THE EVOLUTION OF SOCIAL DOMINANCE
II: MULTI-PLAYER MODELS

by

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Summary

The social hierarchies observed in natural systems often show a high degree of transitivity. Transitive hierarchies do not only require rank differentiation within pairs of individuals but also a higher level ordering of relations within the group. Several authors have suggested that the formation of linear hierarchies at the group level is an emergent property of individual behavioural rules, referred to as winner and loser effects. Winner and loser effects occur if winners of previous conflicts are more likely to escalate the current conflict, whereas the losers of previous conflicts are less likely to do so. According to this idea, an individual's position in a hierarchy may not necessarily reflect its fighting ability, but may rather result from arbitrary historical asymmetries, in particular the history of victories and defeats. However, if this is the case, it is difficult to explain from an evolutionary perspective why a low ranking individual should accept its subordinate status. Here we present a game theoretical model to investigate whether winner and loser effects giving rise to transitive hierarchies can evolve and under which conditions they are evolutionarily stable. The main version of the model focuses on an extreme case in which there are no intrinsic differences in fighting ability between individuals. The only asymmetries that may arise between individuals are generated by the outcome of previous conflicts. We show that, at evolutionary equilibrium, these asymmetries can be utilized for conventional conflict resolution. Several evolutionarily stable strategies are based on winner and loser effects and these strategies give rise to transitive hierarchies.

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Introduction

In a companion paper (Van Doorn *et al.*, this issue), we investigated the evolution of conflict resolution strategies in repeated conflicts between isolated pairs of individuals. We demonstrated that asymmetries generated by the outcome of previous interactions can be used for the resolution of future conflicts, even when the outcome of previous conflicts is not related to differences in resource holding potential (RHP, Parker, 1974). In particular, evolution may lead to behavioural strategies known as winner and loser effects (Chase *et al.*, 1994), which, once established, cannot be replaced by alternative strategies.

Winner and loser effects generate a positive feedback between past performance and future probabilities of winning, which will automatically result in rank differentiation within isolated pairs of players. However, rank differentiation within pairwise relations will not automatically lead to a social hierarchy. When dominance within a pair is arbitrarily determined by winner and loser effects, it need not necessarily be true that, if individual A is dominant over B, and B is dominant over C, that then also A is dominant over C. In other words, the resulting social structure would most likely be intransitive, which is in contrast to the (almost) linear, transitive, social hierarchy that is observed in many biological systems (a classical example being the pecking order in a group of chickens, Schjelderup-Ebbe, 1922).

Apparently, it is not arbitrarily determined which of the two individuals in a pair becomes dominant. A linear hierarchy will arise if this decision depends not only on the history of interactions within the pairs, but also on relations with other individuals than the current opponent. Such a dependency could arise if winner and loser effects do not only act within pairs, but also between pairs. In other words, the individuals in a group would not only have to behave dominantly when they encounter an individual from which they previously won, as before, but also when they are dominant over many other group members. Similarly, individuals would not only have to act subordinately when they encounter individuals from which they previously lost, but also when they are subordinate to many other group members. These behavioural rules will have the effect that an individual has a higher probability of becoming dominant if it is already dominant in its relations with other individuals. Indeed, theoretical models have shown that between-pair winner and loser effects (or bystander effects) can give rise to stable linear dominance hierarchies (Landau, 1951b; Hogeweg & Hesper, 1983; Bonabeau *et* *al.*, 1996). Moreover, experimental studies (Chase, 1982; Chase *et al.*, 1994, and references therein) have demonstrated between-pair winner and loser effects based on various proximate mechanisms (*e.g.* mediated by hormones influencing aggressiveness Oliviera *et al.*, 2001).

There are alternative explanations for the transitivity of hierarchies in natural systems. A certain degree of transitivity could be induced by RHP-asymmetries between individuals. For example, if an individual has a very high RHP relative to its competitors, then this individual is likely to become the highest-ranking individual, since it will win most of its escalated conflicts. However, the conclusion that the transitivity of social hierarchies in natural systems is caused by underlying RHP asymmetries in this direct way seems implausible. In fact, the probability of finding a linear hierarchy in a group of modest size, where rank differences are determined directly by RHP asymmetries, is negligibly small even for high levels of RHP asymmetries (Landau, 1951a; Mesterton-Gibbons & Dugatkin, 1995; but see Appleby, 1983). Alternatively, social conventions based on RHP assessment (Maynard Smith & Parker, 1976; Hammerstein, 1981), could lead to transitive social hierarchies. For example, if individuals adhere to the convention that larger individuals are always allowed to win, then this will result in a transitive hierarchy in which ranks are directly related to size. However, the idea that dominance rank is completely determined by individual attributes such as RHP cannot explain experimental results (in coackroach, Dugatkin *et al.*, 1994, and cichlid fish, Chase *et al.*, 2002) showing that repeatedly reconstituting groups of individuals may result in completely different dominance hierarchies.

Without completely denying the importance of RHP asymmetries, the idea that social dominance emerges from winner and loser effects within and between pairs of individuals, immediately implies that dominance status is assigned, at least to some extent, arbitrarily. This is quite puzzling, at least from the perspective of the subordinate individual. If dominance rank is assigned arbitrarily, why should a subordinate individual accept its unfortunate position?

A possible answer to this question is that it is simply too costly for a low ranking individual to break the conflict resolution convention that (arbitrarily) assigned it to its subordinate status. A subordinate individual wanting to break the social convention would have to behave aggressively, despite its subordinate status. At the same time, its opponent will still treat it as a subordinate, and, hence, will behave aggressively as well. Consequently, a low ranking individual would have to go through many escalated and costly fights in order to ascend the social hierarchy.

In the companion paper (Van Doorn *et al.*, this issue), we showed that this argument does indeed apply to within-pair winner and loser effects. In the present study, we investigate whether the evolutionary validity of this argument extends to between-pair winner and loser effects. To this end, we construct a game-theoretical model, in which the evolution of social conflict resolution strategies can be studied. Specifically, we are interested in the question whether between-pair winner and loser effects can evolve, and, once they have evolved, whether they are stable against invasion by alternative strategies.

Model description and analysis

As in the companion paper, we model conflicts between two individuals by a slightly modified Hawk-Dove game (Maynard Smith, 1982). For simplicity, we focus on that version of the model where not only Hawk-Hawk, but also Dove-Dove interactions create an asymmetry: when two 'Doves' meet they do not divide the resource, but either one of them obtains the resource with equal probability. Hence, the payoffs for a focal individual are given by

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	$\begin{cases} \frac{1}{2}V, & \text{if the focal obtains the resource} \\ 0, & \text{if the opponent obtains the resource} \end{cases}$

The parameter V denotes the value of the resource, C denotes the cost of losing an escalated fight, and there is a small cost D associated with playing Hawk. For the sake of our argument, we deliberately restrict ourselves for the moment to the special case where all individuals have an equal probability of winning escalated conflicts. This represents a worst-case scenario in which there are no underlying RHP asymmetries between individuals.

We assume that individuals participate in a large number of conflicts. On average, individuals interact T times. Individuals can only remember the outcome of the preceding conflict and have no information about earlier conflicts. In the companion paper, we studied in detail how different asymmetries generated by the outcome of the previous conflict between an individual and its opponent may influence the course of actions in the current conflict. This aspect of conflict resolution is kept as simple as possible in the current paper: with respect to the outcome of the previous conflict, individuals are assumed to remember only whether they obtained the resource or not. Instead, the current model explores a different dimension of biological complexity. Individuals may now base their behaviour not only on the preceding conflict between them and their current opponent, but also on their previous interaction with another individual (allowing for an effect of overall social rank on behaviour) or on the previous interaction of their opponent with another individual (allowing for bystander effects, Chase, 1982). To keep things as simple as possible, let us first focus on a group of three individuals only (hence, we refer to this model as the three-player model). Individuals remember whether they obtained the resource or not in the previous conflict with both of their group members. An individual may therefore be in three states, which can be interpreted as different social ranks: it may have won from both other group members (we refer to such an individual as the α-individual), it may have won one conflict, but may have lost the other (β-individual), or it may have lost both conflicts (γ-individual).

Since the relation between the individuals in a pair is always asymmetric (by assumption), there can only be two social configurations within a group of three players. The first one is a transitive hierarchy, where one player is an α-individual, another is a β-individual and the third player is a γ-individual. The second possible social configuration is an intransitive hierarchy. Intransitive hierarchies occur when the first player won its previous conflict with the second player, the second player won its previous conflict with the third player, and the third player won its previous conflict with the first player. In such a case, all three players are in the same individual state (all three are β-individuals), but this does not mean that there are no asymmetric relations within pairs of players. The two possible social configurations are schematically shown below, with arrows pointing towards the loser of the previous conflict.

$$\begin{tikzcd} & \alpha \arrow[dl] \arrow[dd] \\ \beta \arrow[dr] & \\ & \gamma \end{tikzcd} \qquad \begin{tikzcd} & \beta \arrow[dl] \\ \beta \arrow[dr] & \\ & \beta \arrow[uu] \end{tikzcd}$$

transitive intransitive

A transition from a transitive to an intransitive social configuration occurs when the α-individual loses a conflict from the γ-individual. Similarly, an intransitive social configuration transforms into a transitive one when an individual wins a conflict with the opponent from which it previously lost.

In a transitive hierarchy, individuals can find themselves in six different conflict situations, depending on their own rank and on the rank of their opponent. In an intransitive hierarchy, all conflicts are between β-individuals, but there are nevertheless two different conflict situations: a player could encounter either the individual from which it previously won or the individual from which it previously lost. In total, there are therefore eight different conflict situations. Consequently, a conflict resolution strategy $\vec{p}$ consists of eight parameters, each prescribing the probability of playing Hawk for an individual that finds itself in the corresponding conflict situation:

$$\vec{p} = (p_{\alpha\beta}\ p_{\beta\alpha}\ p_{\alpha\gamma}\ p_{\gamma\alpha}\ p_{\beta\gamma}\ p_{\gamma\beta}\ p_{\beta^+\beta^-}\ p_{\beta^-\beta^+}). \tag{1}$$

The first letter of the subscripts indicates the state of the focal individual and the second letter the state of its opponent, where '$+$' ('$-$') is used, when necessary, to denote the β-individual that won (lost) the previous conflict.

We have supposed that individuals can recognize each other individually, or at least can accurately remember the outcome of conflicts with each of their group members. We deliberately made this assumption, since errors in individual recognition would automatically generate between-pair winner and loser effects if within-pair winner and loser effects have evolved. In other words, we will assume, at least initially, that individual recognition is perfect in order to be to be able to study the evolution of within-pair and between-pair winner and loser effects independently. Later, we will check the robustness of the results with respect to errors in individual recognition.

We consider a number of variants of the model that differ in the assumptions regarding the cognitive abilities of the players. We assume that individuals belonging to species with low cognitive abilities are unable to process all available social information, which translates into constraints on the strategic parameters. For example, if individuals remember the outcome of their previous interaction with all group members, but not the outcome of their opponent's previous interactions with other group members, then they cannot distinguish all conflict situations. For instance, the conflict situations

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

Level	Constraints	Interpretation
1	$p_{\alpha\beta} = p_{\beta\alpha} = p_{\alpha\gamma} = p_{\gamma\alpha} =$ $p_{\beta\gamma} = p_{\gamma\beta} = p_{\beta^+\beta^-} = p_{\beta^-\beta^+}$	No information about any previous conflict is used
2	$p_{\alpha\beta} = p_{\alpha\gamma} = p_{\beta\gamma} = p_{\beta^+\beta^-}$ $p_{\beta\alpha} = p_{\gamma\alpha} = p_{\gamma\beta} = p_{\beta^-\beta^+}$	Only the outcome of the previous conflict between the focal and its opponent is used
3[a]	$p_{\alpha\beta} = p_{\alpha\gamma}, p_{\gamma\alpha} = p_{\gamma\beta}$ $p_{\beta\alpha} = p_{\beta\gamma} = p_{\beta^+\beta^-} = p_{\beta^-\beta^+}$	Individuals base their decision on their own rank
3[b]	$p_{\beta\alpha} = p_{\gamma\alpha}, p_{\alpha\gamma} = p_{\beta\gamma}$ $p_{\alpha\beta} = p_{\gamma\beta} = p_{\beta^+\beta^-} = p_{\beta^-\beta^+}$	Individuals base their decision on their opponent's rank
4[a]	$p_{\alpha\beta} = p_{\alpha\gamma}, p_{\beta\gamma} = p_{\beta^+\beta^-}$ $p_{\beta\alpha} = p_{\beta^-\beta^+}, p_{\gamma\alpha} = p_{\gamma\beta}$	Individuals disregard their opponent's relation with the bystander
4[b]	$p_{\beta\alpha} = p_{\gamma\alpha}, p_{\alpha\beta} = p_{\beta^+\beta^-}$ $p_{\gamma\beta} = p_{\beta^-\beta^+}, p_{\alpha\gamma} = p_{\beta\gamma}$	Individuals disregard their own relation with the bystander
5	none	All available social information is used

$$\begin{tikzcd} & \text{opponent} \arrow[dl] \arrow[dd] \\ \text{focal} \arrow[dr] & \\ & \text{bystander} \end{tikzcd} \quad \text{and} \quad \begin{tikzcd} & \text{opponent} \arrow[dl] \\ \text{focal} \arrow[dr] & \\ & \text{bystander} \arrow[uu] \end{tikzcd}$$

would be indistinguishable for the focal individual. The fact that individuals cannot discriminate between two conflict situations implies that their behaviour must be the same in both situations. Therefore, we must impose a constraint on the strategic parameters ($p_{\beta\alpha} = p_{\beta^-\beta^+}$ for this example).

Different assumptions regarding the complexity of the information used by individuals result in seven model variants characterized by different 'information levels' (Table 1). The seven variants of the model allow us to investigate how social information, besides the information obtained from previous interactions with the current opponent, may influence conflict resolution strategies. In particular, we are interested in the question whether conflict resolution strategies may evolve that give rise to between-pair winner and loser effects.

As in the companion paper, the evolution of the system was investigated by means of an adaptive dynamics approach (see the Appendix for details).

Equilibria of the model

For each information level, we ran a large number of simulations from random initial conditions until convergence to an equilibrium. At most levels, multiple stable equilibria exist. The equilibria can be classified into five categories (Table 2). The first category (hereafter labelled by 'M', for 'mixed') contains the mixed strategy equilibrium, in which no social information is used. Equilibrium strategies belonging to the second category (labelled by 'D', for 'dominance') are characterized by winner and loser effects. They lead to more or less stable transitive hierarchies. The third category (labelled by 'A', for 'alternating') contains equilibrium strategies that result in very unstable hierarchies, in which individuals continuously switch their social positions. The fourth category (labelled by 'T', for 'triangular') consists of equilibrium strategies that lead to stable intransitive social configurations. The final category contains hybrid strategies, which combine features of dominance, alternating and triangular strategies.

The distinguishing properties of dominance, alternating and triangular equilibria are further explained in Fig. 1. An overview of all the equilibria that were found in the simulations is presented in Fig. 2. In order to illustrate the social dynamics corresponding to the different equilibrium types, we generated time series of the decisions and ranks of the three players. These will be discussed below.

The simplest equilibrium type is the mixed equilibrium. This occurs only at information level 1, where no information about previous conflicts is used. Consequently, the game is equivalent to a simple Hawk-Dove game, and all strategic parameters evolve towards the evolutionarily stable probability of playing Hawk

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

Since no social information is used, the time series of ranks (upper rows) and decisions (lower rows) of the three players shows no obvious structure. It is given here to allow for a comparison with the time series for dominance, alternating and triangular strategies.

$$\begin{array}{l|ccccccccccccccccccccccccccccc}
\text{player 1:} & \beta & & \gamma & \beta & & \gamma & \gamma & \beta & & \alpha & & & & & \beta & \gamma & \beta & \beta & \alpha & \beta & & & & & \gamma & \beta & & \beta & \gamma & \ldots \\
\text{player 2:} & \beta & & \alpha & \alpha & & \beta & \alpha & \beta & & \beta & & & & & \beta & \alpha & \beta & \gamma & \gamma & \gamma & & & & & \beta & \beta & & \alpha & \alpha & \ldots \\
\text{player 3:} & \beta & & \beta & \beta & & \alpha & \beta & \beta & & \gamma & & & & & \beta & \beta & \beta & \alpha & \beta & \alpha & & & & & \alpha & \beta & & \gamma & \beta & \ldots \\
\hline
\text{player 1:} & 0 & d & d & d & d & 0 & h & 0 & h & 0 & d & d & d & d & d & h & 0 & d & d & d & 0 & h & d & d & d & 0 & 0 & d & h & \ldots \\
\text{player 2:} & d & d & 0 & 0 & d & d & d & d & 0 & h & d & 0 & d & 0 & d & d & d & 0 & 0 & d & d & h & 0 & d & 0 & d & d & 0 & h & \ldots \\
\text{player 3:} & d & 0 & d & d & 0 & d & 0 & d & h & d & 0 & h & 0 & d & 0 & 0 & d & d & h & 0 & h & 0 & h & 0 & d & d & d & h & 0 & \ldots
\end{array} \tag{3}$$

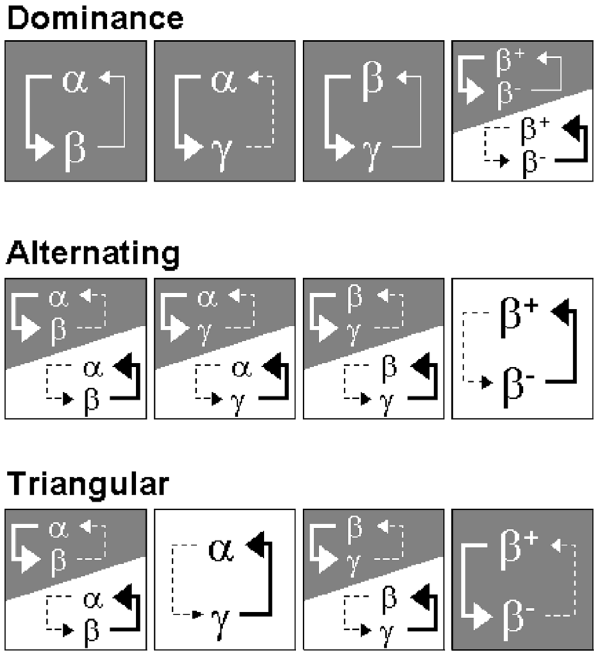

Fig. 1. Characteristics of the different types of equilibria. Within the framework of our three-player model, conflicts are possible between α- and β-individuals, between α- and γ-individuals, between β- and γ-individuals, and, finally, between two β-individuals in case of an intransitive hierarchy. For dominance (D), alternating (A) and triangular (T) equilibrium strategies (explained in the text), these four conflict types are represented by four squares. Moreover, the stability of the corresponding social relations is indicated by the grey-scale colouring of the square: white indicates that the social relation changes after every interaction (unstable relation), grey indicates that the social relation will have a low probability of changing after an interaction (stable social relation). The relation between α- and β-individual, for example, is quite stable in a dominance convention. This is because the α-individual always plays Hawk (indicated by the thick arrow), whereas the β-individual plays Hawk far less often (indicated by the thin arrow). Very unstable social relations, as, for example, the relation between α- and γ-individual in a triangular strategy, occur when the individual that previously won, never plays Hawk (dashed arrow), whereas it's opponent always plays Hawk, leading to a reversal of the social relation. The stability of the social relations in a dominance hierarchy is a common feature of dominance strategies that distinguishes them from the alternating strategies: in alternating strategies, at least one, but usually more than one relation in the transitive social configuration is unstable. There are several alternating strategies, each corresponding to a different possible combination of stable and unstable relations (see Table 2). For example, and as indicated by the two alternative representations of the corresponding square, the relation between α- and β-individual may either be stable or unstable in alternating strategies. Triangular strategies are characterized by the fact that the relations in an intransitive hierarchy are stable, whereas the relation between α- and γ-individual is unstable.

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

Type[2]	Label[4]	Level	Values of strategic parameters[1,3]							
			$p_{\alpha\beta}$	$p_{\beta\alpha}$	$p_{\alpha\gamma}$	$p_{\gamma\alpha}$	$p_{\beta\gamma}$	$p_{\gamma\beta}$	$p_{\beta^+\beta^-}$	$p_{\beta^-\beta^+}$
M	M_1	1	**0.25**	**0.25**	**0.25**	**0.25**	**0.25**	**0.25**	**0.25**	**0.25**
D	D_1	2,4[a]	1	0.22	1	0.22	1	0.22	1	0.22
	D_2	3[a]	1	0.46	1	0	0.46	0	0.46	0.46
	D_3	3[b]	1	0.33	1	0.33	1	1	1	1
	D_4	5	**1**	**0.42**	**1**	**0**	**1**	**0.22**	**0.22**	**1**
A	A_1	2, 4[a], 4[b], 5	**0**	**1**	**0**	**1**	**0**	**1**	**0**	**1**
	A_2	3[a]	0	0	0	1	0	1	0	0
	A_3	3[b]	0	1	0	1	0	0	0	0
	A_4	5	1	0	0	1	0	1	0	1
	A_5	5	0	1	0	1	1	0	0	1
	A_6	5	1	0	0	1	1	0	0	1
	A_7	5	0	1	1	0	0	1	0	1
T	T_1	5	**1**	**0**	**0**	**1**	**1**	**0**	**1**	**0**
	T_2	5	1	0	0	1	0	1	1	0
	T_3	5	0	1	0	1	1	0	1	0
	T_4	5	0	1	0	1	0	1	1	0
hybrid	DA_1	5	0	1	1	0	1	0.65	0	1
	DA_2	5	1	0.34	1	0	0	1	0	1
	DT	4[b], 5	1	0.31	1	0.31	1	0	1	0
	AT	5	0	1	1	0	0	1	1	0
	DAT	5	1	0.22	1	0.17	0	1	1	0

[1)] 200 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: $V = 0.3$, $C = 1.0$, $D = 0.025$, $T = 50$.

[2)] Equilibria were classified into five categories: M (mixed), D (dominance), A (alternating), T (triangular) and hybrids of these types.

[3)] Boldface indicates the equilibria that were used to construct the example time series shown in the text.

[4)] Label used in Figs 2 and 3 and text.

Time series (3) shows the social ranks of the three players and their decisions in a series of pairwise conflicts. The decision 'play Hawk' is denoted by 'h' and the decision 'play Dove' by 'd'. We assume that all players start as β-individuals in their first interaction. Dashed lines indicate transitions between different hierarchies and a '0' indicates the player that does not take part in the conflict (*i.e.* the bystander).

The dominance equilibria are characterized by the emergence of a more or less stable dominance hierarchy where the probability of playing Hawk increases with higher social rank. This is illustrated by the following typical time series corresponding to the dominance strategy D_4 (see Table 2) of level 5 (all available information is used):

$$\begin{array}{l|cccccccccccccccccccccccccccccc}
\text{player 1:} & \beta & \gamma & & & & \beta & & & & & & & & & \alpha & & & & & \beta & & & & & \gamma & & & & & \cdots \\
\text{player 2:} & \beta & \alpha & & & & \alpha & & & & & & & & & \beta & & & & & \alpha & & & & & \alpha & & & & & \cdots \\
\text{player 3:} & \beta & \beta & & & & \gamma & & & & & & & & & \gamma & & & & & \gamma & & & & & \beta & & & & & \cdots \\
\hline
\text{player 1:} & d & 0 & d & 0 & h & 0 & h & d & h & d & 0 & h & 0 & h & h & 0 & h & 0 & h & h & h & 0 & h & h & 0 & d & d & d & 0 & \cdots \\
\text{player 2:} & h & h & h & h & 0 & h & 0 & h & 0 & h & h & 0 & h & h & 0 & h & 0 & h & h & 0 & 0 & h & h & 0 & h & 0 & h & 0 & h & \cdots \\
\text{player 3:} & 0 & h & 0 & d & h & d & d & 0 & d & 0 & d & d & d & 0 & d & d & d & d & 0 & d & d & d & 0 & h & d & h & 0 & h & h & \cdots
\end{array} \tag{4}$$

As can be seen from time series (4) and from Table 2, the α-individual always plays Hawk. The β-individual always plays Hawk against the γ-individual, and usually Dove against the α-individual. Finally, the γ-individual plays Hawk with low probability when playing against the β-individual and Dove otherwise. This results in social dominance relations that may persist for quite some time.

Social stability is lacking when an alternating strategy has evolved. For example, in a population playing strategy A_1, the social configuration changes after every conflict

$$\begin{array}{l|cccccccccccccccccccccccccccccc}
\text{player 1:} & \beta & \beta & \gamma & \gamma & \beta & \beta & \gamma & \gamma & \gamma & \beta & \beta & \beta & \gamma & \gamma & \beta & \alpha & \beta & \beta & \alpha & \alpha & \beta & \gamma & \beta & \gamma & \beta & \beta & \alpha & \beta & \gamma & \cdots \\
\text{player 2:} & \beta & \gamma & \beta & \alpha & \beta & \gamma & \beta & \alpha & \beta & \beta & \alpha & \beta & \beta & \alpha & \alpha & \beta & \beta & \gamma & \gamma & \beta & \alpha & \alpha & \beta & \alpha & \alpha & \beta & \gamma & \gamma & \beta & \cdots \\
\text{player 3:} & \beta & \alpha & \alpha & \beta & \beta & \alpha & \alpha & \beta & \alpha & \beta & \gamma & \beta & \alpha & \beta & \gamma & \gamma & \beta & \alpha & \beta & \gamma & \gamma & \beta & \beta & \beta & \gamma & \beta & \beta & \alpha & \alpha & \cdots \\
\hline
\text{player 1:} & 0 & d & 0 & h & 0 & d & 0 & 0 & h & 0 & 0 & d & 0 & h & h & d & 0 & h & 0 & d & d & h & d & h & 0 & h & d & d & h & \cdots \\
\text{player 2:} & d & h & h & d & d & h & h & d & 0 & h & d & 0 & h & 0 & d & 0 & d & 0 & h & h & 0 & d & h & 0 & d & d & 0 & h & 0 & \cdots \\
\text{player 3:} & h & 0 & d & 0 & h & 0 & d & h & d & d & h & h & d & d & 0 & h & h & d & d & 0 & h & 0 & 0 & d & h & 0 & h & 0 & d & \cdots
\end{array} \tag{5}$$

Without any constraints, there are five possible alternating strategies (A_1 and A_4-A_7). All of them occur with approximately equal frequency in level 5, where individuals use all available social information (Fig. 2).

The triangular strategies are similar to the alternating strategies in the sense that they are also pure strategies. They exist only in level 5 (all available information). Triangular strategies occur when (a) the γ-individual always plays 'hawk' against the α-individual, which results in a triangular social configuration, and (b) the social relations in a triangular configuration are stable. There are four possible configurations, which, effectively, do not

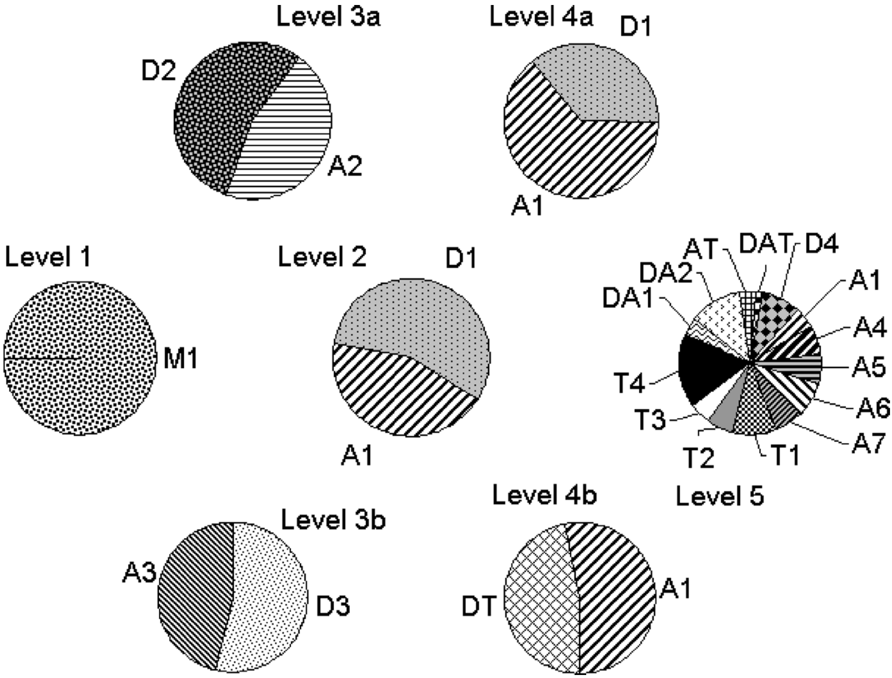

Fig. 2. Equilibria of the three-player model. For every information level, 200 simulations were run, starting from random initial conditions, until convergence to an equilibrium. The pie diagrams show the different equilibria that were found at an information level as well as the proportion of simulations in which they were reached by evolution. As explained in the text, unique labels indicating the strategy type (M, D, A, T, or combinations for hybrid types) were assigned to every equilibrium. These labels can also be found in Table 2, which shows the values of the eight strategic parameters for every equilibrium. The simulation parameters were chosen as follows: $V = 0.3$, $C = 1.0$, $D = 0.025$, $T = 50$.

differ (differences only arise when a player makes a mistake). A typical time series is shown below

$$\begin{array}{l} \text{player 1:}\\ \text{player 2:}\\ \text{player 3:}\\ \hline \text{player 1:}\\ \text{player 2:}\\ \text{player 3:} \end{array} \left(\begin{array}{ccc} & \beta & \\ & \beta & \\ & \beta & \\ \hline h & 0 & d \\ d, & h \text{ or} & 0 \\ 0 & d & h \end{array}\right)_{28} \begin{array}{c} \beta\beta\gamma \\ \beta\gamma\beta \\ \beta\alpha\alpha \\ \hline 0\,d\,h \\ d\,h\,0 \\ d\,0\,d \end{array} \left(\begin{array}{ccc} & \beta & \\ & \beta & \\ & \beta & \\ \hline d, & 0 & h \\ h & d \text{ or} & 0 \\ 0 & h & d \end{array}\right)_{16} \begin{array}{c} \beta \\ \beta \\ \beta \\ \hline h, \\ 0 \\ h \end{array} \left(\begin{array}{ccc} & \beta & \\ & \beta & \\ & \beta & \\ \hline d & 0 & h \\ h & d \text{ or} & 0 \\ 0 & h & d \end{array}\right)_{37} \begin{array}{c} \beta\gamma\gamma\ldots \\ \beta\beta\alpha\ldots \\ \beta\alpha\beta\ldots \\ \hline d\,0\,h\ldots \\ 0\,h\,0\ldots \\ d\,d\,d\ldots \end{array} \quad (6)$$

The brackets are used to abbreviate a repeated series of interactions.

Apart from the equilibria belonging to these categories, a number of equilibrium strategies are hybrids of the different types. For example, a time series corresponding to the strategy DT shows prolonged periods of a triangular social configuration, as in (6), alternating with periods of linear dominance hierarchies as in (4). Switches between these qualitatively different types of social dynamics occur with low probability, that is, when individuals make a mistake. Other interesting hybrid strategies are DA_1 and DA_2, where the rank differences between α- and γ-individual and β- and γ-individual are stable, but α- and β-individuals alternate ranks (DA_1), or where the rank differences between α- and β-individual and α- and γ-individual are stable, but β- and γ-individuals alternate ranks (DA_2).

Evolutionary pathways

Up to here, we have separately analysed the variants of the model for individuals with different cognitive abilities (corresponding to the different information levels). However, it is likely that the complexity of information used in conflict resolution strategies will change in the course of evolution. When selection removes the constraints imposed in the different information levels, and cognitive abilities increase, strategies shift from one information level to another. For example, the ability to remember the outcome of the previous conflict with an opponent could evolve first (corresponding to a transition from level 1, where no information is used, to level 2, where decisions are based only on the previous interaction with the current opponent). This could then be followed by a further elaboration of mental abilities, such that the information from relations with other individuals (level 4^a) and finally the full complexity of social relations within the group (level 5) is taken into account when deciding on the choice of action in a conflict. A second possible pathway would proceed from level 1 (no information is used) via level 3^a (decisions are based on one's own rank) and level 4^a (decisions are based on one's own rank and on the relation with the current opponent) to level 5 (all information is used). Two final, biologically less likely, pathways proceed from level 1 (no information) via level 2 (decisions are based on the relation with the current opponent) or 3^b (decisions are based on opponent's rank) to level 4^b (decisions are based on opponent's rank and on the relation with the current opponent) and finally to level 5 (all information is used).

In order to investigate the evolution of conflict resolution strategies along these evolutionary pathways, we simulated the following transitions between information levels (Fig. 3):

$$\begin{tikzcd}
 & \text{level } 3^{\mathrm{a}} \arrow[r] & \text{level } 4^{\mathrm{a}} \arrow[dr] & \\
\text{level } 1 \arrow[ur] \arrow[r] \arrow[dr] & \text{level } 2 \arrow[ur] \arrow[dr] & & \text{level } 5\ . \\
 & \text{level } 3^{\mathrm{b}} \arrow[r] & \text{level } 4^{\mathrm{b}} \arrow[ur] &
\end{tikzcd}$$

In most cases, simulations started close from an equilibrium in a lower level converge to a unique equilibrium of the same type in the next level. This result shows that most strategies are robust against changes in the amount or detail of social information that is used to base decisions on. There are two exceptions to this rule. First, simulations do not converge to a unique equilibrium, but converge with equal probability to two different equilibria in the transitions from level 1 (no information is used) to higher levels. Second, there is a change of equilibrium type ($D_1/D_3 \rightarrow DT \rightarrow T_1$, see Fig. 3) along the pathways via level 4^{b} (decisions are based on opponent's rank and on the relation with the current opponent). Along these pathways, individuals base their behaviour on their opponent's rank before using information about their own rank, which, on the proximate level, does not seem very likely.

If individuals use information about their own social rank before they use information about their opponent's rank (pathways along levels 2, 3^{a} and 4^{a}), there is a dichotomy between dominance and alternating strategies. This dichotomy occurs already in the first transition along the pathway, implying that already very simple strategies allow for dominance conventions. Moreover, these considerations suggest that, although there are many different equilibria at information level 5 (all information is used), only two of these equilibria (D_4 and A_1) seem relevant as possible outcomes of long term biological evolution.

Asymmetries in resource holding potential

The equilibria of level 2 (decisions are based on the relation with the current opponent), 3^{a} (decisions are based on one's own rank) and 3^{b} (decisions are based on opponent's rank) are reached with equal probability from the mixed strategy ESS of level 1 (no information is used). This is because the mixed equilibrium of level 1 is exactly located at the boundary separating the initial conditions from which the alternative equilibria of levels 2, 3^{a} and

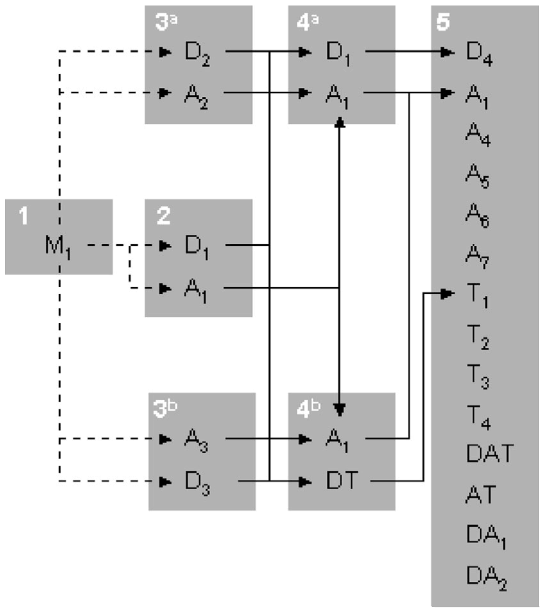

Fig. 3. Transitions between information levels. In the course of evolution, species may shift from lower to higher information levels, as increasingly detailed information is processed. To investigate the effect of a transition between two information levels (say a transition from level x to level y), 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 starting from a particular equilibrium converged to a single equilibrium at the higher information level. This is indicated in the figure by the solid arrows between equilibria at the different information levels (grey rectangles). However, in the transitions from the mixed equilibrium of level 1 (where no information is used) to higher information levels, multiple alternative equilibria can be reached (as indicated by dashed arrows). Parameters as in Fig. 2.

3^b are reached (shown for the transition from level 1 to level 3^a in Fig. 4). This feature disappears as soon as there are RHP asymmetries between the players (Fig. 5). Due to these RHP asymmetries, the boundary plane between the domains of attraction of the dominance and alternating equilibrium shifts slightly. The mixed equilibrium of level 1 is no longer on the border between the two domains of attraction, but in the interior of the domain of attraction of the dominance equilibrium. In our deterministic model, the alternating equilibrium can now no longer be reached from the mixed equilibrium of level 1. However, even with large RHP asymmetries (as in Fig. 5), the mixed equilibrium of level 1 is still very close to the border between the two domains

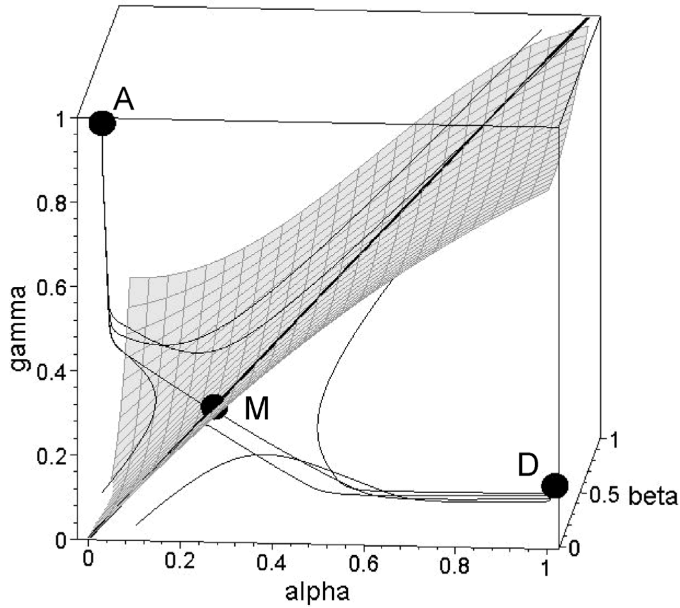

Fig. 4. The dichotomy between dominance strategies and other conventions. At information level 3^a, individuals base their decision on their own rank. Consequently, there are three strategic variables (the probability of playing Hawk when in rank α, β and γ, respectively), which are represented by the three axes of the plot. At information level 1, individuals use no information, and only the overall tendency of playing Hawk can change through evolution. Therefore, if constrained to information level 1, evolution will proceed along the thick black diagonal towards the mixed strategy equilibrium of level 1 (equilibria are represented by black spheres). However, the mixed strategy equilibrium is unstable with respect to movement away from the diagonal, so after a transition to level 3^a (where individuals behave differently depending on their own rank), evolution converges to either the dominance (lower right) or alternating equilibrium (upper left). Since the mixed equilibrium of level 1 is exactly located on the plane separating the domains of attraction of the stable equilibria of information level 3^a, both equilibria are attained with equal probability. The thin black lines represent deterministic evolutionary trajectories of the model at information level 3^a. Parameters as in Fig. 2.

of attraction. Due to stochastic fluctuations, which are likely to be present under natural conditions, the alternating equilibrium may therefore still be attainable in practice.

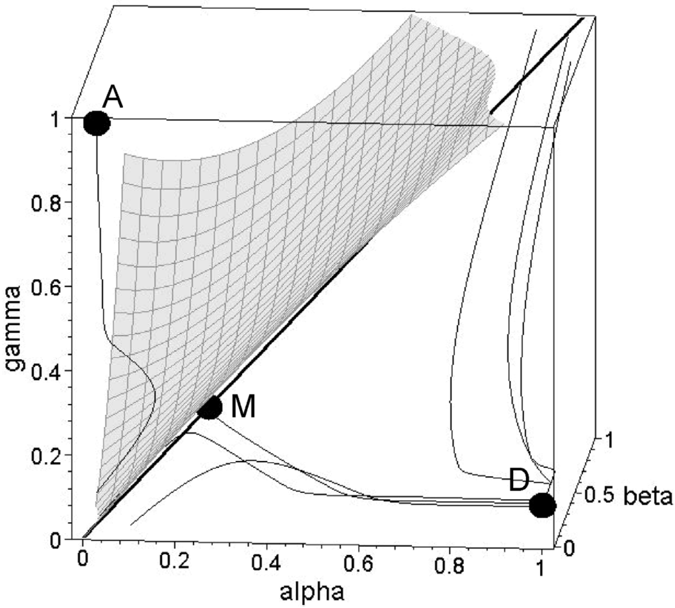

Fig. 5. Effects of RHP differences. This figure is identical to figure 4, except for the fact that this figure is based on an extended version of our model in which hidden RHP asymmetries between individuals were included. To be precise, we assumed that there were two equally frequent RHP classes, representing strong and weak individuals. In an escalated conflict between a strong and a weak individual, the strong individual had a high probability of winning the conflict (87.5%). Due to these RHP asymmetries, the boundary plane between the domains of attraction of the stable equilibria of information level 3[a] (decisions based on own rank) has shifted slightly, such that the mixed equilibrium of information level 1 (no information is used) is now in the interior of the domain of attraction of the dominance equilibrium. Formally, this implies that further evolution from the equilibrium of information level 1 will always converge to the dominance equilibrium, as shown by the deterministic trajectory leading from the mixed equilibrium to the dominance equilibrium.

Interactions in larger groups and the effects of errors in individual recognition

Up to here, we have restricted ourselves to a fixed group size of three individuals and assumed that players had complete information about the outcome of previous conflicts. We refrain from relaxing these assumptions within our deterministic model framework, but instead, we use stochastic individual based simulations to extend our model to arbitrary group size and to check the validity of our results with respect to the assumption that the players can

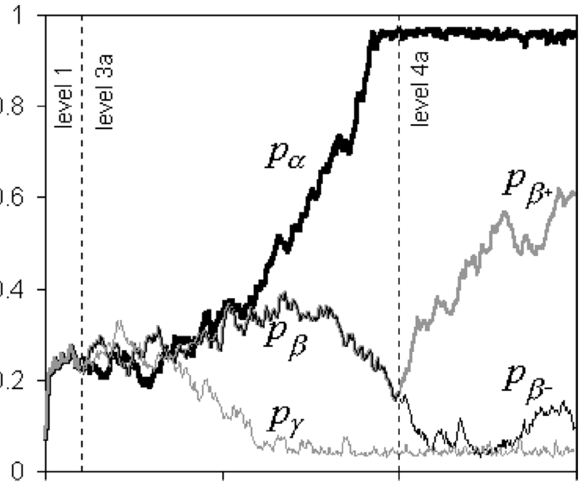

Fig. 6. Individual based simulations. Individual based simulations (see the Appendix for details) were used to extend the model to arbitrary group sizes and to vary our assumptions on the quality of individual recognition. We simulated a population of 50 groups, each consisting of 5 individuals. Errors in individual recognition occurred frequently (individuals made mistakes in 50% of the cases). Transitions to higher information levels occurred at generation 2000 and 20000. The two panels of the figure show the values of the strategic parameters in two replicate simulations, differing only in the seed used to initialise the random number generator. In the upper panel, evolution leads to a dominance strategy, in which higher-ranking individuals behave more aggressively. In the lower panel, the outcome of evolution is an alternating strategy, in which the lowest ranking individuals are most aggressive. The labels shown in the plots denote groups of constrained strategic parameters: $p_\alpha \triangleq p_{\alpha\beta} = p_{\alpha\gamma}$, $p_\beta \triangleq p_{\beta\alpha} = p_{\beta\gamma} = p_{\beta^+\beta^-} = p_{\beta^-\beta^+}$, $p_\gamma \triangleq p_{\gamma\alpha} = p_{\gamma\beta}$, $p_{\beta^+} \triangleq p_{\beta\gamma} = p_{\beta^+\beta^-}$, $p_{\beta^-} \triangleq p_{\beta\alpha} = p_{\beta^-\beta^+}$. Payoffs and other parameters were as in Fig. 2.

accurately remember the outcome of previous conflicts between all players in the group.

There are different ways in which the three-player model can be generalized to arbitrary group sizes. We choose an option that deviates as little as possible from the original model. We assume that an individual bases its decision in a conflict on (1) its relation with its current opponent, (2) its relation with *one* bystander, which is randomly selected from the other group members, and (3) the relation between its opponent and a (potentially different) bystander, which is also randomly selected from the other group members. Individuals can now find themselves in eight qualitatively different social situations, which can be interpreted exactly as in the original three-player model. The different information levels of the three-player model can simi-

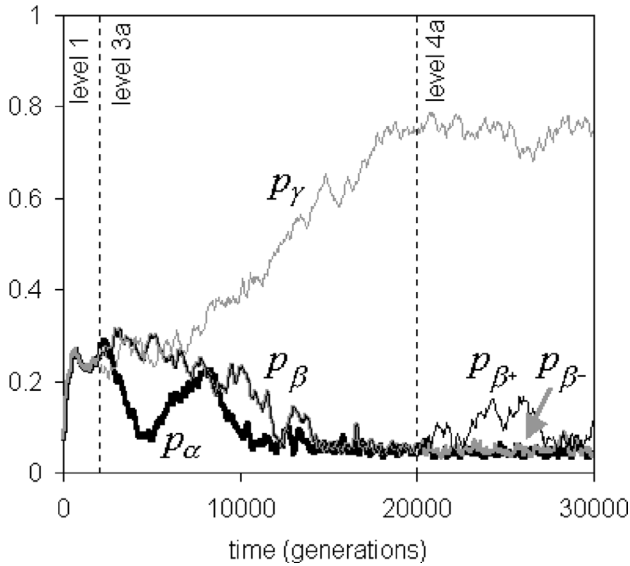

Fig. 6. (Continued).

larly be translated directly to the model with arbitrary group size. We varied the amount of social information that could be accurately remembered by an individual by changing the likelihood of errors in individual recognition. Individuals could either mistake their opponent or the bystander for an arbitrary other individual in the group.

Figure 6 shows the results of two individual based simulations, which differed only in the seed used to initialise the random number generator. In these simulations, groups consisted of five individuals, and errors in individual recognition were quite frequent (50% of the cases). As can be seen from Fig. 6, there are two different evolutionary equilibria. The equilibrium that is attained in the simulation represented in the upper panel is a dominance equilibrium: the α-individual almost always plays Hawk, the β-individual usually plays Hawk against the γ-individual, but hardly ever against the α-individual, and the γ-individual never plays Hawk. The simulation shown in the lower panel of Fig. 6 converges to an equilibrium that corresponds to an alternating equilibrium of the three-player model: this time the γ-individual is the most likely to play Hawk, leading to unstable social configurations.

These results, together with the other simulations we performed, indicate that the presence of multiple qualitatively different conflict resolution conventions is a robust phenomenon. For all combinations of group size (4, 5, 8, 10) and probabilities of errors in individual recognition (0%, 25%, 50%, 100%) tested, we found dominance and alternating equilibria. The analogues of triangular strategies, in which all individuals have exactly the same social rank, never evolved. This is because the maintenance of such maximally intransitive hierarchies in larger groups requires complete social information. In our simulation model, complete social information is unattainable by definition, since the relation with only one of the bystanders is considered in a conflict decision. Replicates of the simulations shown in Fig. 6 moreover indicate that the alternative conventions are reached with equal probability from the mixed equilibrium of level 1 (8 out of 20 replicates converged to the dominance convention). Inclusion of hidden RHP-differences between individuals (as in Fig. 5) biases the outcome towards convergence to the dominance convention (18 out of 20 replicates, data not shown).

Discussion

The outcome of conflicts between individuals in a social group automatically generates historical asymmetries between individuals. Such asymmetries may either pertain to previous conflicts between a focal individual and its opponent, or to previous conflicts with other group members. For example, in a social group in which a linear hierarchy has been established, there are at least two qualitatively different asymmetries between the highest- and lowest-ranking individual. First, there is a direct asymmetry: the highest-ranking individual is obviously dominant over the lowest-ranking one. Second, there is an indirect asymmetry: the highest-ranking individual is dominant over other group members, which, in their turn, are dominant over the lowest-ranking individual. Our results show that both these direct and indirect asymmetries can be used as cues for conventional conflict resolution, leading to within- and between-pair winner and loser effects, respectively. Within-pair winner and loser effects lead to rank differentiation within pairs of individuals, between-pair winner and loser effects lead to the ordering of social relation within the group into a transitive hierarchy. Winner and loser effects may evolve even when the historical asymmetries, generated by the outcomes of previous conflicts between individuals, hold no information about differences in resource holding potential.

Apart from strategies that give rise to transitive dominance hierarchies, our analysis reveals that there are other possible evolutionarily stable conflict resolution strategies. Contrary to the dominance strategies, which are characterized by within- and/or between-pair winner and loser effects, these alternating strategies are comparable to the paradoxical strategies described by Maynard Smith (1982), in the sense that the loser rather than the winner of previous fights is most likely to escalate. This leads to a constantly changing, egalitarian social configuration. In addition to the alternating strategies, evolution may lead to strategies that lock onto an intransitive social configuration that gives equal payoff to all group members (triangular strategies). The occurrence of both alternating and triangular strategies, next to the 'common-sense' dominance strategies is in accordance with game theoretical results, which state that any asymmetry between players (a) must be used for conventional conflict settlement, and (b) can be used in both a paradoxical and common-sense way (Maynard Smith & Parker, 1976; Hammerstein, 1981; Selten, 1980; see also the discussion of the companion paper, Van Doorn *et al.*, this issue).

The triangular strategies do not seem relevant within the context of biological evolution, since they are sensitive to errors in individual recognition and can only evolve when individuals have access to complete social information. The alternating strategies, however, are robust against errors in individual recognition. They can evolve even when individuals have access to only limited social information. In line with the results of previous game theoretical models, paradoxical strategies (alternating and triangular) are less likely to evolve than the common-sense strategies (dominance) if there are underlying RHP asymmetries (Hammerstein, 1981). However, the bias towards evolution of dominance strategies is small, even when the underlying RHP asymmetries are large. The latter finding may change considerably as soon as individuals base their decisions in conflicts not on a single previous conflict (as we assumed for simplicity) but on a large number of previous interactions. The same may be true when the probabilities of interaction between individuals are not fixed (as assumed in our model) but modified by spatial self-structuring (Hemelrijk, 2000).

Together with the companion paper, the present study provides a proof of principle that evolutionarily stable dominance relationships need not necessarily reflect intrinsic differences between individuals, such as RHP asymmetries, but that they may result from arbitrary historical asymmetries. The acknowledgement of the potential of social conventions, which could, in principle, be based on quite arbitrary asymmetries, can help to understand several aspects of social dominance that are difficult to explain with an approach focusing only on intrinsic differences between individuals. Yet, for a full understanding of social dominance and social hierarchy formation these two approaches should not be opposed to one another but combined. In this, and the companion paper, we made only a small step towards this end. Certainly more work is needed to fully integrate social dominance conventions relating to intrinsic differences between individuals, such as direct assessment of the opponent's RHP, and the conventions relating to arbitrary asymmetries, such as winner and loser effects.

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Appendix: Analytical and numerical analysis and individual based simulations

The payoff function

The average expected payoff $W(\vec{q}, \vec{p})$ of a rare mutant playing strategy $\vec{q}$ against resident individuals that play strategy $\vec{p}$ can be derived from the transition probabilities between the different situations in which the mutant individual can find itself. Every mutant individual is in a group with two resident individuals. From here on, we will arbitrarily label the resident individuals as ‘resident 1’ and ‘resident 2’, and we will define the eight possible social situations as follows

$$\begin{array}{cc}
\begin{array}{ccc} & \nearrow & \text{resident 1} \\ \text{mutant} & & \downarrow \\ & \searrow & \text{resident 2} \end{array} & \begin{array}{ccc} & \nearrow & \text{resident 1} \\ \text{mutant} & & \uparrow \\ & \searrow & \text{resident 2} \end{array} \\
\text{social situation 1} & \text{social situation 2} \\
\begin{array}{ccc} & \swarrow & \text{resident 1} \\ \text{mutant} & & \downarrow \\ & \searrow & \text{resident 2} \end{array} & \begin{array}{ccc} & \nearrow & \text{resident 1} \\ \text{mutant} & & \uparrow \\ & \nwarrow & \text{resident 2} \end{array} \\
\text{social situation 3} & \text{social situation 4} \\
\begin{array}{ccc} & \swarrow & \text{resident 1} \\ \text{mutant} & & \downarrow \\ & \nwarrow & \text{resident 2} \end{array} & \begin{array}{ccc} & \swarrow & \text{resident 1} \\ \text{mutant} & & \uparrow \\ & \nwarrow & \text{resident 2} \end{array} \\
\text{social situation 5} & \text{social situation 6} \\
\begin{array}{ccc} & \nearrow & \text{resident 1} \\ \text{mutant} & & \downarrow \\ & \nwarrow & \text{resident 2} \end{array} & \begin{array}{ccc} & \swarrow & \text{resident 1} \\ \text{mutant} & & \uparrow \\ & \searrow & \text{resident 2} \end{array} \\
\text{social situation 7} & \text{social situation 8}
\end{array} \tag{7}$$

with the arrows pointing towards the loser of the previous fight.

We may now compute the transition matrix $\mathbf{M}(\vec{q}, \vec{p})$, the elements $(m_{i,j})$ of which give the transition probability from social situation j to social situation i $(i, j = 1, \dots, 8)$. For example, a transition from social situation 1 to social situation 3 occurs when there is a conflict between mutant and resident 1 (which occurs with probability 1/3) and when the mutant loses this conflict. The latter may occur with probability 1/2 after both mutant and resident 1 play Hawk, or after the mutant plays Dove and resident 1 plays Hawk, or with probability 1/2 after both mutant and resident play Dove. In social situation 1, the mutant is the α-individual, whereas its opponent is the β-individual. Therefore, the mutant plays Hawk with probability $q_{\alpha\beta}$, and resident 1 plays Hawk with probability $p_{\beta\alpha}$. Consequently, we find

$$m_{3,1} = \frac{1}{3}\left(\frac{1}{2}p_{\beta\alpha}q_{\alpha\beta} + p_{\beta\alpha}(1 - q_{\alpha\beta}) + \frac{1}{2}(1 - p_{\beta\alpha})(1 - q_{\alpha\beta})\right). \tag{8}$$

In the same way, the transition probability from social situation 1 to social situation 2 is given by

$$m_{2,1} = \frac{1}{3}\left(\frac{1}{2}p_{\gamma\beta}p_{\beta\gamma} + p_{\gamma\beta}(1 - p_{\beta\gamma}) + \frac{1}{2}(1 - p_{\gamma\beta})(1 - p_{\beta\gamma})\right). \tag{9}$$

Note that this transition probability is independent of the mutant strategy, since a transition from social situation 1 to 2 occurs only after a conflict between the two resident individuals.

After having computed the other elements of $\mathbf{M}(\vec{q}, \vec{p})$ in a similar way, we also need to calculate the expected costs $\vec{c}(\vec{q}, \vec{p})$ and benefits $\vec{b}(\vec{q}, \vec{p})$ (to the mutant) associated with every social situation. For example, in social situation 1, the expected benefit from the previous conflict is $2/3V$. This is because the mutant was involved in the previous conflict with probability 2/3 (it was a mere bystander in 1/3 of the cases). However, if the mutant was involved in the last conflict, it certainly obtained the resource (corresponding to a benefit V). This follows from the fact that the mutant is the α-individual in social situation 1 and, hence, gained the resource in its last conflict with both other group members. In the other social situations the benefits to the mutant are as follows

$$\vec{b}(\vec{q}, \vec{p}) = \left(\frac{2}{3}V \;\; \frac{2}{3}V \;\; \frac{1}{3}V \;\; \frac{1}{3}V \;\; 0 \;\; 0 \;\; \frac{1}{3}V \;\; \frac{1}{3}V\right). \tag{10}$$

The expected costs $\vec{c}(\vec{q}, \vec{p})$ in a given social situation pertain to the expected costs of the *next* conflict. The next conflict may occur between the mutant and resident 1, between the mutant and resident 2, or between the two residents. In the latter cases, the mutant incurs no costs. In the former two cases, there are costs if the mutant plays Hawk and when the conflict escalates and the mutant loses. To be precise, the expected cost $\bar{c}(q, p)$ to a mutant that plays Hawk with probability q in a conflict with another individual playing Hawk with probability p is $\bar{c}(q, p) = 1/2pqC + qD$. Averaging over all possible conflicts that may occur in a social situation, we find

$$\vec{c}(\vec{q},\vec{p}) = \frac{1}{3}\begin{pmatrix} \bar{c}(q_{\alpha\beta}, p_{\beta\alpha}) + \bar{c}(q_{\alpha\gamma}, p_{\gamma\alpha}) \\ \bar{c}(q_{\alpha\beta}, p_{\beta\alpha}) + \bar{c}(q_{\alpha\gamma}, p_{\gamma\alpha}) \\ \bar{c}(q_{\beta\alpha}, p_{\alpha\beta}) + \bar{c}(q_{\beta\gamma}, p_{\gamma\beta}) \\ \bar{c}(q_{\beta\alpha}, p_{\alpha\beta}) + \bar{c}(q_{\beta\gamma}, p_{\gamma\beta}) \\ \bar{c}(q_{\gamma\alpha}, p_{\alpha\gamma}) + \bar{c}(q_{\gamma\beta}, p_{\beta\gamma}) \\ \bar{c}(q_{\gamma\alpha}, p_{\alpha\gamma}) + \bar{c}(q_{\gamma\beta}, p_{\beta\gamma}) \\ \bar{c}(q_{\beta^+\beta^-}, p_{\beta^-\beta^+}) + \bar{c}(q_{\beta^-\beta^+}, p_{\beta^+\beta^-}) \\ \bar{c}(q_{\beta^+\beta^-}, p_{\beta^-\beta^+}) + \bar{c}(q_{\beta^-\beta^+}, p_{\beta^+\beta^-}) \end{pmatrix}^T. \tag{11}$$

Next, we define vectors $\vec{u}_n(\vec{q},\vec{p})$, which contain the probabilities that the mutant finds itself in each of the eight possible social situations in the n-th conflict. The vectors $\vec{u}_n(\vec{q},\vec{p})$ satisfy

$$\vec{u}_n(\vec{q},\vec{p}) = \mathbf{M}(\vec{q},\vec{p})\,\vec{u}_{n-1}(\vec{q},\vec{p}). \tag{12}$$

We assume that the players start in an intransitive hierarchy. Hence,

$$\vec{u}_0(\vec{q},\vec{p}) = \begin{pmatrix} 0 & 0 & 0 & 0 & 0 & 0 & \frac{1}{2} & \frac{1}{2} \end{pmatrix}^T. \tag{13}$$

Equations (12) and (13) together uniquely determine the sequence $\vec{u}_0(\vec{q},\vec{p}), \vec{u}_1(\vec{q},\vec{p}), \vec{u}_2(\vec{q},\vec{p}), \ldots$ which determines the average expected payoff, $W(\vec{q},\vec{p})$, of an individual playing strategy $\vec{q}$ against opponents playing strategy $\vec{p}$.

In order to find $W(\vec{q},\vec{p})$, we must first calculate the expected payoff $w_n(\vec{q},\vec{p})$ to the mutant in the n-th conflict. This quantity is given by

$$w_n(\vec{q},\vec{p}) = \vec{b}(\vec{q},\vec{p})\,\vec{u}_n(\vec{q},\vec{p}) - \vec{c}(\vec{q},\vec{p})\,\vec{u}_{n-1}(\vec{q},\vec{p}). \tag{14}$$

The first term in equation (14) measures the expected benefit to the mutant in the n-th conflict. The second term is the expected cost to the mutant incurred in reaching the current social situation from the $(n-1)$-th conflict.

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

$$W(\vec{q},\vec{p}) = \frac{1}{3T}\sum_{n=1}^{\infty}\left(1-\frac{1}{3T}\right)^{n-1} w_n(\vec{q},\vec{p}). \tag{15}$$

The factor $(1 - 1/(3T))^{n-1}$ is necessary to weigh the expected payoff of the n-th conflict with the probability that this conflict will actually occur.

Evolutionary dynamics

Under the assumption that evolution proceeds in small steps at a rate and in the direction determined by the magnitude and sign of the selection gradient (Hofbauer & Sigmund, 1998, Chapter 9), the evolution of the strategy $\vec{p}$ can be described by

$$\frac{\partial\vec{p}}{\partial t} = \kappa\mathbf{G}\left.\frac{\partial W(\vec{q},\vec{p})}{\partial\vec{q}}\right|_{\vec{q}=\vec{p}}. \tag{16}$$

In this equation, the rate constant κ depends on the population size and the rate of mutations. The matrix **G** is a mutational variance-covariance matrix, which we used to implement the constraints corresponding to the different information levels, as explained in the companion paper. We imposed that all strategic parameters are within the range $[\delta,\ 1-\delta]$, in order to exclude evolution towards equilibrium strategies that are sensitive to occasional errors in decision-making ('trembling hand' approach, Selten, 1975). Throughout this paper, we took $\delta = 0.025$.

Individual based simulations

In the individual based simulations, individuals were distributed at the start of every generation (generations were discrete) into N groups, each consisting of G individuals. Individuals then engaged in repeated Hawk-Dove interactions with other individuals from their group. On average, every pair of individuals interacted T times. At the end of every generation, individuals from all groups were collected in one big mating pool. Offspring was generated by sexual reproduction, and the number of offspring produced by an individual was proportional to the total payoff gained in interactions throughout its lifetime. We furthermore assumed that the 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).