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MATHEMATICAL MODELLING OF DOMINANCE HIERARCHIES

Klodeta Kura

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City, University of London
School of Mathematics, Computer Science and Engineering
Department of Mathematics

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Declaration

This thesis is entirely my own work, except where otherwise indicated.

This thesis is submitted to City, University of London for the Degree of Doctor of Philosophy, and no part of the work included in this thesis has been submitted in fulfilment of the award of any other Degree or qualification.

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Abstract

In this reserach, we analyse the formation of dominance hierarchies from different viewpoints and various models of dominance hierarchy formation have been proposed, one important class being winner-loser models and another being Swiss tournaments.

We start by understanding the structure of hierarchies emerging under the influence of winner and loser effects and two situations are considered: (i) when each individual has the same, fixed (unchanged) aggression threshold, meaning that all of them use the same rule when deciding whether to fight or retreat, and (ii) when individuals select an aggression threshold comparing their own and their opponent's abilities, and fighting if and only if the situation is sufficiently favourable to themselves. For both situations, we investigate if we can achieve hierarchy linearity, and if so, when it is established. We are particularly interested in the question of how many fights are necessary to establish a dominance hierarchy.

To examine these questions we use existing and new statistical measures. Besides understanding the structure and the temporal dynamic of the hierarchy formation, we also analyse the effect of the information that each individual has about the strength of their opponents on linearity.

For the second situation, where individuals choose different aggression threshold, we find the appropriate level of aggression and examine the conditions when an individual needs to be more aggressive and when not.

Lastly, we develop a model which allows only the individuals with the same number of wins and losses to fight each other. We show that linear hierarchies are always established. A formula for the total number of fights is derived, and the effect of group size on the level of aggressiveness is analysed.

Chapter 1

Introduction

Many animals spend their lives, or a part of their lives, living in groups that occupy the same territory. There are a lot of factors why an individual would choose to live in a group, such as mating, foraging benefits [88], etc., but perhaps the most important one, is the anti-predator vigilance [87]. Living in a group allows its members to divide the tasks; while some individuals watch out for predators, the rest can search for food.

On the other hand, living in groups can have different costs. For example, if the resources such as food, mating or territory are limited, individuals often arrange themselves into a ranking system. Those with a higher rank can benefit by a high success in reproduction and access to food resources. This arrangement where everyone or almost everyone has a clear position in the group is called a *dominance hierarchy*. Individuals often establish their position by aggressive fights between themselves.

There are a lot of factors that influence dominance hierarchy formation, two of those are winner and loser effects. Winner and loser effects occur when previous victories lead to an increased probability of winning and previous defeats lead to a decreased probability of winning respectively ([11], [61], [62], [105]).

There is not a large body of theory to predict the position of an individual in a dominance hierarchy [90]. Most theoretical work is concerned with the modelling of winner and loser effects (but see [21], [23] for alternative models). Landau ([75], [76]) showed that intrinsic factors such as age or size alone cannot produce hierarchies similar to ones observed in nature, pointing to the importance of extrinsic factors such as prior experience. Once factors such as winner and loser effects were added to the model, hierarchies similar to those found in nature were obtained. Landau ([75], [76]) considered the combined effects of winner and loser effects on hierarchy formation. Others have seen how winner and loser effects separately influence dominance hierarchy formation ([17], [42], [44], [58]). Dugatkin [42] and Dugatkin & Dugatkin [44] developed a simulation framework which explored the properties of emerging hierarchies in groups of four individuals under different assumptions about the strength of winner and loser effects.

In this research, we analyse and model the formation of dominance hierarchies, in particular the influence of winner and loser effects. Our aim is to find answers to questions such as: Is it possible to find the time when the hierarchy is established and when an individual dominates the others so that the dominance relationship cannot be reversed? So far, in winner-loser models, the temporal dynamic of the hierarchy formation has not been analysed. In addition, we explore the conditions under which an individual should be more aggressive and when it should retreat.

In this work, we combine game-theoretical concepts with the theory of dominance hierarchies. For this reason in the first part of this chapter we introduce such concepts and in the second part, we present the literature on dominance hierarchies.

1.1 Game Theory

Game theory is the study of the decision-making of individuals where an individual's choice might affect the outcomes of others. Its origin is in 1920s with Borel [18] and von Neumann, although there are earlier examples with game theoretical elements involved [36]. It was only in 1944 when von Neumann and Morgenstern published the book *Theory of Games and Economic Behavior* [123] that Game theory was established as a field in its own. In 1950s Game theory was applied to different situations arising in politics, but it has seen an interest from other disciplines as well such as psychology, biology and logic. The basic key elements of a game theoretical model are the following:

Players: In a game we might have a finite or an infinite number of players who are decision-makers. Their decisions affect the outcome of the game. Often the games in biology are characterized by two players for simplicity reasons.

Strategies: During different stages of the game, a player has choices to make and the possible choices in each stage are known as *actions*. A strategy of a player is defined as the action that it chooses at every possible stage of the game. If only one specific strategy is chosen to be played in different positions of the game, this strategy is called a *pure strategy*. For a finite set $\{S_1, S_2, ..., S_n\}$ of pure strategies, we can define a *mixed strategy* as the probability vector **p** $= (p_1, p_2, ..., p_n)$ where p_i is the probability that the player will decide to play strategy S_i.

Payoffs: The "award" that a player gets when playing a game is known as the payoff. When there are only two individuals interacting and each of them has a finite set of pure strategies, the payoffs can be represented by a matrix called the payoff matrix. Such games are called bimatrix games. Suppose that $\{S_1, S_2, ...S_n\}$ is the set of pure strategies of player 1 and $\{T_1, T_2, ..., T_m\}$ is the set of pure strategies for player 2. The payoffs for both payers are determined by the pair of matrices

$$A = (a_{ij})_{i=1,...,n;j=1,...,m}, B = (b_{ij})_{i=1,...,m;j=1,...,n} \tag{1.1}$$

where a_{ij} and b_{ji} are the payoffs of player 1 and 2 respectively, after player 1 chooses strategy S_i and its opponent is playing strategy T_j.

In the case of a symmetric game where both individuals have the same set of strategies $T_1, T_2, ..., T_m$ and the reward gained after using a certain strategy depends only on the other strategies and not who is playing them, the game can be described as an $n \times n$ matrix $A = (a_{ij})_{i,j=1,...,n}$ where the value in the i^{th} row and j^{th} column gives the payoff of the row player that uses strategy T_i against the column player using strategy T_j. The classical Hawk-Dove game described below is an example of a symmetric game.

1.1.1 Nash equilibria

In any game, each player tries to choose a strategy that offers the highest payoff. But how does one find the "best strategy" when its payoff depends on what strategy its opponent is playing? The concept of Nash equilibrium [96] is important to study the strategies used by different players. Before giving its definition, it is useful to first give the definition of the *best response*.

Definition 1. *A strategy S is a best response to strategy U if E[T,U] $\leq$ E[S,U]; for all strategies T, where E[S,U] denotes the payoff to a player using S against a player using U [29].*

Now we give the definition of Nash equilibrium.

Definition 2. *A Nash equilibrium [96], is a set of strategies, one for each player, such that neither player can profitably alter their strategy (i.e. increase their payoff) unilaterally [22].*

If we use the terminology of the best response, we say that a game is in a Nash equilibrium if and only if all the individuals in the group are playing the best response against their opponents' strategies. Mathematically in a two-player game, the strategy S is a Nash equilibrium if

$$E[S,S] \geq E[T,S], \forall T \neq S \tag{1.2}$$

When $E[S,S] > E[T,S], \forall T \neq S$, we say that strategy S is a *strict* Nash equilibrium.

1.2 Evolutionary game theory

In *biology*, game theory is used to model and analyse the conflict and cooperation in different groups of animals [57]. In contrast to the game theory where each player tries to be rational, Evolutionary game theory (EGT) is determined by natural selection which drives different organisms towards the maximisation of reproductive success [57]. An important concept in EGT is that of the *evolutionarily stable strategy* (ESS) introduced by Maynard Smith and Price [84], but it was derived by MacArthur and Hamilton's sex ratio work ([56], [79]) that was based on Fisher's principle and is closely related to the concept of Nash equilibrum.

1.2.1 Evolutionarily stable strategies

In a biological sense the concept of *Evolutionarily Stable Strategy* (ESS) is usually applied to evolutionary processes.

A strategy is an ESS if when adopted by a population (residents) cannot be invaded by a small number of individuals playing any alternative (mutant) strategy. Mathematically an ESS is defined as follows:

Assume that the majority of the population is playing strategy S and a small number of “mutants” (a fraction ε of the total population) adopt strategy T. Then we can give the following definition.

Definition 3. *The strategy S is evolutionarily stable against strategy T if* $E[S,(1-\varepsilon)S+\varepsilon T] > E[T,(1-\varepsilon)S+\varepsilon T]$ *for any sufficiently small value of* $\varepsilon > 0$. *S is an evolutionarily stable strategy* (ESS) *if it is evolutionary stable against T for every other strategy T* $\neq$ *S ([24], [29]).*

This implies that in a population involving randomly selected pairs of individuals playing two-player games, strategy S which can be a pure or mixed strategy, is an ESS if either

$$E[S,S] > E[T,S] \tag{1.3}$$

or

$$E[S,S] = E[T,S] \text{ and } E[S,T] > E[T,T] \tag{1.4}$$

$\forall T \neq S$, where $E[S,S]$ is the expected payoff of an individual playing strategy S against an individual who is playing strategy S .

In a population involving randomly selected groups of N individuals playing N-player games, strategy S is an ESS if either:

$$E[S;S^{N-1}] > E[T;S^{N-1}] \tag{1.5}$$

or

$$E[S;S^{N-1}] = E[T;S^{N-1}] \text{ and } E[S,S^{N-2},T] > E[T,S^{N-2},T] \tag{1.6}$$

$\forall T \neq S$, where $E[S;S^i,T^{N-1-i}]$ is the expected payoff of an individual playing strategy S against i individuals playing strategy S and $N-i-1$ individuals playing strategy T, respectively [24].

If condition (1.3) holds than the individuals (mutants) using strategy T, lose against a population of individuals that are using strategy S, thus they cannot invade the residents. If condition (1.4) holds than even if a mutant individual does equally well as the resident when playing against a resident individual, it cannot invade the population of residents. Thus a strategy S is an ESS if either condition (1.3) or (1.4) holds. Furthermore we note that a game can have more than one ESS simultaneously, or there might be occasions where no ESS are present. When comparing with the Nash equilibria, an ESS is always a Nash equilibria (from conditions (1.3) and (1.4)), but the reverse is not always true. However a strict Nash equilibria is an ESS, because for a strategy to be a strict Nash equilibria, condition (1.3) must hold.

1.2.2 The diagonal rule

The *diagonal rule* allows us to find the ESS in a n-strategy game. Assume that the pure strategies are θ_1, θ_2,...,θ_n with the corresponding $n \times n$ payoff matrix. Now suppose that in the payoff matrix, the i^{th} diagonal payoff E[θ_i, θ_i] is the largest payoff in the i^{th} column. This yields E[θ_i, θ_i] $>$ E[θ_j, θ_i], $\forall j \neq i$.

Let us denote by $\gamma \neq \theta_i$ a mixed strategy which can be written as a combination of the pure strategies θ_i as follows

$$\gamma = p_1\theta_1 + p_2\theta_2 + ... + p_n\theta_n \tag{1.7}$$

where $p_1 + p_2 + ... + p_n = 1$ and each $p_i \geq 0$.

Next, because E[θ_j, θ_i] $<$ E[θ_i, θ_i] we can write the following

$$\begin{aligned} E[\gamma, \theta_i] &= p_1 E[\theta_1, \theta_i] + p_2 E[\theta_2, \theta_i] + ... + p_n E[\theta_n, \theta_i] \\ &< p_1 E[\theta_i, \theta_i] + p_2 E[\theta_i, \theta_i] + ... + p_n E[\theta_i, \theta_i] \\ &= (p_1 + p_2 + ... + p_n) E[\theta_i, \theta_i] \\ &= E[\theta_i, \theta_i] \end{aligned} \tag{1.8}$$

Thus we have proved that E[γ, θ_i] $<$ E[θ_i, θ_i] which yields the following theorem [91]:

Theorem 1.2.1. ***The Diagonal Rule:*** *In a n-strategy game with pure strategies θ_1, θ_2,..., θ_n, if E[θ_i, θ_i] $>$ E[θ_j, θ_i], $\forall j \neq i$, then θ_i is a pure ESS.*

1.2.3 The classical Hawk-Dove model

Here we give a classic example of an evolutionary game, that of the Hawk-Dove game ([83], [84]) which is widely used to model situations where groups of animals compete with each other to gain access to biological resources such as food, territory, mating, etc. The game is described as follows:

Suppose that in a population, individuals fight with each other over a reward $V > 0$. Each individual can choose to either be aggressive, play Hawk (H) or non-aggressive, play Dove (D). When a Hawk meets a Hawk they engage in an aggressive interaction until there is a winner and a loser. The winner gets the reward V and the loser pays a cost of injury C (or gains reward $-C$). Thus the expected reward when a Hawk meets another Hawk, is $E[H, H] = \frac{1}{2}(V - C)$. When a Hawk meets a Dove, the Hawk is aggressive and the Dove always retreats from fighting. Thus the Hawk gets the reward V, the Dove gets 0 and does not pay any cost as it does not engage in a fight. Hence $E[H, D] = V$ and $E[D, H] = 0$. When a Dove meets another Dove they either share the reward V, or only one takes it and the other pays no cost, the winner being selected at random. The overall payoff of Doves in this case is $E[D, D] = \frac{V}{2}$. The following payoff matrix describes this game.

$$\begin{array}{c} \\ Hawk \\ Dove \end{array} \begin{array}{c} \begin{array}{cc} Hawk & Dove \end{array} \\ \begin{pmatrix} \frac{V-C}{2} & V \\ 0 & \frac{V}{2} \end{pmatrix} \end{array}$$

From the payoff matrix, we notice that the Dove strategy cannot be a pure ESS

as $E[H,D] > E[D,D]$ and thus in a population of Doves a Hawk individual always invades. Let us find now the conditions when playing Hawk is a pure ESS. For $V > C$ (the reward of winning is bigger than the cost of losing) we have $E[H,H] > E[D,H]$. In this case, because $E[H,D] > E[D,D]$ and thus playing Hawk is a pure ESS. We can show that playing Hawk is also a pure ESS when $V = C$ as $E[H,D] > E[D,D]$. Let us see now what happens for $V < C$, i.e. when the reward of winning is smaller than the cost of losing so that we have $E[H,H] < E[D,H]$. This means that in a population of residents playing the Hawk strategy, it is best to play Dove. Thus we get a mixed ESS. Denote by $\mathbf{p} = (p, 1-p)$ the mixed strategy where an individual plays Hawk with probability $p \in [0,1]$ and plays Dove otherwise. In order for this mixed strategy to be an ESS, the payoff of an individual playing Hawk needs to be equal to the payoff of an individual playing Dove, i.e.

$$p\frac{V-C}{2} + (1-p)V = p \cdot 0 + (1-p)\frac{V}{2} \tag{1.9}$$

from which we get

$$p = \frac{V}{C} \tag{1.10}$$

For $\mathbf{p}$ to be an ESS we need $E[\mathbf{p},\mathbf{q}] > E[\mathbf{q},\mathbf{q}]$, for all $\mathbf{q} \neq \mathbf{p}$. We have

$$E[\mathbf{p},\mathbf{q}] = q\frac{1}{2}\frac{V}{C}(V-C) + \frac{V}{C}(1-q)V + q(0)\left(1-\frac{V}{C}\right) + \left(1-\frac{V}{C}\right)(1-q)\frac{1}{2}V, \tag{1.11}$$

$$E[\mathbf{q},\mathbf{q}] = q^2\frac{1}{2}(V-C) + q(1-q)V + q(1-q)(0) + \frac{1}{2}V(1-q)^2. \tag{1.12}$$

From (1.11) and (1.12) we obtain

$$E[\mathbf{p},\mathbf{q}] - E[\mathbf{q},\mathbf{q}] = \frac{1}{2}C\left(\frac{V}{C} - q\right)^2 > 0 \tag{1.13}$$

which yields the desired result. This means that a Hawk does better against a Dove than a Dove does against another Dove. Thus we have a unique mixed

ESS where the individuals play Hawk with probability $\frac{V}{C}$ and Dove with probability $1 - \frac{V}{C}$.

1.3 Dominance hierarchies

In this section, we present the literature on dominance hierarchies.

Dominance hierarchies can be linear, so that animal A dominates all others, B dominates all others except A, etc, or can be non-linear where the position of individuals in the group is complex. For example we can have hierarchies in groups of animals where two or more individuals have the same position or when circular triads are present. A circular triad is a subgroup of 3 individuals A, B and C where the relation $A \rightarrow B \rightarrow C \rightarrow A$ holds, ($\rightarrow$ stands for "dominates"). This means that individual A dominates B, individual B dominates C but individual C dominates A.

In this thesis, we are concerned with situations where whole groups form from scratch, with individuals meeting each other for the first time, for example in leks ([60], [71]). In such situations individuals will often enter into a series of pairwise contests, in order to establish their position within the group. In general, linear hierarchies are very stable; for example, when chickens were taken from their group and reintroduced days later, they reoccupied the previous place that they had in the group [23]. Once the hierarchy is formed, the off-springs usually take a place behind or ahead their parents and siblings.

Dominance hierarchies have been the subject of study by behavioral ecologists for a long time and at first sight it is surprising that an individual would accept a subordinate rank within a hierarchy ([4], [41]). However, linear hierarchies are found to be present e.g. in birds, mammals, ants, fish or crustaceans ([1], [10], [31], [55], [85], [92], [93], [106], [110]). When 15 colonies of monogynous queenless ants [93] were put in plaster nets, 6 types of agonistic interactions were observed that were consistent over a period of 2 weeks. The workers ants were then ordered according to these aggressive behavior.

Some animals are more aggressive than others and the level of aggressiveness depends upon many factors such as experience, the value of winning the contest, resource holding potential (RHP) (see e.g., [15], [16], [95], [114], [115]). In our model RHP will simply mean the ability of an individual to win an escalated contest [101], abstracted away from any particular causal effect. In reality, there are a large number of elements that determine the RHP. Very broadly, these elements can be divided into physical attributes, such as size, age and physical strength (intrinsic factors) and psychological attributes, such as prior experience (extrinsic factors).

In more detail, there are a lot of results demonstrating a strong correlation between RHP and body size ([3], [20], [78]). For example it has been observed that larger animals are more aggressive towards smaller ones and that they have more chances of winning an encounter ([54], [69]). However, other results show that such physical attributes are not the only important determinant of RHP. For example [32] showed that 37.5% of a group of house crickets won aggressive interactions, even though they had smaller body size. In [59], bigger individuals lost 30% of the aggressive interactions.

Prior experience as well can have an important effect on the RHP of an individual. For example if an individual has won more fights than it has lost in the past, it may increase its potential to win in the future. In this research, we assume that all individuals have identical physical abilities, so that the outcome of an encounter is significantly determined by past experience (although our results depend upon only a mechanical updating of RHP after a contest, so it would allow for real physical as well as psychological changes, too). In particular we consider so-called “winner and loser effects”, but there can be other extrinsic factors such as the audience and bystander effects that influence the level of aggression. The audience effect ([39], [52], [86]) occurs when an individual changes its strategy as a result of being watched by others and the bystander effect occur when an individual changes the fighting behavior as a result of watching the other individuals in the group.

There is a lot of experimental evidence ([8], [13], [77], [108]) showing the presence of the loser effect in different groups of animals that lasts for several days. On the other hand the winner effect is less common, with only some species showing it. In stickleback fish *Gasterosteus aculeatus* it was observed that the loser effect lasted for twice as long as the winner effect [8]. In copperhead snakes *Agkistrodon contortrix* it was observed that there was no effect after a winning experience, while the effects of losing lasted for more than one day; individuals that had previously lost did not engage in any fight (they retreated), and lost when challenged, whereas those individuals that had previously won, won six of the ten subsequent contests [108].

1.3.1 Dugatkin's model of dominance hierarchy formation

Dugatkin [42] and Dugatkin & Dugatkin [44] developed a model to explore the structure of dominance hierarchies under different strengths of winner and loser effects ($W \geq 0$ and $L \in [0,1]$). The model consists of N individuals who are characterised by their RHP and aggression threshold (θ). The RHP value describes the ability of an individual to win an aggressive interaction (as described in Section 1.3), whereas θ indicates whether an individual engages in a fight in the first place. Further, it is assumed that the outcome of a fight (i.e. win or loss) influences the RHP. While a win increases an individual's ability to win the next fight, a loss decreases it. Two models which differed in the amount of information an individual has about its opponents' fighting abilities were analysed. The *non-updated model* assumes that no information about the current ability is available [42], whereas the *updated model* assumes that information (although with varying levels of accuracy) is accessible [44]. In the following we describe both models in detail.

1.3.1.1 The non-updated model

All individuals possess the same RHP initially (denoted by $RHP_{initial}$) and at each time step two individuals, x and y, are drawn at random to engage in an aggressive interaction. Individual x decides to fight against individual y at time t if

$$\frac{RHP_{x,t}}{RHP_{initial}} \geq \theta \tag{1.14}$$

holds, and it retreats otherwise, where $RHP_{x,t}$ describes the RHP of individual x at time t, and θ is a fixed aggression threshold. In this model, individual x has no information about the current RHP of individual y. Individual y is considered similarly. Each pairwise interaction results in one of three possible outcomes:

(1) both individuals decide to fight and x wins with probability

$$P_{x,y}(t) = \frac{RHP_{x,t}}{RHP_{x,t} + RHP_{y,t}} \tag{1.15}$$

(and consequently y wins with probability $P_{y,x}(t) = 1 - P_{x,y}(t)$);

(2) one chooses to fight and the other retreats;

(3) both individuals retreat, which is known as a double kowtow.

The outcome of the contest is assumed to affect the RHP. If individual x wins or individual y retreats then we obtain

$$RHP_{x,t+1} = (1 + W)RHP_{x,t}. \tag{1.16}$$

Similarly, if x loses or retreats then we have

$$RHP_{x,t+1} = (1 - L)RHP_{x,t}. \tag{1.17}$$

A similar dynamic holds for individual y. Consequently, the RHP of both individuals changes due to the outcome of their pairwise interactions, but in this model individuals are only able to track the changes of their own RHP (this may not be entirely realistic as we touch upon in Section 2.6).

Dugatkin [42] considered a group of four individuals and recorded the number of wins of each individual over each of the others in a single realisation of 1,000 interactions. He defined $\theta = 1$ (meaning that individual x will fight at time t if $RHP_{x,t} \geq RHP_{initial}$ holds) and analysed winner and loser effects of varying strengths ($W = 0; 0.1; 0.2; 0.3; 0.4; 0.5$ and $L = 0; 0.1; 0.2; 0.3; 0.4; 0.5$, respectively).

The results obtained from this simulation are summarised in Table 1.1. When only the winner effect was present each individual had a clear position in the hierarchy; higher-ranked individuals were characterised by a larger total number of wins, and also the ratios of their number of wins compared to their number of losses (excluding double kowtows) against each lower ranked individuals were high. This is true for all values of W. When only the loser effect was present one individual always emerged as the dominant individual and the position of the others was unclear as subordinate individuals started retreating quickly, and so the interactions between them resulted in mutual retreat. However, increasing the winner effect for a given value of the loser effect L increased the number of individuals with a clear position in the hierarchy (nevertheless the hierarchy was not always linear). Dugatkin saw the influence of the winner and loser effect in larger group sizes like when $N = 6, 8, 12$ and concluded that the pattern was the same as for $N = 4$. The loser effect appears to be stronger than the winner effect. For example in a group of 8 individuals, all individuals have a clear rank in the hierarchy when only the winner effect is present, but under a small value of the loser effect and a large value of the winner effect, only the top two to four individuals have a clear position.

	$W = 0$	$W = 0.1$	$W = 0.2$	$W = 0.3$
$L = 0$		– 146 136 140 8 – 8 172 21 170 – 168 6 18 7 –	– 146 172 160 6 – 168 158 7 9 – 167 2 2 3 –	– 4 158 164 161 – 146 172 6 2 – 183 0 1 3 –
$L =$ 0.1	– 0 0 0 171 – 171 163 0 0 −0 0 0 0 –	– 161 195 156 0 – 2 0 0 0 – 0 10 159 153 –	– 177 173 157 0 – 0 0 0 0 – 0 0 0 0 –	– 152 171 159 0 – 0 0 0 0 – 0 4 179 171 –
$L =$ 0.2	– 156 168 174 0 – 3 3 0 0 −0 0 0 0 –	– 156 178 149 0 – 0 0 0 0 – 0 0 0 1 –	– 1 1 0 0 – 0 0 157 173 – 148 1 3 0 –	– 2 173 149 147 – 160 196 0 0 – 0 1 0 3 –
$L =$ 0.3	– 0 3 1 181 – 172 154 0 0 −0 0 0 0 –	– 0 0 0 6 – 0 4 156 178 – 163 0 0 0 –	– 0 1 0 178 – 164 153 0 0 – 0 1 0 5 –	– 0 0 1 0 – 0 0 163 184 – 158 0 0 0 –

Table 1.1: The winner and the loser effects in a population of 4 individuals, $\theta = 1$, 1000 potential interactions. Entries in rows represents the number of times that the row player has defeated the column player (Dugatkin [42]).

1.3.1.2 The updated model

Dugatkin & Dugatkin [44] relaxed the (probably unrealistic) assumption that an individual has no knowledge of its opponent's RHP. They assumed that the opponent's RHP can be estimated and the (error-prone) estimate is drawn uniformly from the interval $[(1-\eta)RHP_{y,t}; (1+\eta)RHP_{y,t}]$ where η describes the accuracy of the estimate. The case $\eta = 0$ models the situation where each individual has perfect knowledge of its opponent's RHP [44]. The estimation of individual y is denoted by $\overline{RHP}_{y,t}$ and thus individual x decides to be aggressive when

$$\frac{RHP_{x,t}}{\overline{RHP}_{y,t}} \geq \theta \tag{1.18}$$

holds and retreats otherwise. The probability that x wins remains

$$P_{x,y}(t) = \frac{RHP_{x,t}}{RHP_{x,t} + RHP_{y,t}}. \tag{1.19}$$

The analysis of the updated model was done under combinations of $\eta = 0; 0.25; 0.75$, $\theta = 0, 0.5, 1$ and for the same values of winner and loser effects as in the non-updated model where $W = 0; 0.1; 0.2; 0.3; 0.4; 0.5$ and $L = 0; 0.1; 0.2; 0.3; 0.4; 0.5$.

Pairwise interactions affect RHP as described in equations (1.16) and (1.17). In total we have 324 combinations of θ, W, L and η and for each of these combinations the following was simulated:

(1) All individuals had $RHP_{initial} = 10$.

(2) All individuals had $RHP_{initial} = 10$, but two individuals always overestimate their opponent's RHP by choosing the maximum of the interval range and two individuals always underestimate their opponent's RHP by choosing the minimum of that range.

(3) $RHP_{initial} = 10, 12, 14, 16$ for the four individuals respectively.

(4) $RHP_{initial} = 10, 12, 14, 16$ for the four individuals respectively, but the two individuals with the lowest RHP always overestimate their opponent's RHP and the two individuals with the highest RHP always underestimate their opponent's RHP.

(5) $RHP_{initial} = 10, 12, 14, 16$ for the four individuals respectively, but the two individuals with the lowest RHP always underestimate their opponent's RHP and the two individuals with the highest RHP always overestimate their opponent's RHP.

For all the analysed cases, clear linear hierarchies were established (i.e. the higher-ranked individuals won more contests in total than lower-ranked individuals, and more direct contests against lower-placed individuals). Interestingly, the three different values of η made no differences to the hierarchy, and thus overestimation or underestimation of the opponent's ability to win a fight had no impact on the establishment of linear hierarchies, as long as some ability to estimate this ability was possessed [44].

1.3.2 A Measurement of linearity

Often the hierarchies found in nature are not perfectly linear (where each individual has a clear rank in the group). Sometimes two or more individuals have the same rank or circular triads might be present. It is of interest to measure how far from linearity hierarchies are. Landau and Kendall ([68], [75]) have both introduced an index of linearity denoted by L and K respectively where both take a value between 0 and 1. A value of 1 indicates a perfect linear hierarchy and a value of 0 represents a non linear hierarchy.

1.3.2.1 Landau's index of linearity

Landau [75] developed a method that measures the linearity of a hierarchy. This index is calculated as follows:

$$h = \left(\frac{12}{N^3 - N}\right) \sum_{x=1}^{N} \left(V_x - \frac{N-1}{2}\right)^2 \qquad (1.20)$$

where N is the group size and V_x is the number of individuals that are dominated by individual x. It was agreed in [12] and [33] that values of $h \geq 0.9$ correspond to 'strong', nearly linear hierarchies. Equation (1.20) is used when there are no individuals with tied rank numbers. However this index can also be used when there are tied ranks by using an adaptation proposed by [97]. Here if two individuals x and y have the same rank, we increase both values V_x and V_y by $1/2$.

1.3.2.2 Kendall's index of linearity

Another measurement of linearity is that developed by Kendall [68]. The method of calculating this index is given by Appleby [6] and the steps are as follows.

	A	B	C	D	E	F	G	Row total (R_i)
A	-	1	1	1	1	1	1	6
B	0	-	1	0.5	0.5	0	0	2
C	0	0	-	0.5	0.5	0	0.5	1.5
D	0	0.5	0.5	-	0	0.5	0.5	2
E	0	0.5	0.5	1	-	0	0.5	2.5
F	0	1	1	0.5	1	-	1	4.5
G	0	1	0.5	0.5	0.5	0	-	2.5

Table 1.2: Matrix of relationships between 7 individuals named A, B, C, D, E, F and G where row individual dominant to column individual is indicated by 1; column individual dominant to row individual is indicated by 0 and the unknown relationships are indicated by 0.5.

(1) Construct a matrix of relationships, in which the row individual i dominant to the column individual is indicated by 1 and the column individual dominant to the row individual is indicated by 0. Unknown relationships are indicated by 0.5.

(2) For each individual ($i = 1, ..., N$) calculate the row sum R_i which represents the number of individuals dominated by i (Table 1.2).

(3) Calculate d which is the number of circular triads (see Section 2.2.1) by

$$d = \frac{N(N-1)(2N-1)}{12} - \frac{1}{2}\sum_{i=1}^{N}(R_i)^2. \tag{1.21}$$

(4) The index of linearity K is calculated as follow:

$$K = \begin{cases} 1 - \frac{24d}{N^3-N} & : \text{N odd} \\ 1 - \frac{24d}{N^3-4N} & : \text{N even} \end{cases}$$

The value of K for odd values of N is the same as Landau's h. In Kendall's original procedure it was assumed that no tied relationships were present. However by indicating unknown relationships by $1/2$, the above procedure could be applied to hierarchies with unknown relationships. On the other hand, if the number of unknown relationships is relatively large the value of

K may be negative. Depending on the number of tied relationships K can overestimate or underestimate the level of linearity. De Vries [38] proposed an improved test of linearity that is not affected by the number of tied relationships. The steps of the procedure are as follows.

(1) Construct the matrix of relationships where the row individual dominant to the column individual is indicated by 1 and the column individual dominant to the row individual is indicated by 0. Unknown relationships are also indicated by 0.

(2) Construct 2^u matrices where u is the number of unknown relationships. Thus for a pair of individuals (A, B), if they have an unknown relationship, in a new matrix the position (A, B) will be indicated by 1 and the position (B, A) by 0 or the other way around. Because there are 2 possibilities for each unknown relationship, the total number of matrices that we construct is 2^u.

(3) For each of the 2^u matrices, calculate the number of circular triads d.

(4) Calculate the number of circular triads d' as the average of all d values.

(5) The index of linearity is defined as

$$K' = 1 - \frac{d'}{\max(d)}. \tag{1.22}$$

De Vries also proposed a *two-step randomisation test* as an alternative one to K' (see [38])

1.3.3 Reproductive skew

In this research we use the concept of reproductive skew to analyse how limited resources are divided between a group of individuals. The distribution of reproduction varies among breeding individuals that share the same territory

[66]. Reproduction skew measures the division of reproduction among group members. In high-skew groups, only the individuals that have a high position in the group obtain a large share of reproduction. In low-skew groups, reproduction is distributed more evenly among group members. A classical example of high reproductive skew is that of eusocial insects where only the queen (dominant individual) reproduces. In *Liostenogaster flavolineata* (hover wasps) it is observed that only one female produces more offspring in the group, even though there might be more females in the group able to mate and lay eggs [112]. On the other hand in *Mungos mungo* (the banded mongoose) a low reproductive skew has been found to be present. There are a lot of factors that influence such variation in different groups of animals (see [19], [46], [47], [48], [66]). Most of the theoretical work is based on the idea that the top-ranked individual has control over reproduction but might share an amount of that with lower-ranked individuals so that they do not leave the group ([45], [120], [121], [122]).

However it is not clear the extent to which top-ranked individuals control reproduction. This leads to the idea of *incomplete control* models of skew, where lower-ranked individuals can have an effect on the distribution of reproduction ([64], [65], [102]). Dominant individuals can allow the lower-ranked individuals to have an influence on the distribution of reproduction because sometimes producing more offspring can be costly for the dominant individual when they can be produced by subordinate individuals at a lower cost.

But how is reproductive skew measured? There are more than 20 indices used to find whether there is an even or uneven distribution of reproduction among group members. The most used index is that by [67] denoted by S and is calculated by equation (1.23)

$$S = \frac{\nu N_b + N_N}{N_b + N_N} \tag{1.23}$$

where N_b is the number of individuals that are breeders, N_N is the number of individuals that are non breeders and ν measures the variation of reproductive output among breeders. S takes values between 0 and 1 where a value of S equal to 0 indicates that reproduction is equally distributed among group members and a value of S equal to 1 indicates that reproduction is only by the dominant individual.

Another popular index of skew is that by Kokko & Lindstrom [70] denoted by λ and calculated by formula 1.24

$$E[p_r] = \frac{\lambda(1-\lambda)^{r-1}}{1-(1-\lambda)^n} \tag{1.24}$$

where $E[p_r]$ is the expected proportion of matings by males that are in rank r. This index also takes a value between 0 and 1, where $\lambda \to 0$ indicates no reproduction skew and $\lambda \to 1$ indicates a high-skew.

1.3.4 Tournament models of dominance hierarchy formation

Different groups of animals can be thought to follow different types of tournaments when they establish the dominance hierarchy. In the following we explain some of the tournaments that we use in our research.

A tournament is a competition consisting of a series of contests and a large number of individuals. In each contest two individuals are paired against each other to fight over a reward. There are a number of tournaments that different groups of animals follow to establish a dominance hierarchy such as the knockout tournament, the round-robin (all-play-all) tournament and the Swiss tournament. In the following we briefly describe these models.

In *knockout tournaments*, 2^n individuals are paired together. In the first round we get 2^{n-1} winners and 2^{n-1} losers. The losers are eliminated from the competition, while the winners are repaired together. This process continues until the last round where one single individual remains undefeated. This yield

$2^n - 1$ contests in total. Knockout tournaments are considered in detail in [25] and [26]. This type of tournament is useful when there is a large group of individuals and only the top-ranked one gets the payoff, otherwise when intermediate rank individuals obtain a reward as well, this model might not be useful.

In *round-robin tournament* (all-play-all) all possible pairings can occur and the number of contests for a group of 2^n individuals is $2^{n-1}(2^n - 1)$. Mesterton Gibbons and Dugatkin [90] used a round-robin tournament to model dominance hierarchy formation, in particular they were interested to see whether the established hierarchy was linear or not. Furthermore they introduced the concept of RHP into this model and analysed its influence on linearity. They concluded that the level of linearity depends on the group size, RHP and aggression threshold. A disadvantage of round robin tournaments is that for larger group sizes there would be a large number of fights which leads to loss of energy and injury [23]. Thus this model works better for smaller groups.

Another disadvantage of this tournament is that it forces those that do not do well in early contests to fight until the end, when they could have been eliminated earlier as they get nothing by fighting. Here is where the Swiss tournament is useful, because it has less fights than the round-robin. In Swiss tournaments for a group of size 2^n there are $2^{n-1}n$ contests in total, which is intermediate between knockout tournaments and round-robin.

1.3.5 A Swiss tournament model by Broom and Cannings

1.3.5.1 Some preliminaries

A Swiss tournament is a tournament which originates with a chess competition taking place in Zurich (hence the name) in 1895. In a group of 2^n players, those with the same score are paired together to compete. If they have different scores, those with a score as close as possible are paired together. Broom

$\&$ Cannings [23] have modelled the Swiss tournament as a Hawk-Dove type games ([83], [84]); the winner gets an extra score and the loser stays on the same score. The payoff matrix in this case is denoted by **M** and is given as follows:

$$\mathbf{M} = \begin{bmatrix} \frac{1}{2}(W+L-C) & W \\ L & \frac{1}{2}(W+L) \end{bmatrix} \tag{1.25}$$

where W is the reward for the winner, L is the reward for the loser and C is the cost for losing. There is always a unique ESS when considering a single interaction of this game. If p is the probability of being aggressive in the ESS then the followings apply:

(1) $p = 0$ means that an individual plays Dove, which happens if $W - L < 0$. The pay-off for this strategy is $\frac{1}{2}(W + L)$.

(2) $p = 1$ means that an individual plays Hawk, which happens if $W - L \geq C$. The payoff for this strategy is then $\frac{1}{2}(W + L - C)$.

(3) For $0 \leq W - L < C$ we have $p = \frac{W-L}{C}$ and the payoff in this case is $\frac{1}{2}(W + L) - \frac{1}{2C}(W - L)^2$.

In general the payoff will be $\frac{1}{2}(W + L - p^2C)$ where $p = mid(0, \frac{W-L}{C}, 1)$ is the second largest value of 0, $\frac{W-L}{C}$ and 1. For the Hawk-Dove model in Swiss tournaments case 1 never happens. Thus the payoff can be written as $\frac{1}{2}(W + L - \frac{1}{C}min(C, (W - L))^2)$. We define

$$R(x, y) = \frac{1}{2}\left(x + y - \frac{1}{C}min(C, (x - y)\right)^2 \tag{1.26}$$

for $x \geq y$, which is the expected payoff at the ESS for $W = x$ and $L = y$. Then the following results are true.

Result 1. *If $x \geq y$ then $x \geq R(x, y) \geq y$.*

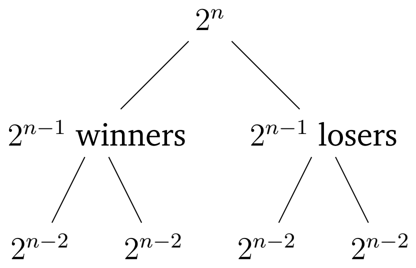


Figure 1.1: The division of individuals using a Swiss tournament

This means that the expected payoff prior to a contest is between the expected payoff of the winner and the payoff of the loser after the contest.

Result 2. *If $x \geq y \geq z$ and $y - z \geq C$ then $R(x, y) - R(y, z) \geq C$.*

This means that the reward for winning twice is x, for winning once and losing once y, and for losing twice is z [23]. Then the reward for winning one contest is at least C greater than the reward for winning no contests.

1.3.5.2 The Model

In a population of size 2^n, each individual starts with the same score $0|0$ (0 wins from 0 contests). At the end of the first round where these 2^n players are randomly paired together, we get 2^{n-1} individuals on a score $1|1$ and 2^{n-1} individuals on a score $0|1$. In the second round, the winners are paired together and the losers together. At the end of this round we get 2^{n-2} individuals on a score $0|2$, 2^{n-1} individuals on a score $1|2$ and 2^{n-2} on a score $2|2$. Then individuals on the same score are paired against each other. We get an almost accurate ordering by using the Swiss tournament and the winner is established in n rounds (if there are no draws). The total number of contests until we stop is $2^{n-1}n$ and after j rounds there are $\binom{j}{i}2^{n-j}$ players on $i|j$ (i.e. i wins from j contests), $\forall i = 0, ..., j$.

The reward for finishing on a score $i|n$ is V_i such that $V_0 \leq V_1 \leq ... \leq V_n$.

In Swiss tournaments the followings are defined:

- W_{ij} is the expected reward for an individual with a score of $i|j$ (i wins until round j). Thus $W_{in} = V_i$, $\forall i$

- M_{ij} is the payoff matrix for an individual with a score $i|j$ playing in round $j+1$. The expected reward for winning is $W_{(i+1)(j+1)}$ and the expected reward for losing is $W_{i(j+1)}$ as $(i+1)|(j+1)$ and $i|(j+1)$ are the only two possible states that an individual on a score $i|j$ can be in subsequently. Thus the matrix M will be:

$$M_{ij} = \begin{bmatrix} \frac{1}{2}(W_{(i+1)(j+1)} + W_{i(j+1)} - C) & W_{(i+1)(j+1)} \\ W_{i(j+1)} & \frac{1}{2}(W_{(i+1)(j+1)} + W_{i(j+1)}) \end{bmatrix} \tag{1.27}$$

- Next, the probability of being aggressive in the ESS of M_{ij} is defined by p_{ij} and is given by

$$p_{ij} = mid(0, \frac{W_{(i+1)(j+1)} - W_{i(j+1)}}{C}, 1) \tag{1.28}$$

The expected reward W_{ij} will then be

$$W_{ij} = \frac{1}{2}(W_{(i+1)(j+1)} + W_{i(j+1)} - p_{ij}^2 C). \tag{1.29}$$

Result 3. *For* $i \leq k \leq j, W_{ij} \leq W_{kj}$.

This means that the expected reward for an individual who has won k contests is at least as large as an individual with less wins i, at the end of round j.

From Result 3, we can write

$$p_{ij} = min\left(\frac{W_{(i+1)(j+1)} - W_{i(j+1)}}{C}, 1\right) \tag{1.30}$$

and

$$W_{ij} = R(W_{(i+1)(j+1)}, W_{i(j+1)}) \; \forall i \leq j \leq N-1. \qquad (1.31)$$

Note that there is a unique choice of p_{ij} for every position, which is the only candidate ESS, but not necessarily an ESS [23]. The following results are also true for Swiss tournaments (see [23] for proofs of these results).

Result 4. $W_{ij} \leq W_{(i+1)(j+1)}$ *if* $i \leq j \leq N-1$.

This result means that the expected reward of an individual cannot decrease after a win.

Result 5. $W_{ij} \geq W_{i(j+1)}$ *if* $i \leq j \leq N-1$.

This result means that the expected reward of an individual cannot increase after a loss.

Result 6. *If* $p_{i(j+1)} = 1$ *then* $p_{ij} = 1$. *Equivalently if* $p_{ij} < 1$ *then* $p_{i(j+1)} < 1$.

This means that if an individual loses after playing any mixed strategy other than pure Hawk, on the next round it cannot play pure Hawk. However, p_{ij} are not necessarily monotonically decreasing with j for a given i.

1.3.6 Outline

This thesis is structured as follows.

In Chapter 2, we analyse the influence of winner and loser effects on dominance hierarchy formation. Two cases are considered: (i) when individuals do not know the strength of their opponents and (ii) when they can estimate the strength of their opponents with varying levels of accuracy. For each case the linearity of hierarchies is measured. We do this by analysing the average number of wins for an individual where we use the index of linearity K and by analysing the temporal change in the RHP where the concept of overlap is used. We then find the time (how many rounds) when the hierarchy is established. For the non-updated model we find analytically the number of wins for the second and third place in a group of four individuals when only the loser effect is present. The probability of having a unique loser is also analysed.

In Chapter 3, we introduce game-theoretical elements in the form of strategic factors to the winner and loser model developed in Chapter 2. For a general strategy, we find its expected payoff and hence find the appropriate range of strategies. We use two payoff functions: the first representing situations where the resources are unlimited, and the other representing situations with limited resources. Using both payoff functions we analyse the level of aggressiveness for an individual and in particular we find that in the second case individuals need to be more aggressive to obtain a higher share of the resources.

In Chapter 4, we develop a new model of dominance hierarchy formation, based upon the Swiss tournament model by Broom & Cannings [23]. Analysis of the model shows that linear dominance hierarchies are always established. We find the number of rounds until the winner, the second place and the full hierarchy is established and a formula for the total number of fights is derived. Furthermore, we explore the effect of group size, reward and cost on the level of aggressiveness and on the expected payoff.

In Chapter 5, we summarise our main findings, the contributions of this study and give some directions of future research.

Chapter 2

Modelling Dominance Hierarchies Under Winner and Loser Effects

2.1 Introduction

For a long time, the question as to what stops a lower-ranked individual to overturn its social rank, has been a big puzzle in biology. A Substantial amount of work is carried out on this subject, but only the last couple of decades, the focus has been on the winner and loser effects. These factors have an important role on the level of aggressiveness for an individual and are found to be one of the possible mechanisms of dominance hierarchy formation in different groups of animals ([8], [13], [77], [108]). Therefore, in this chapter, we analyse in more detail the influence of winner and loser effects on dominance hierarchy formation.

Our starting point is the model developed by Dugatkin and Dugatkin & Dugatkin ([42], [44]) (see Chapter 1 for the model description and results). For each combination of the winner and loser effect, he analysed the number of wins of each individual in the group. Although this model makes good predictions about how different species arrange themselves into a ranking order, his results are based on a single observation for each of the analysed cases. We are interested in looking at the distribution of the number of wins for each case, to ascertain if different observations will always yield effectively the same results (in most cases they do, but there are exceptions, as we see in Section 2.3). The average is important as the logical representative of the distribution.

We start by extending the framework developed in ([42], [44]). For ease of comparison, we will use the same model that Dugatkin has used with the only difference being in the updated model where the errors are treated differently (see Section 2.5). We start by analysing the average behaviour of the original model (as opposed to considering a single realisation) by recording the average number of wins of each individual over any other individual present in the population on the basis of 10,000 simulations and consider appropriate statistics to describe the properties of the emerging hierarchies. To this end we evaluate the linearity of the hierarchy by adapting the index of linearity introduced by Kendall [68], denoted by K $(0 \leq K \leq 1)$. Values of K close to one are indicative of linear hierarchies and values of K close to zero indicate no linear hierarchy to be present. We calculate the index of linearity based on the averaged number of wins for all considered parameter combinations and this systematic investigation of the model from [42] reveals that a near linear hierarchy is achieved for all the analysed cases.

Besides understanding the structure of the emerging hierarchy we are interested in understanding the temporal dynamic of the hierarchy formation, in particular we want to explore when (or after how many interactions) a hierarchy is established. This knowledge can be of importance for experimentalists as it gives a guideline for the number of interactions that need to be observed.

To do so we firstly need to define when we consider a hierarchy as established. This will be based upon pairwise comparisons, and we will use the term “distinguishable” to indicate when two individuals can be thought to clearly occupy different positions in the hierarchy.

Additionally, we are interested in the role of information in the process of hierarchy formation. Based on [42] and [44], we consider the situations where:

i. an individual has no information about the current RHP of its opponent,

ii. an individual is fully aware of the current RHP of its opponent and

iii. an individual can make a noisy estimate about the current RHP of its opponent.

Next for each pair of individuals and different parameter combinations, we calculate the time until both individuals are considered to be distinguishable regarding their rank in the hierarchy. We discuss our results in Sections 2.3-2.5. This chapter prepares the platform for developing game-theoretical models, where levels of aggression (for example) are strategic factors, with the best choice depending upon the natural parameters, including species or habitat-specific features which affect how resources are divided (the reproductive skew).
Parts of this chapter are published in [73].

2.2 Methods

In the following we use the non-updated and updated (with different levels of accuracy) model to explore the properties of the process of hierarchy formation; in particular we explore its temporal dynamics. To do so, for each model, we firstly analyse the number of wins of each individual over all other individuals present in the population after 1000 interactions (and therefore at a fixed point in time) and secondly the temporal changes in the RHP of each individual over these 1000 interactions for the non-updated and updated model. We note that in both analyses, the rank of an individual is calculated differently. While in the first analysis the rank is determined by the total number of wins in the second analysis it is determined by the size of the RHP. However, the two definitions are highly correlated as equations (1.16) and (1.17) guarantee that a high number of wins corresponds to a high value of RHP. All results presented in the following are based on averaging over 10,000 simulations and we explore the same parameter constellations as in [42] to allow for a direct comparison of the results. Therefore we mainly consider groups of size four but we have additionally analysed the behaviour of larger groups and obtained similar patterns. We occasionally comment on the results for larger group sizes in later sections.

2.2.1 Analysis of the average number of wins

We start our analysis by determining the rank of all individuals at all times t. Since we allow multiple contests between the individuals, it makes sense to arrange individuals according to their number of wins; the higher the number of wins, the higher the position in the hierarchy (this was the case in the models of [42] and [44] as well). If two individuals have the same number of wins, the rank is assigned at random. We note that an alternative way of deciding the ordering of the hierarchy would be by placing an individual above another if it had won more of their pairwise contests (although this latter definition has the significant disadvantage of sometimes not yielding an ordering). Theoretically on some occasions, these two definitions can produce different orderings of a given hierarchy, but in practice this is very rare, and so there is no practical difference. Next we determine the matrix $\mathbf{W} = [w_{ij}]_{i,j=1,\dots,N}$ which contains the average number of wins of the individual with rank i over individual with rank j under different strengths of the winner and loser effects, noting that there is a one-to-one correspondence between individuals and ranks. The resulting hierarchy is perfectly linear ($K = 1$) if all individuals have a different number of wins, and have won (lost) all of their decisive contests against those lower (higher) in the hierarchy than them. To quantify the degree of linearity we calculate in the next step the index of linearity [68] using the following procedure.

(1) From the matrix of wins **W** we construct an index matrix **F**=(f_{ij}) where (f_{ij}) is the fraction of decisive interactions between individuals i and j (i.e. from those contests not involving a double kowtow) which were won by individual i (so that $f_{ij} + f_{ji} = 1$). This matrix will be called the matrix of fractions.

(2) For this matrix **F** calculate the row sum R_i for $i = 1, ..., N$.

(3) Calculate the index of linearity

$$K = 1 - \frac{d}{d_{max}}, \tag{2.1}$$

(see [6]), where

$$d = \frac{1}{12}N(N-1)(2N-1) - \frac{1}{2}\sum_{i=1}^{N}(R_i)^2, \;\; d_{max} = \frac{1}{24}(N^3 - N). \tag{2.2}$$

The method used above is an adaptation of that developed by Kendall [68]. In that case the interaction between a pair of individuals was a single contest with a unique top individual, so that exactly one of f_{ij} and f_{ji} was 1 and the other was 0. The parameter d was the number of circular triads of matrix **F**, where a circular triad is a subgroup of three individuals denoted by A, B and C in a larger group which has the form $A \rightarrow B \rightarrow C \rightarrow A$ which means that A dominates B, B dominates C but C dominates A. No circular triads corresponds to a completely linear hierarchy.

Below we show that the original definition of d as the number of circular triads, in the case where there was a single contest between each pair of individuals, is a special case of our definition from (2.2). For the single contest case, d is the total number of triples minus the total number of transitive triples [9]. The number of transitive triples is $\sum_{i=1}^{N}\binom{R_i}{2}$ (see [9]), and so

$$\begin{aligned}
d &= \binom{N}{3} - \sum_{i=1}^{N}\binom{R_i}{2} \\
&= \frac{N(N-1)(N-2)}{6} - \frac{1}{2}\sum_{i=1}^{N}(R_i)^2 + \frac{1}{2}\sum_{i=1}^{N}R_i \\
&= \frac{N(N-1)(N-2)}{6} - \frac{1}{2}\sum_{i=1}^{N}(R_i)^2 + \frac{1}{2}\frac{N(N-1)}{2} \\
&= \frac{N(N-1)(2N-1)}{12} - \frac{1}{2}\sum_{i=1}^{N}(R_i)^2, \qquad (2.3)
\end{aligned}$$

which is the form for d that we apply in our model for more general values of R_i (see also [38]). For the formula (2.1), d_{max} corresponds to the maximum value that d can take. In general this is given by

$$d_{max} = \frac{1}{24}(N^3 - N). \qquad (2.4)$$

For the case where f_{ij} was 0 or 1 [6], this was also the formula for odd values of N, but for even values this is not achievable, and the maximum is

$$d_{max} = \frac{1}{24}(N^3 - 4N). \qquad (2.5)$$

In our model we use d_{max} from (2.4) as this is achievable for fractional f_{ij}, even though our group size is generally even ($N = 4$).

2.2.2 Analysis of the temporal change in RHP

It is assumed that each aggressive interaction changes the RHP of the individuals involved according to equations (1.16) and (1.17). In the following we investigate the temporal dynamics of the hierarchy formation by analysing the change in RHP for each individual over time. To do so we define the rank of an individual at time $t \in [1, \infty]$ based on its RHP (higher-ranked individuals have a higher RHP than lower-ranked individuals) and determine the probability distribution of the RHP values of the first, second, ..., Nth rank based on the 10,000 simulations at each point in time. This allows us to ask how distinguishable individuals of different ranks are based on the ability to win an aggressive interaction. The degree of distinguishability between two individuals at time t is determined by the overlap $\nu_{xy}(t)$ (see the grey area in Figure 2.1) of the density of the RHP values, denoted by $f_x(t)$ and $f_y(t)$ (note that this overlap was termed OVL by Schmid & Schmidt [107]). We have $0 \leq \nu_{xy}(t) \leq 1, \; \forall t$ and

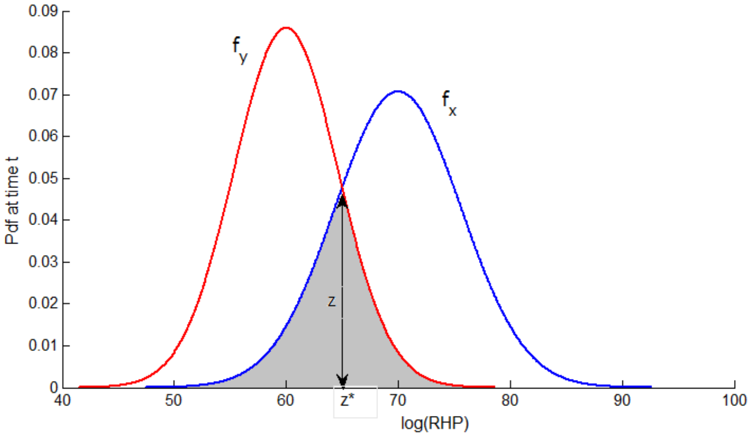


Figure 2.1: Probability distributions functions of the RHP of two individuals at time t. The shaded area describes the overlap between the two distributions.

the smaller $\nu_{xy}(t)$, the clearer the distinction between the ranks of the individuals. If there is complete overlap then the individual with the higher rank is effectively chosen at random. In the following we call two individuals x and y *distinguishable* if $\nu_{xy}(t) < 0.1$ holds. The overlapping area $\nu_{xy}(t)$ is determined using the Kolomogorov distance $\max_{\forall z}|F_{x,t}(z) - F_{y,t}(z)|$ between the distributions $F_{x,t}$ and $F_{y,t}$. Assuming that the Kolmogorov distance is realised at position z^* we obtain

$$\begin{aligned}\nu_{xy}(t) &= \int_{z^*}^{\infty} f_{y,t}(z)dz + \int_{-\infty}^{z^*} f_{x,t}(z)dz = 1 + (F_{x,t}(z^*) - F_{y,t}(z^*)) \\ &= 1 - \max_{\forall z}|F_{x,t}(z) - F_{y,t}(z)|.\end{aligned}$$

In our model, the values of RHP are discrete rather than continuous, but except for very early in the process (and with the single exception of the top individual when only the loser effect is present, as we discuss later) the number of possible discrete values becomes large and our discrete distribution can be approximated by a continuous distribution. We use this procedure to determine the overlap ν_{xy} for all combinations of individuals and every point in time. In this way we are able to determine when $\nu_{xy}(t)$ falls below 0.1 for all x, y, and consequently when all ranks become distinguishable. We note that it is possible that $\nu_{xy}(t)$ can increase above 0.1 again (though this never in practice happens except at the very early stages of certain cases). In the following we call the (final) time when $\nu_{xy}(t)$ falls below 0.1, a *domination event*.

2.3 Results for the non-updated model

In the following we assume a group of four individuals which are initialised with $RHP_{\text{initial}} = 10$ and an aggression threshold $\theta = 1$, unless stated otherwise. We explore the dynamics of hierarchy formation by analysing the average number of wins and the temporal change in the RHP. These dynamics are analysed for various combinations of winner and loser effects where both W and L take values from 0 up to 0.5. We show only W and L in the range from 0 to 0.3 in intervals of increment 0.1, as the behaviour at other values is consistent with the values shown, and 0.3 is a large value for a winner or a loser effect (see how large RHP becomes in Figure 2.11 leading to predictable contest outcomes).

2.3.1 Analysis of the average number of wins

For different strengths of winner and loser effects we record the average number of wins of each individual after 1000 aggressive interactions. Table 2.1 shows the matrix of wins $\mathbf{W} = [w_{ij}]_{i,j=1,\ldots,N}$ for each set of parameters. Each single entry w_{ij} indicates the number of wins of individual with rank i over individual with rank j. Following our definition, it is clear that every individual has a clear rank in the hierarchy as the average number of wins for all individuals in all cases are different. When only the loser effect is present, all individuals in the group score except the individual that takes the last place. This is because the first to lose a fight will retreat in all subsequent contests, as its RHP is lower than $RHP_{initial}$ and therefore equation (1.14) does not hold. Increasing the loser effect in the absence of the winner effect does not make any difference to the structure. When only the winner effect is present, all individuals in the group score and have a clear position in the hierarchy. When increasing the winner effect in the absence of the loser effect, we notice that higher ranked individuals win an increasing fraction of the individual contests. In particular, each individual scores increasingly better against those individu-

	$W = 0$	$W = 0.1$	$W = 0.2$	$W = 0.3$
$L = 0$		$\begin{matrix} - & 153.51 & 161.59 & 163.67 \\ 15.13 & - & 150.21 & 158.38 \\ 7.52 & 15.48 & - & 148.63 \\ 4.57 & 7.34 & 14.46 & - \end{matrix}$	$\begin{matrix} - & 160.71 & 164.99 & 166.37 \\ 7.33 & - & 158.32 & 162.98 \\ 3.21 & 7.29 & - & 157.42 \\ 1.78 & 2.93 & 6.67 & - \end{matrix}$	$\begin{matrix} - & 162.67 & 166.23 & 167.01 \\ 4.91 & - & 160.88 & 164.36 \\ 2.04 & 4.81 & - & 160.19 \\ 0.99 & 1.81 & 4.11 & - \end{matrix}$
$L = 0.1$	$\begin{matrix} - & 166.12 & 166.91 & 166.79 \\ 0 & - & 1.55 & 1.69 \\ 0 & 0.06 & - & 0.51 \\ 0 & 0 & 0 & - \end{matrix}$	$\begin{matrix} - & 161.81 & 167.47 & 168.01 \\ 4.27 & - & 104.83 & 105.28 \\ 0.06 & 0.09 & - & 0.61 \\ 0 & 0 & 0 & - \end{matrix}$	$\begin{matrix} - & 162.58 & 167.61 & 168.12 \\ 3.69 & - & 147.53 & 148.61 \\ 0.32 & 0.74 & - & 8.01 \\ 0 & 0 & 0 & - \end{matrix}$	$\begin{matrix} - & 163.48 & 167.51 & 168.38 \\ 2.76 & - & 152.81 & 153.92 \\ 0.28 & 0.81 & - & 30.78 \\ 0 & 0 & 0 & - \end{matrix}$
$L = 0.2$	$\begin{matrix} - & 166.33 & 166.56 & 166.64 \\ 0 & - & 1.57 & 1.75 \\ 0 & 0.06 & - & 0.51 \\ 0 & 0 & 0 & - \end{matrix}$	$\begin{matrix} - & 165.09 & 167.21 & 167.17 \\ 1.28 & - & 14.71 & 14.89 \\ 0.006 & 0.05 & - & 0.51 \\ 0 & 0 & 0 & - \end{matrix}$	$\begin{matrix} - & 164.45 & 167.41 & 167.62 \\ 1.81 & - & 93.29 & 93.61 \\ 0.03 & 0.06 & - & 0.51 \\ 0 & 0 & 0 & - \end{matrix}$	$\begin{matrix} - & 164.56 & 167.37 & 167.91 \\ 1.86 & - & 136.76 & 137.72 \\ 0.14 & 0.21 & - & 1.11 \\ 0 & 0 & 0 & - \end{matrix}$
$L = 0.3$	$\begin{matrix} - & 164.05 & 166.62 & 166.81 \\ 0 & - & 1.54 & 1.74 \\ 0 & 0.06 & - & 0.51 \\ 0 & 0 & 0 & - \end{matrix}$	$\begin{matrix} - & 165.79 & 166.91 & 167.09 \\ 0.35 & - & 2.68 & 2.91 \\ 0.01 & 0.06 & - & 0.51 \\ 0 & 0 & 0 & - \end{matrix}$	$\begin{matrix} - & 165.28 & 167.31 & 167.36 \\ 1.02 & - & 32.81 & 33.01 \\ 0.02 & 0.05 & - & 0.52 \\ 0 & 0 & 0 & - \end{matrix}$	$\begin{matrix} - & 165.29 & 167.71 & 167.46 \\ 0.94 & - & 78.09 & 78.11 \\ 0.02 & 0.05 & - & 0.37 \\ 0 & 0 & 0 & - \end{matrix}$

Table 2.1: Matrices of wins **W** in the non-updated model for different strengths of the winner and loser effect ($W = 0; 0.1; 0.2; 0.3$ and $L = 0; 0.1; 0.2; 0.3$), $N = 4$, $\theta = 1$ and *t*=1000.

als that are lower in rank, and increasingly worse against those that are higher in rank. In Figure 2.2 we plot the total average number of wins for each position in the hierarchy for different combinations of W and L. To check how far

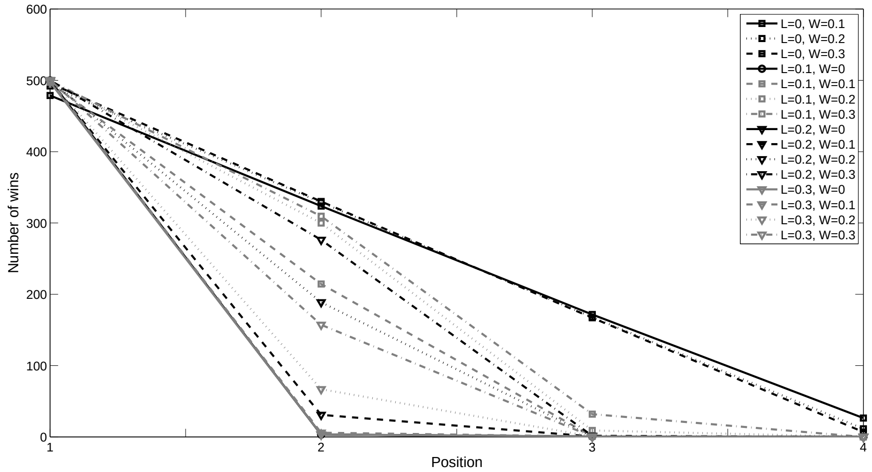


Figure 2.2: The total average number of wins for positions 1, 2, 3 and 4 for different combinations of W and L in the non-updated model as given in Table 2.1.

from linearity a hierarchy is we calculate the index of linearity K as described in equation (2.1). The following example calculates K for when $W = 0.1$ and $L = 0$. The corresponding matrix of wins for this case is

$$\mathbf{W} = \begin{bmatrix} - & 153.51 & 161.59 & 163.67 \\ 15.13 & - & 150.21 & 158.38 \\ 7.52 & 15.48 & - & 148.63 \\ 4.57 & 7.34 & 14.46 & - \end{bmatrix} \tag{2.6}$$

Then the matrix of fractions **F** will be

$$\mathbf{F} = \begin{bmatrix} - & \frac{153.51}{168.64} & \frac{161.59}{169.11} & \frac{163.67}{168.24} \\ \frac{15.13}{168.64} & - & \frac{150.21}{165.69} & \frac{158.38}{165.72} \\ \frac{7.52}{169.11} & \frac{15.48}{165.69} & - & \frac{148.63}{163.09} \\ \frac{4.57}{168.24} & \frac{7.34}{165.72} & \frac{14.46}{163.09} & - \end{bmatrix} = \begin{bmatrix} - & 0.91 & 0.96 & 0.97 \\ 0.09 & - & 0.91 & 0.96 \\ 0.04 & 0.09 & - & 0.91 \\ 0.03 & 0.04 & 0.09 & - \end{bmatrix} \tag{2.7}$$

From the matrix of fractions **F**, now we calculate the row sums $R_i, i = 1, 2, 3, 4$

$$R_i = \begin{bmatrix} 2.84 \\ 1.96 \\ 1.04 \\ 0.16 \end{bmatrix} \tag{2.8}$$

Next we calculate the average number of circular triads d by using equation (2.2) as follows

$$d = \frac{N(N-1)(2N-1)}{12} - \frac{1}{2}\sum_{i=1}^{N}(R_i)^2 = 7 - 6.51 = 0.49.$$

Thus in this example there are on average 0.49 circular triads. To find K we need to know the maximum number of circular triads (maximum value that d can take) and this is found by

$$d_{max} = \frac{1}{24}(N^3 - N) = 2.5.$$

Finally we can calculate the value of K for when $W = 0.1$ and $L = 0$ which is $K = 1 - \frac{d}{d_{max}} = 0.804$. This shows that in this case we obtain a near linear hierarchy.

Figure 2.3 shows the values of the index of linearity K calculated by equation (2.1) for different values of W and L. We observe that K is close to 1 for all parameter combinations considered, indicating a near linear hierarchy in almost all of the cases. Further, we see that, as expected, K increases with W. When the loser effect is increased for a given positive value of W, each individual except the first placed individual does worse than before. This has a mild impact on K.

When both winner and loser effects are present, we observe two different outcomes.

i. Hierarchies with a clear first and second place, a bottom individual with zero wins and the third place individual which does not differ much from the fourth place individual.

ii. Hierarchies with a clear first place individual, but the second place individual is not that different from the third placed one (see the case when W=0.1 and L=0.3).

These outcomes depend on the values of winner and loser effects. If we simultaneously increase winner and loser effects, we get a slight increase in the index of linearity (see Figure 2.3). These results also hold for larger group sizes. Figure 2.4 describes the index of linearity K under the influence of the loser effect only.

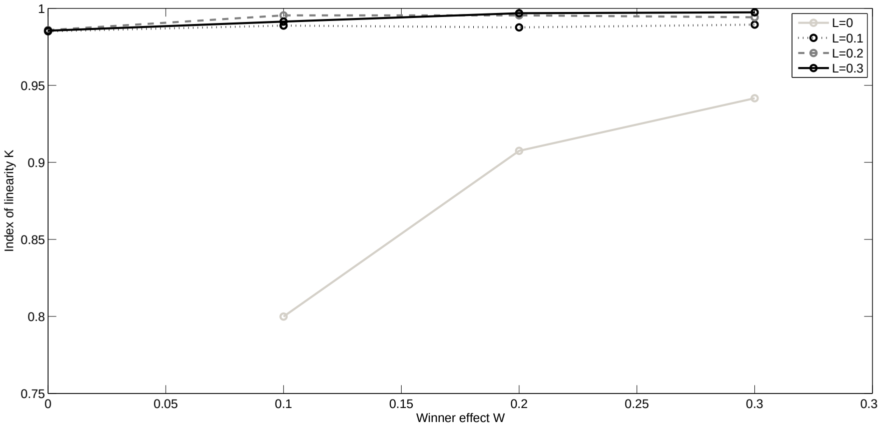


Figure 2.3: Index of linearity for different values of W and L, calculated from the (unrounded) values of the average number of wins from Table 2.1.

2.3.2 Analytical results for the loser effect only

In this section, we present some analytical results for dominance hierarchies emerging under the influence of the loser effect. We consider only the loser effect because (i) there is more documented evidence in different species that

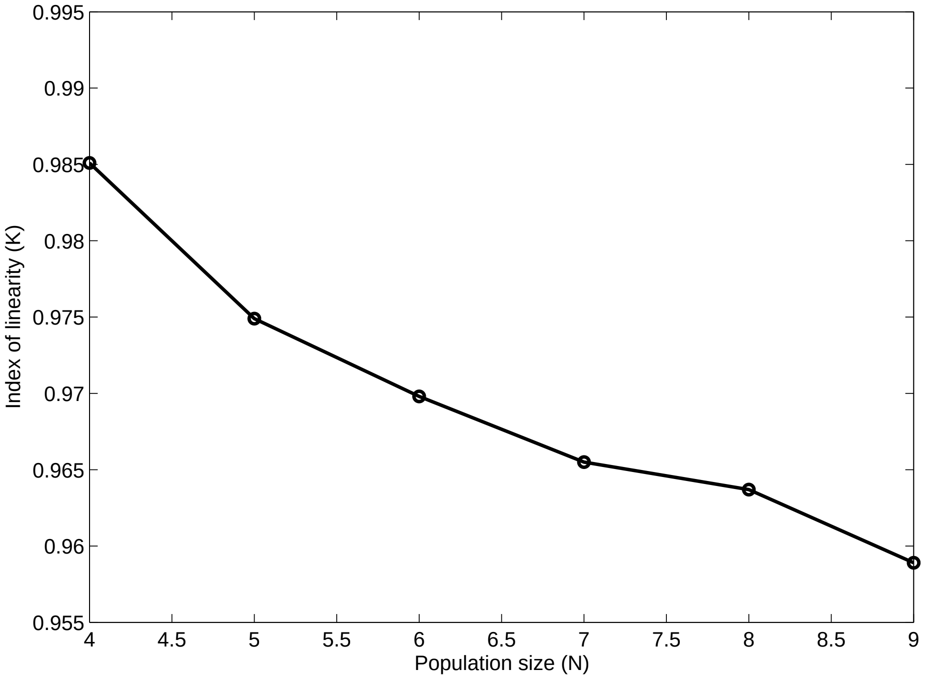


Figure 2.4: Change of index of linearity K when the group size is increased from 4 to 9 under the influence of the loser effect only.

show the presence of this effect, and (ii) the precise value of the loser effect does not have any influence on dominance hierarchy formation or the number of wins for each individual.

In Section 2.3.1, we found that such hierarchies have a clear first place individual with a large number of wins and a last place individual with zero wins. The average number of wins of the second place does not differ much from the average number of wins of the third place. Here, we are interested to find analytically how many wins on average the second and the third place individuals have.

Let us denote by A, B, C and D the four individuals in the group. At each point in time, two random individuals are pitted against each other to engage in an aggressive interaction. From the model we know that if an individual loses a fight, it is going to retreat afterwards (as it does not meet the aggression threshold θ). This means that the first individual to lose, will occupy the last place in the hierarchy.

We start by finding the total number of rounds where pairings between unbeaten individuals (that have not lost any fight) happen. Without loss of generality, we assume that in round 1, individual A wins against individual B. We denote this relation by $A \rightarrow B$. Thus individual B will retreat every time that it is picked by another in the group to fight. From Figure 2.5, we find that

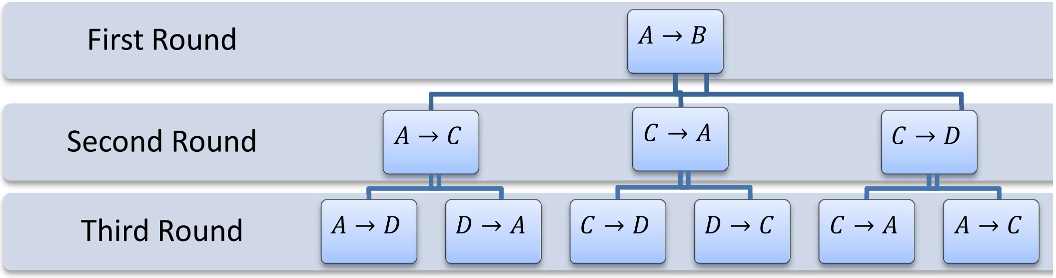


Figure 2.5: Rounds of fights between unbeaten individuals, where in each of them, one individual is losing for the first time. There are six possible hierarchical structures represented by the six branches, e.g., the first one follows the path $A \rightarrow B$, $A \rightarrow C$, $A \rightarrow D$.

there are three rounds of fights between unbeaten individuals. In this figure we have 6 branches (e.g., the first branch represents the sequence $A \rightarrow B$, $A \rightarrow C$, $A \rightarrow D$), where each of the branches represents a hierarchical structure with a sequence of losses. In each round one individual is losing for the first time. Because we assumed that in the first round $A \rightarrow B$, in the following round we can have either $A \rightarrow C$, $C \rightarrow A$ or $C \rightarrow D$ and in the third round we can have either, $A \rightarrow D$, $D \rightarrow A$, $C \rightarrow D$, $D \rightarrow C$, $C \rightarrow A$ or $A \rightarrow C$.

Between these three rounds we can have pairings of unbeaten individuals with individuals that have previously lost and hence are going to retreat. These types of pairings contribute to the average number of wins that an individual has over the others. So the next step is to find how often these happen.

In the following, we denote by x_n the number of times that an unbeaten individual chooses a particular individual that has previously lost, until a new pairing between unbeaten individuals happens. Then x_n has a geometric (0) distribution which we denote by $x_n \sim Geo(p)$, where p is the probability that conditioned upon the next game involving the above contest or two unbeaten individuals, it is the two unbeaten individuals that play.

From the first round, we have individual B as the only loser. Thus between round one and round two, we can have these possible pairings: $A \rightarrow B$, $C \rightarrow B$ or $D \rightarrow B$ and assume that these combinations occur x_1, x_2 and x_3 times respectively.

In other words, x_1 for example, represents the number of wins of individual A over individual B until one of the pairings $A \rightarrow C$, $C \rightarrow A$ or $C \rightarrow D$ in round two happens. Each of these pairings happens with a probability $1/4$. Thus we have $x_1 \sim Geo\,(3/4)$. The same applies to x_2 and x_3 and so $x_2 \sim Geo\,(3/4)$ and $x_3 \sim Geo\,(3/4)$.

Now we find the number of pairings between an unbeaten individual and an individual that has previously lost between the second and the third round. After the second round we have two losers. From the path $A \rightarrow B$, $A \rightarrow C$ in Figure 2.5, the two losers are B and C. Thus the possible pairings are: $A \rightarrow B$, $A \rightarrow C$, $D \rightarrow B$, $D \rightarrow C$. We assume that these happen x_4, x_5, x_6 and x_7 times, respectively. Again, for the same reasons as in round 1, they are geometrically distributed with probability $p = 1/2$. Thus $x_n \sim Geo\,(1/2)\,, \forall n = 4, 5, 6, 7$.

From the second path in Figure 2.5 ($A \rightarrow B$, $C \rightarrow A$) we can have these possible pairings: $C \rightarrow B$, $C \rightarrow A$, $D \rightarrow B$, $D \rightarrow A$, which again happen x_4, x_5, x_6 and x_7 times respectively. They are geometrically distributed with probability $p = 1/2$ ($x_n \sim Geo\,(1/2)\,, \forall n = 4, 5, 6, 7$).

From the third path in Figure 2.5 ($A \rightarrow B$, $C \rightarrow D$) we can have these possible pairings: $C \rightarrow B$, $C \rightarrow D$, $A \rightarrow B$, $A \rightarrow D$, which again happen x_4, x_5, x_6 and x_7 times respectively. They are geometrically distributed with probability $p = 1/2$ ($x_n \sim Geo\,(1/2)\,, \forall n = 4, 5, 6, 7$).

The analysis of the 6 branches in Figure 2.5, will assign a rank to each individual in the hierarchy. These results are shown in Table 2.2. The orderings

	1stbranch	**2ndbranch**	**3rdbranch**
1st	**A:**$3 + x_1 + x_4 + x_{5+..}$	**D:**$1+x_3+x_6+x_7$+..	**C:**$2+x_2+x_4+x_5$+..
2nd	**D:**$x_3 + x_6 + x_7$	**A:**$2 + x_1 + x_4 + x_5$	**D:**$x_3 + x_6 + x_7$
3^{d}	**C:**x_2	**C:**x_2	**A:**$1 + x_1$
4th	**B:** 0	**B:** 0	**B:**0

	4thbranch	**5thbranch**	**6thbranch**
1st	**D:**$1+x_3+x_6+x_7+..$	**C:**$2+x_2+x_4+x_5+..$	**A:**$2+x_1+x_6+x_7+..$
2nd	**C:**$1 + x_2 + x_4 + x_5$	**A:**$1 + x_1 + x_6 + x_7$	**C:**$1 + x_2 + x_4 + x_5$
3^{d}	**A:**$1 + x_1$	**D:**x_3	**D:**x_3
4th	**B:** 0	**B:** 0	**B:**0

Table 2.2: The rank and the number of wins of each individual in Figure 2.5.

of individuals are the reverse of the order of their first loss. For example the first individual to lose will occupy the last place, the second individual to lose will occupy the third place and so on. The second and the third place in Table 2.2 represent the second and the third place by losses. This structure (based on the number of losses) will be called the *sequence hierarchy*, which is a linear one. The ranks that we are interested to work out are in order of the highest number of wins. This hierarchy, based on the number of wins, will be called the *real hierarchy*. For example, if $x_3 + x_6 + x_7 < x_2$, means that individual C has more wins than individual D and thus it will occupy the second position and D will occupy the third position in the real hierarchy. The combined number of wins between the second and the third place in the sequence hierarchy is the same as in the real hierarchy and by averaging over the all branches we find it to be

$$\frac{6 + 4x_1 + 4x_2 + 4x_3 + 3x_4 + 3x_5 + 3x_6 + 3x_7}{6}. \tag{2.9}$$

We know that the expected value of variable x_n that is geometrically distributed, $x_n \sim Geo(p)$, is $E[x_n] = \frac{1}{p} - 1$. Then the expected average number of wins between the second and the third place is

$$E[\frac{6 + 4x_1 + 4x_2 + 4x_3 + 3x_4 + 3x_5 + 3x_6 + 3x_7}{6}]$$

$$= \frac{6 + 4\frac{3}{4} + 4\frac{3}{4} + 4\frac{3}{4} + 3\frac{1}{2} + 3\frac{1}{2} + 3\frac{1}{2} + 3\frac{1}{2}}{6} = \frac{23}{6} \approx 3.833. \tag{2.10}$$

because $E[x_1] = E[x_2] = E[x_3] = \frac{1}{\frac{3}{4}} - 1 = \frac{1}{3}$ and $E[x_4] = E[x_5] = E[x_6] = E[x_7] = \frac{1}{\frac{1}{2}} - 1 = 1$.

But how do we find the average number of wins for the second and the third place respectively? To answer this question, for every branch in Figure 2.5, we analyse the case when the second place by losses is the third place by wins and when the third place by losses is the second place by wins.

We denote by Y_i and Z_i the total number of wins for the second and third place respectively in branch $i, \forall i = 1, 2, 3, 4, 5, 6$. We need to work out the values of Z_i and Y_i and for every particular value of Z_i, we need to find the probability of Z_i being less than Y_i. In particular we need to calculate

$$\sum_{z_i=0}^{\infty} z_i P(Z_i = z_i \ and \ Z_i \leq Y_i) + \sum_{y_i=0}^{\infty} y_i P(Y_i = y_i \ and \ Z_i > Y_i). \tag{2.11}$$

In the following we calculate the value of equation (2.11) for every branch in Table 2.2.

Number of wins for the third position in the first branch

In the first branch we have $Z_1 = x_2$ and $Y_1 = x_3 + x_6 + x_7$. In this case equation (2.11) becomes:

$$\sum_{z_1=0}^{\infty} z_1 P(Z_1 = z_1 \ and \ Z_1 \leq Y_1) + \sum_{y_1=0}^{\infty} y_1 P(Y_1 = y_1 \ and \ Z_1 > Y_1) \tag{2.12}$$

In order to calculate equation (2.12), we separately calculate $\sum_{z_1=0}^{\infty} z_1 P(Z_1 = z_1 \ and \ Z_1 \leq Y_1)$ and $\sum_{y_1=0}^{\infty} y_1 P(Y_1 = y_1 \ and \ Z_1 > Y_1)$ and add them together. We start by calculating the second summation. We have

$$\sum_{y_1=0}^{\infty} y_1 P(Y_1 = y_1 \ and \ Z_1 > Y_1) = \sum_{y_1=0}^{\infty} y_1 P(Y_1 = y_1) P(Z_1 > Y_1). \tag{2.13}$$

In order to calculate (2.13), we need to first calculate P[Y_1=y_1]
Y_1 is given as the sum of three independent variables x_3, x_6, x_7 that are all geometrically distributed with probabilities $3/4$, $1/2$ and $1/2$ respectively. We also know that the sum of 2 independent geometrically distributed random variables that have the same probability p, is a negative binomial random variable denoted by $NB(r;p)$ where r is the number of random variables and p is the probability that a new pairing with unbeaten individuals happens. Hence, we find that $Y = x_6 + x_7$ has a negative binomial distribution with pdf

$$P[Y = y] = \left(\frac{1}{2}\right)^2 \left(\frac{1}{2}\right)^y (y+1) \tag{2.14}$$

We can now calculate

$$\begin{aligned}
P[Y_1 = y_1] &= \sum_{x_3=0}^{y_1} P(X_3 = x_3) P(Y = y_1 - x_3)(y_1 - x_3 + 1) \\
&= \sum_{x_3=0}^{y_1} \left(\frac{3}{4}\right) \left(\frac{1}{4}\right)^{x_3} \left(\frac{1}{2}\right)^2 \left(\frac{1}{2}\right)^{y_1 - x_3} (y_1 - x_3 + 1) \\
&= \sum_{x_3=0}^{y_1} \left(\frac{3}{16}\right) \left(\frac{1}{4}\right)^{x_3} \left(\frac{1}{2}\right)^{y_1} \left(\frac{1}{2}\right)^{-x_3} (y_1 - x_3 + 1) \\
&= \sum_{x_3=0}^{y_1} \left(\frac{3}{16}\right) \left(\frac{1}{2}\right)^{x_3} \left(\frac{1}{2}\right)^{y_1} (y_1 - x_3 + 1) \\
&= \sum_{x_3=0}^{y_1} \left(\frac{3}{16}\right) \left(\frac{1}{2}\right)^{x_3} \left(\frac{1}{2}\right)^{y_1} \left(\frac{1}{2}\right)^{y_1} \left(\frac{1}{2}\right)^{-y_1} (y_1 - x_3 + 1) \\
&= \sum_{x_3=0}^{y_1} \left(\frac{3}{16}\right) \left(\frac{1}{4}\right)^{y_1} \left(\frac{1}{2}\right)^{x_3 - y_1} (y_1 - x_3 + 1) \\
&= \sum_{x_3=0}^{y_1} \left(\frac{3}{16}\right) \left(\frac{1}{4}\right)^{y_1} 2^{y_1 - x_3} (y_1 - x_3 + 1)
\end{aligned}$$

$$= \sum_{k=0}^{y_1} \left(\frac{3}{16}\right) \left(\frac{1}{4}\right)^{y_1} 2^k (k+1) \tag{2.15}$$

where $k = y_1 - x_3$.

In order to calculate (2.15) we need to first calculate the sum $\sum_{k=0}^{y_1} 2^k(k+1)$ and then substitute into (2.15). Doing this we have

$$\begin{aligned}
\sum_{k=0}^{y_1} 2^k(k+1) &= \sum_{k=0}^{y_1} t^k (k+1) \\
&= \sum_{k=0}^{y_1} \frac{d}{dt}(t^{k+1}) \\
&= \frac{d}{dt}(t) + \frac{d}{dt}(t^2) + ... + \frac{d}{dt}(t_1^y) + \frac{d}{dt}(t^{y_1+1}) \\
&= \frac{d}{dt}(t + t^2 + ... + t_1^y + t^{y_1+1}) \\
&= \frac{d}{dt}\left[\frac{1 - t^{y_1+1}}{1-t}\right] \\
&= \frac{1}{(1-t^2)}\left[1 - t^{y_1+2} - (y_1+2)t^{y_1+1} + (y_1+2)t^{y_1+2}\right] \\
&= \frac{1}{(1-t)^2}\left[1 + (y_1+1)t^{y_1+2} - (y_1+2)t^{y_1+1}\right] \qquad (2.16)
\end{aligned}$$

where $t = 2$.

Evaluating (2.16) for t=2 we have

$$\sum_{k=0}^{y_1} 2^k(k+1) = 1 + (y_1+1)2^{y_1+2} - (y_1+2)2^{y_1+1}. \tag{2.17}$$

Now we substitute (2.17) into (2.15) and obtain:

$$\begin{aligned}
P[Y_1 = y_1] &= \sum_{k=0}^{y_1} \left(\frac{3}{16}\right)\left(\frac{1}{4}\right)^{y_1} 2^k(k+1) \\
&= \left(\frac{3}{16}\right)\left(\frac{1}{4}\right)^{y_1} \left[1 + (y_1+1)2^{y_1+2} - (y_1+2)2^{y_1+1}\right] \\
&= \left(\frac{3}{4}\right)\frac{1}{4}\left(\frac{1}{4}\right)^{y_1} \left[1 + (y_1+1)2^{y_1+2} - (y_1+2)2^{y_1+1}\right] \\
&= \left(\frac{3}{4}\right)\left(\frac{1}{4}\right)^{y_1+1} \left[1 + (y_1+1)2^{y_1+2} - (y_1+2)2^{y_1+1}\right]
\end{aligned}$$

$$
\begin{aligned}
&= \left(\frac{3}{4}\right)\left(\frac{1}{4}\right)^{y_1+1}\left[1+(y_1+1)2^{y_1+1}2-(y_1+1+1)2^{y_1+1}\right]\\
&= \left(\frac{3}{4}\right)\left(\frac{1}{4}\right)^{y_1+1}+\left(\frac{3}{2}\right)(y_1+1)\left(\frac{1}{2}\right)^{y_1+1}-\frac{3}{4}(y_1+1)\left(\frac{1}{2}\right)^{y_1+1}-\left(\frac{3}{4}\left(\frac{1}{2}\right)^{y_1+1}\right.\\
&= \left(\frac{3}{4}\right)\left(\frac{1}{4}\right)^{y_1+1}+\left(\frac{3}{4}\right)(y_1+1)\left(\frac{1}{2}\right)^{y_1+1}-\left(\frac{3}{4}\right)\left(\frac{1}{2}\right)^{y_1+1}\\
&= \left(\frac{3}{4}\right)\left(\frac{1}{4}\right)^{y_1+1}+y_1\left(\frac{3}{4}\right)\left(\frac{1}{2}\right)^{y_1+1}.
\end{aligned}
$$

Finally we can calculate:

$$\sum y_1 P[Y_1 = y_1 \; and \; Z_1 > Y_1]. \tag{2.18}$$

We know that $Z_1 \sim Geo\,(3/4)$ so we can write $P(Z_1 > Y_1)$=$(1/4)^{y_1+1}$. Thus equation (2.18) can be calculated as follows

$$
\begin{aligned}
&\sum_{y_1=0}^{\infty} y_1 P[Y_1 = y_1 \; and \; Z_1 > Y_1] = \sum_{y_1=0}^{\infty} y_1 P(Y_1 = y_1) P(Z_1 > Y_1)\\
&= \sum_{y_1=0}^{\infty} y_1\left[\left(\frac{3}{4}\right)\left(\frac{1}{4}\right)^{y_1+1}+y_1\left(\frac{3}{4}\right)\left(\frac{1}{2}\right)^{y_1+1}\right]\left(\frac{1}{4}\right)^{y_1+1}\\
&= \sum_{y_1=0}^{\infty} y_1\left[\left(\frac{3}{4}\right)\left(\frac{1}{4}\right)^{2y_1+2}+y_1\left(\frac{3}{4}\right)\left(\frac{1}{8}\right)^{y_1+1}\right]\\
&= \sum_{y_1=0}^{\infty}\left[y_1\left(\frac{3}{4}\right)\left(\frac{1}{4}\right)^{2y_1+2}+\left(\frac{3}{4}\right)\left(\frac{1}{8}\right)^{y_1+1}y_1^2\right]\\
&= \left(\frac{3}{4}\right)\sum_{y_1=0}^{\infty} y_1\left(\frac{1}{4}\right)^{2y_1+2}+\left(\frac{3}{4}\right)\sum_{y_1=0}^{\infty}\left(\frac{1}{8}\right)^{y_1+1}y_1^2\\
&= \frac{592}{25725}.
\end{aligned} \tag{2.19}
$$

So far we have calculated the second sum in equation (2.12), and now we calculate the first sum which is

$$\sum_{z_1=0}^{\infty} z_1 P(Z_1 = z_1 \; and \; Z_1 \leq Y_1). \tag{2.20}$$

First we need to evaluate $P(Z_1 = z_1)$.

We have $P(Z_1 = z_1) = (3/4)\,(1/4)^{z_1}$ because $Z_1 \sim Geo\,(3/4)$. Thus we have

$$\begin{aligned}
P(Z_1 = z_1 \; and \; Z_1 \leq Y_1) &= P(Z_1 = z_1) \sum_{y_1=z_1}^{\infty} P(Y_1 = y_1) \\
&= \left(\frac{3}{4}\right)\left(\frac{1}{4}\right)^{z_1} \sum_{y_1=z_1}^{\infty} \left(\frac{3}{4}\right)\left(\frac{1}{4}\right)^{y_1+1} + y_1 \left(\frac{3}{4}\right)\left(\frac{1}{2}\right)^{y_1+1} \\
&= \left(\frac{3}{4}\right)\left(\frac{1}{4}\right)^{z_1} \left(\frac{3}{4}\right) \sum_{y_1=z_1}^{\infty} \left(\frac{1}{4}\right)^{y_1+1} + \left(\frac{3}{4}\right) \sum_{y_1=z_1}^{\infty} y_1 \left(\frac{1}{2}\right)^{y_1+1} \\
&= \left(\frac{3}{4}\right)\left(\frac{1}{4}\right)^{z_1} [\left(\frac{3}{4}\right)\left(\frac{1}{3}\right)\left(\frac{1}{4}\right)^{z_1} + \left(\frac{3}{4}\right)\left(\frac{1}{2}\right)^{z_1} (z_1 + 1) \\
&= \left(\frac{3}{4}\right)\left(\frac{1}{4}\right)^{(2z_1+1)} + \left(\frac{9}{16}\right)\left(\frac{1}{8}\right)^{z_1} (z_1 + 1). \qquad (2.21)
\end{aligned}$$

Substituting (2.21) into (2.20) we obtain

$$\begin{aligned}
&\sum_{z_1=0}^{\infty} z_1 P(Z_1 = z_1 \; and \; Z_1 \leq Y_1) = \sum_{z_1=0}^{\infty} z_1 \left[\left(\frac{3}{4}\right)\left(\frac{1}{4}\right)^{2z_1+1} + \left(\frac{9}{16}\right)\left(\frac{1}{8}\right)^{z_1} (z_1 + 1)\right] \\
&= \left(\frac{3}{4}\right) \sum_{z_1=0}^{\infty} z_1 \left(\frac{1}{4}\right)^{2z_1+1} + \left(\frac{9}{16}\right) \sum_{z_1=0}^{\infty} z_1 (z_1 + 1) \left(\frac{1}{8}\right)^{z_1} \\
&= \left(\frac{3}{4}\right) \cdot \left(\frac{4}{225}\right) + \left(\frac{9}{16}\right) \cdot \left(\frac{128}{343}\right) \\
&= \frac{5743}{25725}. \qquad (2.22)
\end{aligned}$$

Substituting (2.19) and (2.22) into (2.12) we obtain

$$\begin{aligned}
&\sum_{z_1=0}^{\infty} z_1 P(Z_1 = z_1 \; and \; Z_1 < Y_1) + \sum_{y_1=0}^{\infty} y_1 P(Y_1 = y_1 \; and \; Z_1 > Y_1) \\
&\quad = \frac{5743}{25725} + \frac{592}{25725} \\
&\quad = \frac{181}{735} \approx \mathbf{0.2463}.
\end{aligned}$$

This means that the average number of wins of the third place in the first branch of the tree is 0.2463. We will repeat the same procedure for the other five branches in order to find the average number of wins of the third place.

Number of wins for the third position in the second branch

In the second branch the second place has $Y_2 = 2 + x_1 + x_4 + x_5$ wins. We have that x_1 has the same form as x_3; they are both geometrically distributed with the same probability p. Also x_4 and x_5 are of the same form as x_6 and x_7 respectively. Thus $Y_1 = x_1 + x_4 + x_5 = x_3 + x_6 + x_7$. This means that the number of wins of the second place is then $2 + Y_1$.

The third place has $Z_2 = x_2 = Z_1$ wins, which is the same as in the first branch of the tree.

Again, we are interested to calculate equation (2.11) which in this branch becomes

$$\sum_{z_1=0}^{\infty} z_1 P(Z_1 = z_1 \; and \; Z_1 \leq Y_1+2) + \sum_{y_1=0}^{\infty} (y_1+2) P[Y_1+2 = y_1+2 \; and \; Z_1 > Y_1+2]. \tag{2.23}$$

As in the first branch, we first calculate

$$\sum_{y_1=0}^{\infty} (y_1 + 2) P[Y_1 + 2 = y_1 + 2 \; and \; Z_1 > Y_1 + 2] \tag{2.24}$$

and we have

$$\begin{aligned}
&\sum_{y_1=0}^{\infty} (y_1 + 2) P[Y_1 + 2 = y_1 + 2 \; and \; Z_1 > Y_1 + 2] \\
&= \sum_{y_1=0}^{\infty} (y_1 + 2) P[Y_1 + 2 = y_1 + 2] P[Z_1 > Y_1 + 2] \\
&= \sum_{y_1=0}^{\infty} (y_1 + 2) P(Y_1 = y_1) \left(\frac{1}{4}\right)^{y_1+3} \\
&= \sum_{y_1=0}^{\infty} (y_1 + 2) \left[\left(\frac{3}{4}\right) \left(\frac{1}{4}\right)^{y_1+1} + y_1 \left(\frac{3}{4}\right) \left(\frac{1}{2}\right)^{y_1+1} \right] \left(\frac{1}{4}\right)^{y_1+3} \\
&= \sum_{y_1=0}^{\infty} (y_1 + 2) \left[\left(\frac{3}{4}\right) \left(\frac{1}{4}\right)^{2y_1+4} + \left(\frac{3}{16}\right) \left(\frac{1}{8}\right)^{y_1+1} y_1 \right]
\end{aligned}$$

$$
\begin{aligned}
&= \left(\frac{3}{4}\right)\sum_{y_1=0}^{\infty}(y_1+2)\left(\frac{1}{4}\right)^{2y_1+4} + \left(\frac{3}{64}\right)\sum_{y_1=0}^{\infty} y_1(y_1+2)\left(\frac{1}{8}\right)^{y_1+1} \\
&= \frac{3}{4}\cdot\frac{31}{3600} + \frac{3}{64}\cdot\frac{23}{343} \\
&= \frac{247}{25725} \\
&\approx \mathbf{0.0096}. \qquad (2.25)
\end{aligned}
$$

Secondly we calculate the rest of equation (2.23) which is:

$$
\sum_{z_1=0}^{\infty} z_1 P(Z_1 = z_1 \ and \ Z_1 \le Y_1 + 2). \qquad (2.26)
$$

In order to calculate (2.26) we find first $P(Z_1 = z_1 \ and \ Z_1 \le Y_1 + 2)$. We have

$$
\begin{aligned}
&P(Z_1 = z_1 \ and \ Z_1 \le Y_1 + 2) \\
&= P(Z_1 = z_1)\sum_{y_1=z_1-2}^{\infty} P(Y_1 + 2 = y_1 + 2) \\
&= P(Z_1 = z_1)\sum_{y_1=z_1-2}^{\infty} P(Y_1 = y_1) \\
&= \left(\frac{3}{4}\right)\left(\frac{1}{4}\right)^{z_1}\sum_{y_1=z_1-2}^{\infty}\left[\left(\frac{3}{4}\right)\left(\frac{1}{4}\right)^{y_1+1} + \left(\frac{3}{4}\right)\sum_{y_1=z_1-2}^{\infty} y\left(\frac{1}{2}\right)^{y_1+1}\right] \\
&= \left(\frac{3}{4}\right)\left(\frac{1}{4}\right)^{z_1}\left[\left(\frac{3}{4}\right)\left(\frac{1}{3}\right)\left(\frac{1}{4}\right)^{z_1-2} + \left(\frac{3}{4}\right)\left(\frac{1}{2}\right)^{z_1-2}(z_1-1)\right] \\
&= \left(\frac{3}{4}\right)\left(\frac{1}{4}\right)^{2z_1-1} + \left(\frac{9}{4}\right)\left(\frac{1}{8}\right)^{z_1}(z_1-1). \qquad (2.27)
\end{aligned}
$$

Now we substitute equation (2.27) into equation (2.26) and obtain

$$
\begin{aligned}
&\sum_{z_1=0}^{\infty} z_1 P(Z_1 = z_1 \ and \ Z_1 \le Y_1 + 2) \\
&= \sum_{z_1=0}^{\infty} z_1\left[\left(\frac{3}{4}\right)\left(\frac{1}{4}\right)^{2z_1-1} + \left(\frac{9}{4}\right)\left(\frac{1}{8}\right)^{z_1}(z_1-1)\right] \\
&= \left(\frac{3}{4}\right)\sum_{z_1=0}^{\infty} z_1\left(\frac{1}{4}\right)^{2z_1-1} + \left(\frac{9}{4}\right)\sum_{z_1=0}^{\infty} z_1(z_1-1)\left(\frac{1}{8}\right)^{z_1}
\end{aligned}
$$

$$= \left(\frac{3}{4}\right) \cdot \left(\frac{64}{225}\right) + \left(\frac{9}{4}\right) \cdot \left(\frac{16}{343}\right)$$
$$= \frac{8188}{25725}$$
$$\approx \mathbf{0.31829}. \tag{2.28}$$

Finally we substitute equation (2.24) and equation (2.28) into equation (2.23) and we have

$$\sum_{z_1=0}^{\infty} z_1 P(Z_1 = z_1 \; and \; Z_1 \leq Y_1 + 2) + \sum_{y_1=0}^{\infty} (y_1 + 2) P(Y_1 + 2 = y_1 + 2 \; and \; Z_1 > Y_1 + 2)$$
$$= \frac{8188}{25725} + \frac{247}{25725}$$
$$= \frac{241}{735}$$
$$\approx \mathbf{0.32789}.$$

Thus the average number of wins of the third place in the second branch of the tree is 0.32789.

Number of wins for the third position in the third branch

As in the previous branches, in this branch as well we calculate the average number of wins for the third place, which is found by equation (2.11). In the third branch, the second place has $Y_3 = x_3 + x_6 + x_7 = Y_1$ wins, which is the same as in the first branch. The third place has $Z_3 = 1 + x_1 = 1 + Z_1$ wins, because x_1 and x_2 are both geometrically distributed with probability $p = 3/4$. Thus equation (2.11) in the third branch becomes:

$$\sum_{z_1=0}^{\infty} (z_1+1) P[Z_1+1 = z_1+1 \; and \; Z_1+1 \leq Y_1] + \sum_{y_1=0}^{\infty} y_1 P[Y_1 = y_1 \; and \; Z_1+1 > Y_1] \tag{2.29}$$

where $Z_1 = z_1$ and $Y_1 = x_3 + x_6 + x_7$.

Again we see the two sums in (2.29) separately and then add them together.

We start by calculating

$$\begin{aligned}
&\sum_{y_1=0}^{\infty} y_1 P[Y_1 = y_1 \ and \ Z_1 + 1 > Y_1] = \sum_{y_1=0}^{\infty} y_1 P(Y_1 = y_1) P(Z_1 + 1 > Y_1) \\
&= \sum_{y_1=0}^{\infty} y_1 \left[\left(\frac{3}{4}\right) \left(\frac{1}{4}\right)^{y_1+1} + y_1 \left(\frac{3}{4}\right) \left(\frac{1}{2}\right)^{y_1+1} \right] \left(\frac{1}{4}\right)^{y_1} \\
&= \sum_{y_1=0}^{\infty} y_1 \left[\left(\frac{3}{4}\right) \left(\frac{1}{4}\right)^{2y_1+1} + y_1 \left(\frac{3}{8}\right) \left(\frac{1}{8}\right)^{y_1} \right] \\
&= \left(\frac{3}{4}\right) \sum_{y_1=0}^{\infty} y_1 \left(\frac{1}{4}\right)^{2y_1+1} + \left(\frac{3}{8}\right) \sum_{y_1=0}^{\infty} y_1^2 \left(\frac{1}{8}\right)^{y_1} \\
&= \frac{3}{4} \cdot \frac{4}{225} + \frac{3}{8} \cdot \frac{72}{343} \\
&= \frac{2368}{25725} \\
&\approx \mathbf{0.09205}. \qquad (2.30)
\end{aligned}$$

Next we calculate

$$\sum_{z_1=0}^{\infty} (z_1 + 1) P[Z_1 + 1 = z_1 + 1 \ and \ Z_1 + 1 \leq Y_1]. \qquad (2.31)$$

First we work out the value of

$$P[Z_1 + 1 = z_1 + 1 \ and \ Z_1 + 1 \leq Y_1].$$

which is

$$\begin{aligned}
&P[Z_1 + 1 = z_1 + 1 \ and \ Z_1 + 1 \leq Y_1] = P(Z_1 + 1 = z_1 + 1) \sum_{y_1=z_1+1}^{\infty} P(Y_1 = y_1) \\
&= P(Z_1 = z_1) \sum_{y_1=z_1+1}^{\infty} P(Y_1 + y_1) \\
&= \frac{3}{4} \left(\frac{1}{4}\right)^{z_1} \sum_{y_1=z_1+1}^{\infty} \left[\frac{3}{4} \left(\frac{1}{4}\right)^{y_1+1} + y_1 \frac{3}{4} \left(\frac{1}{2}\right)^{y_1+1} \right] \\
&= \frac{3}{4} \left(\frac{1}{4}\right)^{z_1} \left[\frac{3}{4} \sum_{y_1=z_1+1}^{\infty} \left(\frac{1}{4}\right)^{y_1+1} + \frac{3}{4} \sum_{y_1=z_1+1}^{\infty} y_1 \left(\frac{1}{2}\right)^{y_1+1} \right]
\end{aligned}$$

$$\begin{aligned}
&= \frac{3}{4}\left(\frac{1}{4}\right)^{z_1}[\frac{3}{4}\cdot\frac{1}{3}\left(\frac{1}{4}\right)^{z_1+1}+\frac{3}{4}\left(\frac{1}{2}\right)^{z_1+1}(z_1+2)\\
&= \frac{3}{4}\left(\frac{1}{2}\right)^{2z_1+2}+\frac{9}{32}\left(\frac{1}{8}\right)^{z_1}(z_1+2).
\end{aligned}\tag{2.32}$$

Now we substitute (2.32) into (2.31) and obtain

$$\begin{aligned}
&\sum_{z_1=0}^{\infty}(z_1+1)P(Z_1+1=z_1+1\ and\ Z_1+1\leq Y_1]\\
&=\sum_{z_1=0}^{\infty}(z_1+1)\left[\frac{3}{4}\left(\frac{1}{4}\right)^{2z_1+2}+\frac{9}{32}\left(\frac{1}{8}\right)^{z_1}(z_1+2)\right]\\
&=\frac{3}{4}\sum_{z_1=0}^{\infty}(z_1+1)\left(\frac{1}{4}\right)^{2z_1+2}+\frac{9}{32}\sum_{z_1=0}^{\infty}(z_1+1)(z_1+2)\left(\frac{1}{8}\right)^{z_1}\\
&=\frac{3}{4}\cdot\frac{16}{225}+\frac{9}{32}\cdot\frac{1024}{343}\\
&=\frac{22972}{25725}\\
&\approx \mathbf{0.89298}.
\end{aligned}\tag{2.33}$$

Now that we have calculated (2.30) and (2.33) separately, we substitute them in (2.29) and have

$$\begin{aligned}
\sum_{z_1=0}^{\infty}(z_1+1)P[Z_1+1=z_1+1\ and\ Z_1+1\leq Y_1]+\sum_{y_1=0}^{\infty}y_1P[Y_1=y_1\ and\ Z_1+1>Y_1]&\\
&=\frac{22972}{25725}+\frac{2368}{25725}\\
&=\frac{724}{735}\\
&\approx \mathbf{0.985}.
\end{aligned}$$

Thus the average number of wins of the third place in the third branch of the tree is 0.985.

Number of wins for the third position in the fourth branch

In the fourth branch of the tree, the second place has $Y_4 = 1 + x_2 + x_4 + x_5 =$

$1 + Y_1$ wins, because $x_2 + x_4 + x_5 = x_3 + x_6 + x_7 = Y_1$. The third place has $Z_4 = 1 + x_1 = 1 + Z_1$ wins.

Then, equation (2.11) that calculates the average number of wins of the third place, in this branch becomes:

$$\begin{aligned}&\sum_{z_1=0}^{\infty}(z_1+1)P[Z_1+1=z_1+1 \; and \; Z_1+1 \leq Y_1+1]+\\&\sum_{y_1=0}^{\infty}(y_1+1)P[Y_1+1=y_1+1 \; and \; Z_1+1 > Y_1+1]. \qquad (2.34)\end{aligned}$$

Again as on the previous branches, we calculate the two sums in (2.34) separately and add them together.

First let us evaluate the value of

$$\sum_{y_1=0}^{\infty}(y_1+1)P[Y_1+1=y_1+1 \; and \; Z_1+1 > Y_1+1]; \qquad (2.35)$$

we have

$$\begin{aligned}&\sum_{y_1=0}^{\infty}(y_1+1)P[Y_1+1=y_1+1 \; and \; Z_1+1 > Y_1+1]\\&=\sum_{y_1=0}^{\infty}(y_1+1)P(Y_1+1=y_1+1)P(Z_1+1 > Y_1+1)\\&=\sum_{y_1=0}^{\infty}(y_1+1)P(Y_1=y_1)P(Z_1+1 > Y_1+1)\cdot\\&\sum_{y_1=0}^{\infty}(y_1+1)\left[\frac{3}{4}\left(\frac{1}{4}\right)^{y_1+1}+y_1\frac{3}{4}\left(\frac{1}{2}\right)^{y_1+1}\right]\left(\frac{1}{4}\right)^{y_1+1}\\&=\sum_{y_1=0}^{\infty}(y_1+1)\left[\frac{3}{4}\left(\frac{1}{4}\right)^{2y_1+2}+y_1\frac{3}{4}\left(\frac{1}{8}\right)^{y_1+1}\right]\\&=\frac{3}{4}\sum_{y_1=0}^{\infty}(y_1+1)\left(\frac{1}{4}\right)^{2y_1+2}+\frac{3}{4}\sum_{y_1=0}^{\infty}y_1(y_1+1)\left(\frac{1}{8}\right)^{y_1+1}\\&=\frac{3}{4}\cdot\frac{16}{225}+\frac{3}{4}\cdot\frac{16}{343}\\&=\frac{2272}{25725}\end{aligned}$$

$$\approx \mathbf{0.08832}. \tag{2.36}$$

Now we evaluate the second part of (2.34) which is

$$\sum_{z_1=0}^{\infty}(z_1+1)P[Z_1+1=z_1+1 \; and \; Z_1+1 \leq Y_1+1]. \tag{2.37}$$

In order to calculate (2.37) we first find the value of

$$P(Z_1+1=z_1+1 \; and \; Z_1+1 \leq Y_1+1] \tag{2.38}$$

and we have

$$\begin{aligned}
&P(Z_1+1=z_1+1 \; and \; Z_1+1 \leq Y_1+1] \\
&= P(Z_1=z_1)\sum_{y_1=z_1}^{\infty}P(Y_1=y_1) \\
&= \frac{3}{4}\left(\frac{1}{4}\right)^{2z_1+1}+\frac{9}{16}\left(\frac{1}{8}\right)^{z_1}(z_1+1).
\end{aligned} \tag{2.39}$$

Substituting (2.39) into (2.37) we obtain

$$\begin{aligned}
&\sum_{z_1=0}^{\infty}(z_1+1)P[Z_1+1=z_1+1 \; and \; Z_1+1 \leq Y_1+1] \\
&= \sum_{z_1=0}^{\infty}(z_1+1)\left[\frac{3}{4}\left(\frac{1}{4}\right)^{2z_1+1}+\frac{9}{16}\left(\frac{1}{8}\right)^{z_1}(z_1+1)\right] \\
&= \frac{3}{4}\sum_{z_1=0}^{\infty}(z_1+1)\left(\frac{1}{4}\right)^{2z_1+1}+\frac{9}{16}\sum_{z_1=0}^{\infty}(z_1+1)^2\left(\frac{1}{8}\right)^{z_1} \\
&= \frac{3}{4}\cdot\frac{64}{225}+\frac{9}{16}\cdot\frac{576}{343} \\
&= \frac{29788}{25725} \\
&\approx \mathbf{1.15794}.
\end{aligned} \tag{2.40}$$

Substituting (2.36) and (2.40) into (2.34) we obtain

$$\begin{aligned}
&\sum_{z_1=0}^{\infty}(z_1+1)P[Z_1+1=z_1+1 \; and \; Z_1+1 \leq Y_1+1] \\
&+\sum_{y_1=0}^{\infty}(y_1+1)P[Y_1+1=y_1+1 \; and \; Z_1+1 > Y_1+1] \\
&=\frac{29788}{25725}+\frac{2272}{25725} \\
&=\frac{916}{735} \\
&\approx \mathbf{1.2463}. \qquad (2.41)
\end{aligned}$$

Thus the average number of wins of the third place in the fourth branch of the tree is 1.2463.

Number of wins for the third position in the fifth branch

In the fifth branch, the second place has $Y_5 = 1+x_1+x_6+x_7 = 1+Y_1$ wins. The third place here has $Z_5 = x_3 = Z_1$ wins. Proceeding exactly as in the previous branches, what we need to calculate is

$$\sum_{z_1=0}^{\infty} z_1 P[Z_1=z_1 \; and \; Z_1 \leq Y_1+1]+\sum_{y_1=0}^{\infty}(y_1+1)P[Y_1+1=y_1+1 \; and \; Z_1 > Y_1+1]. \qquad (2.42)$$

Let us first start by calculation the second sum of (2.42) which is as follows:

$$\begin{aligned}
&\sum_{y_1=0}^{\infty}(y_1+1)P[Y_1+1=y_1+1 \; and \; Z_1 > Y_1+1] \\
&=\sum_{y_1=0}^{\infty}(y_1+1)P(Y_1=y_1)P(Z_1>Y_1+1) \\
&=\sum_{y_1=0}^{\infty}(y_1+1)\left[\frac{3}{4}\left(\frac{1}{4}\right)^{y_1+1}+y_1\frac{3}{4}\left(\frac{1}{2}\right)^{y_1+1}\right]\left(\frac{1}{4}\right)^{y_1+2} \\
&=\sum_{y_1=0}^{\infty}(y_1+1)\left[\frac{3}{4}\left(\frac{1}{4}\right)^{2y_1+3}+y_1\frac{3}{16}\left(\frac{1}{8}\right)^{y_1+1}\right]
\end{aligned}$$

$$\begin{aligned}
&= \sum_{y_1=0}^{\infty}(y_1+1)\left(\frac{1}{4}\right)^{2y_1+3} + \frac{3}{16}\sum_{y_1=0}^{\infty} y_1(y_1+1)\left(\frac{1}{8}\right)^{y_1+1} \\
&= \frac{3}{4}\cdot\frac{4}{225}+\frac{3}{16}\cdot\frac{16}{343} \\
&= \frac{568}{25725} \\
&\approx \mathbf{0.0221}. \qquad (2.43)
\end{aligned}$$

The first sum of (2.42) is

$$\sum_{z_1=0}^{\infty} z_1 P(Z_1 = z_1 \; and \; Z_1 \leq Y_1 + 1). \qquad (2.44)$$

First we calculate

$$\begin{aligned}
&P(Z_1 = z_1 \; and \; Z_1 \leq Y_1+1) = P(Z_1 = z_1)\sum_{y_1=z_1-1}^{\infty} P(Y_1 = y_1) \\
&= \frac{3}{4}\left(\frac{1}{4}\right)^{z_1}\sum_{y_1=z_1-1}^{\infty}\left[\frac{3}{4}\left(\frac{1}{4}\right)^{y_1+1} + y_1\frac{3}{4}\left(\frac{1}{2}\right)^{y_1+1}\right] \\
&= \frac{3}{4}\left(\frac{1}{4}\right)^{z_1}\left[\frac{3}{4}\sum_{y_1=z_1-1}^{\infty}\left(\frac{1}{4}\right)^{y_1+1} + \frac{3}{4}\sum_{y_1=z_1-1}^{\infty} y_1\left(\frac{1}{2}\right)^{y_1+1}\right] \\
&= \frac{3}{4}\left(\frac{1}{4}\right)^{z_1}\left[\frac{3}{4}\cdot\frac{1}{3}\left(\frac{1}{4}\right)^{z_1-1} + \frac{3}{4}\left(\frac{1}{2}\right)^{z_1-1} z_1\right] \\
&= \frac{3}{4}\left(\frac{1}{4}\right)^{2z_1} + \frac{9}{8}\left(\frac{1}{8}\right)^{z_1} z_1. \qquad (2.45)
\end{aligned}$$

Substituting (2.45) into (2.44) we obtain

$$\begin{aligned}
\sum_{z_1=0}^{\infty} z_1 P(Z_1 = z_1 \; and \; Z_1 \leq Y_1+1) &= \sum_{z_1=0}^{\infty} z_1\left[\frac{3}{4}\left(\frac{1}{4}\right)^{2z_1} + \frac{9}{8}\left(\frac{1}{8}\right)^{z_1} z_1\right] \\
&= \frac{3}{4}\sum_{z_1=0}^{\infty} z_1\left(\frac{1}{4}\right)^{2z_1} + \frac{9}{8}\sum_{z_1=0}^{\infty}(z_1)^2\left(\frac{1}{8}\right)^{z_1} \\
&= \frac{3}{4}\cdot\frac{16}{225}+\frac{9}{8}\cdot\frac{72}{343}. \qquad (2.46)
\end{aligned}$$

Substituting (2.43) and (2.46) into (2.42) we obtain

$$\begin{aligned}\sum_{z_1=0}^{\infty} z_1 P(X_1 = z_1 \; and \; Z_1 \leq Y_1 + 1) + \sum_{y_1=0}^{\infty}(y_1+1)P[Y_1+1 = y_1+1 \; and \; Z_1 > Y_1+1]\\ = \frac{7447}{25725} + \frac{568}{25725}\\ = \frac{229}{735}(\approx \mathbf{0.3116}). \qquad (2.47)\end{aligned}$$

Thus the average number of wins of the third place in the fifth branch of the tree is equal to 0.3116.

Number of wins for the third position in the sixth branch

In the sixth branch, the second place has $Y_6 = 1 + x_1 + x_6 + x_7 = 1 + Y_1$ wins. The third place has $Z_6 = x_3 = Z_1$ wins. We notice that the number of wins of the second and third place in this branch is the same as the number of wins of the second and the third place in the fifth branch. Thus the average number of wins for the third place is

$$\begin{aligned}\sum_{z_1=0}^{\infty} z_1 P(X_1 = z_1 \; and \; Z_1 \leq Y_1 + 1) + \sum_{y_1=0}^{\infty}(y_1+1)P[Y_1+1 = y_1+1 \; and \; Z_1 > Y_1+1]\\ = \frac{229}{735}(\approx \mathbf{0.3116}).\end{aligned}$$

Having found the average number of wins for the third place in every branch of Table 2.2, we can now calculate the average number of wins over all branches and this is $\frac{181+241+724+916+229+229}{735} \cdot \frac{1}{6} = \frac{4}{7}(\approx \mathbf{0.5714})$.

Thus the average number of wins of the third place in a group of 4 individuals equally able to win a fight in a situation when only the loser effect is present is equal to 0.5714.

We can now calculate the number of wins for the second place, because we have the combined number of wins of the second and third place given in equation (2.10). Then, the average number of wins of the second placed individual is $\frac{23}{6} - \frac{4}{7} = \frac{137}{42} (\approx \mathbf{3.2619})$.

2.3.2.1 Nonlinearity due to ties in the final positions

The number of wins in Table 2.1 are an average over 10,000 simulations, and in fact the simulations do not always yield linear hierarchies. The fact that in every case they sometimes do, is enough to demonstrate linearity on average. Nonlinearity in real dominance hierarchies can occur through a number of bottom-ranked individuals having equivalent (lack of) status, and this can also happen in our model. We now consider the probability of having a unique last-placed individual when only the loser effect is in place (this is the simplest case as we get the same structure for different values of the loser effect), and observe the large probability of ties here. The set of all possible structures with at least two individuals with zero wins will be denoted by **A**. When an individual has lost a contest in this version of our model, it will always concede any subsequent contest. Thus if our population enters the set **A** it can never leave it, and the final dominance hierarchy will not have a unique last-placed individual. We denote all *final* hierarchies not in **A** as the set **B**.

The first encounter will give us a winner denoted by W and a loser denoted by $L(0)$ where $L(0)$ stands for a loser with 0 wins. This leads to a state of the population $S_{WL(0)}$ (in our notation we list the individuals that have fought, omitting any individual that has not engaged in a contest). Conditional on the next fight not being between the two existing individuals, we have either:

1) A new individual fights the original loser and wins. This means that $S_{WL(0)} \mapsto S_{WWL(0)}$ with a probability $2/5$.

2) A new individual fights the original winner and loses. This means that $S_{WL(0)} \mapsto S_{WL(0)L(0)}$, an element of the set **A**, with a probability $1/5$.

3) A new individual fights the original winner and wins. This means that $S_{WL(0)} \mapsto S_{WL(+)L(0)}$ with a probability $1/5$, where $L(+)$ denotes a loser that has won a previous contest (the original winner).

4) The next fight is between the two new individuals. This means that $S_{WL(0)} \mapsto S_{WWL(0)L(0)}$, an element of **A**, with a probability $1/5$.

Similar working from the states $S_{WWL(0)}$ and $S_{WL(+)L(0)}$ yields the transition diagram from Figure 2.6. Adding all the above probabilities for the four cases, we obtain the final probability of ending up in state **A**, as opposed to **B**, as $11/20$. Thus the probability of finishing in a hierarchy with a unique last-placed individual, in set **B**, is $9/20$. Note that this does not necessarily mean that in this case we have a linear hierarchy, because we might have a tie between the second and the third place (note that this is another way for linearity on average not to translate to linearity in every simulation).

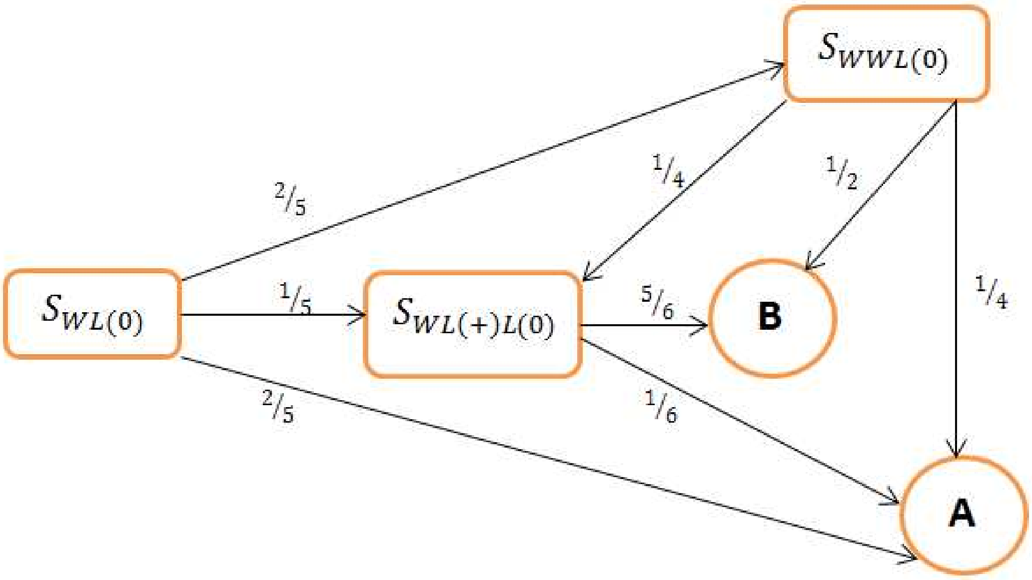


Figure 2.6: Transition probabilities between states for $N = 4$. **A** represents a structure with two losers with zero wins, W is a winner that has not yet lost a fight, L(+) is a previous winner that has now lost, L(0) is a loser with no wins and **B** represent all final structures with only one loser with zero wins.

The case when N=5

Now we increase the group size from 4 to 5. We have the same possibilities as when $N = 4$. Thus starting with $S_{WL(0)}$ and conditional upon the next fights not being between the two existing individuals we have either:

1) A new individual fights the original loser and wins. This means that $S_{WL(0)} \mapsto S_{WWL(0)}$ with a probability $1/3$.

2) A new individual fights the original winner and loses. This means that $S_{WL(0)} \mapsto S_{WL(0)L(0)}$, an element of the set **A**, with a probability $(3/9)(1/2) = (1/6)$, where $3/9$ is the probability for a new individual to meet the previous winner and $1/2$ is the probability of winning.

3) A new individual fights the original winner and wins. This means that $S_{WL(0)} \mapsto S_{WL(+)L(0)}$ with a probability $1/6$.

4) The next fight is between the two new individuals. This means that $S_{WL(0)} \mapsto S_{WWL(0)L(0)}$, an element of **A**, with a probability $1/3$.

Similar working from the states $S_{WWL(0)}$ and $S_{WL(+)L(0)}$ yields the transition diagram from Figure 2.7. Adding all the above probabilities for the four cases, we obtain the final probability of ending up in state **A**, as opposed to **B**, as 0.234. Thus the probability of finishing in a hierarchy with a unique last-placed individual, in set **B**, is 0.234. As expected, we notice that when the group size is increased, the probability of everyone scoring except for the last placed individual, decreases.

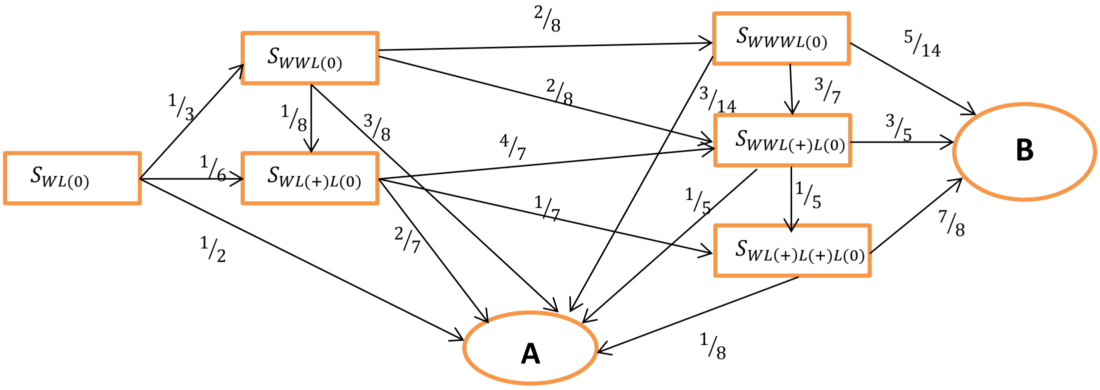


Figure 2.7: Transition probabilities between states for $N = 5$. **A** represents a structure with two losers with zero wins, W is a winner that has not yet lost a fight, L(+) is a previous winner that has now lost, L(0) is a loser with no wins and **B** represent all final structures with only one loser with zero wins.

General group size N

In general from the state $S_{\alpha,\beta,1}$, where α=number of winners W, β=number of L(+)'s and 1 means that we have one loser with zero, L(0), we can go to 4 different possible states as shown in Figure 2.8. Thus for example if we start

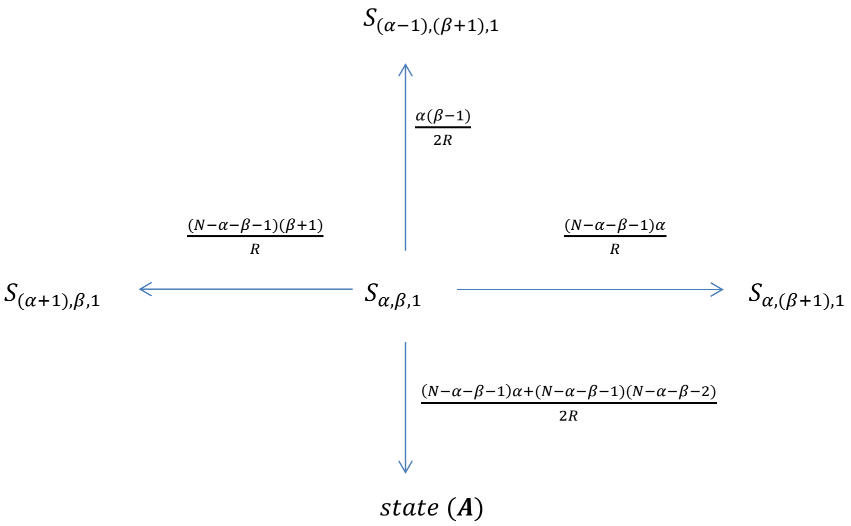


Figure 2.8: Possible states with the corresponding transition probabilities, where $R = \dfrac{\alpha(\alpha-1)}{2} + (N-\alpha-\beta-1)(\alpha+\beta+1) + \dfrac{(N-\alpha-\beta-1)(N-\alpha-\beta-2)}{2}$.

from the state $S_{WL(0)}$ which is the result of the first contest between 2 random individuals in a population of size N, in the next round of fights we can go to state $S_{WWL(0)}$, state $S_{WL(+)L(0)}$ and state **A** with the corresponding transition probabilities given in Figure 2.8. In the first round of the pairwise interactions we have α=1, β=0.

2.3.3 Analysis of the temporal change in RHP

In this section we analyse the temporal dynamic of the change in overlap $\nu_{xy}(t)$, $x, y = 1, \ldots, 4,\ x \neq y, t \geq 1$ of the probability distributions of the four ranks at time t. For the sake of brevity we present the results for only one combination of the winner and loser effect in three different situations: i. only the loser effect is present in the population, ii. only the winner effect is present and iii. both effects are present.

2.3.3.1 The loser effect only

Figure 2.9 shows the probability distributions of the four ranks at time $t = 500$ when $W = 0, L = 0.1$ and Figure 2.10 the corresponding areas of overlap $\nu_{xy}(t),\ \forall t \leq 500$. There is a clear first place individual if only the loser effect is present (we reached the same conclusion when analysing the average number of wins). Further, the second and the fourth place are distinguishable as $\nu_{24}(t)$ decreases below the threshold point 0.1 (see Figure 2.10 and again the same conclusion could be drawn on the basis of Table 2.1). However, Figure 2.9 shows clearly that the second to fourth place individuals all appear close in RHP in comparison to the dominant first individual. The areas of overlaps $\nu_{23}(t)$ and $\nu_{34}(t)$ are almost the same and the pairs corresponding to these overlaps are not distinguishable. The RHP of the top individual stays unchanged, equal to $RHP_{initial}$, meaning that the top individual has a distribution which takes the value 10 with probability 1. Its RHP at time $t = 500$ over 10,000 simulations is shown by the vertical line $x = log(10)$ (Figure 2.9).

Due to the discrete nature of the RHP, it is possible in the very early time steps that the overlap ν can decrease below 0.1 and then increase above 0.1 again (as mentioned previously) several times, but this never happens later on (in practice; theoretically this would be possible), and a dominance event is defined as the time when two individuals became distinguishable in this way

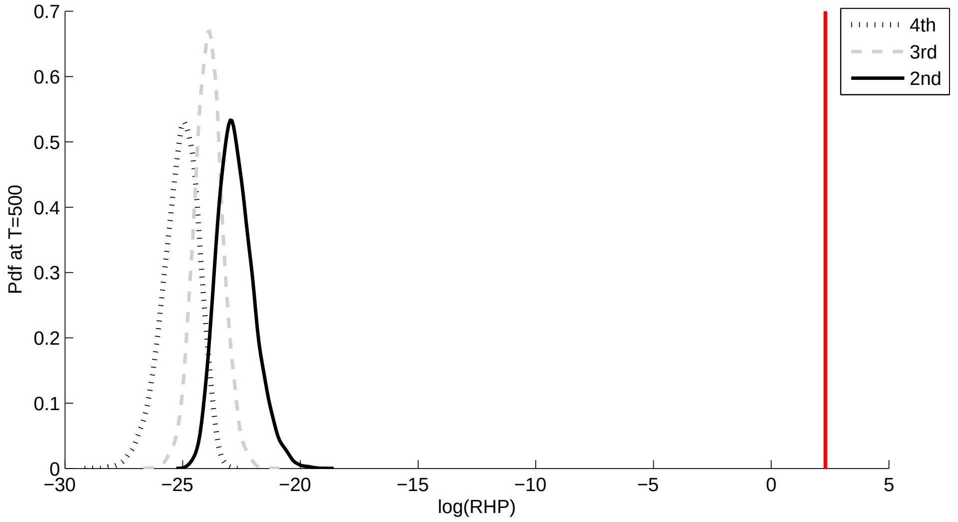


Figure 2.9: Probability distribution for the second, third, forth place individuals for $W = 0$ and $L = 0.1$ at $t = 500$. The probability distribution for the first place individual is represented by the vertical line ($x = log(10)$) because it's RHP stays unchanged.

for the last time. The obtained temporal dynamic in the change of the area of overlap allows us to ask when (meaning after how many fights) the dominance hierarchy is established, i.e. when the last domination event occurs.

We cannot calculate the overlap between the top individual and the other individuals in the same way, as the RHP of the top individual stays unchanged at 10. In this case we say that the top individual will be distinguishable from the second placed individual when the 90% quantile of the distribution of the RHP of the second individual is less than 10 (i.e. we effectively consider the probability of the second placed individual to be 10 as the overlap). The same method will be used to distinguish the top individual from the third and the fourth placed individuals. For the time of domination events of other pairs of individuals, the overlap concept will be used. In the case considered the hierarchy is established quite early; 11 fights are needed for the first and the second place to become distinguishable, which is the final domination event.

It should be noted that this overlap criterion is possibly a rather conservative measure. It is based upon the comparison between randomly selected second

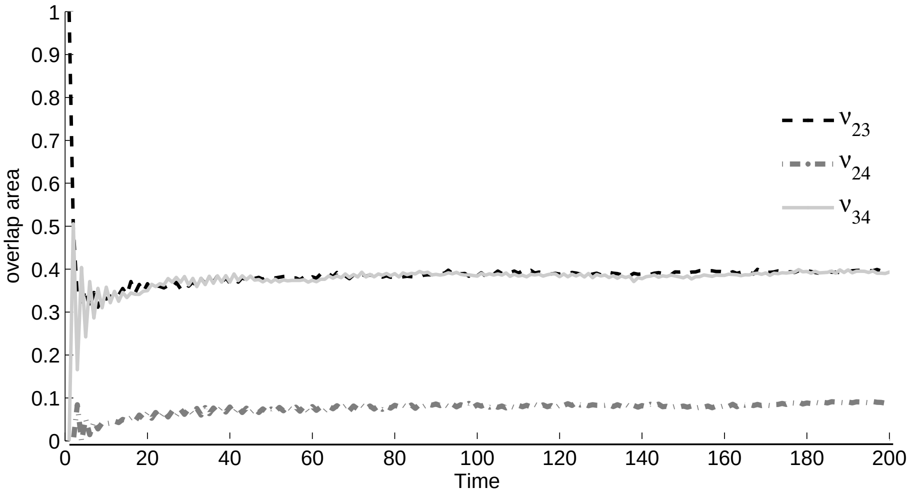


Figure 2.10: Time course of the corresponding area of overlap $\nu_{xy}(t)$, $x = 2,3,4, y = 3,4$ when $W = 0$ and $L = 0.1$. $\nu_{23}(t)$ and $\nu_{34}(t)$ overlap with each other. The overlap between the top individual and the other individuals becomes close to 0 very quickly.

place and third place individuals, whereas in a real hierarchy there would be a pair of individuals in the second and third places, for example. The values of their RHP will not be independent, and are likely to be negatively correlated; the better the second place does, the more likely the third place would do worse. Increasing the loser effect does not make any change in domination events as we obtain the same structure.

2.3.3.2 The winner effect only

Now we consider the situation where only the winner effect is present and assume $W = 0.1$ and $L = 0$. We know from Table 2.1 that in this situation all individuals have a clear position in the hierarchy and this result is confirmed by Figures 2.11 and 2.12. It is clear that the area of overlap $\nu_{xy}(t)$ falls below 0.1 for all combinations of x and y and we are interested in when the domination event occurs.

We note that at the start the RHP of the different individuals can only take some discrete values causing the fluctuations of the area of overlap (see Figure

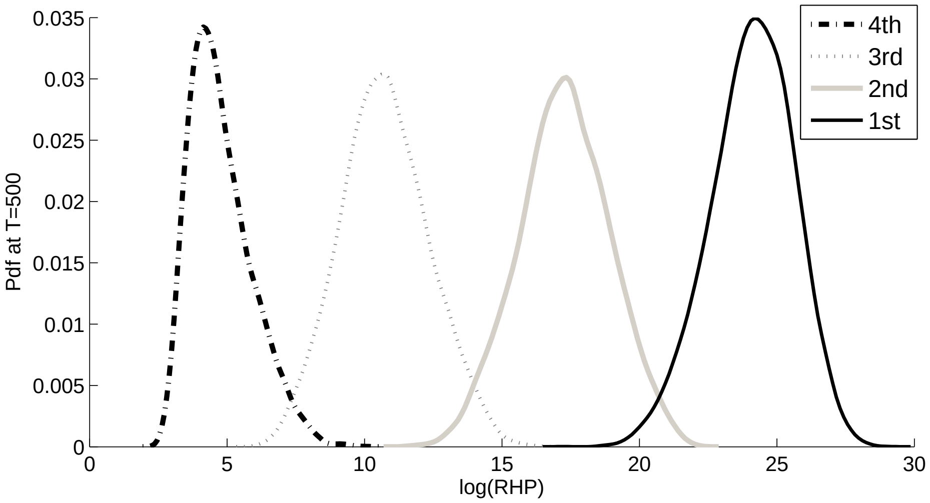


Figure 2.11: Probability distribution for the 4 individuals in the non-updated model when $W = 0.3$ and $L = 0$

2.12). Further, from Figure 2.12 we observe that the final domination event occurs quite late. The last domination event occurs between the second and the third place individuals, which finally become distinguishable at time point $t = 395$. Hence roughly 400 fights are enough to specify the place of each individual in the hierarchy. Increasing the winner effect in the absence of the loser effect does greatly decrease the time needed to establish a hierarchy. The times of domination event for different values of the winner effect are shown in Table 2.3

2.3.3.3 Winner and Loser effects

In this analysis we assume that both the winner and loser effect are present and possess the values $W = 0.3$ and $L = 0.2$. We know from the matrix of wins given in Table 2.1 that the third place individual scores an average of approximately one win, whereas the last individual never wins (as it is the first one to lose and retreats afterwards). Thus the third and the fourth place individuals are expected to have almost identical RHP, confirmed by Figures 2.13 and 2.14. The overlapping probability distributions are concentrated around low values. We further observe that the first place individual is clearly distinguish-

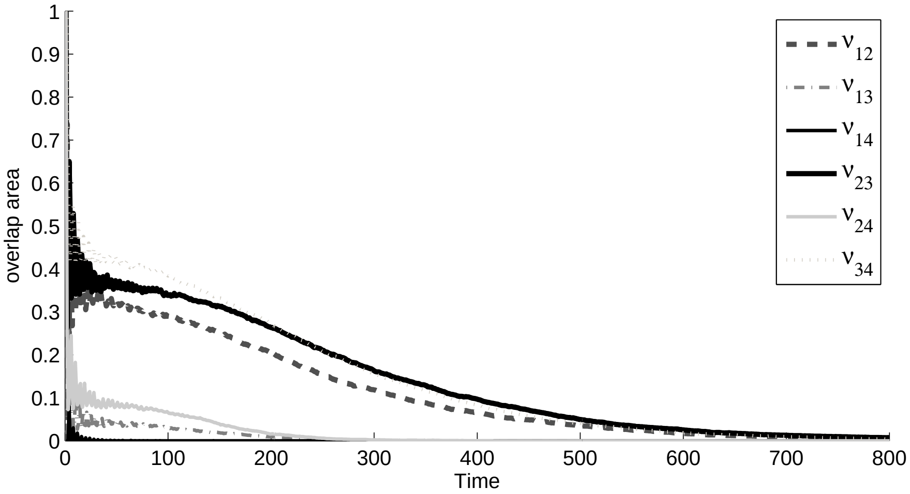


Figure 2.12: Time course of the corresponding area of overlap $\nu_{xy}(t)$, $x, y = 1, \ldots, 4$, $x \neq y$, when $W = 0.1$ and $L = 0$.

able from the others. Interestingly, the RHP of the second place individual has a bi-modal distribution. This implies that sometimes (in most cases) the second place individual is distinguishable from the third, and sometimes it is not. This phenomenon is caused by the outcomes of the very early interactions: through "bad luck" the second place individual can lose sufficiently many early fights and its RHP fall below 10 (implying that it will never fight another contest again), or it can win sufficiently many early fights and its RHP will never fall below 10. Whether an individual will be in a given part of the bi-modal distribution is thus determined in the early contests.

Based on Figure 2.14 we conclude that the second and the fourth places are distinguishable as $\nu_{24}(t) < 0.1$ from a very early time. The second and the third place individuals appear to be clearly different based on the analysis of the average number of wins, with the second place individual doing much better, but the area of the overlap $\nu_{23}(t)$ decreases only to 0.18 (at $t = 45$) and then stays unchanged. This means that for 82% of hierarchies they are clearly different and for 18% they are effectively the same. These values (18% and 82%) correspond to the right and left area of the bi-modal distribution, respectively. We note that this result contradicts the claim of repeatability for

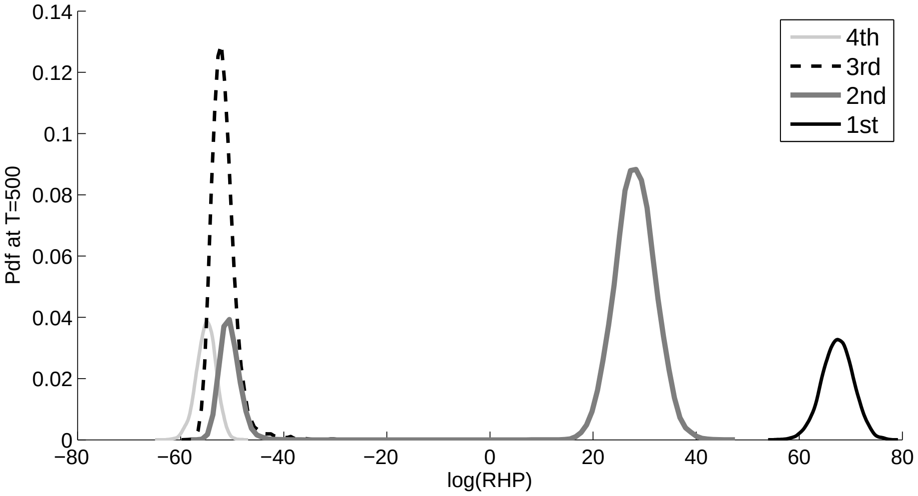


Figure 2.13: Probability distribution functions for the 4 individuals in the non-updated model when $W = 0.3$ and $L = 0.2$ at $t = 500$.

the simulations from [42] as different individual simulations will yield very different results. In general in this type of winner-loser model, this only occurs when there is bimodality in one of the individuals; in all of our cases the second individual out of four, though it is possible for very large winner effects for this to happen for the third individual. In hierarchies with more individuals, theoretically this could happen for any individual except the first or the last.

The last pair of individuals to become distinguishable is the first and the second place, and this happens at $t = 47$ (the time of the final domination event). Summarizing, when both the winner and loser effect are present, the first place individual always becomes distinguishable. For $W = 0.3$ and $L = 0.2$ the second place individual has a bi-modal distribution. In general however, if the ratio between the loser and the winner effect is sufficiently large then the bi-modal shape disappears (individuals will eventually have RHP under 10), but as the ratio becomes smaller, a small upper area appears, which is of increasing size the smaller the ratio. The times of all of the domination events for different combinations of winner and loser effects are shown in Table 2.3.

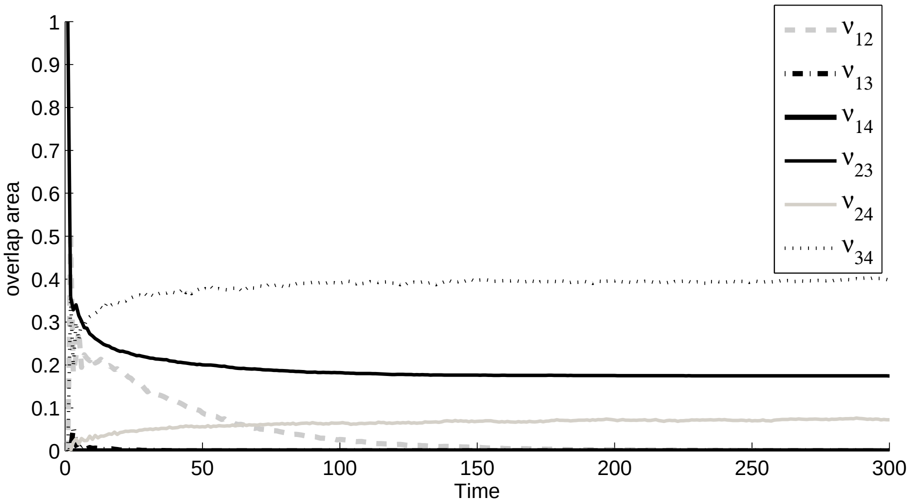


Figure 2.14: Area of overlap ν_{xy} over time when $W = 0.3$ and $L = 0.2$. $\nu_{13}(t)$ and $\nu_{14}(t)$ become close to 0 very quickly, and so are close to the x-axis

2.4 Results for the updated model with perfect assessment

We will now consider the hierarchy structures which emerge when each individual is aware not only of its own RHP through time, but likewise that of its opponent. This corresponds to $\eta = 0$ in [44]. All other features of the model are the same as in the previous section.

2.4.1 Analysis of the average number of wins

We start by analysing the average number of wins in the updated model. Table 2.4 shows the matrices of wins for $W, L = 0; 0.1; 0.2; 0.3$. We observe that for every combination of W and L linear hierarchies are established. The strength of the winner and the loser effects do not have any significant influence on the number of wins of the first, second and third place individuals; they only affect the last place. This individual always scores zero when only the winner effect is present, but generally scores something when the loser effect or both effects are operating. This is the opposite behaviour that we get from the non-

	$W = 0$	$W = 0.1$	$W = 0.2$	$W = 0.3$
$L = 0$		$T_{12} = 328$ $T_{13} = 15$ $T_{14} = 1$ $T_{23} = 395$ $T_{24} = 29$ $T_{34} = 373$	$T_{12} = 169$ $T_{13} = 8$ $T_{14} = 1$ $T_{23} = 204$ $T_{24} = 26$ $T_{34} = 196$	$T_{12} = 115$ $T_{13} = 4$ $T_{14} = 1$ $T_{23} = 153$ $T_{24} = 27$ $T_{34} = 136$
$L = 0.1$	$T_{12} = 11$ $T_{13} = 9$ $T_{14} = 1$ $T_{23} = \infty$ $T_{24} = 1$ $T_{34} = \infty$	$T_{12} = 74$ $T_{13} = 1$ $T_{14} = 1$ $T_{23} = \infty$ $T_{24} = 800$ $T_{34} = \infty$	$T_{12} = 82$ $T_{13} = 1$ $T_{14} = 1$ $T_{23} = 207$ $T_{24} = \infty$ $T_{34} = \infty$	$T_{12} = 67$ $T_{13} = 1$ $T_{14} = 1$ $T_{23} = 109$ $T_{24} = 1$ $T_{34} = \infty$
$L = 0.2$	$T_{12} = 11$ $T_{13} = 9$ $T_{14} = 1$ $T_{23} = \infty$ $T_{24} = 1$ $T_{34} = \infty$	$T_{12} = 28$ $T_{13} = 1$ $T_{14} = 1$ $T_{23} = \infty$ $T_{24} = 679$ $T_{34} = \infty$	$T_{12} = 39$ $T_{13} = 1$ $T_{14} = 1$ $T_{23} = \infty$ $T_{24} = \infty$ $T_{34} = \infty$	$T_{12} = 47$ $T_{13} = 1$ $T_{14} = 1$ $T_{23} = \infty$ $T_{24} = 1$ $T_{34} = \infty$
$L = 0.3$	$T_{12} = 11$ $T_{13} = 9$ $T_{14} = 1$ $T_{23} = \infty$ $T_{24} = 1$ $T_{34} = \infty$	$T_{12} = 19$ $T_{13} = 1$ $T_{14} = 1$ $T_{23} = \infty$ $T_{24} = 1$ $T_{34} = \infty$	$T_{12} = 32$ $T_{13} = 1$ $T_{14} = 1$ $T_{23} = \infty$ $T_{24} = 1$ $T_{34} = \infty$	$T_{12} = 30$ $T_{13} = 1$ $T_{14} = 1$ $T_{23} = \infty$ $T_{24} = 1$ $T_{34} = \infty$

Table 2.3: The times of the domination events for the non-updated model with $\theta = 1$ and various values of W and L. T_{xy} is the (final) time when $\nu_{xy}(t)$ falls below 0.1.

updated model. In Figure 2.15 we plot the total average number of wins for each position in the hierarchy for different combinations of W and L.

2.4.2 Analysis of the temporal change in RHP

Following the same process as in the non-updated model, in this section we analyse the RHP values of all individuals. Firstly and in accordance with the results obtained above, we observe that for all combinations of W and L, all ranks in the hierarchy are distinguishable (see Figures 2.16, 2.17, 2.18, 2.19, 2.20 and 2.21). Additionally we calculate the final time when the dominance hierarchy is established and find three different outcomes depending on W and L values.

	$W = 0$	$W = 0.1$	$W = 0.2$	$W = 0.3$
$L = 0$		$\begin{matrix} - & 164.07 & 165.79 & 166.04 \\ 1.01 & - & 163.39 & 164.74 \\ 0.12 & 0.46 & - & 163.38 \\ 0 & 0 & 0 & - \end{matrix}$	$\begin{matrix} - & 164.09 & 165.72 & 166.18 \\ 1.01 & - & 163.38 & 164.72 \\ 0.11 & 0.47 & - & 163.33 \\ 0 & 0 & 0 & - \end{matrix}$	$\begin{matrix} - & 164.04 & 165.82 & 166.12 \\ 1.01 & - & 163.41 & 164.66 \\ 0.12 & 0.46 & - & 163.34 \\ 0 & 0 & 0 & - \end{matrix}$
$L = 0.1$	$\begin{matrix} - & 163.38 & 164.76 & 166.10 \\ 0 & - & 163.21 & 165.84 \\ 0 & 0.48 & - & 164.15 \\ 0 & 0.11 & 0.99 & - \end{matrix}$	$\begin{matrix} - & 163.85 & 165.33 & 166.48 \\ 0.10 & - & 163.60 & 165.26 \\ 0.0048 & 0.15 & - & 163.99 \\ 0.0004 & 0.01 & 0.19 & - \end{matrix}$	$\begin{matrix} - & 163.92 & 165.35 & 166.58 \\ 0.26 & - & 163.59 & 165.28 \\ 0.01 & 0.16 & - & 163.77 \\ 0.0002 & 0.003 & 0.06 & - \end{matrix}$	$\begin{matrix} - & 164.04 & 165.41 & 166.62 \\ 0.36 & - & 163.39 & 165.28 \\ 0.02 & 0.18 & - & 163.64 \\ 0.0001 & 0.001 & 0.03 & - \end{matrix}$
$L = 0.2$	$\begin{matrix} - & 163.44 & 164.69 & 166.06 \\ 0 & - & 163.37 & 165.74 \\ 0 & 0.46 & - & 164.14 \\ 0 & 0.11 & 1 & - \end{matrix}$	$\begin{matrix} - & 163.81 & 165.17 & 166.68 \\ 0.03 & - & 163.44 & 165.33 \\ 0.001 & 0.18 & - & 163.99 \\ 0.0001 & 0.02 & 0.35 & - \end{matrix}$	$\begin{matrix} - & 163.84 & 165.20 & 166.58 \\ 0.1 & - & 163.65 & 165.30 \\ 0.005 & 0.15 & - & 163.96 \\ 0.0003 & 0.01 & 0.20 & - \end{matrix}$	$\begin{matrix} - & 163.93 & 165.27 & 166.56 \\ 0.19 & - & 163.59 & 165.29 \\ 0.01 & 0.15 & - & 163.85 \\ 0.0004 & 0.004 & 0.10 & - \end{matrix}$
$L = 0.3$	$\begin{matrix} - & 163.37 & 164.67 & 166.10 \\ 0 & - & 163.37 & 165.82 \\ 0 & 0.46 & - & 164.08 \\ 0 & 0.11 & 1.01 & - \end{matrix}$	$\begin{matrix} - & 163.64 & 165.17 & 166.68 \\ 0.01 & - & 163.37 & 165.44 \\ 0.0002 & 0.21 & - & 163.98 \\ 0.0001 & 0.03 & 0.46 & - \end{matrix}$	$\begin{matrix} - & 163.88 & 165.24 & 166.49 \\ 0.06 & - & 163.58 & 165.35 \\ 0.004 & 0.17 & - & 163.94 \\ 0.0003 & 0.01 & 0.27 & - \end{matrix}$	$\begin{matrix} - & 163.89 & 165.23 & 166.58 \\ 0.08 & - & 163.58 & 165.32 \\ 0.004 & 0.15 & - & 163.89 \\ 0.003 & 0.01 & 0.0.23 & - \end{matrix}$

Table 2.4: Matrices of wins **W** in the updated model for different strength of the winner and loser effect ($W = 0; 0.1; 0.2; 0.3$ and $L = 0; 0.1; 0.2; 0.3$), $N = 4$, $\theta = 1$ and 1000 aggressive interactions.

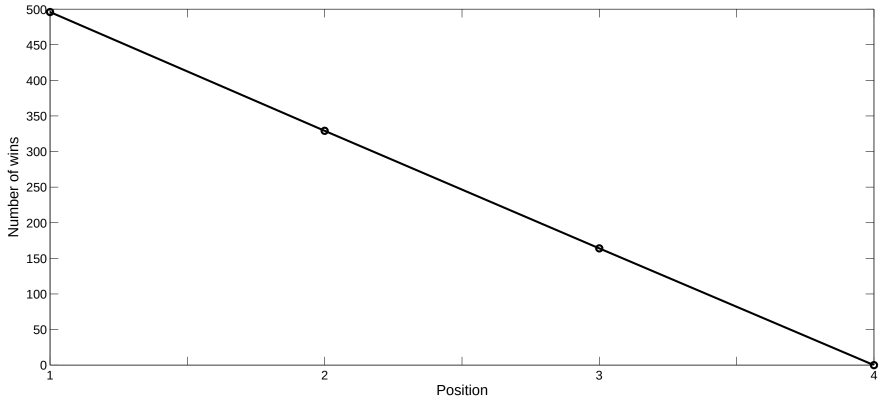


Figure 2.15: The total average number of wins for positions 1, 2, 3 and 4 for $W = 0, 0.1, 0.2, 0.3$ and $L = 0, 0.1, 0.2, 0.3$ in the updated model as given in Table 2.4. Note that all of the plots for these combinations are overlapping and thus are represented by a single line.

When only the winner effect is present (Figure 2.16 and 2.17), on average 41 fights are necessary to establish a linear hierarchy. After this nothing new happens to the hierarchy and the rank of the individuals. The last domination event between a pair of individuals is that between the second and the third place individuals. We note that the value of W does not have any effect on the time to establish the hierarchy.

We obtained a similar pattern when only the loser effect is present (Figure 2.18 and 2.19). Irrespective of the value of L the structure is established at the point $t = 44$ and the last pair to become distinguishable are the second and third place individuals.

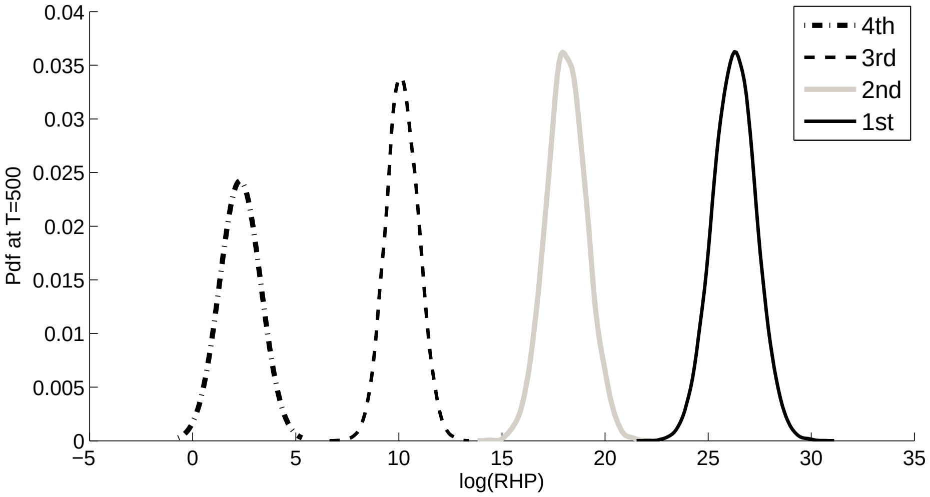


Figure 2.16: Probability distribution functions of RHP for the 4 individuals in the updated model: $t = 500$, only W is present ($L = 0$).

Lastly, when winner and loser effects are both present in the population at varying strengths, hierarchies are established latest at time point $t = 32$ (Figures 2.20 and 2.21). Again, as in the two cases above, the last pair to become distinguishable are the second and third place individuals.

Table 2.5 shows the times of the dominance events between all pair of individuals for various values of winner and loser effects. In general, the best scenario for fast hierarchy formation is when both the winner and loser effects are present in a group of individuals as the dominance hierarchy is established earlier than when only one is present. The first pair to become distinguishable is the first and the fourth place individuals, whereas the last pair is again that of the second and the third place individuals. This is the case for all the possible values of the winner and loser effects. In the following we consider the influence of the fighting threshold θ on the dynamics of hierarchy formation. So far we considered $\theta = 1$ and from equation (1.18) it is clear that a lower fighting threshold θ means that the number of possible fights is increased. When decreasing θ to 0.8 the qualitative dynamic of the updated model is unchanged but the time needed to establish a dominance hierarchy is increased. In particular for $0 < W \leq 0.2$ and $0 < L \leq 0.2$, the final domination events occur

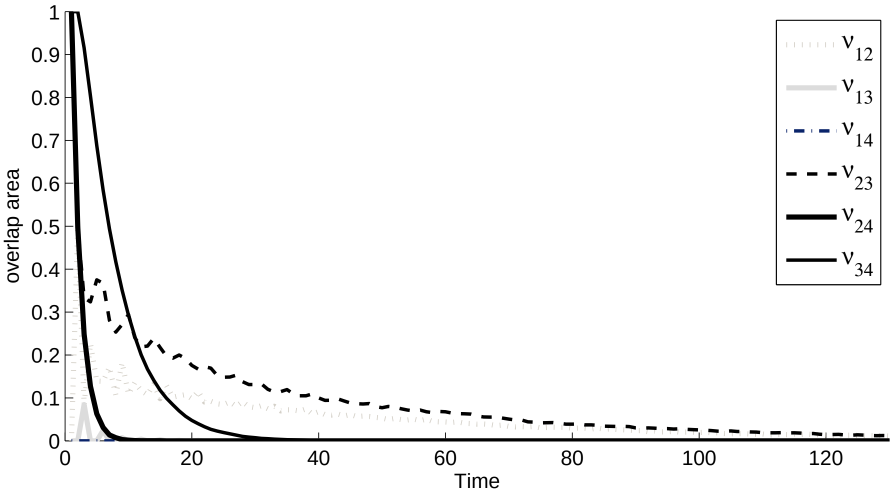


Figure 2.17: ν_{xy} over time when only W is present. $\nu_{14}(t)$ becomes close to 0 very quickly, and so is close to the x-axis.

later than for the situation with $\theta = 1$. Once we increase the values of the winner and loser effects, however, we notice that the time of the final domination events do not differ much from the previous case when $\theta = 1$.

The results obtained for the updated model hold also for larger groups. Table 2.6 shows the time of the domination event for each pair in a group of 8 individuals. As expected the hierarchy is established much later compared to a group of four individuals.

2.5 Results for the updated model with assessment error

In this section we relax the assumption that an individual has perfect knowledge of the RHP of its opponent. As described in Section 2.1 we assume that an individual assesses an opponent with a real RHP of $RHP_{y,t}$ as having a value of $(1+\varepsilon)RHP_{y,t}$, where ε is normally distributed with mean 0 and standard deviation 0.2 (truncated above at 1 and below at -1). This type of error is somewhat different to that used in [44], who used uniformly distributed intervals, although the results do not hugely depend upon the distribution of

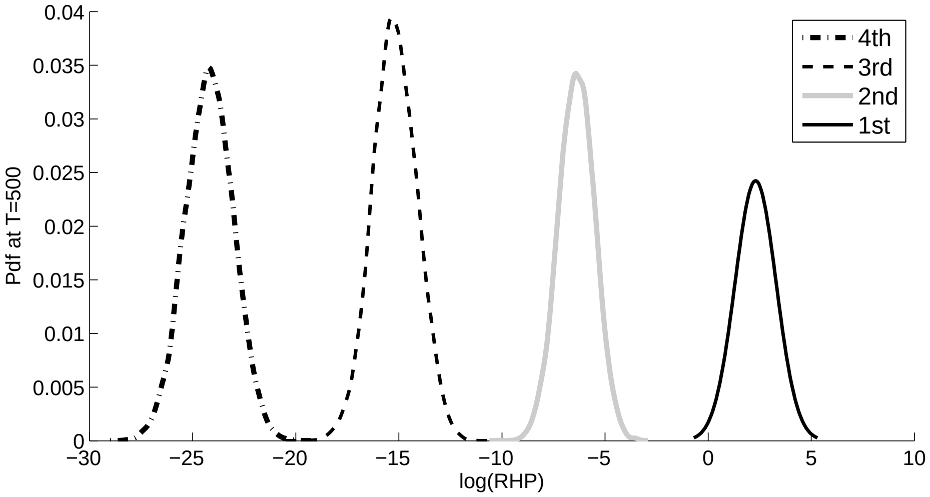


Figure 2.18: Probability distribution functions of RHP for the 4 individuals in the updated model: $t = 500$, only L is present.

error used. In the following we again consider 4 individuals with an aggression threshold $\theta = 1$ and analyse the RHP through time. We note that the analysis of the number of wins leads to similar results as in Section 2.4.1 and for brevity we exclude this.

When $\theta = 1$ and ε is normally distributed with mean 0 and standard deviation 0.2, linear hierarchies are formed for all combinations of W and L. Even though the individuals can make only an approximate estimation of their opponent's RHP with a normally distributed error ε, this does not have any significant effect on the linearity of the hierarchy. The only impact that ε has is on the time to hierarchy establishment. In this case the individuals need to interact more with each other (compared with the case when ε=0) in order to establish a linear hierarchy.

We can conclude that ε stabilizes linear hierarchies, meaning that only a little information about your opponents strength is necessary in order to establish a linear hierarchy. Lowering the aggression threshold leads to a similar dynamic as described in Section 2.4. We still obtain linear hierarchies for all combinations of W and L, however the time until the hierarchy is established is increased. Table 2.7 shows that for $\theta = 0.8$ and imperfect information, lin-

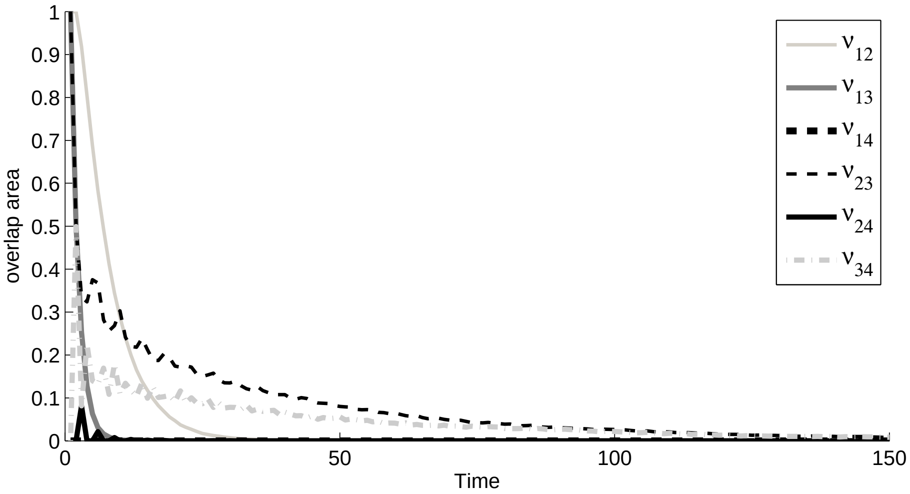


Figure 2.19: ν_{xy} over time when only L is present. $\nu_{14}(t)$ coincides with the x-axis after $t = 1$.

ear hierarchies are achieved on all the analysed cases. The time of domination events depends on the values of the winner and loser effects, with an increase in the size of either effect generally reducing the time to the domination events. Comparing this with the results of the updated model with $\theta = 1$ and perfect assessment from Table 2.5, we can see that the hierarchy generally takes longer to be established, but that the difference is not large. This is a cumulative effect of making individuals more aggressive by reducing θ and reducing the accuracy of their information; when we make one of these changes only, we find times between those from the two extremes (we have omitted tables corresponding to these cases).

Summarizing, in this section we showed that using the updated model with different levels of accuracy, linear hierarchies are always achievable. When individuals have perfect information about their opponent's RHP, the linear hierarchy is established earlier than when they overestimate or underestimate their opponents. More interactions are necessary in the second case, but after a certain point in time (depending on the values of the winner and the loser effects) the hierarchy is stabilized. When we lowered the aggression threshold, the linear hierarchies were established later than in the first two cases. We

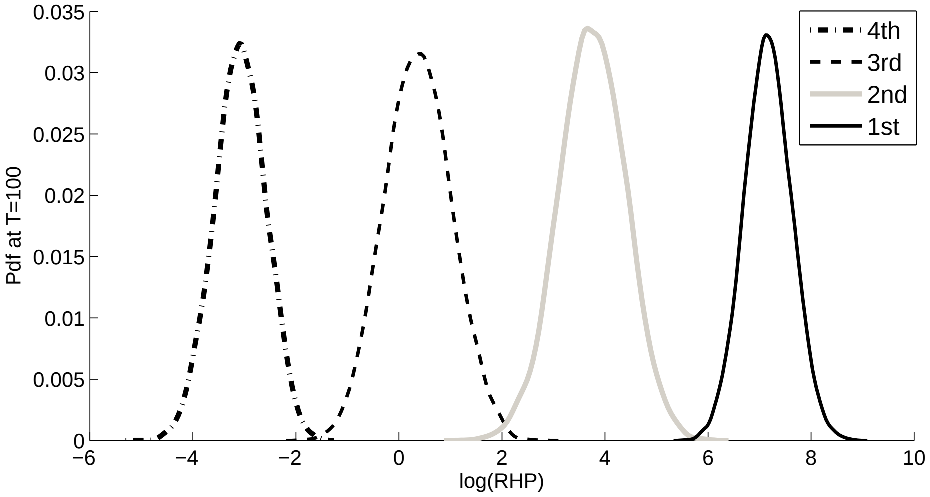


Figure 2.20: Probability distribution functions of RHP for the 4 individuals in the updated model: $t = 500$, both W and L are present.

can conclude that the updated model with different levels of accuracy always produces linear hierarchies. The time when these are established depends upon the level of information that individuals have about others in the group, and upon the value of the aggression threshold, where the higher the threshold and the smaller the error, the shorter the time to hierarchy formation.

2.6 Discussion

In this chapter we explored how winner and loser effects influence dominance hierarchy formation using a simulation based model developed first in Dugatkin [42] and Dugatkin & Dugatkin [44]. We considered two main situations: the non-updated model, when an individual has no information about the current resource holding potential (RHP) of its opponent, and the updated model, when an individual can estimate the RHP of its opponent with various levels of accuracy. We built on the model of [42] and [44] by providing a more complete analysis of the non-updated and updated model. All of our results are based on 10,000 simulations rather than one single realisation. In particular we developed new statistical measures for the time when a dominance

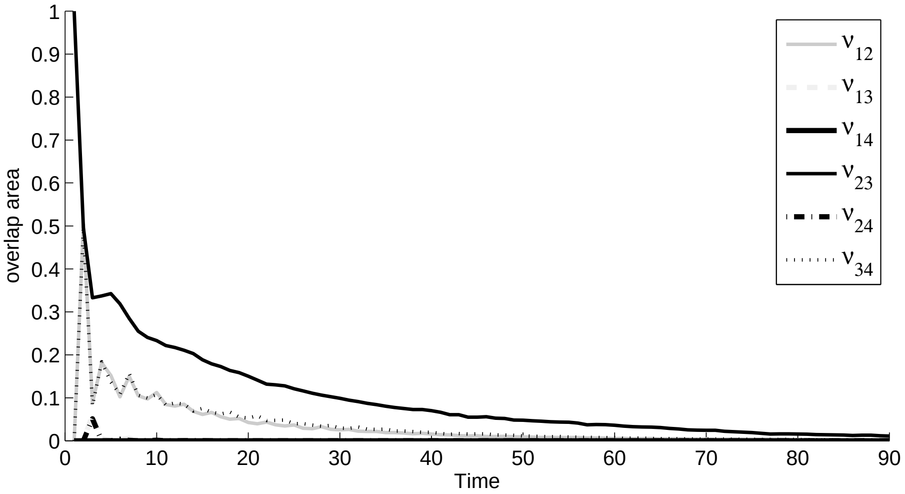


Figure 2.21: ν_{xy} through time when both W and L are present. $\nu_{13}(t)$, $\nu_{14}(t)$ and $\nu_{24}(t)$ become close to 0 very quickly, and so are close to the x-axis.

hierarchy is established.

These methods include a more detailed analysis of large numbers of interactions and an extension of the classical idea of the index of linearity K (developed by Kendall [68]) to this general number of interactions. An important consideration was the time to establishment of the hierarchy, and we have introduced a new measure to distinguish pairs of individuals, and to establish when dominance has been achieved. We have then been able to find when our hierarchy has been established for each of the different models that we consider, and make comparisons between them.

The values of the index of linearity K are perhaps exaggerated as a measure because high scores looks like they predict high linearity, when the reality can be more complex. We have used fractions of interactions experienced by one individual over the others where it has emerged as the winner, but this ratio is not the only important aspect, the absolute values of the number of wins is potentially important as well. For example the ratio $20/2$ indicates more distinguishability between two individuals scoring 20 and 2 wins, than the ratio $2/0.2$ for those with 2 and 0.2 wins. These low numbers can indicate an averaging which can include hierarchies with indistinguishable final individuals,

	$W = 0$	$W = 0.1$	$W = 0.2$	$W = 0.3$
$L = 0$		$T_{12} = 22$ $T_{13} = 1$ $T_{14} = 1$ $T_{23} = 40$ $T_{24} = 5$ $T_{34} = 16$	$T_{12} = 22$ $T_{13} = 1$ $T_{14} = 1$ $T_{23} = 41$ $T_{24} = 5$ $T_{34} = 17$	$T_{12} = 22$ $T_{13} = 1$ $T_{14} = 1$ $T_{23} = 41$ $T_{24} = 5$ $T_{34} = 16$
$L = 0.1$	$T_{12} = 16$ $T_{13} = 5$ $T_{14} = 1$ $T_{23} = 44$ $T_{24} = 1$ $T_{34} = 24$	$T_{12} = 11$ $T_{13} = 1$ $T_{14} = 1$ $T_{23} = 30$ $T_{24} = 1$ $T_{34} = 11$	$T_{12} = 11$ $T_{13} = 1$ $T_{14} = 1$ $T_{23} = 31$ $T_{24} = 1$ $T_{34} = 11$	$T_{12} = 11$ $T_{13} = 1$ $T_{14} = 1$ $T_{23} = 31$ $T_{24} = 1$ $T_{34} = 11$
$L = 0.2$	$T_{12} = 16$ $T_{13} = 5$ $T_{14} = 1$ $T_{23} = 40$ $T_{24} = 1$ $T_{34} = 22$	$T_{12} = 11$ $T_{13} = 1$ $T_{14} = 1$ $T_{23} = 32$ $T_{24} = 1$ $T_{34} = 11$	$T_{12} = 11$ $T_{13} = 1$ $T_{14} = 1$ $T_{23} = 29$ $T_{24} = 1$ $T_{34} = 11$	$T_{12} = 11$ $T_{13} = 1$ $T_{14} = 1$ $T_{23} = 30$ $T_{24} = 1$ $T_{34} = 11$
$L = 0.3$	$T_{12} = 16$ $T_{13} = 5$ $T_{14} = 1$ $T_{23} = 41$ $T_{24} = 1$ $T_{34} = 22$	$T_{12} = 11$ $T_{13} = 1$ $T_{14} = 1$ $T_{23} = 32$ $T_{24} = 1$ $T_{34} = 11$	$T_{12} = 11$ $T_{13} = 1$ $T_{14} = 1$ $T_{23} = 30$ $T_{24} = 1$ $T_{34} = 11$	$T_{12} = 11$ $T_{13} = 1$ $T_{14} = 1$ $T_{23} = 31$ $T_{24} = 1$ $T_{34} = 11$

Table 2.5: The time of the domination events for the updated model with perfect estimation: $\theta = 1$, various values of W and L. T_{xy} is the (final) time when $\nu_{xy}(t)$ falls below 0.1.

although even high numbers can be the result of bimodality in RHP. One possible (simplistic) solution is to add a baseline value of wins to all table entries when calculating K, which necessarily will have a smaller effect, the larger the number of decisive contests.

For the non-updated model we found different types of hierarchy formation for each of the three main cases, although the values of the index of linearity show that almost linear hierarchies are established. When only the winner effect is present, each individual scores in the group, three of them with a high number of wins, and all interactions lead to fights. It appears that this structure is the simplest one and that it can be achieved quite early, however

Individual	**2**	**3**	**4**	**5**	**6**	**7**	**8**
1	$T_{12} = 782$	$T_{13} = 17$	$T_{14} = 5$	$T_{15} = 1$	$T_{16} = 1$	$T_{17} = 1$	$T_{18} = 1$
2		$T_{23} = 806$	$T_{24} = 29$	$T_{25} = 8$	$T_{26} = 3$	$T_{27} = 3$	$T_{28} = 3$
3			$T_{34} = 745$	$T_{35} = 48$	$T_{36} = 13$	$T_{37} = 6$	$T_{38} = 6$
4				$T_{45} = 635$	$T_{46} = 57$	$T_{47} = 10$	$T_{48} = 10$
5					$T_{56} = 522$	$T_{57} = 46$	$T_{58} = 18$
6						$T_{67} = 321$	$T_{68} = 34$
7							$T_{78} = 85$

Table 2.6: The time of domination events between each pair of individuals in the updated model with $\theta = 1$ and perfect estimation: $W = 0.1, L = 0$ for a group of size 8. T_{xy} is the (final) time when ν_{xy} falls below 0.1.

our analysis of the RHP showed that up to 400 interactions are needed to establish a linear hierarchy. When only the loser effect was present, the first place individual scores a high number of wins, and all others a small number. The analysis of the RHP through time showed that the overlap between the second and the third place individuals is almost 0.4 which is much bigger than the threshold 0.1 where we consider two individuals to be distinguishable. This structure (with second and third positions indistinguishable) is established very early compared with the case when only the winner effect is present, with only 11 possible interactions needed.

When both winner and loser effects are present we obtained a structure where the first place is always clear with an individual who has a high number of wins, and the second place individual has quite a high average number of wins, with a high number of wins on some simulations and on other simulations the number of wins does not differ much from the number of wins of the third placed individual; this corresponds with the RHP analysis where the second place individual often has a bimodal distribution of the RHP. This means that different individual simulations will yield different results, where some-

	$W = 0$	$W = 0.1$	$W = 0.2$	$W = 0.3$
$L = 0$		$T_{12} = 122$ $T_{13} = 4$ $T_{14} = 1$ $T_{23} = 151$ $T_{24} = 22$ $T_{34} = 134$	$T_{12} = 68$ $T_{13} = 4$ $T_{14} = 1$ $T_{23} = 91$ $T_{24} = 13$ $T_{34} = 78$	$T_{12} = 41$ $T_{13} = 1$ $T_{14} = 1$ $T_{23} = 61$ $T_{24} = 9$ $T_{34} = 50$
$L = 0.1$	$T_{12} = 123$ $T_{13} = 18$ $T_{14} = 1$ $T_{23} = 137$ $T_{24} = 4$ $T_{34} = 110$	$T_{12} = 59$ $T_{13} = 1$ $T_{14} = 1$ $T_{23} = 78$ $T_{24} = 1$ $T_{34} = 59$	$T_{12} = 33$ $T_{13} = 1$ $T_{14} = 1$ $T_{23} = 51$ $T_{24} = 1$ $T_{34} = 38$	$T_{12} = 31$ $T_{13} = 1$ $T_{14} = 1$ $T_{23} = 52$ $T_{24} = 1$ $T_{34} = 37$
$L = 0.2$	$T_{12} = 67$ $T_{13} = 14$ $T_{14} = 1$ $T_{23} = 77$ $T_{24} = 4$ $T_{34} = 58$	$T_{12} = 43$ $T_{13} = 1$ $T_{14} = 1$ $T_{23} = 57$ $T_{24} = 1$ $T_{34} = 36$	$T_{12} = 25$ $T_{13} = 1$ $T_{14} = 1$ $T_{23} = 44$ $T_{24} = 1$ $T_{34} = 27$	$T_{12} = 25$ $T_{13} = 1$ $T_{14} = 1$ $T_{23} = 39$ $T_{24} = 1$ $T_{34} = 23$
$L = 0.3$	$T_{12} = 48$ $T_{13} = 9$ $T_{14} = 1$ $T_{23} = 58$ $T_{24} = 4$ $T_{34} = 40$	$T_{12} = 32$ $T_{13} = 1$ $T_{14} = 1$ $T_{23} = 49$ $T_{24} = 1$ $T_{34} = 27$	$T_{12} = 22$ $T_{13} = 1$ $T_{14} = 1$ $T_{23} = 39$ $T_{24} = 1$ $T_{34} = 20$	$T_{12} = 19$ $T_{13} = 1$ $T_{14} = 1$ $T_{23} = 35$ $T_{24} = 1$ $T_{34} = 17$

Table 2.7: The time of domination events for the updated model with $\theta = 0.8$ and imperfect estimation for various values of W and L. T_{xy} is the (final) time when $\nu_{xy}(t)$ falls below 0.1.

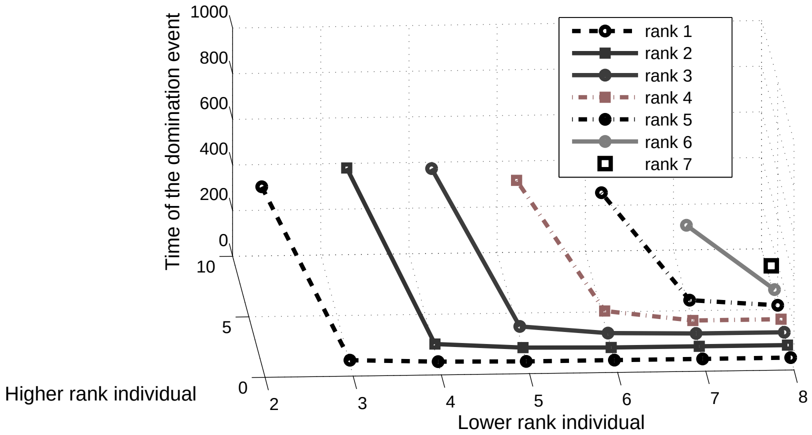


Figure 2.22: The time of domination events between each pair of individuals in the updated model with $\theta = 1$ and perfect estimation: $W = 0.1, L = 0$ for a group of size 8. T_{xy} is the (final) time when ν_{xy} falls below 0.1.

times the second place individual will be distinguishable from the third and sometimes not (this partially contradicted previous results from [42]); which occurs is decided very early in the process.

The non-updated model has some limitations as in reality the individuals could potentially approximate what the average “strength” of another individual would be at a certain time and then use this estimation when deciding whether to fight or retreat. If only the winner effect is in operation, for example, then an individual may be able to estimate the rate of increase of RHP of an average opponent just by considering the time elapsed, as the RHP of all will tend to increase. Thus the updated model, with varying levels of accuracy, is more realistic.

For the updated model, with perfect information of the strength of the others, we conclude that a linear hierarchy is always established. The values of the winner and loser effects, and whether they are considered alone or both to be present in the group, do not have any influence on linearity. When the RHP was analysed we calculated that the linear hierarchy is established at the time $t = 41$ when only the winner effect is present, at time $t = 32$ when only the loser effect is present and at $t = 44$ when both the winner and the loser effect are present. If individuals do not have perfect information about the strength of their opponents, this does not have any real influence on the linearity (as was shown previously by [44]). The only effect that it has is on the time when these linear hierarchies are established. More interactions are needed in this case than when individuals have perfect information about the RHP of others. The same results are achieved when the aggression threshold θ is lowered from 1 to 0.8, when the establishment of the dominance hierarchy occurs later than when $\theta=1$. Thus, as long as individuals know something about the strength of their opponents, a dominance hierarchy is always likely to be established in this model, and the precise model parameters have only a relatively small effect.

Our model thus predicts that for real biological populations, provided that animals can estimate the strength of their groupmates (and this estimation does not have to be accurate), then an unambiguous dominance hierarchy can be established in a relatively small number of interactions. Thus if contests are not too costly, and the group stays together for a sufficiently long time, a linear hierarchy will be formed. We predict some variation, so that when information is more reliable, or when loser effects dominate, the time to hierarchy formation will be the shortest. For the group as a whole a short hierarchy formation phase is of course beneficial, as risk of injury and lost time and energy are minimised [116]. If animals cannot estimate their groupmates' strength at all, then our model predicts far longer periods of hierarchy formation often with less clear-cut results. It seems unreasonable, however, to assume that even after a number of contests animals can possess so little information. Thus it seems likely that, as often observed in real populations, linear hierarchies should form relatively quickly. Of course it should be noted that many real populations are more complex, with group membership in a state of flux, or coalitions between group-mates (e.g. close relatives) ([37],[111]), and so often our idealised conditions will not apply.

In the model analysed in this chapter, no strategic elements are considered. This is in contrast to other models of dominance hierarchy formation, such as that of Broom and Cannings [23], where individuals differed in their level of aggressiveness, and evolutionarily stable strategies were found. In the following chapter we introduce such game theoretical elements to our winner and loser models, considering strategic choices of the aggression threshold, for instance (in conjunction to varying rewards and costs for winning or losing different types of contests, we note that in the current model there is no benefit to not fighting, and individuals retreat at a certain threshold due to a loss of confidence).

Chapter 3

A Game-Theoretical Winner and Loser Model of Dominance Hierarchy Formation

3.1 Introduction

In [42] and [44] (as well as [73]), each individual had the same fixed level of aggression; they would retreat for the same excess of the number of wins over the number of losses. In this chapter we introduce game-theoretical elements in the form of aggressiveness level into this model. The motivation behind this is that in real populations, individuals behave in a more complex way. They can adopt different strategies when deciding whether to fight or retreat as opposed to adopting the same fixed strategy. We assume that each individual can choose its own strategy, independent of their opponent's strategy. We are particularly interested in determining the appropriate level of the aggression threshold and exploring whether a unique strategy, or mixture of strategies, emerges in the population considered. Our model set up allows us to answer questions such as, under what circumstances should an individual fight more in order to establish a higher rank in the hierarchy and when should it retreat? We use a framework similar to the Hawk-Dove model [83], where an individual can choose to either fight or concede, with each individual making its choice simultaneously. When two individuals choose to fight they engage in an aggressive interaction; the winner will increase its RHP by a factor $1 + V_1$ and the loser will reduce its RHP by a factor $1 - C_1$. When one individual fights and the other concedes, the individual that chooses to fight increases its RHP by a factor $1 + V_2$ and the retreating individual has its RHP reduced by a factor $1 - C_2$. In the case when both individuals retreat, they have their RHP multiplied by $1 - C_2$. Individuals adopt their own strategies, meaning whether to fight and or to concede in an aggressive interaction given their history of fights won and lost, from a range of possible strategies. For each of these possible strategies we will determine the resulting expected payoff and conclude whether the adopted strategy is beneficial to the individual or not. We will analyse two cases: when each individual adopts a strategy that enables them to fight in all interactions, and when they adopt strategies that enables them to fight until a certain point in time (based upon how many contests they have won or lost) and retreat afterwards. We will determine the evolutionarily stable strategies ($ESSs$) for this fighting game, calculate the possible stopping times of the game for different strategies, and analyse the relationship between the stopping time and the difference between the number of wins and the number of losses for an individual. We find that a unique strategy evolves, as opposed to a mixture of strategies. Thus in any scenario there exists a unique ESS, and individuals should not switch between strategies. We find that the hierarchy forms quickly, after which there are no mutually aggressive contests. As explained above, individuals fight for more access to resources and we will investigate the effects of different payoff functions on the $ESSs$ within our model. In particular we compare payoffs which depend upon the level of resource an individual receives to those which depend upon the proportion of the overall resource that it receives. The latter payoff function is particularly appropriate when resources are scarce. Once the dominance hierarchy is established it is easier for the group to divide resources between them: the higher the position in the hierarchy the higher the payoff. The division of resources has been analysed by different authors (see e.g., [28], [66]). We will use the concept of *reproductive skew* ([27], [66], [103], [109], [121]), which refers to the distribution of reproductive rights in a group of animals. We will use the term more generally to refer to how limited resources and hence payoffs (which are generally proportional to reproductive levels in evolutionary games) are divided among our group. When the reproductive skew is high the division of resources is uneven with the high ranking individuals obtaining more resources than the lower ranking ones (for examples see [40], [94], [104]). In contrast, if the reproductive skew is low the division of resources is even and all ranks of individuals have similar resource levels (see [30], [81]). Further, we will explore the interplay between all three game-theoretical elements, V_i, C_i and strategies θ, and analyse whether there is a general pattern for the ESS when the V_i and C_i are increased (or decreased). Additionally, we develop a simulation framework to investigate the effect of the group size on the level of aggression.

We note that Andersen et al. [5] developed an alternative optimization based model to analyse the effect of group size on aggression level and showed that the theoretical results obtained are supported by experimental data observed in domesticated pigs; we discuss this in Section 3.6. Lastly we compare our theoretical results with experimental evidence which is rather different for different groups of animals such as birds, farmed animals or fish (see e.g.,[5], [14],[50], [51], [72], [98], [113] [117]). Parts of this chapter are published in [74].

3.2 The model

We assume a large population of social individuals living together in groups. At the beginning of the consideration, groups of size N are randomly formed, so that all individuals are members of a group and we analyze a specific group of N individuals. Each individual has an RHP value, which, as mentioned in Chapter 1, is a measure of its ability to win an aggressive interaction (cf. [42] and [44]) and which is altered by the outcome of each interaction. At the beginning, as in the previous chapters, all individuals are assigned the same initial RHP, denoted by $RHP_{initial}$. We assume that all individuals know their own RHP, and that of any opponent. In each round t ($t = 1, ..., T$), two individuals are randomly chosen to engage in an aggressive interaction, while the rest of individuals do not engage in any aggressive interactions. Through time an individual's RHP changes due to winning or losing (in reality it will be mainly the extrinsic factors than change, but our model could cope with other eventualities equally well); while a win increases the RHP, a loss decreases it and each individual keeps track of the changes in their own RHP and that of its opponents. More precisely, suppose that at time t the two individuals pitted against each other are x and y. We denote by $RHP_{x,t}$ individual x's RHP at time t. Individual x can decide to be aggressive or retreat once it has been chosen and this decision is based on the strategy $\theta_x \geq 0$ which is its aggression threshold.

Individual x fights individual y at this time (plays Hawk) if

$$\frac{RHP_{x,t}}{RHP_{y,t}} \geq \theta_x \tag{3.1}$$

holds, otherwise it will retreat (play Dove), where $RHP_{y,t}$ and θ_y are the individual's y RHP at time t and its aggression threshold respectively. The pairwise interaction lead to one of the following outcomes:

(1) Both individuals x and y decide to engage in an aggressive interaction and the probability that x wins is given by

$$P_{x,y}(t) = \frac{RHP_{x,t}}{RHP_{x,t} + RHP_{y,t}}, \tag{3.2}$$

and consequently individual y wins with a probability $P_{y,x}(t) = 1 - P_{x,y}(t)$.

(2) One individual engages in the aggressive interaction and the other retreats.

(3) Both individuals decide not to fight.

After a win the RHP increases and after a loss it decreases. More precisely, if individual x wins and individual y loses then they increase and decrease respectively their own RHP as follows:

$$RHP_{x,t+1} = (1 + V_1) RHP_{x,t} \tag{3.3}$$

$$RHP_{y,t+1} = (1 - C_1) RHP_{y,t}. \tag{3.4}$$

If individual x wins and individual y retreats then they increase and decrease respectively their own RHP as follows:

$$RHP_{x,t+1} = (1 + V_2) RHP_{x,t} \tag{3.5}$$

$$RHP_{y,t+1} = (1 - C_2) RHP_{y,t}. \tag{3.6}$$

Equivalent changes to the RHPs apply if individual y wins.

If both individuals retreat (double kow-tow) then they decrease their RHPs as follows:

$$RHP_{x,t+1} = (1 - C_2) RHP_{x,t}, \tag{3.7}$$

$$RHP_{y,t+1} = (1 - C_2) RHP_{y,t}. \tag{3.8}$$

In this model V_1, V_2 are proportional increases in RHP and C_1, C_2 are proportional decrease in RHP where $V_1, V_2 \geq 0$ and $C_1, C_2 \in [0, 1]$.

The aim of each member of the population is to maximise its payoff at time T. In the following we assume that the payoff function is defined as the natural logarithm of the RHP (which corresponds to the situation of unlimited resources) but consider in Section 3.3.5 the effects of an alternative payoff function (which corresponds to the situation of limited resources). Now there are two main reasons for considering the natural logarithm of the RHP. Firstly, while we want to keep to Dugatkin's terminology as much as possible, the multiplicative nature of how the RHP increases, means that RHP values can become large very quickly. If we would assume the expected RHP as the payoff, then even a minuscule chance of winning enough contests to be the top individual would be worth almost any risk. Considering the logarithm means that winning (losing) any contest increases (decreases) the payoff by the same amount irrespective of the current RHP. Secondly, taking the natural logarithm of the RHP guarantees that the payoffs increase in precisely the same way as in evolutionary matrix games, and in particular the Hawk-Dove game, which we use as an analogy in this chapter.

This model set-up allows us to track the changes in RHP of all N individuals at the time points $t = 1, \ldots, T$ and therefore to evaluate which strategy θ results in the highest payoff over time. In this context, the ESS [82] as defined in Chapter 1, proves to be an important concept.

3.3 The two-individual model

For simplicity, in this section we consider groups of two individuals only. This will allow us to find some analytical results which will give us general insights into the dynamics of our model. We will then generalise to larger groups in Section 3.4.

3.3.1 Expected payoffs when players always fight (θ_x=$\theta_y = 0$)

We assume that both individuals, denoted by x and y, possess the same $RHP_{initial}$ values. Further, individuals x and y play the strategies $\theta_x = \theta_y = 0$, meaning that both individuals will fight until time T (cf. equation (3.1)). In this section and throughout the chapter we assume $V_1 = V_2 = V$, $C_1 = C$, $C_2 = 0$. $V_1 = V_2 = V$ implies that winning a fight and having your opponent retreat has the same effect on the RHP. Retreating is seen as a recognition of the opponent's superiority and therefore is treated similar to a loss. But contrary to the model analysed in Chapters 1 and 2, here we do not assume that losing a fight and retreating has the same effect on the RHP. This seems plausible as it is similar to the Hawk-Dove model to which we refer, in the sense that the loss of a fight is like an injury (whether a real injury or a psychological one). Figure 3.1 illustrates the possible RHP values of individual x at times $t = 1$ and $t = 2$. For example, the expected payoff of individual x at $t = 1$, denoted by $E[\ln(RHP_{x,1})]$ is equal to

$$E[\ln(RHP_{x,1})] = \frac{1}{2}\ln(RHP_{initial}(1+V)) + \frac{1}{2}\ln(RHP_{initial}(1-C)).$$

An individual either wins or loses a fight, and we denote a win (loss) in the kth contest by $j_k = 1$ ($j_k = 0$). Thus at time t individual x has a_t wins and b_t losses which are given as follows:

$$a_t = \sum_{k=1}^{t} j_k \tag{3.9}$$

and

$$b_t = t - \sum_{k=1}^{t} j_k. \tag{3.10}$$

The RHP for individual x, having won a_t contests and lost b_t, will be denoted

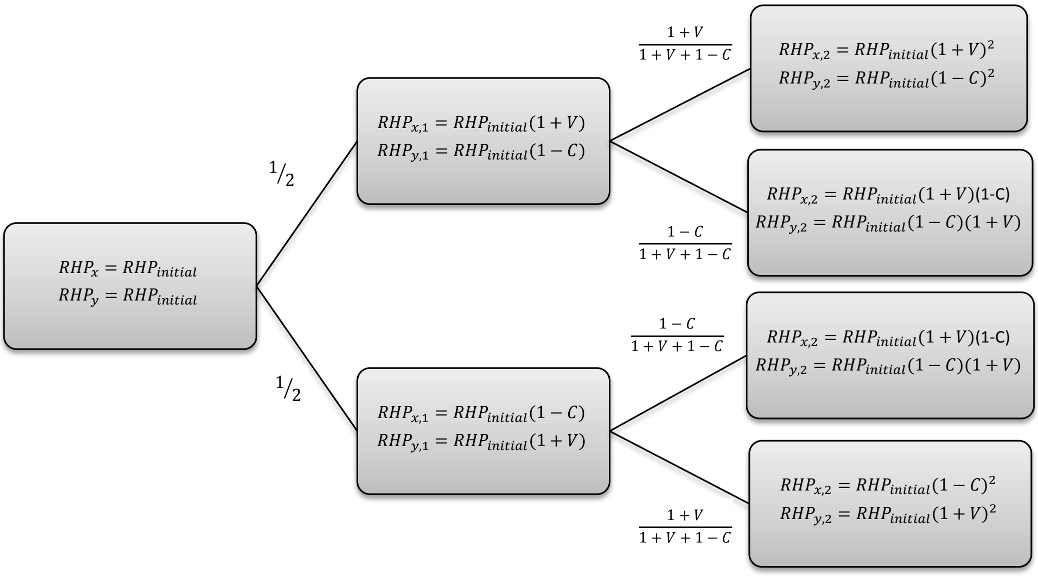


Figure 3.1: RHP of individual x and individual y at times $t = 1$ and $t = 2$ when they both start with the same $RHP_{initial}$ and always fight ($\theta_x = \theta_y = 0$).

by R_{a_t,b_t} and is given by (cf. equations (3.3) and (3.4))

$$R_{a_t,b_t} = RHP_{initial}(1+V)^{a_t}(1-C)^{b_t} = RHP_{initial}(1+V)^{\sum_{k=1}^{t} j_k}(1-C)^{t-\sum_{k=1}^{t} j_k}.$$

The probability of winning after a_t wins and b_t losses at time t will be denoted by W_{a_t,b_t}, whereas the probability of losing will be denoted by $L_{a_t,b_t} = 1 - W_{a_t,b_t}$. From equation (3.2) we obtain

$$W_{a_t,b_t} = \frac{(1+V)^{a_t}(1-C)^{b_t}}{(1+V)^{a_t}(1-C)^{b_t} + (1+V)^{b_t}(1-C)^{a_t}}.$$

If we consider all combinations of wins and losses and consider $\ln(RHP)$, then the overall expected payoff is given by

$$E[\ln(RHP_{x,T})] = \sum_{j_1=0}^{1}\sum_{j_2=0}^{1}\sum_{j_3=0}^{1}\cdots\sum_{j_T=0}^{1} \ln(R_{a_T,b_T})\prod_{i=1}^{T} W_{a_T,b_T}^{j_i} L_{a_T,b_T}^{1-j_i} \tag{3.11}$$

where a_T and b_T are given by equations (3.9) and (3.10).

3.3.2 Individuals with general strategies θ_x and θ_y

In this section we analyse the expected payoffs for individuals x and y when they have potentially non-zero and different strategies θ_x and θ_y, respectively. We start by deriving a general criterion for the number of losses necessary so that an individual retreats. Suppose that at time t individual x has won a_t contests against individual y and lost b_t. Then it's RHP will be $RHP_{x,t} = R_{a_t,b_t}$. In contrast, individual y has won b_t contests and lost a_t against individual x resulting in a RHP of $RHP_{y,t} = R_{b_t,a_t}$. Thus from equations (3.3)-(3.6) we obtain

$$R_{a_t,b_t} = RHP_{initial}(1+V)^{a_t}(1-C)^{b_t}$$

and

$$R_{b_t,a_t} = RHP_{initial}(1+V)^{b_t}(1-C)^{a_t}.$$

The next interaction between the individuals x and y will result in a fight if equation (3.1) holds for both individuals. In other words, the following two equations have to be satisfied simultaneously

$$\frac{RHP_{x,t}}{RHP_{y,t}} = \frac{R_{a_t,b_t}}{R_{b_t,a_t}} = (1+V)^{a_t-b_t}(1-C)^{b_t-a_t} = \left(\frac{1+V}{1-C}\right)^{a_t-b_t} \geq \theta_x \tag{3.12}$$

and

$$\frac{RHP_{y,t}}{RHP_{x,t}} = \frac{R_{b_t,a_t}}{R_{a_t,b_t}} = (1+V)^{b_t-a_t}(1-C)^{a_t-b_t} = \left(\frac{1+V}{1-C}\right)^{b_t-a_t} \geq \theta_y. \tag{3.13}$$

Next, we take the logarithm of equations (3.12) and (3.13) on both sides and obtain

$$(a_t - b_t) \geq \frac{\ln(\theta_x)}{\ln(1+V) - \ln(1-C)} \tag{3.14}$$

and

$$(b_t - a_t) \geq \frac{\ln(\theta_y)}{\ln(1+V) - \ln(1-C)}. \tag{3.15}$$

We define

$$d_x = \frac{-\ln(\theta_x)}{\ln(1+V) - \ln(1-C)} \tag{3.16}$$

and

$$d_y = \frac{-\ln(\theta_y)}{\ln(1+V) - \ln(1-C)} \tag{3.17}$$

where d_x and d_y are both positive numbers for any pair of individuals which do not concede immediately. As equations (3.14) and (3.15) have to be fullfilled simultaneously we obtain

$$-d_x \leq a_t - b_t \leq d_y. \tag{3.18}$$

This means that if the excess of the number of wins over the number of losses is within $[-d_x, d_y]$, individuals x and y will engage in a fight. If both individuals start by fighting and the first condition to not hold is $a_t - b_t \leq d_y$, then we have a case where individual y decides to retreat and individual x to fight. After retreating for the first time, an individual then retreats in every contest until time T. Consequently, after y has retreated, individual x increases its RHP for every contest. By contrast, if the first condition to not hold is $-d_x \leq a_t - b_t$ then individual x decides to retreat and individual y increases its RHP for every contest. The situation where both individuals retreat only occurs if this happens at $t = 1$.

We define the time when individual x retreats by

$$T_s(x) = \min\{t \geq 1 : a_t - b_t < -d_x\}. \tag{3.19}$$

$T_s(x)$ will be called the x-stopping time. The y-stopping time $T_s(y)$ is defined similarly. Clearly, in any contest exactly one of these values will be finite; the time of the last contest where both individuals fight is given by the stopping time T_s, where

$$T_s = \min\{T_s(x), T_s(y)\}. \tag{3.20}$$

Then the expected payoff $E[\ln(RHP_{x,T})]$ at time T is given by:

$$E[\ln(RHP_{x,T})] = \sum_{j_1=0}^{1}\sum_{j_2=0}^{1} \dots \sum_{j_{T_s}=0}^{1} \ln[R_{a_T,b_T}(1+V)^{(T-T_s)I_1}] \prod_{i=1}^{T_s} W_{a_T,b_T}^{j_i} L_{a_t,b_t}^{1-j_i} \tag{3.21}$$

where

$$I_1 = \begin{cases} 0 & \text{if } a_t - b_t < d_x \\ 1 & \text{if } a_t - b_t > d_y \end{cases}$$

and $(1+V)^{(T-T_s)I_1}$ is the multiplicative increase in RHP that individual x gets after the stopping time T_s. It follows from inequality (3.18) and the fact that $a_t - b_t$ is an integer that all θ values within a certain interval result in the same expected payoff (for fixed V and C). We denote those intervals of strategy values by $[\theta_{x,min}, \theta_{x,sup})$ where $\theta_{x,sup}$ is the value of θ_x that corresponds to $\lfloor d_x \rfloor$ and $\theta_{x,min}$ the value of θ_x that corresponds to $\lceil d_x \rceil$. The intervals are closed at the lower bound and open at the upper bound and $\theta_{x,min} < \theta_{x,sup}$. We set

$$k'_x = \lfloor d_x \rfloor = \left\lfloor \frac{-\ln(\theta_{x,sup})}{\ln(1+V) - \ln(1-C)} \right\rfloor \tag{3.22}$$

and obtain

$$\theta_{x,sup} = \left(\frac{1-C}{1+V}\right)^{k'_x}.$$

Further, we set $k_x = \lceil d_x \rceil$. The corresponding strategy value θ_x for k_x is $\theta_{x,min}$ and we have

$$k_x = \lceil d_x \rceil = \left\lceil \frac{-\ln(\theta_{x,min})}{\ln(1+V) - \ln(1-C)} \right\rceil \tag{3.23}$$

which results in

$$\theta_{x,min} = \left(\frac{1-C}{1+V}\right)^{k_x}.$$

Similarly to the above, for given V and C there is a range of θ values that correspond to a given k. Importantly, each strategy θ from that range results in the same payoff. We note, however, that this range changes for different V and C. For simplicity, we shall assume that individual x chooses the middle value from $[\theta_{x,min}, \theta_{x,sup})$, and this strategy will be denoted by $\theta_{x,rep}$ as the representative strategy of the $[\theta_{x,min}, \theta_{x,sup})$ range

$$\theta_{x,rep} = \left(\frac{1-C}{1+V}\right)^{k_x} \left(\frac{2+V-C}{2(1-C)}\right). \tag{3.24}$$

3.3.3 Stopping time T_s

The expected payoff $E[\ln(RHP_{x,T})]$ given by equation (3.21) depends on the stopping time T_s. In this section we explore the properties of T_s as defined by equation (3.20), in particular its distribution.

To do so we firstly determine the values of k_x and k_y for individuals x and y with strategies θ_x and θ_y, respectively. The time when the random process $a_t - b_t$ is equal to k_x or k_y represents the stopping time. For instance, individual x would not engage in aggressive interactions when $a_t - b_t \leq -k_x$ and the stopping time defined in equation (3.19) can be written alternatively as

$$T_s(x) = min\{t \geq 1 : a_t - b_t \leq -k_x\}. \tag{3.25}$$

But which values can the stopping time $T_s(x)$ assume? The earliest possible x-stopping time is $T = k_x$, i.e. individual y has k_x consecutive wins from the start of the interaction. The next possible stopping time will be at $k_x + 2$, where a single win by individual x within the first k_x interactions has to be met by a total of $k_x + 1$ wins by y. In general the stopping times for individual x will be given by $k_x + (2n)_{n\geq 0}$. Consequently, the stopping times for individual y will be given by $k_y + (2n)_{n\geq 0}$. Thus $T_s = \min\{T_s(x), T_s(y)\}$ can assume the following values

$$T_s = \begin{cases} 1 & : k_x = k_y = 1 \\ min\{k_x, k_y\} + (2n)_{n\geq 0} & : k_x + k_y \text{ even} \\ max\{k_x, k_y\} + n + \text{even numbers in } [min\{k_x, k_y\}, max\{k_x, k_y\}] & : k_x + k_y \text{ odd}, \\ & \quad min\{k_x, k_y\} \\ & \text{odd} \\ max\{k_x, k_y\} + n + \text{odd numbers in } [min\{k_x, k_y\}, max\{k_x, k_y\}] & : k_x + k_y \text{ odd}, \\ & \quad min\{k_x, k_y\} \\ & \text{even} \end{cases} \tag{3.26}$$

In summary, the stopping time defines the exact round when one individual starts to retreat for different strategy combinations. It also gives the number of possible interactions that need to be observed in order to distinguish between a pair of individuals, so that in our model the second individual will always concede to the first (for a different interpretation of this concept, see [73]).

Note that it is possible for our model to generate one experience, a winner effect or a loser effect, without the other. For example for $V > 0$ and $C = 0$ we have a case when only the winner effect is in place. Table A.1 and Table A.2 (see Appendix) show the expected payoffs for different strategic values when $V = 0.1$ and $C = 0$. On the other hand when $C > 0$ and $V = 0$, illustrated by Table A.3 and Table A.4 (see Appendix), we have a case where only the loser effect is operating.

In the next section we derive the distribution of T_s for the parameter constellation $V = C = 0.1$ (both winner and loser effect are influencing the RHP).

3.3.4 Example: $V = C = 0.1$

To illustrate the findings of the last sections we consider an example by assuming the parameters $V = 0.1$, $C = 0.1$ and $T = 20$. In particular, we calculate the expected payoffs $E[\ln(RHP_{x,20})]$ for different combinations of strategies θ_x and θ_y, determine the unique ESS and derive the distribution of the stopping time T_s. In this section and throughout the chapter we will assume that $RHP_{initial} = 10$.

Firstly we determine the representative strategies to $k_x = 1, 2, 3, 4, 5, 6, 7, 8$ by using equation (3.24). Note that there is a range of strategies θ_x that correspond to the same value of k_x and we take the middle one as described in Section 3.3.2. We obtain the following mappings (the same values apply for individual y as well.).

$k_x = 1 \Rightarrow \theta_{x,rep} = 0.91$, $k_x = 2 \Rightarrow \theta_{x,rep} = 0.74$, $k_x = 3 \Rightarrow \theta_{x,rep} = 0.61$, $k_x = 4 \Rightarrow \theta_{x,rep} = 0.50$, $k_x = 5 \Rightarrow \theta_{x,rep} = 0.41$, $k_x = 6 \Rightarrow \theta_{x,rep} = 0.33$, $k_x = 7 \Rightarrow \theta_{x,rep} = 0.27$, $k_x = 8 \Rightarrow \theta_{x,rep} = 0.22$.

For this set of strategies we then calculate the expected payoffs $E[\ln(RHP_{x,20})]$ for individual x and $E[\ln(RHP_{y,20})]$ for individual y by using equation (3.21). Table 3.1 represents the matrix of payoffs for different combinations of strategies θ_x and θ_y. We plot these values in Figure 3.2.

	k_y=1(θ_y=0.91)	k_y=2(θ_y=0.74)	k_y=3(θ_y=0.61)	k_y=4(θ_y=0.50)	k_y=5(θ_y=0.41)	k_y=6(θ_y=0.33)	k_y=7(θ_y=0.27)	k_y=8(θ_y=0.22)
k_x=1(θ_x=0.91)	3.2000	2.8700	2.7300	2.6500	2.6000	2.5800	2.5600	2.5400
k_x=2(θ_x=0.74)	3.4400	3.0600	2.8700	2.7600	2.7000	2.6600	2.6200	2.6000
k_x=3(θ_x=0.61)	3.5000	3.1000	2.8900	2.7700	2.6900	2.6500	2.6100	2.6000
k_x=4(θ_x=0.50)	3.5100	3.0800	2.8700	2.7400	2.6700	2.6200	2.5600	2.5600
k_x=5(θ_x=0.41)	3.5000	3.0500	2.8400	2.700	2.6200	2.5700	2.5400	2.5200
k_x=6(θ_x=0.33)	3.4600	3.0200	2.7900	2.6600	2.6000	2.5300	2.5000	2.4700
k_x=7(θ_x=0.27)	3.4300	2.9900	2.7700	2.6200	2.5600	2.5000	2.4800	2.4500
k_x=8(θ_x=0.22)	3.4200	2.9500	2.7300	2.6000	2.5100	2.4800	2.4400	2.4100

Table 3.1: The matrix of payoffs where each entry represent the expected payoff $E[\ln(RHP_{x,T})]$ at time $T = 20$ (calculated by equation (3.21)) for different strategies θ_x and θ_y.

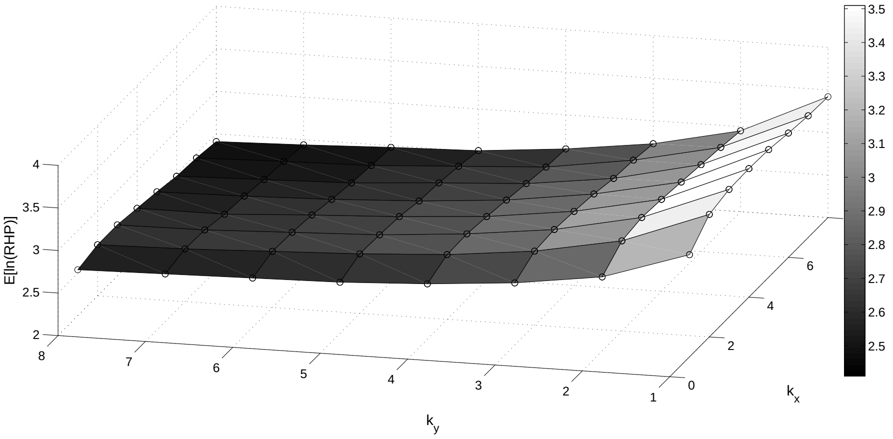
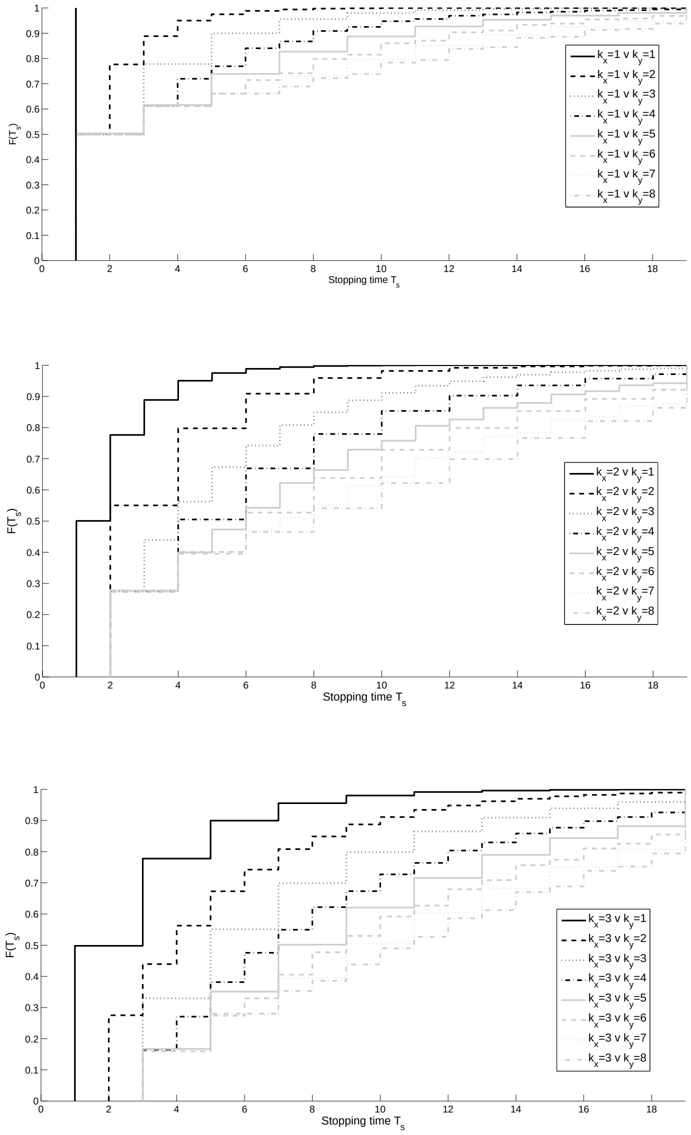


Figure 3.2: The payoffs $E[\ln(RHP_{x,T})]$ at time $T = 20$ (calculated by equation (3.21)) for different strategies θ_x and θ_y.

Now for each strategy we can find the best response, i.e. for each column of Table 3.1 we find the highest payoff and use the "diagonal rule" (see Chapter 1) to find the ESS. We note that for a pure ESS, all our results satisfy ESS condition (1.3); condition (1.4) is only achieved when mixtures are present, which we do not get in our example. In this example we obtain $\theta = 0.61$, corresponding to $k = 3$, as the unique ESS. Note that there is a range of strategies $[\theta_{x,min}, \theta_{x,sup}) = [0.55, 0.67]$ that corresponds to $k = 3$. Thus any strategy from this range results in the same expected payoff and is therefore equivalent to our ESS. Lastly we derive the distribution of the stopping time T_s. For example, when $\theta_x = 0.5$ (corresponding to $k_x = 4$) and $\theta_y = 0.7$ (corresponding to $k_y = 2$), T_s can only assume the values $(k_y + 2n)_{n \geq 0}$ because $k_x + k_y = 6$ is an even number (see equation (3.26)). But how does this distribution change when k_x and k_y are varied? To explore this we assume that individual x has a strategy θ_x corresponding to $k_x = 1, 2, 3$ and his opponent has strategies θ_y corresponding to $k_y \in [1, 8]$. We choose the value 8 as an upper bound for k_y as an arbitrary large cut-off value which corresponds to small values of θ, but we could have chosen any other high value. Figure 3.3 shows the distribution functions of the stopping time for various combinations of k_x and k_y for $V = C = 0.1$.



(a)

(b)

(c)

Figure 3.3: The distribution function of the stopping time for the case when $V = C = 0.1$, $k_y = 1, 2, \ldots, 8$ and (a) $k_x = 1$, (b) $k_x = 2$, (c) $k_x = 3$. Note that parts of the distribution functions are overlaid by other distribution functions, e.g. all lines in (a), include the segment with starting coordinate $(1, 0)$ and ending coordinate $(1, \frac{1}{2})$.

Figures 3.3 illustrates that a pair of individuals will fight longer for higher values of k_x and k_y. In this example one of the individuals x and y has started retreating before time T, for most of the possible cases. This means that observing 20 interactions would allow us to distinguish between the two individuals almost with certainty. As we increase the values of k_x and k_y, the probability of retreating before $T = 20$ is decreased.

3.3.5 An alternative payoff function

Table 3.1 shows the expected payoff of individuals x and y after $T_{max} = 20$ possible interactions using equation (3.21). In this section we explore how limited resources are divided between the two individuals based on an alternative payoff function. We will use the concept of reproductive skew as discussed in ([27], [66], [103], [109], [121]). In this case the expected payoff for individual x after 20 interactions is given by function:

$$E[\theta_x, \theta_y] = E\left[\frac{\ln(RHP_{x,20})}{\ln(RHP_{x,20}) + \ln(RHP_{y,20})}\right]. \tag{3.27}$$

Consequently the expected payoff for individual y is given by function

$$E[\theta_y, \theta_x] = E\left[\frac{\ln(RHP_{y,20})}{\ln(RHP_{x,20}) + \ln(RHP_{y,20})}\right].$$

The results are given in Table 3.2 and Figure 3.4.

	k_y=1(θ_y=1)	k_y=2(θ_y)=0.7	k_y=3(θ_y)=0.6	k_y=4(θ_y=0.5)	k_y=5(θ_y=0.4)	k_y=6(θ_y=0.35)	k_y=7(θ_y=0.27)	k_y=8(θ_y=0.23)
k_x=1(θ_x=1)	0.5000	0.4585	0.4417	0.4353	0.4344	0.4354	0.4360	0.4385
k_x=2(θ_x)=0.7	0.5415	0.5000	0.4825	0.4777	0.4765	0.4777	0.4806	0.4825
k_x=3(θ_x)=0.6	0.5583	0.5175	0.5000	0.4941	0.4928	0.4949	0.4973	0.4999
k_x=4(θ_x=0.5)	0.5647	0.5223	0.5059	0.5000	0.4992	0.5013	0.5034	0.5066
k_x=5(θ_x=0.4)	0.5656	0.5235	0.5072	0.5008	0.5000	0.5014	0.5046	0.5077
k_x=6(θ_x=0.35)	0.5646	0.5223	0.5051	0.4987	0.4986	0.5000	0.5026	0.5054
k_x=7(θ_x=0.27)	0.5640	0.5194	0.5027	0.4966	0.4954	0.4974	0.5000	0.5033
k_x=8(θ_x=0.23)	0.5615	0.5175	0.5001	0.4934	0.4923	0.4946	0.4967	0.5000

Table 3.2: Division of resources for different values of k, when $V = C = 0.1$

From Table 3.2, we find that $\theta = 0.4$ (corresponding to $k = 5$) is the ESS. Comparing this result with the result obtained from Table 3.1, we notice that they differ; when using this alternative payoff function we obtain $k = 5$ as the ESS, while for the original payoff function used in Section 3.3.4 the ESS is $k = 3$. This difference is related to the amount of available resources, in

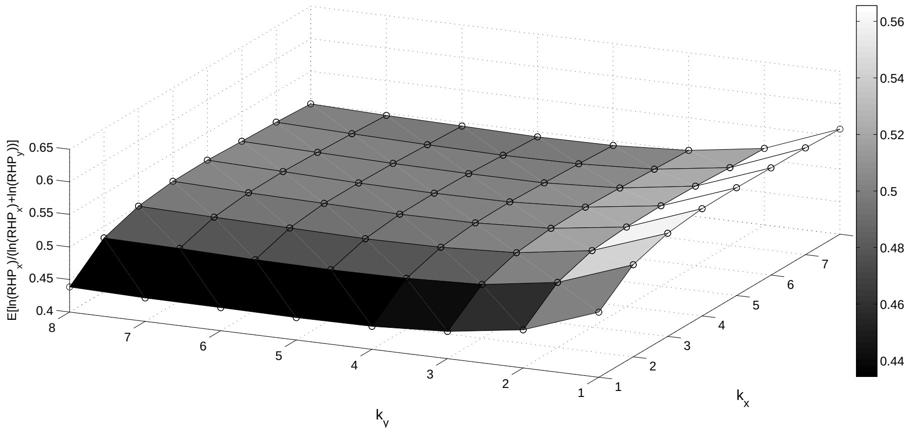


Figure 3.4: Division of resources for different values of k, when $V = C = 0.1$

particular whether they are plentiful or limited. We assume that for plentiful resources, the absolute RHP is more important, but for scarce resources shared between group-members, the relative RHP is the key element. If an individual needs to maximize the RHP then it should fight less compared to the situation where it needs to maximise the division of limited resources. In this latter case the individual needs to be more aggressive so that it can win a greater share than its opponent, since "hurting" its opponent leads directly to improving its proportion in equation (3.27).

3.3.6 How the expected payoffs and the division of resources change when varying V and C

In this section we will vary the values of V and fix the value of C ($C = 0.1$), noting that different combinations of V and C correspond to different values of k for any given value of θ. For each of these combinations we find the ESS (θ and the corresponding k) when $\ln(RHP)$ is considered as the payoff function and when the alternative payoff function is used. The results are summarised in Figures 3.5 and 3.6 where we plot the ratio $\frac{V}{C}$ with $C = 0.1$ on the x-axis and the ESS on the y-axis (k value in Figure 3.5 and θ value in Figure 3.6).

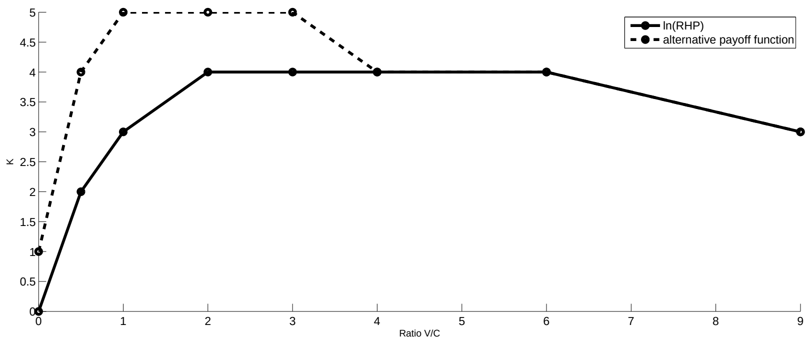


Figure 3.5: The evolutionarily stable strategy k for variable V and fixed C ($C = 0.1$) for $\ln(RHP)$ and alternative payoff function. When $C = 0$ the ESS will be the highest possible value of k ($C \to 0 \implies k \to \infty$).

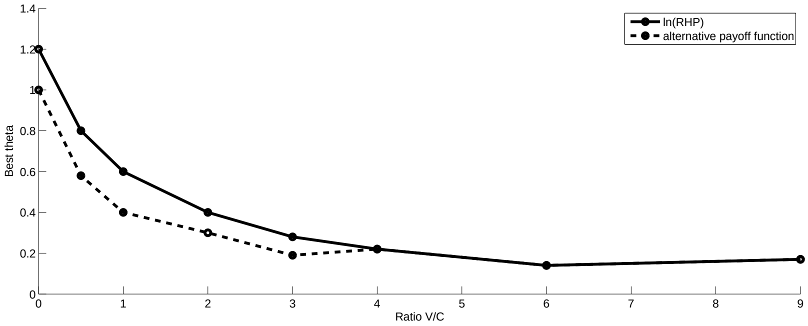


Figure 3.6: The evolutionarily stable strategy θ for variable V and fixed C ($C = 0.1$) for $\ln(RHP)$ and alternative payoff function. When $C = 0$ the ESS will be the highest possible value of k ($C \to 0 \implies k \to \infty$).

For the case when $V = 0$ and $C > 0$, we expect the ESS to be the strategy where an individual retreats immediately. This is true when $\ln(RHP)$ is considered as the payoff function. When the alternative payoff function is used we obtain $k = 1$ ($\theta = 1$) as the ESS (for $C = 0.1$). Thus in this case it is best to fight initially to potentially reduce the RHP of the opponent, as this increases the individual's payoff function. On the other hand for $C = 0$ and $V > 0$, we obtain $k \to \infty$ as the ESS. This is the expected result as since there is no cost for losing, it is best to fight until the end of the competition. When $V \leq 4$ we obtain lower values of θ as an ESS for the alternative payoff function than for the payoff function given by $\ln(RHP)$. This means that when resources are scarce, individuals need to be more aggressive in order to get a high payoff.

For sufficiently high V ratio, (e.g., for $V > 4$), we obtain the same value of θ as an ESS for both payoff functions. The corresponding tables showing the expected payoffs for different combinations of k_x and k_y when V and C vary are given in Appendix A.

3.4 The N-individual model

In Section 3.3 we demonstrated how the expected payoff can be derived analytically for the situation of two interacting individuals. Generalisations of these results to situations with more than two individuals, however, have proven to be analytically intractable. To nevertheless gain insights into the behaviour of larger groups we develop a simulation approach which determines the ESS for N interacting individuals. We imagine a population of $10000N$ individuals, which at the start of the game is divided into 10000 groups of size N at random. Members within each group interact as previously described, for a total of 200 contests and record their payoff (this correspond to steps *S1*-*S2.3*). The individuals then produce offspring proportional to their payoff to form a new generation of $10000N$ individuals. This process is repeated for 10000 generations (this corresponds to step *S3*). The algorithm which generates our approach is defined as follows.

S1 Initially, the N individuals can choose their strategies from the range

$$\Theta = [\theta_1, \theta_2, \ldots, \theta_{10}] = [0.1, 0.2, \ldots, 1]$$

with probability $p(\theta = \theta_k) = \frac{1}{10}$, $k = 1, \ldots, 10$.
Set $i = 0$.

S2.0 Set $H = [0, 0, \ldots, 0]$ (H has dimension 10) and $j = 0$.

S2.1 Each of the N individuals chooses a strategy θ_{x_l}, $l = 1, \ldots, N$ according to the probability function $p(\theta = \theta_k)$.

S2.2 Repeat the following for $T_{max} = 200$ times steps.

Randomly choose two individuals with their strategies θ_{x_l} and θ_{x_m}, $l, m = 1, \ldots, N$ out of the N individuals and update their RHP according to equations (3.3-3.6).

S2.3 Update the vector H as follows

$$H(10\theta_{x_l}) = H(10\theta_{x_l}) + \ln(RHP_{x_l,200}), \quad l = 1, \ldots, N.$$

Set $j = j + 1$. If $j < 10,000$ go to *S2.0* otherwise to *S3*.

S3 Update probability function $p(\theta = \theta_k)$ as follows

$$p(\theta = \theta_k) = \frac{H(10\theta_k)}{\sum\limits_{k=1}^{10} H(10\theta_k)}.$$

Set $i = i+1$. If $i < 10,000$ go to *S2.0* otherwise the simulation is finished.

The outcome of this algorithm is the probability vector $p(\theta = \theta_k)$ and in most cases the probability mass will be concentrated in a single strategy θ_k which represents the ESS. When this is not the case, the mean value of the strategies at the end of the simulation (i.e. after 10000 generations) will be considered as the ESS. In order to analyse the accuracy of the simulation algorithm we consider the same parameter constellation as in Section 3.3.4, namely $N = 2$ and $V = C = 0.1$, and determine the ESS. We obtain $p(\theta = 0.6) = 1$ and conclude that $\theta = 0.6$ is the ESS, which falls within the $[0.55, 0.67]$ range; the result that we obtained from equation (3.21). We considered other values of V and C as well and in all situations analytical and simulation results coincided.

3.4.1 Example: population size $N = 4$

Now we consider a group of $N = 4$ individuals and use the simulation algorithm described above to determine the $ESSs$. We do this for different combinations of V and C and the results are shown in Table 3.3 and Figure 3.7.

	C=0.025	C=0.05	C=0.075	C=0.1	C=0.125	C=0.15
V=0.01	0.9400	0.9900	1.0000	1.0000	1.0000	1.0000
V=0.02	0.8800	0.9000	0.9200	0.9500	0.9700	0.9900
V=0.03	0.7000	0.8100	0.9000	0.9000	0.9200	0.9400
V=0.04	0.6000	0.8000	0.8000	0.8700	0.9000	0.9100
V=0.05	0.4900	0.7000	0.7900	0.8000	0.8000	0.9000
V=0.06	0.4000	0.6200	0.7000	0.7700	0.8000	0.8000
V=0.07	0.3700	0.6000	0.6900	0.7000	0.7600	0.8000
V=0.08	0.3000	0.5000	0.6000	0.6900	0.7000	0.7000
V=0.09	0.2900	0.5000	0.6000	0.6000	0.6500	0.6500
V=0.1	0.2600	0.4400	0.5100	0.6000	0.6000	0.6900
V=0.11	0.2100	0.4000	0.5000	0.5300	0.6000	0.6100
V=0.12	0.2000	0.4000	0.5000	0.5100	0.6000	0.6000
V=0.15	0.2000	0.3000	0.4000	0.5000	0.5000	0.5100
V=0.18	0.1400	0.2900	0.3000	0.4000	0.4300	0.4400

Table 3.3: The ESS value of θ for different combinations of V and C.

The ESS values show that when the value of C is increased for a fixed value of V the value of θ is also increased. This means that the individuals fight less as the cost of injury, for example, is increased. On the other hand, when V is increased for a fixed C we notice that the value of θ is decreased, thus individuals are fighting longer. If $V = C$ then the value of the ESS decreases when V and C are simultaneously increased by the same factor. This is supported by the results of $V = C = 0.05$, $V = C = 0.1$ and $V = C = 0.15$ which have respective $ESSs$ 0.6, 0.49 and 0.45.

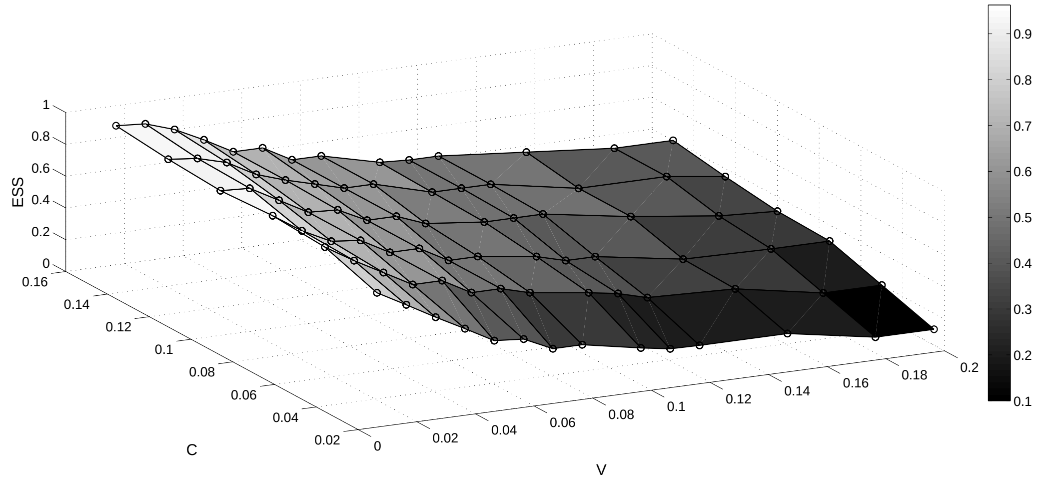


Figure 3.7: The ESS θ for $N = 4$ and different combinations of V and C.

Next, we analyse the level of aggressiveness in a population of 10 individuals for the same combination of V and C as in $N = 4$. The results are plotted in Figure 3.8. From this figure, we notice that increasing the reward (cost) for a fixed value of the cost (reward), increases (decreases) the level of aggressiveness. This was the case for $N = 4$ as well, explained above.

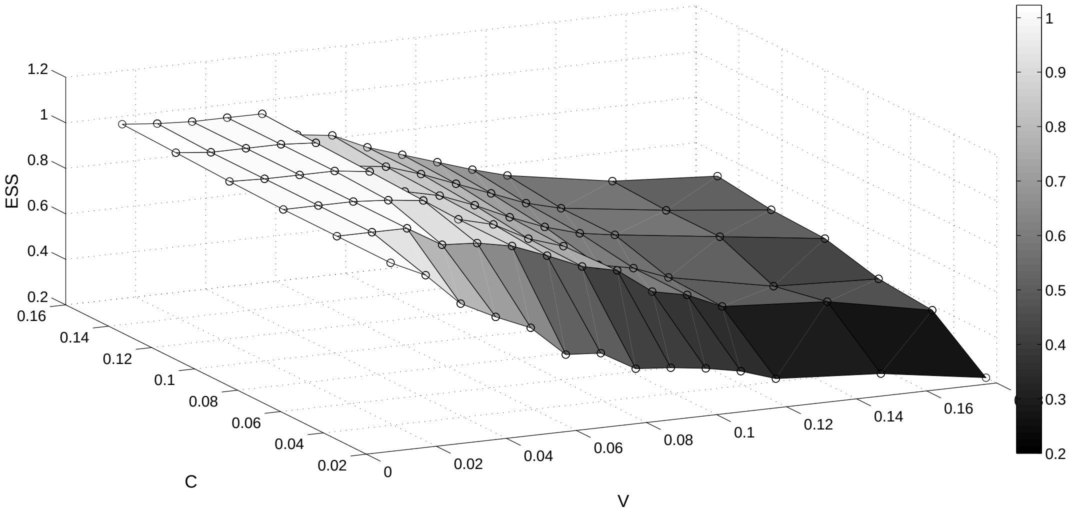


Figure 3.8: The ESS θ for $N = 10$ and different combinations of V and C.

We then, compare the $ESSs$ for $N = 2$, $N = 4$ and $N = 10$. In Table 3.4 we show the values of the ESS for these three group sizes for some combinations of V and C. We conclude that as the group size is increased the values of strategies θ are also increased. This implies less aggressiveness in larger groups. Hence in larger group sizes it is best to fight less than it is in smaller populations, because an individual will suffer a larger loss in RHP for fighting longer and potentially losing against all individuals.

	N=2	N=4	N=10
V=0.1, C=0.2	[0.53, 0.73]	0.9	1.01
V=0,1, C=0.1	[0.55, 0.67]	0.6	0.65
V=0.2, C=0.1	[0.32, 0.42]	0.5	0.5
V=0.3, C=0.1	[0.23, 0.33]	0.35	0.36

Table 3.4: The ESS values for different combinations of V and C for $N = 2$, $N = 4$ and $N = 10$. For $N = 2$ there is a range of strategies θ that correspond to the same critical value of the excess number of defeats k leading to concession. This range is determined by (3.23).

3.5 Comparison of strategies

In the above sections we have derived how the ESS for different values of C and V can be calculated. Now we explore whether the knowledge about the ESS in a specific situation characterized by V and C allows us to infer the ESS for a related situation with αV and αC (for sufficiently small α). Similarly to the Hawk-Dove game, the ratio V/C might be the most important aspect regarding the expected payoffs (if $V < C$ the ESS of the Hawk-Dove game is simply play Hawk with probability $p = V/C$), as opposed to specific values of V and C. This means that if we know the ESS for small values of V and C, we can also calculate the ESS for αV and αC. The following holds

$$d_x = \frac{-\ln(\theta_x)}{\ln(1+V) - \ln(1-C)} \approx \frac{-\ln(\theta_x)}{V - (-C)} = \frac{-\ln(\theta_x)}{V + C} \Rightarrow \tag{3.28}$$

$$d_x(V + C) = -\ln(\theta_x)$$

If we multiply V and C by α we obtain

$$\begin{aligned} d_x &= \frac{-\ln(\theta'_x)}{\ln(1+\alpha V)-\ln(1-\alpha C)} \approx \frac{-\ln(\theta'_x)}{\alpha V+\alpha C} = \frac{-\ln(\theta'_x)}{\alpha(V+C)} \Rightarrow \\ \alpha d_x(V+C) &= -\ln(\theta'_x) \end{aligned} \tag{3.29}$$

where θ'_x is the strategy of individual x when V and C become αV and αC respectively. Now from equations (3.28) and (3.29) we obtain

$$\ln(\theta'_x) = \alpha \ln(\theta_x) \Rightarrow \theta'_x = \theta_x^{\alpha}. \tag{3.30}$$

This means that if for a sequence of wins and losses individual x retreats following strategy θ_x, it will retreat for the same sequence following strategy $\theta'_x = \theta_x^{\alpha}$ when V and C are exchanged for αV and αC, respectively (assuming that changing the value of V using α in this way does not affect the choice of k_x). Thus if only the ratio V/C matters for finding the ESS and θ_x is the ESS for V and C, then θ'_x will be the ESS for αV and αC. We illustrate this point with an example. We assume the parameter constellation $N = 2$, $V = 0.02$, $C = 0.04$ and $\alpha = 3/2$ and use the simulation algorithm given in section 3.4 to determine the ESS. We obtain $\theta_x = 0.91$ (corresponding to $k_x = 2$) as the ESS for $V = 0.02$, $C = 0.04$ and $\theta_x = 0.87$ (corresponding to $k_x = 2$) for $\alpha V = 0.03$ and $\alpha C = 0.06$. When we use formula (3.30) and take $\theta_x = 0.91$ as the ESS baseline ($V = 0.02$, $C = 0.04$), we obtain $\theta'_x = 0.91^{\frac{3}{2}} = 0.868$ as the new ESS which is close to the 0.87 value that we get from the simulations. Thus the results from these simulations support formula (3.30). We have also analysed different values of $\alpha = 2, 1/2, 1/5, 5$ and we obtain ESS corresponding to $k_x = 2$ for all the cases. We can conclude that equation (3.30) gives a good approximation for the ESS. This is always true when we have small values of V and C, however there are some cases when it works less well, principally where V or C is large (or we have an α which will lead to large V or C in the comparative model). We note that the larger V and C, and the bigger T, the more unrealistic multiplying the RHP by a constant after every contest is. On the other hand the smaller T, the more times there are when we cannot distinguish between a pair of individuals as neither of them has retreated. Thus a realistic model should only contain relatively small V and C.

3.6 Discussion

In this chapter we have introduced game-theoretical elements to the winner-loser model developed by Dugatkin ([42], [44], [73]). We considered a group of individuals that are characterised by their RHP and a strategy θ that indicates whether an individual would engage in an aggressive interaction or retreat. All individuals were assumed to possess the same RHP initially. We have developed a model that determines the expected payoff and ESS for different group sizes and payoffs, involving V and C, in such a population.

In the first part of this chapter, we derived analytical results for a group of two individuals for the expected payoff and found the ESS, using $\ln(RHP)$ as the payoff function, which corresponds to situations with unlimited resources. In order to calculate the expected payoff for individual x with strategy θ_x, we first found the condition when this individual would retreat, represented by k. The variable k describes the critical difference between the number of wins and losses, below which individual x retreats. Given that a win increases the value of RHP, the value of k corresponds to the difference in RHP and thus only the individuals with a high RHP relative to their opponents risk engaging in an agonistic interaction to obtain more access to the available resources. We showed that there is a range of strategies θ_x that correspond to the same value of k, meaning that they will give the same payoff. Furthermore different combinations of V and C yield different ranges of θ_x for any given value of k.

We illustrated this analytical part with an example where we assumed $V =$

$C = 0.1$. We found the expected payoff for different strategies $\theta \geq 0$. In this case we obtained a pure ESS which was achieved for $k = 3$, corresponding to the θ range $[0.55, 0.67]$. Any strategy from this range gives the same payoff and is an ESS. We next varied V and C and saw the effect of this variation on the expected payoff and the ESS. As expected, if V is increased for a fixed C the individuals will fight more, corresponding to lower values of θ. On the other hand, if C is increased for a fixed V, we get bigger values of θ as an ESS. This means that individuals will fight less as C is increased.

We also used the idea of the reproductive skew ([27], [66], [103], [109], [121]) to study how scarce resources are divided between a pair of individuals by using an alternative payoff function given in equation (3.27). When comparing the results with the ones obtained for the original payoff function we observe smaller values of θ as an ESS. This means that in this case individuals need to be more aggressive in order to obtain a larger share of the available resources.

Enquist and Leimar [49], developed a mathematical model to study the evolution of fighting behavior. The model consists of a pair of individuals with different fighting abilities which have only noisy information about this difference prior to an aggressive interaction, although they can gain some information during the game by keeping track of the outcomes of the fights (wins and losses). This gives them an idea of the probability of winning the next contests. The individuals are fighting over a resource of value V and in each round, there is a cost for both of them. Depending on the value of the costs and reward, each individual fights until it meets a given threshold. Note that in our model, we assume that the individuals start with the same fighting ability (denoted RHP) which then changes following the results of interactions, and they have perfect knowledge of this ability at every point in time. The ESS for an individual against the strategy of its opponent was calculated and similarly to our result, they concluded that there is a unique, pure ESS that evolves as opposed to a mixture of strategies.

Whilst in our model, and in those of [42] and [44], linear hierarchies are generally formed efficiently when (i) winner and loser effects are both present, (ii) only the winner effect or (iii) only the loser effect is present, the three models give clearly distinct predictions. With only the winner effect present individuals in our model (for optimal strategy choice) and that of [42] will continue fighting indefinitely, whereas in [44] individuals start fighting, but eventually contests cease. With only the loser effect present, individuals would give up immediately in our model (at least for the plentiful resources case defined by payoff function (3.11)), would give up after the first loss in the model of [42], and would fight for some longer period in the model of [44]. These differences in the results of the three models are rooted in the modelling assumptions. In [42] there is no strategic choice and individuals do not know their opponent's RHP, in [44] there is no strategic choice but they do know their opponent's RHP and in our model there is strategic choice and their opponent's RHP is known. Thus [44] can be thought of as an intermediate model between the other two. However, the predictions of our model are closer to that of [42] than [44] and we would argue that these are more realistic.

Other authors have considered alternative game-theoretical models of dominance hierarchy formation. A good recent survey, which raises some interesting questions and suggestions for further modelling is [89]. We shall discuss two such models. Van Doorn and co-workers [118] analysed the evolution of dominance hierarchies by assuming that individuals are identical in ability throughout the time of their interaction, and so while their strategic choices depend upon past results, the actual probability of winning a contest depends upon the strategic choices of individuals, rather than their actual abilities. This is an example of what Maynard Smith [83] called an uncorrelated asymmetry (as opposed to a correlated asymmetry, as in our model). They found several evolutionary equilibria, one of them was the "dominance" equilibrium with the winner and loser effect where previous winners were more likely to take part in aggressive interactions and previous losers less likely to be aggressive. They also found a paradoxical equilibrium where the higher position was occupied by the loser of an aggressive interaction rather than the winner. These results are very similar to those from the owner-intruder game [83] where paradoxical convention-based outcomes can occur. For example in *Oecibus civitas* spiders, it has been observed that owners of the webs give up their webs to the intruders [83]. They then extended this model to larger group sizes [119], where the individuals still had limited information about previous fights. The results were the same as in the two-player model. The assumptions and outcomes are thus rather different to our model.

Fawcett & Johnstone [53] developed a model to analyse the level of aggression where each individual differed in strength, but where they had no information about this difference. They predicted that the level of aggression is related to the amount of information that an individual has about prior contests. While the young individuals should be more aggressive as they are not sure about their fighting ability, the older ones are not. They have knowledge of prior experience and they retreat after a series of losses. Although the mechanisms differ, the actual way that the populations evolve is quite similar to ours. In their model there are real differences between individuals, but the individuals start with no knowledge and learn over time; in our model individuals have varying probabilities of being able to win a contest, which change (perhaps due to psychological factors) over time. In each case, after a time it is clear which individuals are the better ones, and the level of aggressive interactions declines, as more individuals play the more passive strategy. We note that in their model, the eventual division into mainly aggressive strong individuals and mainly passive weak individuals is dependent upon an intermediate number of strong/ weak individuals, and that this divide would not happen for all population divisions.

In each of the strategic models discussed above ([53], [118] and [119], in addition to ours) individuals face a potentially long sequence of contests where they have two options at each step. Thus, in the same way as in games such as the classical iterated prisoner's dilemma [7], there is a vast array of potential strategies. Each model reduces the dimensions of this strategy space in different ways. In the models of [118], [119], individuals were constrained to have a memory only of the latest interaction with an individual, and so could base their play only on the results of this latest interaction (from the iterated prisoner's dilemma "tit for tat" is such a strategy). Fawcett & Johnstone [53] allow individuals to know their performance from all past contests, but allow them only to condition play on the total number of contests encountered, together with the number of wins in these contests. Our model behaves in a similar way to that of [53], basing strategy on the RHP, which in turn depends directly upon the number of won and lost contests of the participating individuals.

Similar results to those from our model concerning aggression levels have been found in experimental settings. Kotrschal et al. [72] performed a feeding experiment with greylag geese. Grained food was given in high, medium and low density. The geese were fed twice daily and the level of aggression was recorded. They found a low number of agonistic interactions in the high food density setting and an increase in those aggressive interactions when the food density was decreased. Nie et al. [99] conducted feeding experiments with varying levels of predation with root voles. They considered four treatments by combining different levels of predation and food supply (i.e. (no predation, food), (predation, food), (predation, no food), (no predation, no food)). They observed higher levels of aggressiveness in the groups treated with unfavourable conditions (predation, no food) compared to groups treated with (no predation, food). When the groups were treated with (predation, food) and (no predation, no food) the level of aggression observed was intermediate. These findings support our model's predictions that if resources are scarce, then an individual needs to be more aggressive in order to obtain a larger share.

An important concept related to the expected payoff is that of the stopping time. The stopping time is defined as the first time when one of the two individuals hits its stopping value of k. It gives a guideline for how many agonistic interactions we need to observe in a pair of individuals before one retreats. After hitting the stopping time an individual would then always retreat afterwards. We showed in our example that twenty possible interactions is enough for an individual to retreat in almost all cases. Note that if T_{max} is relatively larger than the stopping time, the continued increase of the winner's RHP after the stopping time is unrealistic. If, however, T_{max} is smaller than the stopping time, it is more difficult to distinguish between a pair of individuals in terms of their ranks in the hierarchy.

Analytical results can be derived for a group of two individuals but for larger group sizes those derivations become effectively intractable. To explore the behaviour of larger group sizes, in particular to find the ESS, we developed in the second part of the chapter a simulation approach. Analysing a group of four individuals we found that the value of the ESS is increased when V is increased (for a fixed C) and by contrast the value of the ESS is decreased when C is increased (for a fixed V). Comparing the values of ESS for a group of two individuals with the ones obtained for a group of four individuals leads to the conclusion that individuals should be less aggressive (i.e. fight less) in larger groups.

While this result is commonly observed in behavioural experiments, there are experimental settings leading to contradictory conclusions. For example, Nicol et al. [98] conducted a feeding experiment with Isa brown hens. They analysed the behaviour of the birds in groups of four different sizes (72, 168, 264 and 368). The birds were fed twice a day and the number of aggressive pecking interactions were recorded. The results suggested a higher level of aggression in the smallest group (72) compared to the larger groups (168, 264, 368). Further, Anderson et al. [5] compared their model predictions (larger group sizes result in lower aggression levels) with results from an experiment with crossbred pigs. They considered three groups of 6, 12 and 24 pigs (which had not interacted with each other previously) which were put into pens and the space per individual was kept the same. There was one feeder per six pigs and they were fed on ‘Format Start’ every morning. The aggressive interactions in each group were then recorded. It was observed that the level of aggression decreased with increasing group size. This result was also supported by further experiments ([50], [51], [113] [117]). However, Bilvci et al. [14] observed the aggressive behaviour in a feeding experiment with groups of 15, 30, 60 and 120 Hisex white hens and noticed higher level of aggression in larger groups of birds than in the smaller ones.

Summarizing, we presented a game-theoretical model which determines the evolutionarily stable aggression level in a populations of N individuals and different payoff functions, involving V and C, within a winner-loser framework. Within a group, we found that the population evolves to a unique aggression threshold, indicating that relative to their strength, all individuals adopt the same decision rule against whom to fight. Typically the hierarchy is established quickly, with aggressive fights happening only in the early contests.

While higher values of C for losing an aggressive interaction (keeping the value of V constant) lead to lower aggression levels in the population the reverse is true for increasing the value V for winning an aggressive interaction (keeping C constant): the higher the value of V the higher is the aggression level in the population. Further, we predict lower aggression levels in larger populations. Our results are largely supported by experimental evidence so that we conclude that the introduction of game-theoretical elements to Dugatkin’s winner-loser model, provides a further step towards a realistic description of aggressive interactions.

It is clear from our model that winner-loser effects can produce linear hierarchies similar to the ones found in different groups of animals. However, in nature, animals tend to fight opponents of the same strength [23]. In the following chapter, we analyse the Swiss tournament that describes exactly such scenarios.

Chapter 4

An Alternative Swiss Tournament Model of Dominance Hierarchy Formation

4.1 Introduction

In Chapters 2 and 3, we analysed dominance hierarchies formed under the influence of the winner and the loser effect, where individuals of a population are randomly paired together and fighting only when the conditions are favorable for both of them. As explained in Section 1.3.4, winner and loser effects are one possible mechanism to understand how different groups of animals arrange themselves into a ranking order. There are other types of tournaments that animals can follow in order to establish a dominance hierarchy. In this chapter we present an alternative model of dominance hierarchy formation where only individuals with the same strength fight each other. The model that we consider is the Swiss tournament developed by Broom & Cannings [23] and we refer to this model as the usual Swiss tournament. Initially, it is assumed that each individual has the same ability to win a fight. At each round only the individuals with the same number of wins fight each other. Although this is a very structured model, it can happen due to different features of the environment, possibly spatial. For example [23] consider the example of carpenter bees *Xylocopa (Neoxylocopa) varipuncta*, (see [2]), that live in an environment where higher positions in altitude are preferred as opposed to the lower ones. At first, bees might meet at an intermediate level (height) with the winners going up in height and the losers down. Thus at every level only the individuals with the same success rate are aggregated together. There are two issues when considering dominance hierarchies following this type of model. The first one is that the dominance relation is not clear for all the pairs in the group, thus we do not get a linear hierarchy if we follow the definition of linearity given in Chapter 1. The second issue is related to the correlation between the outcome of consecutive contests of an individual. While a win increases the probability of winning the next fight (winner effect), a loss decreases it (loser effect). The winner and the loser effect are not used in the Swiss tournament developed by [23] as individuals with the same success rate fight each other and thus the outcome of a fight is not affected by the sequence of wins and losses and two justifications are given for this. The first one is that there is a long time from one contest to the next and the individuals have a short memory and thus they cannot use the prior experience. The next justification is that each individual measures its strength by the position where it is at a specific moment (the height on the hill for the bees) and that it is not important how it arrived in that position.

One of the limitations of this tournament is that it can be used only for population of size 2^n. In this chapter, we generalise this model to be applied in populations of size N by introducing the concept of “byes” . A number of assumptions are the same as in the Swiss tournament developed by [23].

(1) We still consider populations where individuals have the same strength initially.

(2) The winners go one level up and the losers go one level down. If there are unpaired individuals, they will get a bye and be classed as a winner.

As in [23] the prior experience is not taken into consideration as only the individuals with the same number of wins and losses fight each other. Thus the probability of winning is 0.5.

We prove that linear hierarchies are always established in Swiss tournaments with byes and that we can distinguish between each pair of individuals. As we mentioned above, this was an issue in the first model. Hence Swiss tournaments with byes are better designed for groups of individuals that want to establish a linear hierarchy, where everyone has a clear position in the group.

The fact that we can distinguish between each pair of individuals means that the Swiss tournament with byes has more fights and hence last longer than the usual Swiss model where the hierarchy was established in n rounds. In Section 4.2.1 and 4.2.2 we find how many round are needed for the winner and the second place to be unique. In Section 4.2.3 we give an approximation for the total number of rounds until the dominance hierarchy is established and in Section 4.2.4 the formula for the total number of fights is derived. In Section 4.2.5 we find the expected reward for an individual that has won i contests out of j and the probability of being aggressive (playing Hawk). We illustrate this with an example. In Section 4.2.6 the effect of the group size and cost on the level of aggressiveness is analysed and in Section 4.2.7 we analyse how the probability of being aggressive changes when an individual with a score $i|j$ wins any consecutive round. In Section 4.2.8 we compare the properties of Swiss tournaments with byes with winner and loser models. Another point of interest is finding the total number of fights until the last round. This is analysed in Section 4.2.4.

4.2 Swiss tournaments with byes

In this section we extend further the usual Swiss tournament by analysing populations of size N rather than 2^n. We use the same principles as in the usual Swiss tournament [23]. The only difference is in the fact that in the Swiss tournament with byes in each round we might have individuals that are not paired, due to the general group size N. In this case those individuals get a 'bye' and will end up in a winner's group. As in [23], the Swiss tournament with byes is modelled as a Hawk-Dove game, the matrix of payoffs is given by M_{ij} in Section 1.3.5.2 and the results 3, 4, 5 and 6 hold for this model as well.

Consider a population of size N and let us denote by $S_{i,k}$ the number of individuals with a score i in round k. At the beginning, each individual starts with 0 wins. Thus $S_{00} = N$. In each round, the individuals with the same score are paired together to fight. The winner gets an extra win and the loser gets an extra loss. Those individuals that are not being paired (due to having unique scores or not being selected to fight from an odd-numbered group), get an extra win. Assume that in round k we have $S_{i,k}$ individuals. We are interested to analyse how the individuals are divided in each round. To do so we first need to give the definition of an unbroken sequence as follows:

Definition 4. *An unbroken sequence is one where* $S_{i,k} > 0$ *and* $S_{l,k} > 0 \Rightarrow S_{j,k} > 0 \ \forall i < j < l$.

In other words, by an unbroken sequence we mean an uninterrupted ordering of losses.

If each individual has a different score at round k we say that we reach a unique sequence. The round where we get a unique sequence will be considered as the last round of the competition. Equation (4.1) below gives the number of individuals with a score i at round $k+1$;

$$S_{i,k+1} = \lfloor \frac{S_{i,k}}{2} \rfloor + \lceil \frac{S_{i-1,k}}{2} \rceil \tag{4.1}$$

where $\lfloor \frac{S_{i,k}}{2} \rfloor$ gives the number of individuals with i wins that lose in round k and $\lceil \frac{S_{i-1,k}}{2} \rceil$ gives the number of individuals with $i-1$ wins that win in round k. Figure 4.1 gives the number of individuals and their corresponding scores in rounds 1 and 2.

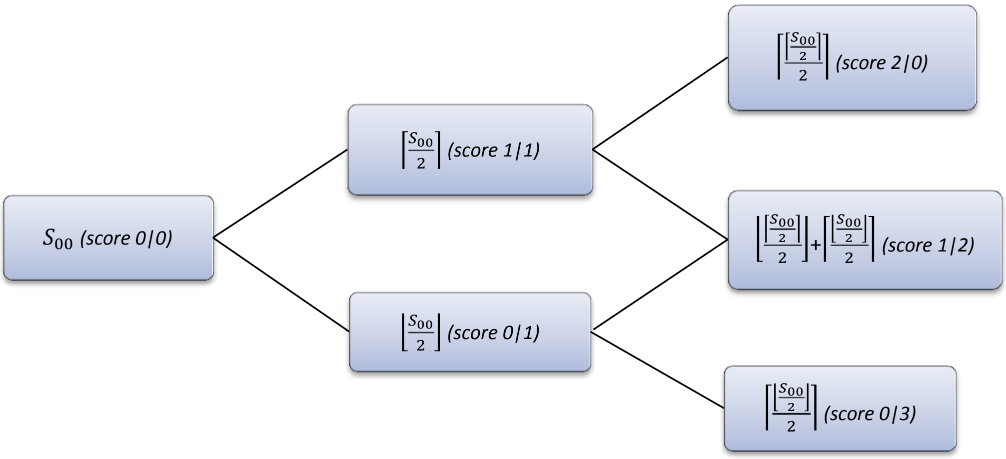


Figure 4.1: The number of winners and losers in round 1 and 2. For example, if we have $S_{0,0}$ individuals at the beging with 0 wins and losses, we would have $\lceil \frac{S_{0,0}}{2} \rceil$ individuals on the next round with one win and no losses, and $\lfloor \frac{S_{0,0}}{2} \rfloor$ individuals with one loss and no wins.

In Figures 4.2 and 4.3 we show how the individuals are divided in every round for $N = 3, 4$

Lemma 4.2.1. *If $S_{i,k} > 0$ and $S_{l,k} > 0$ then $S_{j,k} > 0$ $\forall i < j < l$ and $\forall k$. This means that in each round we have an unbroken sequence.*

Proof. As mentioned earlier $S_{00} = N$ and $S_{i,0} = 0$ otherwise. Thus at the beginning (round 0), we have an unbroken sequence of zeros.

Suppose that we have an unbroken sequence in round k so that $S_{i,k} > 0$ for $m \leq i \leq M$ and $S_{i,k} = 0$ for $i < m$ or $i > M$.

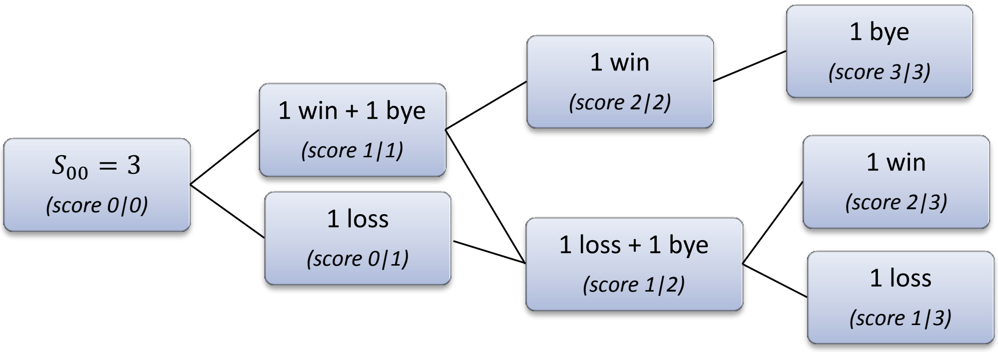


Figure 4.2: The number of winners and losers in every round in a group of 3 individuals. For example at the begining we have 3 individuals on a score $0|0$ (0 wins out of 0 rounds), in the first round we have 2 individuals on a score $1|1$ (one gets this score after fighting and winning and the other gets to this score by getting a bye as it was not paired with any oponent), and 1 individual on a score $0|1$.

From equation (4.1) we have that $S_{i,k} > 0 \Rightarrow S_{i+1,k+1} > 0$. Similarly $S_{j,k+1} = 0$ for $j < m$ or $j > M + 1$. $S_{m,k+1} = 0$ if and only if $S_{m,k} = 1$, but whether it is or not, we have an unbroken sequence in round $k + 1$. Thus by induction the sequence is always unbroken in every round. $\square$

Corollary 4.2.2. *Note that as $S_{00} > 0$, from equation (4.1) we have $M = k$, $\forall k$.*

Lemma 4.2.3. *The Swiss tournament with byes produces linear hierarchies where each individual has a unique profile. Thus if the hierarchy is established in $\widetilde{U}_N$ rounds, then $S_{i,\widetilde{U}_N} = 1 \; \forall i \in [\widetilde{U}_N - N + 1, \widetilde{U}_N]$.*

Proof. From Corollary 4.2.2 we have that $S_{k,k} > 0 \, \forall k$. If $S_{k,k} > 1$ then $S_{k+1,k+1} < S_{k,k}$ and so eventually $S_{k_1,k_1} = 1$, and moreover $S_{k,k} = 1 \; \forall k > k_1$.
Next we consider the remaining $N - 1$ individuals. Eventually we will obtain a unique high score where $S_{k_2-1,k_2} = 1$ (from Lemma 4.2.1 we have $S_{k_2-1,k_2} > 0$) and this score cannot be reached by other individuals in the group. Similarly we can consider the remaining $N - 2$ individuals and so on. We thus obtain a unique sequence, where each individual ends the competition with a unique score. $\square$

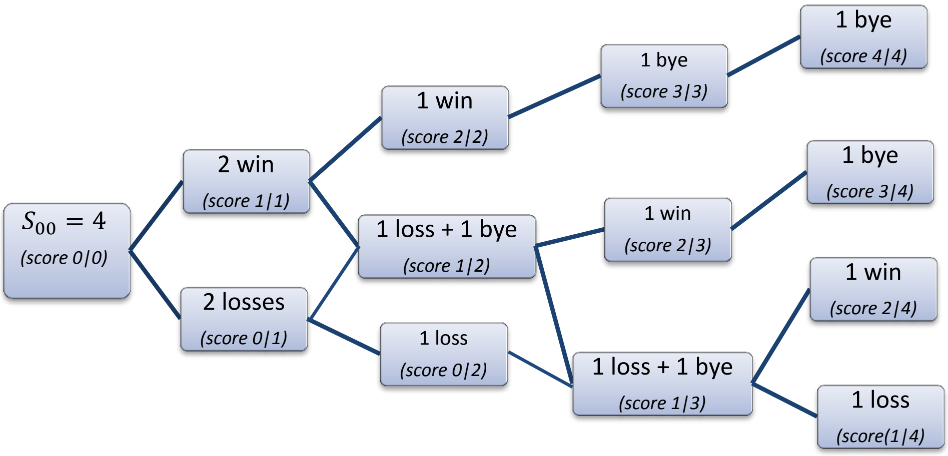


Figure 4.3: The number of winners and losers in every round in a group of 4 individuals. For example at the begining we have 4 individuals on a score $0|0$ (0 wins out of 0 rounds), in the first round we have 2 individuals on a score $1|1$ (they both get to this score by fighting and winning), and 2 individuals on a score $0|1$.

4.2.1 The exact number of rounds until a unique winner

In this section we find the number of rounds needed in order to have a unique winner. The winner will be that individual that has not lost a fight. In the first round of the tournament there are $\lceil \frac{N}{2} \rceil$ winners. In the following round there are $\lceil \frac{\lceil \frac{N}{2} \rceil}{2} \rceil$ undefeated individuals and this continues until there is a single winner which happens in round $\lceil log_2(N) \rceil$. Then the time t_1 when the first place is established is

$$t_1 = \lceil \frac{log(N)}{log(2)} \rceil \tag{4.2}$$

In Figure 4.4 we have plotted the time when the first place is established for group size from 2 to 100. Clearly, the time of establishment of the first place is either constant or increased by one. After the winner is decided (at round t_1), it will get a bye (getting a bye is the same as winning) until the end of the competition and no other individual can ever catch it.

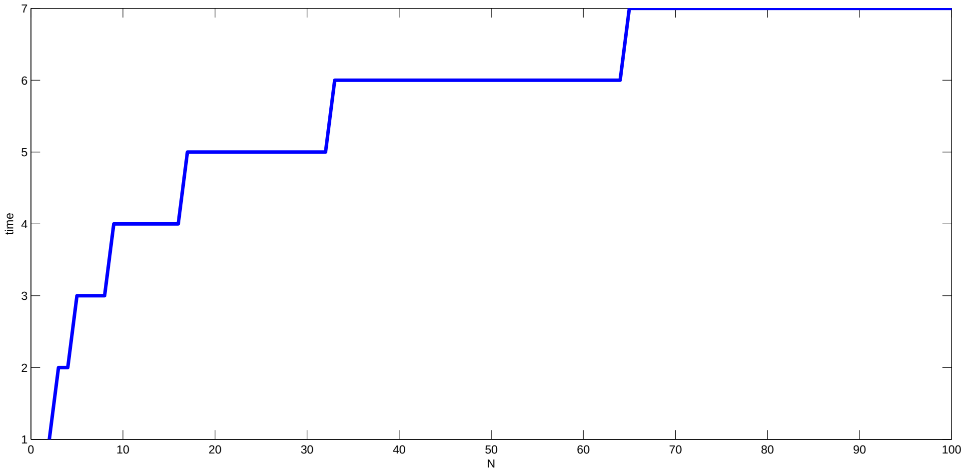


Figure 4.4: The time of establishment for the first place when $N = 2, ..., 100$

4.2.2 The exact number of rounds until a unique second place

We are interested in finding the number of rounds until the second place is decided. We consider populations of size 2^n and N individuals

4.2.2.1 Populations of 2^n individuals

Firstly, we need to find the number of individuals that are at the second place at time t_1 (when the winner is decided). In other words we need to find S_{t_1-1,t_1}.

Consider Pascal's triangle in Figure 4.5. Row 2 contains two number 1's. Equation (4.3)

$$\binom{n}{k} = \frac{n!}{k!\,(n-k)!} \tag{4.3}$$

gives the numbers in the triangle where n is the number of the row and k is the element in that row. The sum of numbers in each row is equal to 2^n. We relate this triangle with the division of individuals at round t_1, where t_1 is the round where we get a unique winner and is found by formula 4.2. For example the sixth row gives how the individuals are split in a group of 2^5 individuals,

$$\begin{array}{c}
1 \\
1 \quad 1 \\
1 \quad 2 \quad 1 \\
1 \quad 3 \quad 3 \quad 1 \\
1 \quad 4 \quad 6 \quad 4 \quad 1 \\
1 \quad 5 \quad 10 \quad 10 \quad 5 \quad 1 \\
1 \quad 6 \quad 15 \quad 20 \quad 15 \quad 6 \quad 1
\end{array}$$

Figure 4.5: Pascal's triangle

when the winner is established. The second value of this row (which is 5) gives the number of individuals that are in the second place at this moment. In general for 2^n individuals, we have n individuals at time $t_1 = n$, because the value of the second element is increased by one when we go from row i to row $i+1$, $\forall i \leq n$. Thus $S_{t_1-1,t_1} = n$. To find the time when the second place is established, which we denote it by t_2, we use the same procedure as we did for the winner (see Section 4.2.1). Thus the time (round) when the second place is unique is given by the following equation

$$t_2 = n + \lceil \frac{log(n)}{log(2)} \rceil. \tag{4.4}$$

where n is the time when the winner is established (in a group of size 2^n) and $\lceil \frac{log(n)}{log(2)} \rceil$ is the time when the winner is established in a group of n individuals.

4.2.2.2 Populations of N individuals

So far we found the round t_1 where we have a unique winner in a group of N individuals and also S_{t_1-1,t_1} and t_2 (the round when we have a unique second place) in a group of 2^n individuals. We are interested to find t_2 for a group of size N. First we need to find how many individuals are on the second place

(S_{t_1-1,t_1}) when the winner becomes unique. If we denote the following

$$G(N) = \lceil \frac{N}{2} \rceil \tag{4.5}$$

and

$$F(N) = \lfloor \frac{N}{2} \rfloor \tag{4.6}$$

then, for the early rounds the N individuals will be divided as in Figure 4.6

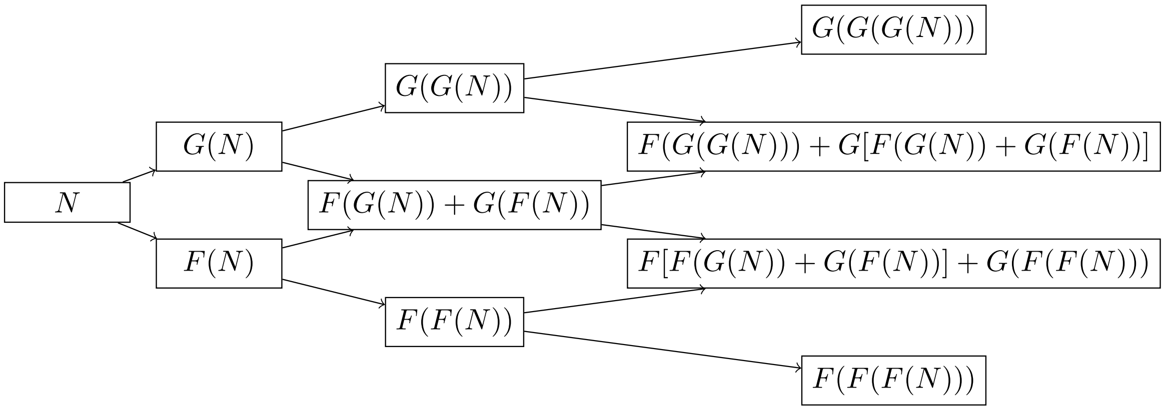


Figure 4.6: How N individuals are split in rounds 1, 2 and 3.

From Figure 4.6 we can generalize and say that the number of individuals at the second place, at time t_1 is:

$$S_{t_1-1,t_1} = FG^{t_1-1} + G(FG^{t_1-2} + G(FG^{t_1-3} + G(FG^{t_1-4} + ... + G(FG + GF)))...) \tag{4.7}$$

where e.g. $FG^2 = F(G(G(N)))$. Note that $FG^{t_1-1} = 1$ as this represent a single individual that has lost to the winner. Thus equation (4.7) becomes

$$S_{t_1-1,t_1} = 1 + G(FG^{t_1-2} + G(FG^{t_1-3} + G(FG^{t_1-4} + ... + G(FG + GF)))...). \tag{4.8}$$

From equation (4.2) we find that it takes $\lceil \frac{log(S_{t_1-1,t_1})}{log(2)} \rceil$ rounds to have a unique winner in a group of S_{t_1-1,t_1} individuals. This means that the time when the second place is unique is given by t_2 as follows

$$t_2 = t_1 + \lceil \frac{log(S_{t_1-1,t_1})}{log(2)} \rceil = \lceil \frac{log(N)}{log(2)} \rceil + \lceil \frac{log(S_{t_1-1,t_1})}{log(2)} \rceil. \tag{4.9}$$

Note that for populations of size 2^n, equation (4.9) reduces to equation (4.4).

4.2.2.3 An approximation for the number of rounds until the second place is unique in a group of N individuals

Above we derived a formula that gives the exact number of rounds until we have a unique second place individual. Sometimes for large group sizes, it takes a lot of steps to calculate t_2. For this reason, here we give an approximation for t_2 which we denote it by $\widetilde{t_2}$ so that we can distinguish with t_2. For 2^n individuals we found that there are n individuals at the second place and that $t_1 = n$. This means that for N individuals we have $t_1 = \lceil \frac{log(N)}{log(2)} \rceil$ and$S_{t_1-1,t_1} = \lceil \frac{log(N)}{log(2)} \rceil$. Thus the time step when the second place is unique will be

$$\widetilde{t_2} = \lceil \frac{log(N)}{log(2)} \rceil + \lceil \frac{log(\lceil \frac{log(N)}{log(2)} \rceil)}{log(2)} \rceil. \tag{4.10}$$

Most of the times $\widetilde{t_2}$ gives the right value for when the second place is unique and occasionally it gives one less than the exact one.

We found analytically the round when the winner and the second place are unique. For the other ranks in the group, it is not easy to find analytically the time when they are unique. In Figure 4.7, we have plotted the time of establishment for each rank in different group sizes.

4.2.3 The total number of rounds

In this section we find how many rounds are needed in total in order to have a unique sequence (linear hierarchy). We know that the winner wins every contest until a unique sequence is established. This means that the total number

N	2	3	4	5	6	7	8	9	10	...	1000
$\widetilde{U}_N$	1	3	4	6	8	10	11	13	15	...	1968

Table 4.1: Number of wins for the first place at the end of the tournament for different group sizes.

of rounds until a linear hierarchy is established, is equal to the total number of wins of the first place, which consists of real fights and byes.

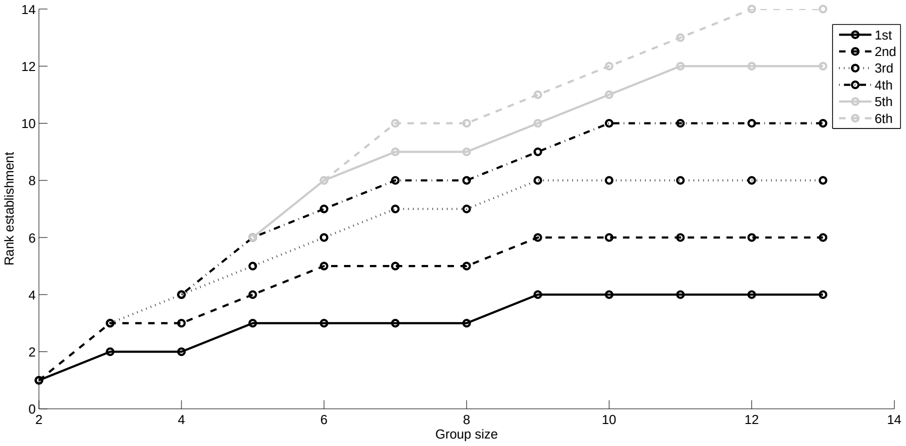


Figure 4.7: The time of establishment for ranks from 1 to 6.

Following the procedure given in Figure 4.1 we compute the number of wins for $N = 2, 3, ..., 1000$. We denote the total number of wins for the first place, until a unique sequence, in a group of N individuals by $\widetilde{U}_N$. Some of the results are given in Table 4.1. In general we find that when we go from a group of size N to $N + 1$ the number of wins for the first place is increased by 2 except for when $N =$ 4, 8, 15, 24, 32,48, 62, 80, 101, 122, 147, 171, 202, 230, 267, 299, 339, 377, 418, 464, 509, 559, 611, 664, 719, 776, 836, 896, 960,... where the total number of wins is increased by one (a jump of one). We plot the group sizes with a jump of one in Figure 4.8 where on $x-$ axis we have $N = 2, ..., 1000$ and on $y-$ axis we have the times when a jump of one happens.

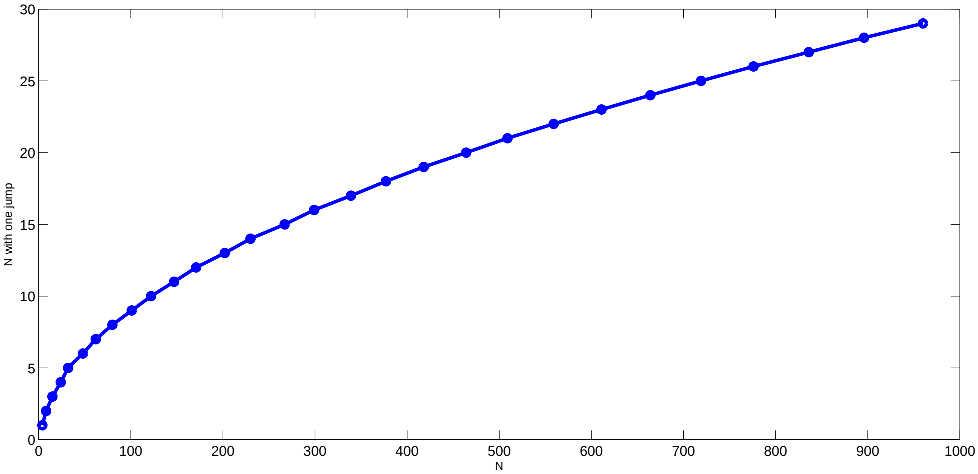


Figure 4.8: Group sizes where a jump of one happens in the number of wins of the first place individual.

We find that the curve with equation

$$C_f = 1.047N^{0.4878} - 0.912 \tag{4.11}$$

fits these data with $R^2 = 0.99$. Then

$$U_N = 2(N-1) - 1.047N^{0.4878} + 0.912 \tag{4.12}$$

gives an approximation for the number of wins for the first place in a population of size N.

As the number of wins is an integer, we round the equation (4.12) to the nearest integer. Then the number of wins $\widetilde{U}_N$ for the first place is

$$\widetilde{U}_N = [U_N] = [2(N-1) - 1.047N^{0.4878} + 0.912], \tag{4.13}$$

where [.] stands for the nearest integer. For most values equation (4.13) gives the exact result for the number of wins, but occasionally it overestimates it or underestimates it by 1.

4.2.4 The number of real fights

In this section we find the total number of real fights in the tournament.

If we denote by $A = [a_1, a_2, ..., a_{\widetilde{U}N}]$ the number for fights in each round, where a_j corresponds to the number of fights at round j, then $\sum_{j=1}^{\widetilde{U}_N} a_j$ gives the total number of fights. For example, for $N = 4, 5, 6, 7, 8, 9, 10$ we have the following:

$N = 5 \Rightarrow A = [2, 2, 2, 2, 1, 1, 0] \Rightarrow$ The number of total fights is 10

$N = 6 \Rightarrow A = [3, 2, 2, 2, 2, 2, 1, 1, 0] \Rightarrow$ The number of total fights is 15

$N = 7 \Rightarrow A = [3, 3, 3, 2, 2, 2, 2, 2, 1, 1, 0] \Rightarrow$ The number of total fights is 21

$N = 8 \Rightarrow A = [4, 4, 4, 2, 3, 2, 3, 2, 2, 1, 1, 0] \Rightarrow$ The number of total fights is 28

$N = 9 \Rightarrow A = [4, 4, 4, 3, 3, 3, 3, 3, 3, 2, 2, 1, 1, 0] \Rightarrow$ The number of total fights is 36

$N = 10 \Rightarrow A = [5, 4, 4, 4, 4, 3, 3, 3, 3, 3, 3, 2, 2, 1, 1, 0] \Rightarrow$ The number of total fights is 45

We notice that the total number of fights in a group of N individuals is equal to $N(N-1)/2$, which corresponds with the number of fights in a round-robin tournament.

Now we prove analytically that the total number of fights in a group of N individuals is equal to $N(N-1)/2$.

For any particular group of individuals we are able to find their deficit with the maximum (winner) and the number of fights. Assume that $S_{i,k}$ is the number of individuals at round k that have scored i wins (denoted by $i|k$) where each individual has a deficit of $(k-i)$ from the maximum. The number of fights for this group is $\lfloor \frac{S_{i,k}}{2} \rfloor$. Then the total deficit below the maximum at round k which we denote by d_k will be

$$d_k = \sum_{i=0}^{k} S_{i,k}(k-i) \tag{4.14}$$

Furthermore the total number of fights at round k will be denoted by f_k and is equal to

$$f_k = \sum_{i=0}^{k} \lfloor \frac{S_{i,k}}{2} \rfloor \tag{4.15}$$

Theorem 4.2.4. *The deficiency d_k below the maximum at round k is equal to the number of fights prior to this round and because the deficit in the last round is*

$$d_{\widetilde{U}_N} = \frac{N(N-1)}{2}$$

then the total number of fights is $\frac{N(N-1)}{2}$, where $\widetilde{U}_N$ and N are the index of the last round and the group size respectively.

Proof. For the $S_{i,k}$ group where the number of fights is $\lfloor \frac{S_{i,k}}{2} \rfloor$, each individual before the fight has a deficit of $(k-i)$. Let us see what happens at the next round $(k+1)$. We know that a bye or a win does not change the number of losses, whereas a loss increases the number of losses by 1. Then on the next round we have $\lfloor \frac{S_{i,k}}{2} \rfloor$ individuals on a score $i|(k+1)$ where each individual has a deficit of $k+1-i$ and the rest of individuals $S_{i,k} - \lfloor \frac{S_{i,k}}{2} \rfloor$ have a score $(i+1)|(k+1)$ where each individual has a deficit of $(k-i)$. The total deficit in round k is d_k given in equation (4.14) and the total deficit in round $k+1$ will be

$$\begin{aligned} d_{k+1} &= \sum_{i=0}^{k} [\lfloor \frac{S_{i,k}}{2} \rfloor (k+1-i) + (S_{i,k} - \lfloor \frac{S_{i,k}}{2} \rfloor)(k-i] \\ &= \sum_{i=0}^{k} \lfloor \frac{S_{i,k}}{2} \rfloor + \sum_{i=0}^{k} S_{i,k}(k-i) \\ &= f_k + d_k \end{aligned} \tag{4.16}$$

Thus we have shown that

$$d_{k+1} = d_k + f_k \tag{4.17}$$

which means that the new deficit in round $k+1$ is equal to the total sum of the deficit and number of fights at round k.

Let us show now that $d_k = \sum_{j=0}^{k} f_j$ is equal to the total number of fights.

The deficit in round 0 is $d_0 = f_0 = 0$. Assume that equation (4.18) is true.

$$d_k = \sum_{j=0}^{k} f_j \tag{4.18}$$

Then from equation (4.17) we have $d_{k+1} = d_k + f_k \Rightarrow d_{k+1} = \sum_{j=0}^{k+1} f_j$.

Thus we proved that if equation (4.18) is true for k, then it is also true for $k+1$. By induction equation (4.18) holds for every k and in particular it is true for the last round $\widetilde{U}_N$ where we have

$$d_{\widetilde{U}_N} = \sum_{j=0}^{\widetilde{U}_N} f_j = \frac{N(N-1)}{2} \tag{4.19}$$

But we know the deficit in the last round is

$$d_{\widetilde{U}_N} = \frac{N(N-1)}{2}. \tag{4.20}$$

Thus the total number of fights in a group of N individuals is $\frac{N(N-1)}{2}$. $\square$

In summary, in previous sections, we have analysed the model with respect to the fighting structure. We have seen how long it takes until the winner and the second place are established and we also found the total number of real fights. In the following section we find the expected reward for an individual after any win or loss.

4.2.5 The expected reward for an individual on a score $i|j$

In this section we find the expected reward for an individual that is on a score $i|j$ (having won i contests until round j). As in the Swiss tournament developed by Broom & Cannings [23], the Swiss tournament with byes is modelled as a Hawk-Dove model where individuals always interact with each other with the winners getting an extra point and the losers staying on the same score. The only difference is on the rewards where the payoff matrix is as follows:

$$M_{ij} = \begin{bmatrix} \frac{1}{2}(W_{(i+1)(j+1)} + W_{i(j+1)} - C) & W_{(i+1)(j+1)} \\ W_{i(j+1)} & \frac{1}{2}(W_{(i+1)(j+1)} + W_{i(j+1)}) \end{bmatrix} \tag{4.21}$$

where again, $W_{i,j}$ is the expected reward for an individual with a score $i|j$, $W_{(i+1),(j+1)}$ is the expected reward for an individual with a score $i|j$ to win the next contest, $W_{i,(j+1)}$ is the expected reward if it loses and C is the cost that the loser pays if the contest is Hawk-Hawk. If p_{ij} is the probability of playing Hawk in the ESS (for an individual on a score $i|j$) then the followings apply.

(1) $p_{ij} = 0$ means that an individual plays Dove. This happens if $W_{(i+1),(j+1)} - W_{i,(j+1)} < 0$. The expected payoff for this strategy is $\frac{1}{2}(W_{(i+1),(j+1)} + W_{i,(j+1)})$.

(2) $p = 1$ means that an individual plays Hawk, which happens if $W_{(i+1),(j+1)} - W_{i,(j+1)} \geq C$. The expected payoff for this strategy is then $\frac{1}{2}(W_{(i+1),(j+1)} + W_{i,(j+1)} - C)$.

(3) For $0 \leq W_{(i+1),(j+1)} - W_{i,(j+1)} < C$ we have $p = \frac{W_{(i+1),(j+1)} - W_{i,(j+1)}}{C}$ and the expected payoff in this case is $\frac{1}{2}(W_{(i+1),(j+1)} + W_{i,(j+1)}) - \frac{1}{2C}(W_{(i+1),(j+1)} - W_{i,(j+1)})^2$.

In [23] (2^n individuals) the expected payoff is given by the following single expression:

$$W_{ij} = \frac{1}{2}(W_{(i+1)(j+1)} + W_{i(j+1)} - p_{ij}^2 C) \tag{4.22}$$

In the Swiss tournament with byes, equation (4.22) becomes

$$W_{ij} = \frac{\lceil \frac{S_{i,j}}{2} \rceil}{S_{i,j}} W_{i+1,j+1} + \frac{\lfloor \frac{S_{i,j}}{2} \rfloor}{S_{i,j}} W_{i,j+1} - \frac{\lfloor \frac{S_{i,j}}{2} \rfloor}{S_{i,j}} p_{ij}^2 C. \tag{4.23}$$

where $S_{i,j}$ is the number of individuals on a score $i|j$, C is the cost and p_{ij} is the probability of being aggressive when on score $i|j$. Thus $\frac{\lceil\frac{S_{i,j}}{2}\rceil}{S_{i,j}}$ is the probability that an individual will win or get a bye and $\frac{\lfloor\frac{S_{i,j}}{2}\rfloor}{S_{i,j}}$ is the probability that it loses. The probability p_{ij} is as follows:

$$p_{ij} = mid\left(0, \frac{W_{i+1,j+1} - W_{i,j+1}}{C}, 1\right). \tag{4.24}$$

As in the Hawk-Dove model, $p_{ij} = 0$ does not occur, and so equation (4.24) becomes

$$p_{ij} = min\left(\frac{W_{i+1,j+1} - W_{i,j+1}}{C}, 1\right). \tag{4.25}$$

We found that the total number of rounds until a linear hierarchy is established, is equal to the total number of wins of the first place, which is given by $\widetilde{U}_N$, thus the reward for finishing on a score $i|\widetilde{U}_N$ is V_i where $V_0 \leq V_1 \leq ... \leq V_{\widetilde{U}_N}$ $\forall i$.

Note then when $S_{i,j} = 0$ (no individual is on a score $i|j$), the expected reward W_{ij} will be equal to the expected reward if there was to be one individual on $i|j$. In this case as $S_{i,j} = 1$ the individual will get a bye and end up on a score $(i+1)|(j+1)$. Thus in this case we have $W_{i,j} = W_{(i+1),(j+1)}$. In the matrix of payoffs we put brackets around W_{ij} when the corresponding $S_{i,j} = 0$. We use the same logic for the probability p_{ij} when $S_{i,j} = 0$ as for when $S_{i,j} = 1$.

4.2.5.1 A Numerical example

Consider a game with $N = 4$ individuals, cost $C = 1$ and rewards $V_i = i$ for $i = 1, .., \widetilde{U}_N$. For example the expected reward for an individual finishing on a score 1|3 is. $W_{1,3} = \frac{1}{2}2 + \frac{1}{2}1 - \frac{1}{2}1 = 1$ where $p_{1,3} = min\left(\frac{2-1}{1}, 1\right) = 1$. We find the successive values of W_{ij} and p_{ij} by using (4.23) and (4.25).

The results for $W_{i,j}$ and $p_{i,j}$ are given in Tables 4.3 and 4.4.

$i\|j$	0	1	2	3	4
4	-	-	-	-	1
3	-	-	-	1	1
2	-	-	1	1	1
1	-	2	2	2	1
0	4	2	1	0	1

Table 4.2: The number of individuals on a score $i|j$ ($S_{i,j}$)

$i\|j$	0	1	2	3	4
4	-	-	-	-	4
3	-	-	-	4	3
2	-	-	4	3	2
1	-	$\frac{9}{4}$	$\frac{3}{2}$	1	1
0	$\frac{19}{16}$	$\frac{9}{8}$	1	(1)	0

Table 4.3: Expected pay-offs to individuals on a score $i|j$ (W_{ij})

$i\|j$	0	1	2	3	4
4	-	-	-	-	-
3	-	-	-	(1)	-
2	-	-	(1)	(1)	-
1	-	1	1	1	-
0	1	$\frac{1}{2}$	(1)	(1)	-

Table 4.4: The probability of playing Hawk on a score $i|j$ (p_{ij})

4.2.6 The effect of group size and cost on the level of aggressivenes

Another important concept is that of the weighted average of the probability p_{ij}, which is a general measure of aggressiveness, and we will denote it by $\overline{p}_N$

and calculate it as follows

$$\overline{p}_N = \frac{\sum_{i,j=0}^{\widetilde{U}_N} \lfloor \frac{S_{i,j}}{2} \rfloor p_{i,j}}{\sum_{i,j=0}^{\widetilde{U}_N} \lfloor \frac{S_{i,j}}{2} \rfloor}. \tag{4.26}$$

For the numerical example in section 4.2.5.1, we find he weighted average of probability p_{ij} to be

$$\overline{p}_N = 0.9.$$

We are interested to see how the weighted probability $\overline{p}_N$ changes when we increase the cost C and the group size. Firstly we calculate $\overline{p}_N$ for $N = 4$ and $C = 1, 2, ..., 100$ and the results are plotted in Figure 4.9. We find that when the cost C is sufficiently large, the product $C\overline{p}_N$ tends towards the value 1. Next, we plot $\overline{p}_N$ multiplied by the value of cost on the y-axis, and the value of the cost on the x-axis. We do this for $N = 5, 6, 7, 8, 9, 10, 48$ and $C = 1, 2, ..., 1000$. The results are plotted in Figure 4.10. From this figure we find that when the cost is increased, the value of $\overline{p}_N$ decreases. This means that for very large values of cost, individuals are less aggressive. For each of the group sizes we notice that the product $C\overline{p}_N$, converges to a value that we denote by l_N

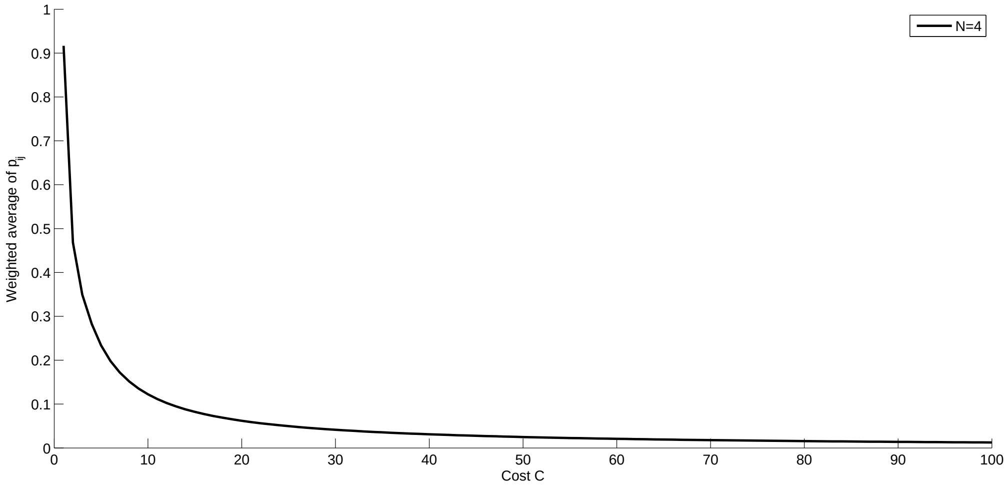


Figure 4.9: Weighted average of probability p_{ij} for $N = 4$, when C ranges from 1 to 100.

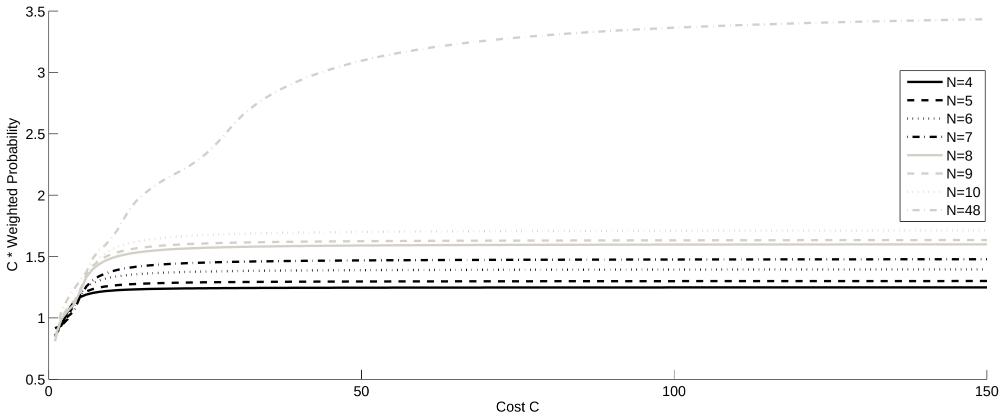


Figure 4.10: Weighted average of probability p_{ij} $*C$ when we increase the cost from 1 to 1000 in different group sizes

For each group size we find the value of l_N for when $C = 1000$. We plot these results in Figure 4.11.

When the group size is increased, the value of l_N also increases which implies that $\overline{p}_N$ also increases. This is related to the expected number of fights that an individual has when it wins the first fight and when it loses the first fight. For example when $N = 4$ (see Figure 4.3), the following sequences are possible:

(1) An individual wins two fights in a row. We denote this sequence WW. In this case, the total number of fights is equal to two.

(2) If an individual follows the sequence WLW (win-lose-win), it will finish with a total of three fights.

(3) If an individual follows the sequence LWW (lose-win-win), it will finish with a total of three fights.

(4) If the first two outcomes are LL (two loses in a row), it will finish with a total of three fights.

(5) When it follows the sequence WLL or LWL, this individual will finish with a total of four fights

Thus, in general, an individual has more fights if it loses the first contest than it has if it wins it. This is why the level of aggressiveness increases at round 1, as an individual does not benefit by ending up in a group of losers. As the group size is increased, the difference between the first place and the last one, increases.

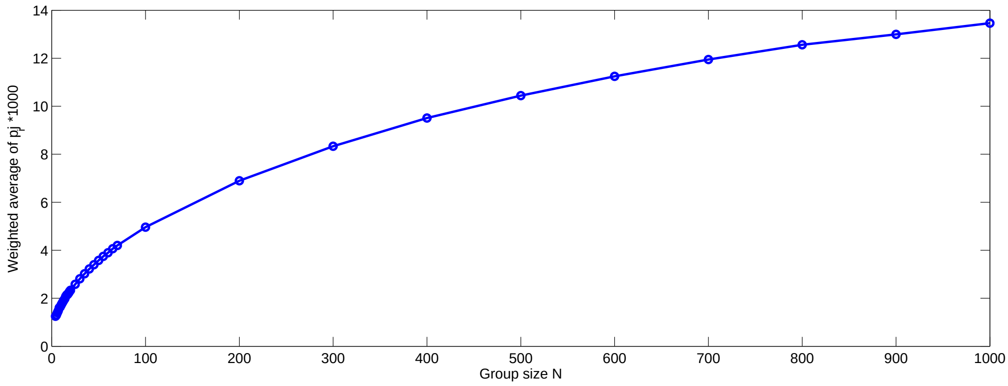


Figure 4.11: Weighted average of probability p_{ij} $*C$ when we increase the cost from 1 to 1000 in different group sizes

Note that in Figure 4.11 we have calculated l_N for some other group sizes as well. We find that the function

$$l_N = 0.704(N+1)^{0.4329} - 0.1765 \tag{4.27}$$

fits the data in Figure 4.11 with $R^2 = 0.999$. Finally, we can say that the weighted average of probability p_{ij} is given by the following approximation:

$$\overline{p}_N = \frac{1}{C}(0.704(N+1)^{0.4329} - 0.1765) \tag{4.28}$$

For example for $N = 2$ we get $\overline{p}_N = \dfrac{1}{C}$ which is exactly what we expect as $l_N = 1$.

4.2.7 The effect of winning or losing a fight on the level of aggressivenes

In this section we analyse the probability p_{ij} in more detail. Denote by $P = [p_{ij}]_{i,j=1,\ldots,\widetilde{U}_N}$ the matrix of probabilities p_{ij} where p_{ij} represent the probability of being aggressive if an individual has won i rounds until round j. If we look at the leading diagonal, it gives us the probability of aggressiveness for an individual when it wins all the fights. The next diagonal, parallel with the leading one, gives us the probability of being aggressive for an individual that starts with one loss and wins every round. Then the following parallel diagonal gives us the probability of being aggressive for an individual that starts with two losses and wins every other fight, and so on for the next diagonals. Now, we analyse the behavior on each of these diagonals. For example for a tournament with 5 rounds the matrix P is as follows

$$P = \begin{bmatrix} p_{00} & p_{01} & p_{02} & p_{03} & p_{04} & p_{05} \\ - & p_{11} & p_{12} & p_{13} & p_{14} & p_{15} \\ - & - & p_{22} & p_{23} & p_{24} & p_{25} \\ - & - & - & p_{33} & p_{34} & p_{35} \\ - & - & - & - & p_{44} & p_{45} \\ - & - & - & - & - & p_{55} \end{bmatrix} \tag{4.29}$$

The leading diagonal has $j - i = 0$. We will call this diagonal 0. The values in this diagonal are: $p_{00}, p_{11}, p_{22}, p_{33}, p_{44}, p_{55}$

The next diagonal parallel with diagonal 0 has values: $p_{01}, p_{12}, p_{23}, p_{34}, p_{45}$ where the difference $j - i = 1$, we will call this diagonal 1. We repeat this for all diagonals parallel with the main one. We are interested only in those p_{ij} values that have corresponding $S_{i,j} \geq 2$ as they represent the 'real fights'.

4.2.7.1 Example: N=20

In this example we consider a group of 20 individuals. We find the total number of rounds given by $\widetilde{U}_N$ as follows:

$$\widetilde{U}_N = [2(N-1) - 1.047N^{0.4878} + 0.912] = 34 \tag{4.30}$$

Thus it takes approximately 34 rounds (which coincide with the exact number of rounds) for the hierarchy to be established. We calculate the values in matrix P and the values on each diagonal corresponding to $S_{i,j} \geq 2$ are plotted in Figure 4.12.

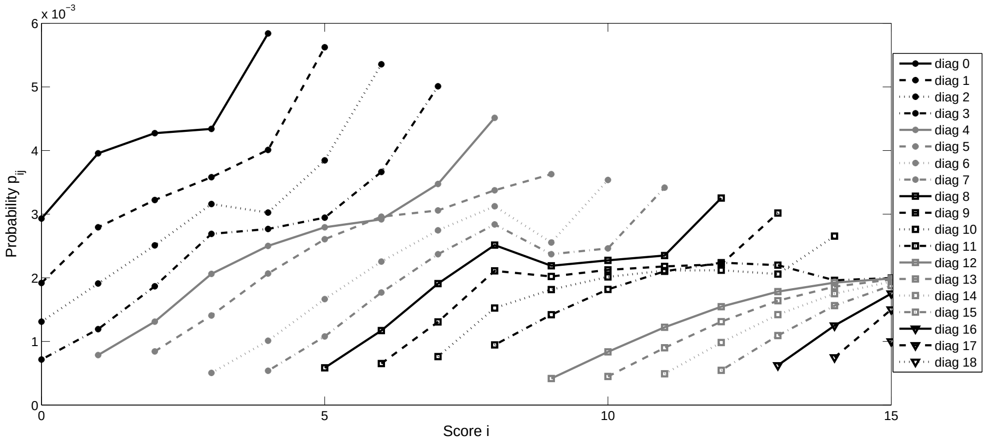


Figure 4.12: Diagonal probabilities in P for $N = 20$. On the x-axis we have the score i. The corresponding round for this score is $i + \xi$.

On the x-axis we have the score i and on y-axis the corresponding p_{ij} where $j = (i + \xi)$, and ξ correspond to the diagonal number. For example if we consider diagonal 4, the first value correspond to $i = 1$. Then we can find the round j as $j = 1 + 4 = 5$. This means that the first value in diagonal 4 is $p_{1,5}$, the following one will be $p_{2,6}$ and so on. We notice in Figure 4.12 that the maximum for each diagonal is reached when there are only two individuals fighting, and that is the final fight before the corresponding position is decided. We are interested to see whether consecutive wins increase the probability of

Diagonal (ξ)	0	1	2	3	4	5	6	7	8	9	10	11
No ind. in ξ+1, ξ+2, ξ+3, ξ+4 place	1, 4, 6, 6	1,4,5,6	1,4,5,5	1,4,5,4	1,4,4,4	1,3,4,4	1,3,3,4	1,3,3,3	1,3,3,3	1,3,3,2	1,3,2,2	1,2,2,2

Table 4.5: The number of individuals at the ξ+1, ξ+2, ξ+3, ξ+4 place in diagonal ξ at the time when we have a unique winner. For example in diagonal 0 at the time when we have a unique winner $k_{t_1,t_1} = 1$ there are 4 individual at the second place, 6 individuals at the third place and 6 individuals at the fourth place.

being aggressive. In other words we want to check if $p_{(i+1),(j+1)} \geq p_{i,j}$, as for the original Swiss tournament [23]. While in most cases this is true, winning a fight does not guarantee a higher level of aggressiveness. This can be seen on diagonal 2 where $p_{3,5} = 0.0032$ and $p_{4,6} = 0.003$ and thus $p_{4,6} < p_{3,5}$.

Another point of interest is to see how the level of aggressiveness changes from one diagonal to the other. In order to do so we plot the maximum probability (corresponding to the last fight) for each diagonal, in Figure 4.13. We know that in each diagonal ξ, the position $\xi + 1$ is determined. For example the winner is decided on diagonal 0, the second place is determined on diagonal 1, and so on. From Figures 4.12 and 4.13, we see that the level of aggressiveness is higher in diagonals 0, 1, 2, 3 and 4. In diagonal 5 there is a jump, the pattern changes and there is less aggression. This is because the consequences of winning and losing are less when we shift the diagonals. To understand this better, for each diagonal ξ, we find the number of individuals that are at position $\xi + 2$ (one win less than the winner of that diagonal). These results are given in Table 4.5 From diagonal 0 to diagonal 4 there are 4 individuals with one win less than the winner, whereas at diagonal 5 there are 3 individuals with one win less than the winner of this diagonal. Being in a group of 3 is better than being in a group of 4, because in a group of 4, an individual needs to win 2 fights to be at the top of the group, and in a group of 3 it needs to win an average of $\frac{3}{2}$ fights to be at the top. Thus a loss in diagonal 5 is not as costly as a loss in the previous diagonals. This is the reason why the pattern changes, because it is affected by the cost of losing.

For the same reasons the pattern changes in diagonal 11, because here if an individual loses, it would end up in a group of two individuals. In this case it takes only one round to be the next best individual.

In general this means that the level of aggressiveness is higher when individuals are fighting for a higher position in the group and lower when they are fighting for the last positions in the hierarchy, as the reward is smaller.

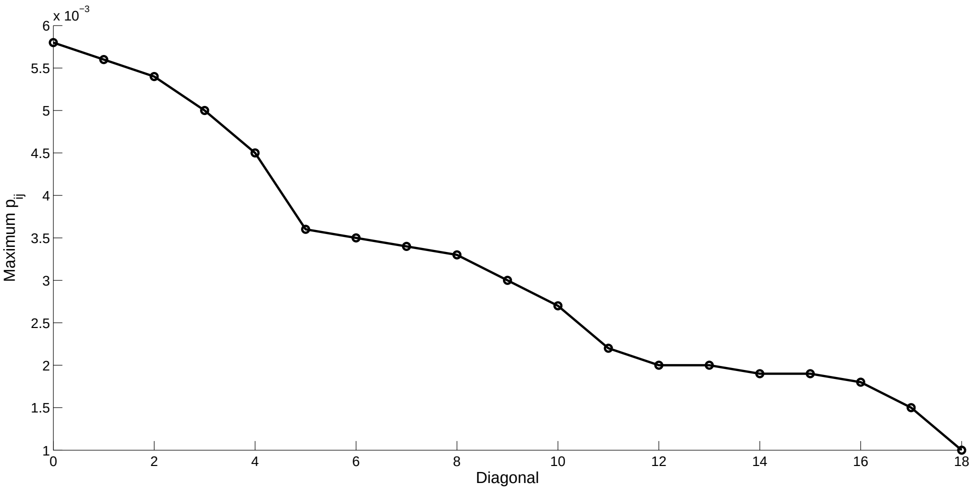


Figure 4.13: The maximum of each diagonal in matrix P when $N = 20$

4.2.7.2 Example: N=44

In this example we consider a group of $N = 44$ individuals. In Figure 4.14 we plot the probabilities for each diagonal.

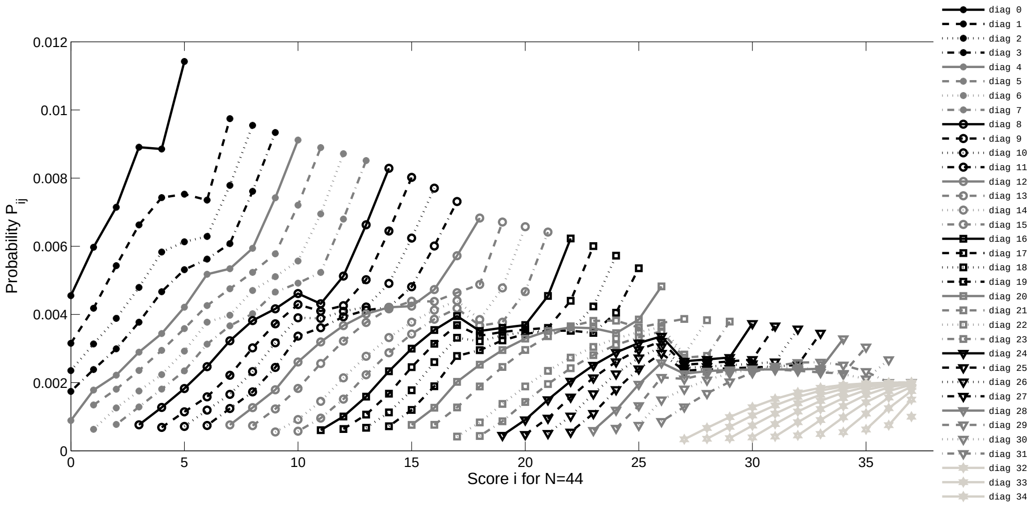


Figure 4.14: Diagonal probabilities in P for $N = 44$. On x-axis we have the score i. The corresponding round for this score is i + diagonal number.

Now we plot the maximum for each diagonal in Figure 4.15

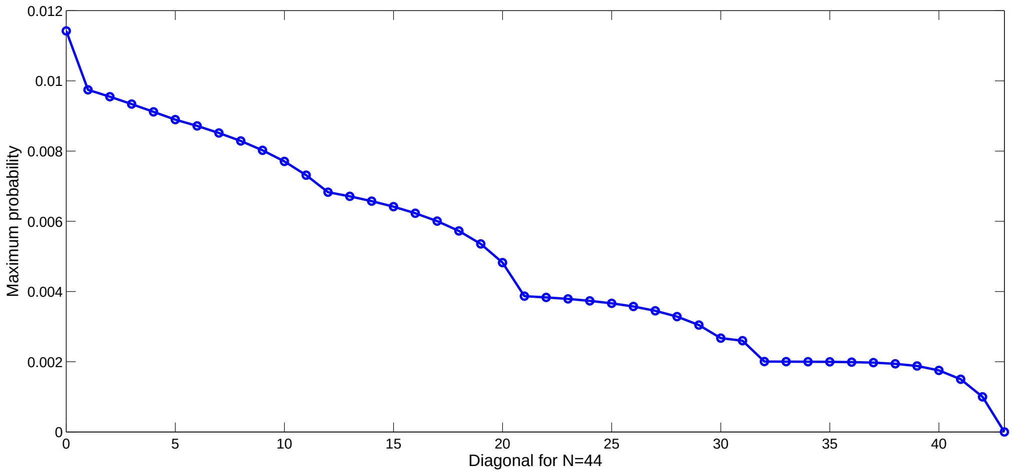


Figure 4.15: The maximum of each diagonal of matrix P for $N = 44$

From Figure 4.15 we see that the level of aggressiveness changes when we go form one diagonal to the other, in particular there are five significant changes. For the same reasons as in the previous example, these changes are related with the number of individuals that are at positions ξ+2 and ξ+3 respectively, at the time that the winner for each diagonal is established. These numbers are given in Table 4.6. The first change in the level of aggressiveness happens in diagonal 1, because here if an individual loses ends up in a group of

Diagonal(ξ)	0	1	2	3	4	5
No ind. in ξ+1, ξ+2, ξ+3, ξ+4 place	1, 5, 10, 14	1,4,7,10	1,4,7,10	1,4,7,9	1,4,7,9	1,4,7,9

Diagonal (ξ)	6	7	8	9	10	11
No ind. in ξ+1, ξ+2, ξ+3, ξ+4 place	1,4,7,8	1,4,7,7	1,4,7,7	1,4,7,7	1,4,7,7	1,4,7,6

Diagonal (ξ)	12	13	14	15	16	17
No ind. in ξ+1, ξ+2, ξ+3, ξ+4 place	1,4,6,6	1,4,5,6	1,4,5,5	1,4,5,5	1,4,5,5	1,4,5,5

Diagonal (ξ)	18	19	20	21	22
No ind. in ξ+1, ξ+2, ξ+3, ξ+4 place	1,4,5,5	1,4,5,4	1,4,4,4	1,3,4,4	1,3,3,4

Diagonal (ξ)	23	24	25	26	27
No ind. in ξ+1, ξ+2, ξ+3, ξ+4 place	1,3,3,3	1,3,3,3	1,3,3,3	1,3,3,3	1,3,3,3

Diagonal (ξ)	28	29	30	31	32
No ind. in ξ+1, ξ+2, ξ+3, ξ+4 place	1,3,3,3	1,3,3,2	1,3,2,2	1,2,2,2	1,2,2,2

Table 4.6: The number of individuals at the ξ+1, ξ+2, ξ+3, ξ+4 place at the moment that we have a unique winner for diagonal i and N=44. For example in diagonal 0 at the time when we have a unique winner ($k_{t_1,t_1} = 1$), there are 5 individual at the second place, 10 individuals at the third place and 14 individuals at the fourth place.

four individuals. Again being in a group of four individuals is better than being in a group of five individuals (main diagonal). The next change in the level of aggressiveness happens in diagonal 12, where for the first time we go from having 7 individuals at the ξ+3 place to having 6 individuals. This means that if an individual loses there can be 4 other individuals that can reach its score when there are 7 individuals with one win less than this individual, and there can be 3 individuals that can reach it if there are 6 individuals with one win less than this individual. The next change in the level of aggressiveness happens in diagonal 21, where we go from having 4 individuals at the ξ+2 place to 3 individuals. In diagonal 31 we have the first time that if an individual loses it would end up in a group of two individuals.

4.2.8 Swiss tournaments with byes vs. winner-loser models

In this section we compare Swiss tournaments with byes with winner and loser models. In both models we consider a population of size N. In winner-loser models each individual has a score RHP (resource holding potential). At each point in time two individuals are chosen at random to fight each other. Individual x will fight individual y if $RHP_x/RHP_y \geq \theta$ where RHP_x and RHP_y are the resource holding potential of individuals x and y respectively. θ is the aggression threshold that indicates whether an individual fights or not. Thus in winner-loser models we randomly pair individuals against each other, so there will be extra fights that will not feature in the Swiss tournament. In winner-loser models we have a fixed group interacting together. Thus the Swiss tournament is better designed for larger population size where individuals react locally and locality is influenced by the success of an individual.

The probability of winning in the Swiss tournament with byes is equal to $1/2$ and the winner is decided at random. In winner and loser model this probability is equal to $RHP_x/(RHP_x + RHP_y)$. If we consider the Swiss tournament in terms of the RHP, the probability of winning will be still $1/2$ as only the individuals with the same score (RHP) will fight each other. Hence we are in the same world in terms of probability of winning.

Linearity: Both Swiss tournaments with byes and winner-loser models produce linear hierarchies. In the updated winner-loser model the time when the hierarchy is established depends on whether the winner effect is considered alone, the loser effect is considered alone or both the winner and loser effect are present. We have considered mostly groups of four individuals as it is time-consuming to calculate after how many rounds the hierarchy is established in larger groups. On the other hand, the Swiss tournament produces linear hierarchies in less rounds than the winner-loser model. For example, in a group of 4 individuals, only 4 rounds are needed to establish a linear hierarchy. In winner and loser models (with $\theta = 1$, $W, L = 0, 0.1, 0.2, 0.3$) the linearity is established after 41 rounds when only the winner effect is present, after 44 rounds when only the loser effect is present and after 32 rounds when both the winner and the loser effects were present. In all three cases the last pair to be distinguishable is the second and the third place.

The Swiss tournament with byes is similar to the winner-loser model when only the loser effect is present, where not fighting (retreating) is considered as winning. The loser effect is found to be present in a variety of species where it lasts longer than the winner effect. This might be due to the fact that after a loss, an individual would think that has less chances of winning an aggressive interaction.

Strategies: Now we compare the ESS in the winner-loser model with strategic factors, with the weighted probability in the Swiss tournament with byes. Figure 4.16 show the level of aggressiveness in the winner loser model for a group of two individuals. When the cost is increased the values of θ are also increased which means that individuals are less aggressive. Also in the Swiss tournament, when the cost is increased the values of the weighted probability are decreased which means that individuals are less aggressive (see Figure 4.9). Thus the effect of the cost on the level of aggressiveness is the same in both models.

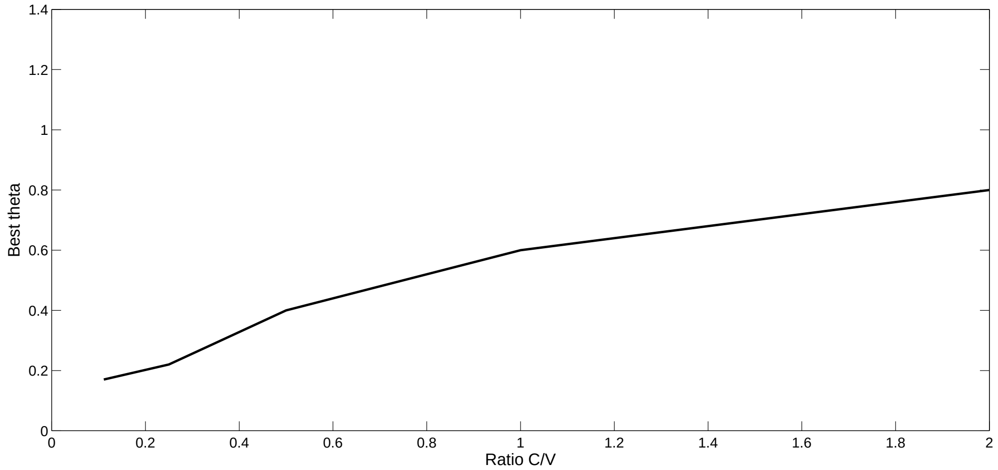


Figure 4.16: The evolutionarily stable strategy θ for different combinations of reward and cost for $ln(RHP)$. When $C = 0$ the ESS will be the highest possible value of k ($C \to 0 \Longrightarrow k \to \infty$)

4.3 Discussion

In this chapter we have introduced an alternative Swiss tournament model of dominance hierarchy formation, following a Hawk-Dove type of model. Our starting point of interest was the model developed by Broom & Cannings [23], where 2^n individuals were pitted against each other. This model can be applied to groups of individuals that are meeting for the first time with no dominance relationships established between pairs of individuals. In order to establish the dominance hierarchy, individuals need to participate in a series of aggressive interactions with each other. Their position in the hierarchy (and their reward) is based upon the number of conflicts won and lost by an individual. In [23] only individuals with the same sequence of wins and losses fight each other. As a result, the hierarchies established were not linear, there were pairs of individuals that we cannot distinguish in ranks. This was one of the limitations of the usual Swiss tournament, the other one was that only populations of size 2^n were considered. We extended this model to overcome these limitations, by considering a group of N individuals and introducing the concept of byes. For example if there is an unpaired individual (N odd), it will get a bye on the next round which is considered the same as winning. We call the new model the Swiss tournament with byes. At each round individuals with the same number of wins and losses are paired together. In the Swiss tournament with byes the sequence of wins and losses is not important. This means that a pair of individuals can fight each other more than once.

We showed that our model produces linear hierarchies all the time, because if a group of individuals has the same number of wins and losses, they will fight until this number is different. The individual with the highest number of wins will occupy the highest position in the group. Our model predicts that the winner will be that individual that has not lost a single fight while in the winner-loser model the winner does not necessary wins all the fights. We found the point in time when the winner is established and see that after this point, the winner will get a bye until the end, because no other individual can ever catch it. We did the same for the second place and showed that for the rest of the ranks it is not easy to find analytically the time when they are established. We also showed that the ranks are established in numerical ordering; the first to be decided is the winner, the second is the second place and so on until the last place individual. The last fight will be between bottom-ranked individuals. Because the first place has won all the contests, means that the total number of rounds coincides with the total number of wins for the first place individual. We derived a formula which gives a good approximation of the total number of rounds.

We continued our research and found the expected reward for an individual on a score $i|j$ (having won i contests until round j). There are examples from real populations where the division of resources is uneven, where only the top-ranked individuals have more access to the limited resources. The numerical example in Section 4.2.5.1 illustrates such scenarios.

Our model predicts that the level of aggressiveness is higher in individuals that are fighting for the top positions than it is in individuals fighting for the lower positions in the hierarchy. Those that are fighting for the lower positions are less aggressive as the reward is small for them. This model also predicts that the level of aggressiveness is higher when there are only two individuals left fighting for the higher rank. The winner then cannot be reached by any other individual as it will get a bye until the end of the competition. The level of aggressiveness for an individual x depends on the number of individuals that are one win less than this individual. If this number is large, the level of aggressiveness for x will be high and if it is small the level of aggressiveness will be low. The reason is that the larger the number of individuals with one win less than x, the larger the group that x would end up if it loses. Being in a smaller group is better than being in a larger one; we have less fights in smaller groups. Group size affect the level of aggression at the beginning as well, the larger the group size, the larger $p_{0,0}$ is. Thus individuals need to be more aggressive at the beginning. Other factors such as rewards and costs, influence the level of aggression as well. We see that as the cost is increased, the level of aggression decreases.

An important feature is that of the weighted average of the probability $p_{i,j}$ (being aggressive when on a score $i|j$). Using this model set up we found that as the group size is increased, the average probability is also increased.

If we compare the Swiss tournament with byes with the usual Swiss tournament, it is easy to prove that Results 1 - 6 in [23], hold in our model as well. Another important result is that while on most cases winning a fight, increases the level of aggression, this is not always true. We found that when $N = 4$ we have $p_{4,6} < p_{3,5}$. Furthermore, we found analytically that for a group of N individuals, $N(N-1)/2$ gives the total number of real fights.

Lastly, we compared Swiss tournaments with byes with the winner and loser models. They are both models that produce linear hierarchies, but Swiss tournament is better designed for larger populations where the linear hierarchy is quickly decided. This is not the case in winner and loser models where two random individuals are repeatedly paired against each other.

In summary, this model produces linear hierarchies if a group of individuals stays together for a long time, and it will be of future interest to test our predictions.

Chapter 5

Conclusions and future work

In this research study, we have explored the formation of dominance hierarchies. In particular, we were interested in analysing the relationship between key parameters, for example, reward size, population structure, prior experience and the level of aggressiveness in the population. We were concerned with situations where groups of individuals are meeting for the first time with no prior dominance relationships between pairs of individuals.

We have focused on the influence of the winner and loser effects on the formation of dominance hierarchies and aimed to understand different types of hierarchies that are commonly found in nature. These effects have been documented in different groups of animals which influence the level of aggressiveness and the chances of winning an escalated contest. They are independent of each other, we can have only the winner effect operating, only the loser effect or both to be present in a group of individuals. For decades, experimentalists have analysed the linearity of hierarchies in different species. A linear hierarchy is one where each individual has a clear rank in the group. In this study, we developed a new statistical measure describing the time until the hierarchy is established. This information is important for the experimentalists, as it provides a guideline of how many interactions need to be observed between individuals, until a dominance hierarchy is established. To our best knowledge no such measure has been found so far concerning winner and loser models.

We demonstrated that the level of linearity depends on whether the winner and loser effect are operating alone or both are present, as well as the level of information that each individual has about the strength of their groupmates. Our model, which is based on similar work of Dugatkin, predicts that if we find the winner effect only to be present in real populations, then the hierarchy should be linear. If the hierarchy is quickly decided, like often happens in nature, then it is likely that individuals can estimate the strength of their opponents. We showed that the more reliable the information that one has about its opponents' ability to win a fight, the quicker the linear hierarchy is established. Secondly, if we analyse the aggression in different groups of animals and find the loser effect only to be present, then we predict linear hierarchies if individuals could estimate (at least with some degree of accuracy) their opponents' strength, and less distinct hierarchies if they can not estimate their opponents strength at all. Thirdly, when both the winner and loser effect are found to be present, our model predicts linear hierarchies when individuals only possess a small amount of information about the other individuals in the group. Additionally, hierarchies with a clear winner, clear last place individual, but where the other positions may or may not be distinguishable, are established when they do not have any information about each other's ability to win a fight. Whether these intermediate positions are distinguishable or not is decided early in the fights.

As linear hierarchies are often observed in different groups of animals, we conclude from our research that one of the possible mechanisms to produce such hierarchies is the presence of winner and loser effects and that individuals are likely to posses some information about the strength of their groupmates. This model helps us to make predictions about how hierarchies can be formed under the influence of winner and loser effects, as well as the time when these hierarchies are established.

It will be of future interest to test our predictions in different groups of animals. There is evidence of the winner and loser effect in different species, but no observations have been carried out regarding the type of hierarchies that those species form, and how long they take to be established.

We went on to address questions such as when should individuals be more aggressive and what is the best strategy to play? To answer these questions we introduced game -theoretical elements in the form of strategic factors to the above winner-loser model. We found that in a group of individuals, the population evolves to a unique aggression threshold as opposed to a mixture of strategies. This means that, within any group, they all adopt the same decision rule against whom to fight. This model predicts the time of establishment of the dominance hierarchy to be small and that aggressive interactions only happen at the beginning. Applied to real world situations, this points to the crucial importance of the first few fights for hierarchy formation. Later fights only determine the position of the lower-ranked individuals. The effect of the group size is also analysed, and our model predicts lower aggression threshold levels in larger populations. This result is supported by different experimental evidences ([50], [51], [113] [117]). Another point of interest was to analyse how aggressive individuals are when the resources are limited, and our model predict that they should be more aggressive than when they are plentiful in order to obtain a larger share.

This model is presented in its simplest form as other factors, such as for example coalitions between individuals or migration, are not considered to be present. These effects are worth exploring in the future. In this research, we assume that the level of aggressiveness is determined by the winner and loser effect only, but there are other documented factors such as the audience effect and the bystander effect (see Chapter 1) as described in [43]. Although bystander effects are found to be present in different groups of animals such as fighting fish [100], chickens ([34], [35]) and rainbow trout [63], there is not a lot of empirical work regarding their influence on dominance hierarchy formation.

We note that these effects can only exist in groups larger than two individuals when they do not have a lot of information about the abilities of their opponents. We can develop the non-updated model as described in Chapter 1, so that it includes these factors. For example, we can include the audience effect, where individuals adjust their behaviour as a result of being watched by other individuals, by increasing or decreasing the value of the aggression threshold θ by a factor of $\varepsilon_1 \geq 0$ depending on the type of audience. If an individual increases (decreases) the value of θ, it means that it would be less (more) aggressive. In Siamese fighting fish [80], it was observed that males increase the level of aggressiveness in front of a female audience and decrease it in front of a male audience.

When the bystander effect is present, an individual X would vary its level of aggression according to what it observes in the group. We can include this effect by increasing or decreasing the value of $RHP_{initial}$ by a factor of $\varepsilon_2 \geq 0$. For example if X observes the fight between individuals Y and Z at time t where individual Y wins and Z loses, then X would increase the $RHP_{initial}$ when fighting Y and decrease it when fighting Z. This affects the aggressive behaviour of individual X which would be less aggressive against Y and more aggressive against Z.

This model set up would allow us to see whether a linear hierarchy could be established and if it is possible for a lower ranked individual to overturn its rank. When bystanders effects are present we would expect linear hierarchies to be established as this is similar to the updated model with imperfect information where linear hierarchies are always established.

In the last part of this work we give an alternative dominance hierarchy formation model based on the Swiss tournament as described by Broom & Cannings in [23]. This is a very structured model and the authors do not claim that in real populations animals will follow such model, but as animals often choose to fight opponents of the same strength and try to establish the dominance hierarchy quickly, this type of tournament might be a reasonable approximation. This model produces hierarchies in a relatively small number of rounds, but they are never linear and are applied to groups of 2^n individuals. To overcome these issues, we introduced the concept of byes for the unpaired individuals. The most important result of this part is that we find the exact number of fights until the hierarchy is established to be $N(N-1)/2$. The hierarchies following this model take longer than the usual Swiss tournament to establish, but are better designed than the winner and loser model, especially for large group sizes. Our model predicts that in real biological situations, if individuals are fighting with each other for a long period of time, linear hierarchies are always achieved. This model also predicts that if the group size is increased the level of aggressiveness is also increased. Another result derived from this model is that if an individual wins a number of fights in a row, does not guaranties an increase on aggressiveness. This model is potentially useful for human competitions, for example in chess tournaments, but whether animals behave like this, it still needs to be established through experimental research.

Appendix A

Expected payoffs for different V and C

In this section we give the expected payoffs for different combinations of k_x and k_y as described in Chapter 3 where both the $\ln(RHP)$ and the alternative payoff function are considered as payoffs.

	k=1(θ_y=1)	k=2(θ_y)=0.9	k=3(θ_y)=0.8	k=4(θ_y=0.7)	k=5(θ_y=0.65)	k=6(θ_y=0.6)	k=25(θ_y=0.1)
k=1(θ_x=1)	3.2560	2.8414	2.8414	2.7754	2.7392	2.7131	2.6645
k=2(θ_x)=0.9	3.5456	3.2550	3.1092	3.0271	2.9705	2.9417	2.8767
k=3(θ_x)=0.8	3.6699	3.4022	3.2517	3.1682	3.1168	3.0786	3.0138
k=4(θ_x=0.7)	3.7360	3.4843	3.3432	3.2572	3.1991	3.1643	3.0995
k=5(θ_x=0.65)	3.7721	3.5409	3.3946	3.3123	3.2588	3.2175	3.1514
k=6(θ_x=0.6)	3.7983	3.5697	3.4328	3.3471	3.2939	3.2570	3.1855
k=25(θ_x=0.1)	3.8469	3.6347	3.4976	3.4119	3.3600	3.3259	3.2551

Table A.1: Expected payoffs for different values of k when $V = 0.1, C = 0$

	k=1(θ_y=1)	k=2(θ_y)=0.9	k=3(θ_y)=0.8	k=4(θ_y=0.7)	k=5(θ_y=0.65)	k=6(θ_y=0.6)	k=25(θ_y=0.1)
k=1(θ_x=1)	0.500	0.4555	0.4364	0.4262	0.4207	0.4167	0.4092
k=2(θ_x)=0.9	0.5445	0.500	0.4775	0.4649	0.4562	0.4518	0.4418
k=3(θ_x)=0.8	0.5636	0.5225	0.4994	0.4866	0.4787	0.4728	0.4629
k=4(θ_x=0.7)	0.5738	0.5351	0.5134	0.500	0.4913	0.4860	0.4760
k=5(θ_x=0.65)	0.5793	0.5438	0.5213	0.5087	0.500	0.4941	0.4840
k=6(θ_x=0.6)	0.5833	0.5482	0.5272	0.5140	0.5059	0.500	0.4892
k=25(θ_x=0.1)	0.5908	0.5582	0.5371	0.5240	0.5160	0.5108	0.5000

Table A.2: Division of resources for different values of k when $V = 0.1, C = 0$

	k=0(θ_y=1.2)	k=1(θ_y)=1	k=2(θ_y)=0.9	k=3(θ_y=0.8)	k=4(θ_y=0.7)	k=5(θ_y=0.6)	k=22(θ_y=0.1)
k=0(θ_x=1.2)	2.3026	2.3026	2.3026	2.3026	2.3026	2.3026	2.3026
k=1(θ_x)=1	2.3026	2.2500	2.2122	2.1559	2.1156	2.0843	2.0052
k=2(θ_x)=0.9	2.3026	2.2099	2.1723	2.0648	2.0038	1.9601	1.8634
k=3(θ_x=0.8)	2.3026	2.1452	2.0539	1.9020	1.8218	1.7661	1.6553
k=4(θ_x=0.7)	2.3026	2.0961	1.9798	1.8064	1.7194	1.6621	1.5486
k=5(θ_x=0.6)	2.3026	2.0508	1.9208	1.7315	1.6421	1.5854	1.4706
k=22(θ_x=0.1)	2.3026	1.8927	1.7268	1.5113	1.4190	1.3606	1.2500

Table A.3: Expected payoffs for different values of k when $V = 0, C = 0.1$

	k=0(θ_y=1.2)	k=1(θ_y)=1	k=2(θ_y)=0.9	k=3(θ_y=0.8)	k=4(θ_y=0.7)	k=5(θ_y=0.6)	k=22(θ_y=0.1)
k=0(θ_x=1.2)	0.500	0.500	0.500	0.500	0.500	0.500	0.500
k=1(θ_x)=1	0.500	0.500	0.5004	0.5019	0.5038	0.5068	0.5293
k=2(θ_x)=0.9	0.500	0.4996	0.500	0.5020	0.5049	0.5084	0.5362
k=3(θ_x=0.8)	0.500	0.4981	0.4980	0.500	0.5035	0.5081	0.5395
k=4(θ_x=0.7)	0.500	0.4962	0.4951	0.4965	0.500	0.5048	0.5364
k=5(θ_x=0.6)	0.500	0.4932	0.4916	0.4919	0.4952	0.500	0.5317
k=22(θ_x=0.1)	0.500	0.4707	0.4638	0.4605	0.4636	0.4683	0.5000

Table A.4: Division of resources for different values of k when $V = 0, C = 0.1$

	k=0(θ_y=1.2)	k=1(θ_y)=0.9	k=2(θ_y)=0.7	k=3(θ_y=0.5)	k=4(θ_y=0.4)	k=5(θ_y=0.3)	k=9(θ_y=0.1)
k=0(θ_x=1.2)	2.3026	2.3026	2.3026	2.3026	2.3026	2.3026	2.3026
k=1(θ_x)=0.9	5.9490	4.0724	3.5544	3.3444	3.2392	3.2011	3.1203
k=2(θ_x)=0.7	5.9490	4.4956	3.9443	3.6854	3.5594	3.4934	3.4014
k=3(θ_x=0.5)	5.9490	4.6207	4.0597	3.7925	3.6494	3.5800	3.4715
k=4(θ_x=0.4)	5.9490	4.6521	4.0743	3.8035	3.6629	3.5895	3.4778
k=5(θ_x=0.3)	5.9490	4.6299	4.0573	3.7795	3.6393	3.5616	3.4574
k=9(θ_x=0.1)	5.9490	4.5454	3.9244	3.6488	3.5102	3.4255	3.3109

Table A.5: Expected payoffs for different values of k when $V = 0.2, C = 0.1$

	k=0(θ_y=1.2)	k=1(θ_y)=0.9	k=2(θ_y)=0.7	k=3(θ_y=0.5)	k=4(θ_y=0.4)	k=5(θ_y=0.3)	k=9(θ_y=0.1)
k=0(θ_x=1.2)	0.500	0.2790	0.2790	0.2790	0.2790	0.2790	0.2790
k=1(θ_x)=0.9	0.7210	0.500	0.4430	0.4233	0.4161	0.4161	0.4227
k=2(θ_x)=0.7	0.7210	0.5570	0.500	0.4781	0.4712	0.4701	0.4805
k=3(θ_x=0.5)	0.7210	0.5767	0.5219	0.500	0.4923	0.4916	0.5012
k=4(θ_x=0.4)	0.7210	0.5839	0.5288	0.5077	0.500	0.4991	0.5084
k=5(θ_x=0.3)	0.7210	0.5834	0.5299	0.5084	0.5009	0.500	0.5104
k=9(θ_x=0.1)	0.7210	0.5773	0.5195	0.4988	0.4916	0.4896	0.5000

Table A.6: Division of resources for different values of k when $V = 0.2, C = 0.1$

	k=0(θ_y=1.2)	k=1(θ_y=1)	k=2(θ_y=0.70)	k=3(θ_y=0.50)	k=4(θ_y=0.30)	k=5(θ_y=0.25)	k=8(θ_y=0.10)
k=0(θ_x=1.2)	2.3026	2.3026	2.3026	2.3026	2.3026	2.3026	2.3026
k=1(θ_x=1)	4.2088	3.1454	2.8027	2.6514	2.5755	2.5237	2.4678
k=2(θ_x=0.70)	4.2088	3.2896	2.8714	2.6631	2.5416	2.4852	2.4037
k=3(θ_x=0.50)	4.2088	3.2705	2.8019	2.565	2.4378	2.3715	2.2812
k=4(θ_x=0.30)	4.2088	3.2019	2.7000	2.4429	2.3217	2.2399	2.1442
k=5(θ_x=0.25)	4.2088	3.1383	2.5824	2.3190	2.1796	2.1203	2.0265
k=8(θ_x=0.10)	4.2088	2.9289	2.2914	2.0099	1.8699	1.8030	1.7182

Table A.7: Expected payoffs for different values of k when $V = 0.1, C = 0.2$

	k=0(θ_y=1.2)	k=1(θ_y=1)	k=2(θ_y=0.70)	k=3(θ_y=0.50)	k=4(θ_y=0.30)	k=5(θ_y=0.25)	k=8(θ_y=0.10)
k=0(θ_x=1.2)	0.5000	0.3536	0.3536	0.3536	0.3536	0.3536	0.3536
k=1(θ_x=1)	0.6464	0.5000	0.4630	0.4554	0.4600	0.4679	0.5091
k=2(θ_x)=0.70	0.6464	0.5370	0.5000	0.4938	0.5006	0.5171	0.5786
k=3(θ_x=0.50)	0.6464	0.5446	0.5062	0.5000	0.5092	0.5268	0.5936
k=4(θ_x=0.30)	0.6464	0.5400	0.4994	0.4905	0.5000	0.5177	0.5860
k=5(θ_x=0.25)	0.6464	0.5321	0.4829	0.4732	0.4823	0.5000	0.5684
k=8(θ_x=0.10)	0.6464	0.4909	0.4214	0.4064	0.4140	0.4316	0.5000

Table A.8: Division of resources for different values of k when $V = 0.1, C = 0.2$

	k=0(θ_y=1.2)	k=1(θ_y=0.85)	k=2(θ_y=0.59)	k=3(θ_y=0.41)	k=4(θ_y=0.28)	k=5(θ_y=0.19)	k=6(θ_y=0.13)
k=0(θ_x=1.2)	2.3026	2.3026	2.3026	2.3026	2.3026	2.3026	2.3026
k=1(θ_x=0.85)	7.5500	4.8750	4.1779	3.9227	3.8359	3.7927	3.7710
k=2(θ_x=0.59)	7.5500	5.4765	4.7500	4.4620	4.3284	4.2858	4.2275
k=3(θ_x=0.41)	7.5500	5.6512	4.9101	4.9000	4.4783	4.4089	4.3710
k=4(θ_x=0.28)	7.5500	5.6705	4.9720	4.6375	4.5023	4.4298	4.4038
k=5(θ_x=0.19)	7.5500	5.6573	4.9114	4.6229	4.4937	4.4200	4.3725
k=6(θ_x=0.13)	7.5500	5.6304	4.9107	4.5955	4.4477	4.3944	4.3500

Table A.9: Expected payoffs for different values of k when $V = 0.3, C = 0.1$

	k=0(θ_y=1.2)	k=1(θ_y=0.85)	k=2(θ_y=0.59)	k=3(θ_y=0.41)	k=4(θ_y=0.28)	k=5(θ_y=0.19)	k=6(θ_y=0.13)
k=0(θ_x=1.2)	0.5000	0.2337	0.2337	0.2337	0.2337	0.2337	0.2337
k=1(θ_x=0.85)	0.7663	0.5000	0.4342	0.4131	0.4089	0.4088	0.4104
k=2(θ_x=0.59)	0.7663	0.5658	0.5000	0.4783	0.4711	0.4727	0.4714
k=3(θ_x=0.41)	0.7663	0.5869	0.5217	0.5000	0.4936	0.4926	0.4940
k=4(θ_x=0.28)	0.7663	0.5911	0.5289	0.5064	0.5000	0.4986	0.5016
k=5(θ_x=0.19)	0.7663	0.5912	0.5273	0.5074	0.5014	0.5000	0.5007
k=6(θ_x=0.13)	0.7663	0.5896	0.5286	0.5060	0.4984	0.4993	0.5000

Table A.10: Division of resources for different values of k when $V = 0.3, C = 0.1$

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