976) and later established rigorously by Selten (1980, 1983, 1988). They also demonstrated two aspects of ESSs based on asymmetries that are particularly worth mentioning here.

First, the asymmetry can be used in different ways to resolve the conflict (Maynard Smith & Parker, 1976; Hammerstein, 1981). In our model, the asymmetry generated by the outcome of the previous conflict can be used such that the winner of a previous conflict escalates and the loser retreats, but also the opposite is possible. Hence, we find dominance and alternating strategies, which are counterparts with respect to the way in which the asymmetry after a Hawk-Dove or Dove-Hawk interaction is used. Moreover, we find different alternating strategies, which are a set of mutually opposite conventions with respect to the behaviour after Hawk-Hawk or Dove-Dove interactions, and 'strange' strategies, which are the counterparts of dominance strategies.

The second aspect is that all ESSs that are based on an asymmetry must be pure strategies (Selten, 1980; Van Damme, 1991). For our model, this would imply that an individual should either always escalate or always retreat whenever it observes an asymmetry. Whether an individual can observe the asymmetry or not depends on the information level. This property of ESSs in asymmetric conflicts explains why the alternating strategies are pure strategies and why, in general, the evolved equilibrium strategies at higher levels, where more asymmetries are taken into account, contain more components that are pure (compare for example the strategies P_1 and P_2, or D_2 and D_4). Yet, many of the strategies that evolved in our model (particularly the dominance strategies) seem to be forbidden by Selten's theorem, since they still contain mixed strategic components. We suggest two possible (co-dependent) explanations for this apparent contradiction. First, it strongly depends on the set of alternative strategies whether a given strategy may be considered evolutionarily stable or not. While Selten's theorem presupposes a large strategy set, we have strongly delimited the space of possible options.

In particular, we excluded strategies with perfect recall, which are crucial for Selten's argument (Van Damme, 1991). Second, Selten's theorem relies on the assumption that the payoff function $W(\vec{q}, \vec{p})$ is linear in both the mutant and the resident strategy (Weissing, 1996). In our case, it is easy to see that repeated interactions between a pair of players leads to a payoff function that is highly nonlinear in both of its components. Such nonlinearities result in a decoupling of the properties of evolutionary stability (*i.e.* stability against invasion by rare mutants) and convergence stability (*i.e.* being approachable by a series of gene substitution events), which coincide in games with a linear fitness function (Geritz *et al.*, 1998). As argued by Bulmer (1994, Appendix 8.1), Selten's result only applies to situations where evolutionary stability implies convergence stability, which may not be the case in our model.

Our results regarding the evolutionary pathways along which conflict resolution strategies may change show that evolved strategies obeying an asymmetry are robust against changes in the amount or detail of the available information. That is to say, the type of strategy will not change when a higher information level is reached. Moreover, there will be selection to use increasingly detailed information in populations that play a dominance strategy. The important dichotomy between dominance and other strategies occurs already at low information levels, implying that already very simple strategies allow for a dominance convention.

We checked the robustness of our results with respect to two assumptions. First, hidden RHP asymmetries did not change our results dramatically. This is in line with the conclusions of Hammerstein (1981), who noted that models with payoff-irrelevant asymmetries are valid limiting cases of models with payoff-relevant asymmetries. Our conclusions are also confirmed by a more recent study (Crowley, 2001) on the evolution of memory dependent strategies in a repeated Hawk-Dove game with observable RHP differences. Second, our results were not affected by occasional errors in individual recognition, unless the lower quality of individual memory was accompanied by RHP asymmetries between individuals. In that case, errors in individual recognition tend to favour the evolution of a dominance strategy, since dominance conventions are less vulnerable to errors in individual recognition than alternating or peaceful strategies. This may be one of the reasons why we often find dominance strategies and not alternating strategies in nature: when a dominance hierarchy has formed, mistakes in individual recognition and recollection of previous events do not have large effects, since the outcomes of interactions are positively correlated between opponents and through time.

The two-player approach taken in the present paper has the important limitation that we cannot investigate the important issue of hierarchy formation. The current approach excludes the use of social information other than the information that can be extracted from previous interactions with the current opponent. Hierarchies, or even correlations between the outcomes of interactions with different opponents, can therefore only arise due to strong RHP asymmetries. However, when individuals base their behaviour in a conflict on experiences with other group members than their current opponent, genuinely social hierarchies may arise as a result of bystander effects or transitive inference. A proper investigation of this issue requires a model in which conflict resolution strategies are made dependent on social relations other than the relation between the player and its opponent. The companion paper (Van Doorn *et al.*, this issue) will focus on the importance of such 'third-party' effects on the evolution of social conventions.

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Appendix: Analytical and numerical analysis and individual based simulations

The payoff function

In order to derive equations governing the evolutionary dynamics of the conflict resolution strategies, we must first compute, for every conflict between two individuals, the probability that an individual finds itself in each of the six possible individual states, corresponding to the six possible outcomes of a single Hawk-Dove interaction. This can be done, if we know the strategy of each of the two players and the outcome of the previous conflict, since this determines the behaviour of each player in the current conflict.

We will label the six possible outcomes of a conflict with the numbers 1-6, as follows

Conflict type	Outcome for focal individual	Label
Hawk-Hawk	victory	1
Hawk-Hawk	defeat	2
Hawk-Dove	victory	3
Hawk-Dove	defeat	4
Dove-Dove	victory	5
Dove-Dove	defeat	6

Let us suppose that the first player, which we will arbitrarily regard as the focal individual, has strategy $\vec{p} = (p_{hhw}\ p_{hhl}\ p_{hd}\ p_{dh}\ p_{ddw}\ p_{ddl})$ and that the second player (the opponent) has strategy $\vec{q} = (q_{hhw}\ q_{hhl}\ q_{hd}\ q_{dh}\ q_{ddw}\ q_{ddl})$. By way of example, let us further suppose that the previous conflict between these players ended as an escalated fight, which was won by the second player (hence the conflict ended with outcome 2).

The outcome of the previous conflict uniquely determines the probabilities with which both players will play 'Hawk' in the current conflict. In our example, player 1 will play 'Hawk' in the current conflict with probability p_{hhl} and player 2 will do so with probability q_{hhw}. It is now easy to calculate the likelihood of each of the six possible outcomes of the current conflict. For example, the probability that the current conflict will be resolved by a dominance interaction in which player 1 claims the resource and player 2 retreats (outcome 3) is given by the transition probability $m_{3,2}$, where

$$m_{3,2} = p_{hhl}(1 - q_{hhw}). \tag{3}$$

Similarly, we may compute other transition probabilities m_{ij} $(i, j = 1 \ldots 6)$, which give the probability that the current conflict will end with outcome i, given that the previous conflict ended with outcome j. The 36 transition probabilities, m_{ij}, can be ordered in a transition matrix $\mathbf{M}(\vec{p}, \vec{q})$, such that m_{ij} is the element at the i-th row and j-th column of $\mathbf{M}(\vec{p}, \vec{q})$. The column vectors of $\mathbf{M}(\vec{p}, \vec{q})$ each correspond to one of the six possible outcomes of the *previous* conflict and their elements represent the likelihood of each of the six outcomes of the *current* conflict.

Next, we define vectors $\vec{u}_n(\vec{p}, \vec{q})$, which contain the probabilities that the focal individual finds itself in each of the six possible individual states corresponding to the six outcomes of the n-th conflict between the two players. It is easy to see that

$$\vec{u}_n(\vec{p}, \vec{q}) = \mathbf{M}(\vec{p}, \vec{q})\, \vec{u}_{n-1}(\vec{p}, \vec{q}). \tag{4}$$

We assume that the players both play 'Dove' in their first conflict. Hence,

$$\vec{u}_1(\vec{p}, \vec{q}) = \left(0\,0\,0\,0\,\tfrac{1}{2}\,\tfrac{1}{2}\right)^{\mathrm{T}}. \tag{5}$$

Equations (4) and (5) together uniquely determine the sequence $\vec{u}_1(\vec{p}, \vec{q})$, $\vec{u}_2(\vec{p}, \vec{q})$, $\vec{u}_3(\vec{p}, \vec{q}), \ldots$ from which the average expected payoff, $W(\vec{p}, \vec{q})$, of an individual playing strategy $\vec{p}$ against an opponent playing strategy $\vec{q}$ can be calculated.

In order to find $W(\vec{p}, \vec{q})$, we must first calculate the expected payoff $w_n(\vec{p}, \vec{q})$ to the focal player (*i.e.* player 1) in the n-th conflict. The payoffs associated with the six possible conflict outcomes are represented in a payoff vector $\vec{v}$ as follows

$$\vec{v} = (V - D, -C - D, V - D, 0\ V, 0). \tag{6}$$

The expected payoff $w_n(\vec{p}, \vec{q})$ to the focal player in the n-th conflict quantity can now be obtained by weighing the payoffs associated with every possible conflict outcome with the probability of occurrence of that outcome in the n-th conflict. In other words,

$$w_n(\vec{p}, \vec{q}) = \sum_{i=1...6} (\vec{v})_i (\vec{u}_n(\vec{p}, \vec{q}))_i = \vec{v}\vec{u}_n(\vec{p}, \vec{q}). \tag{7}$$

Under the assumption that individuals interact T times on average, the average expected payoff $W(\vec{p}, \vec{q})$ can now be calculated as

$$W(\vec{p}, \vec{q}) = \frac{1}{T} \sum_{n=1}^{\infty} (1 - 1/T)^{n-1} w_n(\vec{p}, \vec{q}). \tag{8}$$

The factor $(1 - 1/T)^{n-1}$ is necessary to weigh the expected payoff of the n-th conflict with the probability that this conflict will actually occur.

Evolutionary dynamics

We are interested in finding strategies that are (a) stable against invasion by alternative strategies, and (b) attainable by evolution, more specifically, by a series of small phenotypic steps, each corresponding to a mutation and subsequent trait substitution. Such strategies must at least be best replies to themselves (Weissing, 1996). A strategy $\vec{p}$ is a best reply to itself when there are no alternative mutant strategies $\vec{q}$ that would outperform an individual playing the resident strategy $\vec{p}$ against its opponents (which also play the strategy $\vec{p}$). That is to say, a strategy $\vec{p}$ is a best reply to itself when

$$\text{for all alternative strategies } \vec{q}: \quad W(\vec{q}, \vec{p}) \leqslant W(\vec{p}, \vec{p}). \tag{9}$$

If condition (9) holds, the strategy $\vec{p}$ is called a Nash equilibrium strategy. Unfortunately, not all Nash equilibria are evolutionarily stable. That is, Nash equilibria need not be stable against invasion by alternative strategies (problems may arise when there are alternative best replies $\vec{r}$ such that $\vec{r} \neq \vec{p}$ and $W(\vec{r}, \vec{p}) = W(\vec{p}, \vec{p})$). Moreover, condition (9) gives no information regarding the attainability, or convergence stability, of the strategy $\vec{p}$. Convergence stability ensures that a population, which is slightly perturbed away from the strategy $\vec{p}$, will evolve back to the strategy $\vec{p}$. Formally, we would need to check higher order conditions to ensure the evolutionary and convergence stability of the strategy $\vec{p}$ (Eshel, 1983; Geritz *et al.*, 1998). Here, we refrained from doing so. Instead, we took a different approach and derived a dynamical equation for the evolutionary rate of change of the strategy $\vec{p}$. Evolutionarily stable strategies correspond to equilibria of this equation, and the stability of these equilibria will give information about the convergence stability properties of the corresponding strategy.

Let us suppose that the strategy $\vec{q}$ is a rare mutant strategy that has arisen in an otherwise monomorphic resident population, in which all individuals play the strategy $\vec{p}$. The probability that the mutant invades this resident population is determined by the difference between the average expected payoff of the mutant, $W(\vec{q}, \vec{p})$, and the average expected payoff of the resident, $W(\vec{p}, \vec{p})$. Note that the initial rareness of the mutant is responsible for the fact that invasion of the mutant is independent of the performance of the resident against mutant opponents (measured by $W(\vec{p},\vec{q})$) and performance of the mutant against mutant opponents (measured by $W(\vec{q},\vec{q})$). If mutations occur in small steps, the resident and mutant strategies will only be slightly different from each other. In that case, $\|\vec{p}-\vec{q}\|$ is small, which allows us to approximate the fitness difference between mutant and resident as

$$W(\vec{q},\vec{p}) - W(\vec{p},\vec{p}) \approx (\vec{q}-\vec{p})\cdot \left.\frac{\partial W(\vec{q},\vec{p})}{\partial \vec{q}}\right|_{\vec{q}=\vec{p}}. \tag{10}$$

In other words, the fitness difference between mutant and resident is proportional to the local fitness gradient. Therefore, the fitness gradient determines the probability of invasion, which is directly related to the rate of evolution of the strategy $\vec{p}$. Consequently,

$$\frac{\partial \vec{p}}{\partial t} = \kappa \mathbf{G} \left.\frac{\partial W(\vec{q},\vec{p})}{\partial \vec{q}}\right|_{\vec{q}=\vec{p}} \tag{11}$$

(Hofbauer & Sigmund, 1998, Chapter 9). In this equation, the rate constant κ is determined by the population size and the rate of mutations. The matrix $\mathbf{G}$ is a mutational variance-covariance matrix. Evolutionarily stable strategies $\vec{p}$ are also equilibrium solutions of equation (11). Moreover, stable equilibria of equation (11) correspond to convergence stable strategies, usually, but not necessarily (Geritz *et al.*, 1998), continuously stable strategies (that is, convergence stable and evolutionarily stable strategies, Eshel, 1983).

We used the mutational variance-covariance matrix $\mathbf{G}$ to implement the constraints corresponding to the different information levels. For example, we used the 6 × 6 identity matrix as the mutational variance-covariance matrix for information level ALL (that is, all six traits were assumed to evolve independently). Similarly, we used the following matrix as mutational variance-covariance matrix at level DVD (dividable resource scenario),

$$\mathbf{G}^{(\text{DVD, dividable resource})} = \begin{pmatrix} 1 & 0 & 1 & 0 & 0 & 0 \\ 0 & 1 & 0 & 1 & 0 & 0 \\ 1 & 0 & 1 & 0 & 0 & 0 \\ 0 & 1 & 0 & 1 & 0 & 0 \\ 0 & 0 & 0 & 0 & 1 & 1 \\ 0 & 0 & 0 & 0 & 1 & 1 \end{pmatrix}, \tag{12}$$

corresponding to the assumption that evolution of the strategic parameters is controlled by the constraints $p_{hhw} = p_{hd}$ (hence $\mathbf{G}_{1,1} = \mathbf{G}_{3,3} = \mathbf{G}_{1,3} = \mathbf{G}_{3,1}$), $p_{hhl} = p_{dh}$ ($\mathbf{G}_{2,2} = \mathbf{G}_{4,4} = \mathbf{G}_{2,4} = \mathbf{G}_{4,2}$) and $p_{ddw} = p_{ddl}$ ($\mathbf{G}_{5,5} = \mathbf{G}_{6,6} = \mathbf{G}_{5,6} = \mathbf{G}_{6,5}$).

In order to solve equation (11), we used a standard algorithm for the numerical integration of ordinary differential equations. The elements of the local fitness gradient were computed numerically using equations (4)-(8) by calculating the fitness of the six mutant strategies that differed slightly from the resident in one of the strategic variables. The strategic parameters were allowed to vary between δ and $1-\delta$, where δ is a small number (throughout this paper, we used $\delta = 0.025$). This ‘trembling hand’ approach (Selten, 1975) was used in order to exclude equilibrium strategies that are sensitive to occasional errors in decision-making.

Individual based simulations

In the individual based simulations, we traced the evolution of a population of 100 individuals. Each of these had repeated Hawk-Dove interactions as described under 'model description'. The total payoff gained in interactions throughout its lifetime determined the number of offspring produced by an individual. The three strategic parameters of an individual's conflict resolution strategy were each determined by a diploid locus. We assumed normal mendelian inheritance, free recombination between loci and additive interactions between alleles. Mutations, altering the phenotypic effect of an allele slightly (by 1%) occurred at a low frequency (1% per allele per generation).