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Modelling post-injury behaviour in chimpanzees using artificial life

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Abstract
Injury affects individuals' health and fitness in a direct manner, and pain-related behaviours promote escaping, healing and recovery. Therefore, communicating pain might be an advantageous strategy in those social contexts where caregivers are able to recognize the agent in pain and provide help. However, pain expression can also indicate vulnerability, from which predators or conspecifics can take advantage of. For this project, an agent-based model has been developed to study post-injury behaviour in a hierarchical community of wild chimpanzees, where the presence of dominance rank influences the adequacy of certain strategies. The model simulated the effect of injuries on primates' health. Several experiments were performed to analyse the effects of more frequent injury, disparities between social ranks, and the expression of pain. The dynamics observed correlate with behaviours seen in the wild. Moreover, results suggested that in hierarchical communities of chimpanzees, the possible benefits of social grooming and being helped by others do not offset the costs of expressing pain after injury occurs.

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1. Introduction

Injury has a major effect on animals' survival rate and fitness. Therefore, the mechanisms by which individuals promote healing and recovery are crucial for their health. Behaviours associated with pain serve to prioritize efforts, conserving the energy required for immune response and wound care [1]. Moreover, the expression of pain can be an advantage in social contexts where caregivers are able to identify the affected individual and provide help. Hence, whether pain-related behaviours represent an advantage for animal's fitness depends on their environmental and social conditions [1].

Primates in the wild are subject to a range of threats that can cause injuries. These threats include the presence of predators, illnesses, adverse environmental conditions or intra-species conflicts. So far, non-systematic pain-related behaviours have been observed for primates in the wild. Their hierarchical organization determines the access by individuals to resources, which greatly affects their condition and health [2]. Under this social context, expressing pain might indicate vulnerability, resulting in the loss of rank or attacks from predators. Therefore, it is important to understand whether the costs of showing pain might motivate the suppression of pain-related behaviours in the wild.

Conditions hinder behavioural studies of primates in the wild, where researchers keep a distance and do not intervene, and ethics constrain what experimental work can be done with captive primates. It is here that simulation techniques can play a role, helping to test and generate new hypotheses. Agent-based modelling offers a unique way to simulate particular environments under controlled conditions, helping to understand the social dynamics that emerge from individual behaviours. In this report, an agent-based model has been developed to study the role of post-injury behaviours in the dynamics of a hierarchical community of male chimpanzees.

1.1 Injury, pain and associated behaviours

Injury All animals are exposed to a variety of injuries across their lifespan, which affect their survival and health in a direct manner. Many forms of injury do not result in death, but they can significantly reduce their fitness and reproduction rates. Therefore, injury has applied selection pressure on all forms of life throughout history and has consequently selected those mechanisms that provide the best adaptive responses [2].

Pain In humans, pain has been considered a sensory and emotional experience associated with perceived or anticipated injury [2]. The fact that pain has been defined in terms of subjective human experience makes it difficult to verify if these perceptions also occur in non-human species. Nevertheless, observations of similar animal behaviours in response to noxious stimuli have provided models of pain behaviour in animals [2]. Wall (1979) [3] divided the period after injury in three main stages and pointed that the degree of damage is poorly related to the intensity of pain: First, the immediate stage after injury, when activities such as escaping from the source of injury or defensive fighting take priority over the experience of pain. Subsequently, the acute phase begins, when pain and anxiety are experienced. The nature of this state arises from the need to cope with the injury and prepare for recovery. And ultimately, the chronic stage, characterized by more pain, long periods of inactivity and sleep [3].

Pain behaviour and social context Pain behaviours can be separated depending on their function into those that promote protection (e.g., wound care or guarding) and those that have a communicative aim (e.g., facial expressions or vocalizations) [4]. Those behaviours that have a primary communicative function are dependent on social contexts, as they have associated costs and benefits [4]:

Communicative pain expression can be considered a benefit under those scenarios in which social support is present and conspecifics are able to recognize individuals in pain and help them [1]. Experimental studies in mice have reported an increase in pain-related behaviours when noxious stimuli were applied to cage-mate mice that faced each other compared to a situation where they were isolated [5]. Moreover, human patients with chronic pain have proven to report higher levels of pain experience in the presence of relatives [6]. Therefore, pain expression seems to be more frequent in those environments where there is social support.

However, under threatening social environments, communicative pain behaviours can indicate vulnerability [7]. This vulnerability can result in attacks from predators or conflicts with conspecifics. It is known that some animals might mask the signs of pain under certain conditions. Primates in the wild are exposed to different threats that can result in high costs if pain is expressed [8]. Apart from becoming targets to predators, their social status can be threatened, which would have significant consequences on their condition and health [8]. Therefore, in order to understand the advantages and costs of pain behaviours in wild primates, it is important to take into account their hierarchical structure and organization.

1.2 Dominance hierarchies

In this study, dominance rank in male chimpanzees has been modelled. Compared to females, social status in males seems to have more impact on access to resource's and health [9]. However, it is important to note that the influence of social rank varies depending on sex and species [10].

In chimpanzees, dominance relationships between males are based on dyadic interactions. The number of pant-grunt vocalizations between individuals correlates with multiple measures of dominance and is therefore used to determine their social rank in the community [11]. In Figure 1, an example of dominance relationships of a community of chimpanzees can be observed. Dominance relationships were based on the number of times one chimpanzee pant-grunted the other. As a result, an approximate linear hierarchy can be observed, in which individuals at the top of the table clearly dominate over the bottom ones. However, as dominance hierarchies are not always strictly linear, social status is commonly separated between high, middle, and low rank [9] (horizontal bold lines Figure 1).

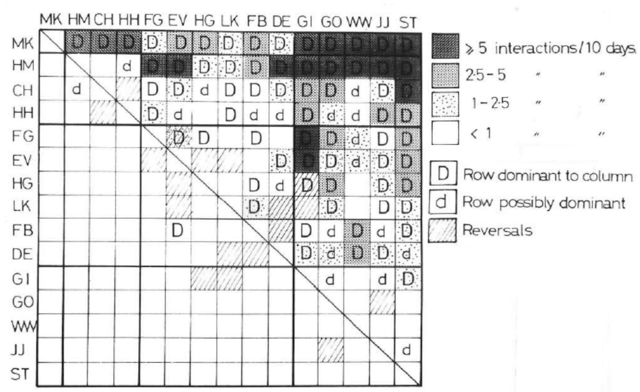


Figure 1. Dominance relationships among adult males in Gombe National Park between 1970 and 1971. Figure from [9].

Dominance ranks change across an individual's lifespan depending on several factors. First, age seems to be closely related with rank. In Figure 2 it can be observed how rank increases from early adulthood to late middle-age, and then drops towards the end of life. Other factors such as body size, coalitions, frequency of aggression or personality have also been reported to determine social rank [9].

High social status has a number of associated benefits. First, a positive relationship has been observed between high rank and reproductive success in many primates [10]. Moreover, dominant males have greater foraging success and access to resources than subordinates [11]. Higher-ranked chimpanzees have been observed to spend longer periods of time grooming, which creates strong relations between conspecifics and has a number of associated health benefits. Recent studies in baboons have also reported differences in immunitary response depending on social status, where faster wound healing rates were found in high-ranking males [12]. However, high rank also comes with an energetic cost and stress. Higher ranked primates spend more time and energy defending territory, foraging, and fighting for social status. As a result, higher ranks are normally maintained for shorter periods of time [13].

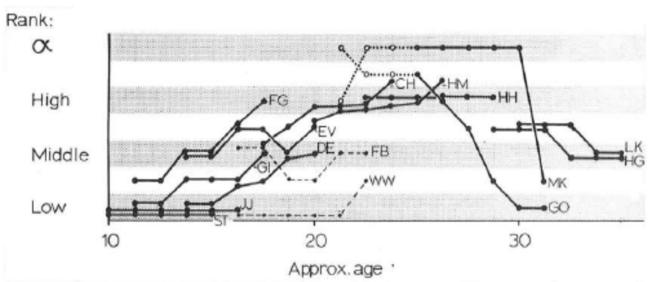


Figure 2. Changes in dominance rank between 1966-1971. Data was taken from chimapnzees between 10 and 35 years. Figure from [9].

1.3 Context and experimental aims

This study aims to analyse post-injury behaviour in a hierarchical society of male chimpanzees through agent-based modelling. With this approach, current knowledge on pain-related behaviour and primate hierarchical organization can be combined to detect emerging dynamics under different scenarios. This is achieved by generating a number of agents that can forage, increase in age, compete for rank, become injured, be born, die, and either express pain or not.

This expands on work carried out in previous studies simulating pain expressiveness and altruistic behaviour in generic mammals [1]. Some findings from previous studies include that the expression of pain was a feasible strategy under those scenarios in which the frequency of injury was low and there was pro-social behaviour in the community. However, when there was frequent injury, or the risk of being exploited by others was high, not expressing pain represented a better strategy [1].

2. Methods

2.1 Agent-Based Modelling

Agent-based modelling is a computational technique in which agents are treated as discrete entities with a set of properties that change over the simulation time according to certain procedural rules. In biology, this ”bottom-up” approach allows researchers to study the big scale dynamics of biological systems emerge from the underlying characteristics of the individuals. Compared to continuous population-level models, more realistic assumptions at an individual scale can be implemented in agent-based models (ABMs). However, it is important to determine the degree of complexity to introduce in an ABM. ABMs offer the possibility to simulate very detailed characteristics on the small scale, but excessive complexity can come with greater uncertainty and hard parametrization.

2.2 Model description

The purpose of this model is to analyse and understand post-injury behaviour in the dynamics of a hierarchical chimpanzee community. Specifically, the effect of increasing the frequency of injury, differences between social statuses, and varying costs and benefits of expressing pain have been studied.

The fundamental entity of the model is a male chimpanzee, which is characterized by the following properties: age, energy, energy increase, social rank and strategy. Some of these properties can change over time according to the processes shown in Figure 3. Across their lifespans, agents can increase their energy (fitness) by foraging or decrease it if they get injured. Their relative energy in the community is used as a proxy for their social rank, which determines their access to resources as well as their probability of getting injured. The final experiments simulated chimpanzees with different strategies: agents were able to express pain when getting injured, which promoted faster recovery rates, but in turn, increased their chance of getting injured (simulating their vulnerability to predators and conspecifics who might challenge them). In the following section, variables characterizing agent's properties and processes will be described in detail.

Simulations occur in a non-spatial environment and the time scale was established at 1 year per iteration, which was small enough to simulate the lifespan of chimpanzees and made simulations computationally feasible. The model was implemented in MATLAB [14], which is a high level programming language and interactive computing environment.

2.3 Agent properties

2.3.1 Age

Agents increased 1 year per iteration until reaching a maximum age, when they died and were replaced by a new agent. In this way, a constant number of individuals was maintained. Maximum ages were randomly assigned according to a normal distribution centred at Age_{MAX}. At the beginning of the simulation, initial ages were taken from a random uniform distribution between 1 and their maximum age.

2.3.2 Energy

The energy level represents the fitness and health of an agent. All agents started with the same initial energy ($E_{initial}$), and by "foraging" they received a certain energy increase. However, energy levels decreased every time the agent was injured. If an agent reached a maximum energy level (E_{MAX}), they continued foraging, maintaining but not increasing energy. E_{MAX} was settled 10 times the maximum possible energy increase (default value of 60). In this way, just a few agents were able to reach the maximum energy level (maximum state of health) at each generation. Finally, if energy levels fell below half the initial energy, the agent died. In Figure 4a, the evolution of energy shows how an agent tries to maximize its health throughout its life, but it is limited by injuries and variable energy increases.

2.3.3 Dominance Rank

The dominance rank was an emergent property of agents. Ranks were assigned according to the energy level that agents had relative to the other members in the community at a certain time. In this way, the agent with highest energy level was always rank 1, whereas the one with the lowest energy level was the one at the bottom of the hierarchy. Higher ranked individuals had more access to resources but also more chances of being injured.

2.3.4 Energy increase

The value of energy increase (E_{inc}) represented the access of each agent to resources. This variable changed as a function of age and rank. The idea behind this implementation is to simulate a linear distribution of the resources according to social rank, but also limited by their age. This dependence follows evidence from experimental studies in male chimpanzees [9]. The relation between energy increase, rank and age was established according to Equation 1 :

$$E_{inc}\ (Rank, Age) = [\Delta_{E_{inc}} \cdot ((Rank_{MAX}+1) - Rank)] \cdot e^{-\frac{(Age-mean)^2}{2 \cdot stdev^2}} \tag{1}$$

The first part of the equation determines the dependence of E_{inc} with rank, where $\Delta_{E_{inc}}$ is the difference in E_{inc} between consecutive ranks. It is important to note that by increasing $\Delta_{E_{inc}}$, larger differences in resources' distribution between ranks are simulated. Therefore, in one of the experiments, the effect of increasing disparities in resource access between ranks was analysed by changing $\Delta_{E_{inc}}$. The second part of the equation is a Gaussian distributed factor centred at $Age_{MAX}/2$ (17.5 years) and standard deviation of 7 years. This factor can take values from 0 to 1, being 1 at $Age_{MAX}/2$. In this way, the E_{inc} was limited by age during juvenile and old ages.

2.3.5 Strategy

Each agent was born with a predefined strategy: expressing or not expressing pain when injured. The benefit of expressing pain was modelled with the assumption that agents received help from conspecifics.

Those agents that expressed pain when injured had the benefit of recovering faster, simulating in this way pro-social behaviour from other individuals in the community. This benefit was implemented using b_{exp}, which can take values from 0 to 1, and increased the E_{inc} by a certain % while expressors were recovering from injuries. In this way, a value of b_{exp} of 0.5 determined an increase in E_{inc} of 50 %. The effects of varying the degree of social support in the community were analysed by changing b_{exp}. However, expressing pain also came at a cost, which was simulated by increasing the chances of getting injured. This cost is explained by the fact that when perceived as vulnerable, predators or conspecifics can take advantage of the injured individual [10]. The costs of showing pain were studied by increasing c_{exp}, which can take values from 0 to 1, where 1 means a 100 % chances of getting injured when showing pain.

Strategies were not inherited during the simulations, and homogeneous communities were simulated in each experiment (either all expressors or non-expressors). As a first approach, base-line experiments were carried out in a community of non-expressors. Then, the costs and benefits of expressing pain were studied in subsequent analyses.

2.4 Injury

The main processes of the model can be observed in Figure 3. Ageing, foraging, expressing pain and death and birth occur according to the rules described in the previous section. However, injury is modelled as an external effect on the agent's energy. The effect of injury in the model pretends to simulate a decrease in health due to natural injuries, illnesses and fights. At each iteration, a number of agents ($n_{injured}$) were selected for injury. Consistent with experimental evidence [15], it was assumed that higher ranks were exposed to more energy-demanding activities (such as mate-guarding, defending territory, or more frequent foraging) and were also more likely to be challenged by lower ranks. Therefore, an exponential probability density function was applied to determine the likelihood of getting injured depending on rank, such that higher ranks had higher chances.

When selected for injury, the agents' energy decreased by a random %. . The percentage of energy decreased when an individual was injured was randomly selected from an exponential distribution with a mean of 20 % ($injury_{severity}$) and limited between 0 and 100 %. In this way, small injuries were simulated to be more common than sever ones.

2.5 Parameters

The main parameters of the model and their respective default values are presented in Table 1. Due to the time limitations of this short study, it is not feasible to investigate the effect of each parameter and their possible combinations. Therefore, a number of key parameters were varied 1 at a time to address different questions while the other remained constant at their default value.

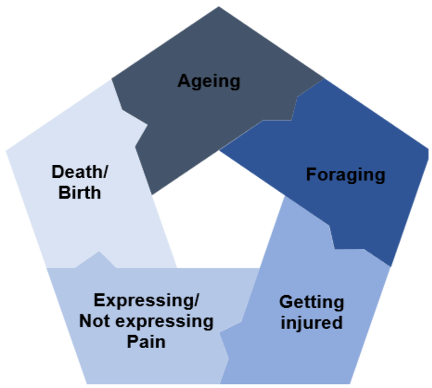


Figure 3. Processes in the model.

Table 1. Default values for the main parameters

Parameter	Default value	Range varied
$n^o agents$	20	–
Age_{MAX}	35	–
$E_{initial}$	10	–
$injury_{severity}$	20 %	–
$n_{injured}$	3	0 – 9
$\Delta_{E_{inc}}$	0.3	0.1 – 0.5
c_{exp}	0.1	0 – 1
b_{exp}	0.1	0 – 1

The number of agents and the average maximum age were maintained constant, and their default values were approximated from field studies in communities of wild chimpanzees [9, 8, 16]. It is important to note that although it has not been analysed in this report, changes in mean injury severity ($injury_{severity}$) have a significant effect on the output. However, an $injury_{severity}$ of 20 % (decrease of E in 20 %) seemed to produce a feasible evolution of energy throughout agents lifespan. On the other hand, the effects of more frequent injury were analysed by varying $n_{injured}$.

In Figure 4, an example of an agent's lifespan is displayed. During the simulation, the agent was injured 4 times. At the age of 18-19 years an injury decreased its energy by 15 units, but a relatively high E_{inc} allowed a fast recovery. However, as E_{inc} decreased as a function of age (and rank), it is clear that the agent was unable to recover from the severe injury that occurred at the age of 30. With this approach, the time that an agent spent recovering from an injury depends on the severity of the injury and the energy increase at that time. For agents expressing pain, during the period of recovery, an increase in E_{inc} was applied, simulating faster recovery rates.

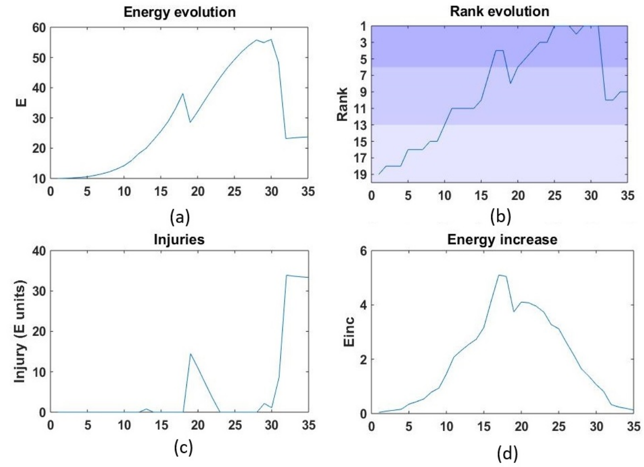


Figure 4. Evolution of (a) Energy, (b) Rank, (c) Injuries and (d) Energy increase across the lifespan of a non-expressor agent.

3. Experiments and results

By using the model previously described, three main experiments were performed to address different questions. First, the effect of injuries on a hierarchical society was studied by varying $n_{injured}$ and analysing how the rank of chimpanzees evolved over their lifespan. Next, the effect of greater disparities in access to resources between consecutive ranks was studied by varying $\Delta_{E_{inc}}$ and comparing the evolution of dominance rank. In those plots displaying the evolution of rank over time, high, middle, and high rank were differentiated with graded blue bands. For simplicity, in these two experiments all agents were considered non-expressors.

Following, further experiments were carried out to evaluate the effect of expressing pain within the context of a hierarchical community by varying c_{exp} and b_{exp} one at a time and displaying the evolution of mean energy (health) and rank. For each simulation, all agents were considered to be expressors, and the results were compared between them and communities of non-expressors. The values of first b_{exp} and then c_{exp} were iteratively increased in the same proportion. It is important to note that a increases of 0.25 in b_{exp} or c_{exp} represented a 25 % increase in the E_{inc} when recovering and 25 % increase in the chances of getting injured respectively.

3.1 Varying injuries per iteration

The aims of this experiment were to study the effect of increasing the dangerousness of the environment and settle a plausible value for $n_{injured}$. In order to do it, $n_{injured}$ was increased systematically from 0 to 9 by steps of 3, and the evolution of rank over time was displayed using box plots (Figure 5). Each plot shows the distribution of ranks when agents were 0, 5, 10, 15, 20, 25, 30 and 35 years of age. The results from Figure 5 were obtained maintaining a constant population size of 20 non-expressor agents, and each plot was generated performing 5 simulations running for 10,000 iterations. With this length and number of simulations, it was ensured that consistent plots were obtained from repeated experiments.

The outputs were presented using box plots in order to visualize the spread and skewness of the data. In each box plot, the edges indicate the 25^{th} and 75^{th} percentiles, whereas the central mark is the median. Whiskers extend until the extreme data points not considered outliers, and the outliers were individually plotted in red using the '+' symbol.

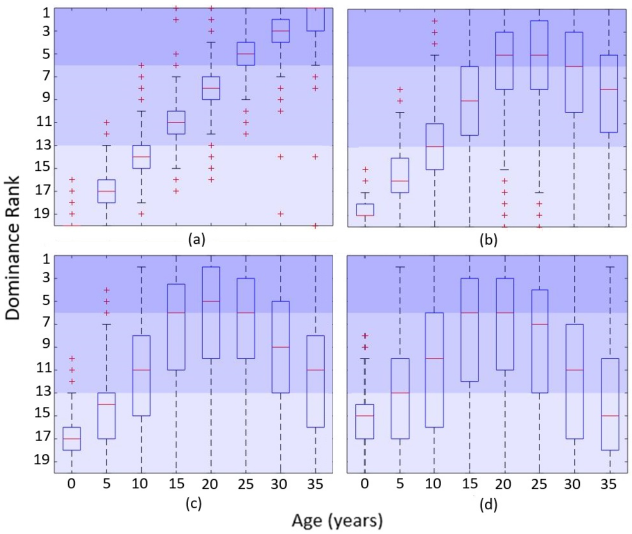


Figure 5. Box plot showing the effect of increasing injuries per iteration on rank evolution. Each simulation ran for 10,000 iterations. (a) 0, (b) 3 (c) 6 (d) 9 injuries per iteration.

3.2 Varying differences between ranks

The disparities in access to resources were simulated by means of gradually increasing $\Delta_{E_{inc}}$ and the emerging dynamics were observed. As previously mentioned, the role of social rank was modelled through its influence on E_{inc}. Without considering the effect of age on E_{inc}, ranks imposed a linear distribution of access to resources where $\Delta_{E_{inc}}$ determined the difference in E_{inc} between consecutive ranks (Equation 1). Therefore, by performing different simulations modifying $\Delta_{E_{inc}}$, greater disparities between ranks were analysed, simulating steeper hierarchical communities.

In this section, $\Delta_{E_{inc}}$ was iteratively increased from 0.1 to 0.5 by steps of 0.1, and the evolution in agents' social rank was displayed (Figure 6). In order to clearly show differences between simulations, the results from this study were presented by plotting the mean rank at different age stages with their respective error bars. Likewise in the previous section, a constant population of 20 non-expressors individuals was maintained through 10,000 iterations, and each plot from Figure 6 was generated with data from 5 simulations under the same conditions.

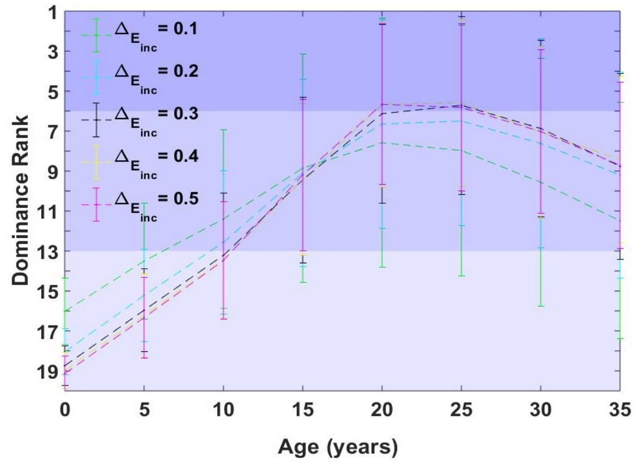


Figure 6. Line plots with error bars displaying the evolution of dominance rank when increasing $\Delta_{E_{inc}}$.

3.3 Varying costs and benefits of expressing pain

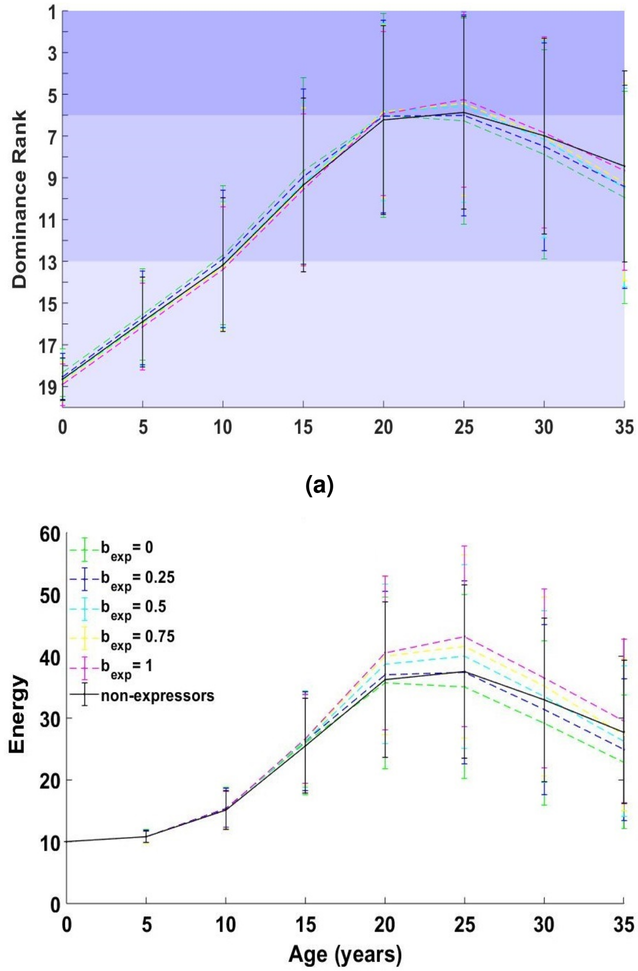
The aim of these experiments was to study whether expressing pain might be an advantageous strategy for chimpanzees in the wild. In order to approach this question, the benefits and costs of expressing pain were modified one at a time. First, b_{exp} was increased from 0 to 1 in steps of 0.25 while c_{exp} kept constant at 0.1. Next, b_{exp} was maintained at 0.1 while c_{exp} was systematically increased in the same way.

As an output, the evolution of rank and energy over the agents' lifespan was displayed to observe the effect on the social hierarchy and the agents' health (Figure 7, 8). The results were obtained from homogeneous populations of expressors and compared with a community of non-expressors. For each value of b_{exp} and c_{exp}, 5 simulations were performed over 10,000 iterations with a constant population of 20 agents.

4. Discussion

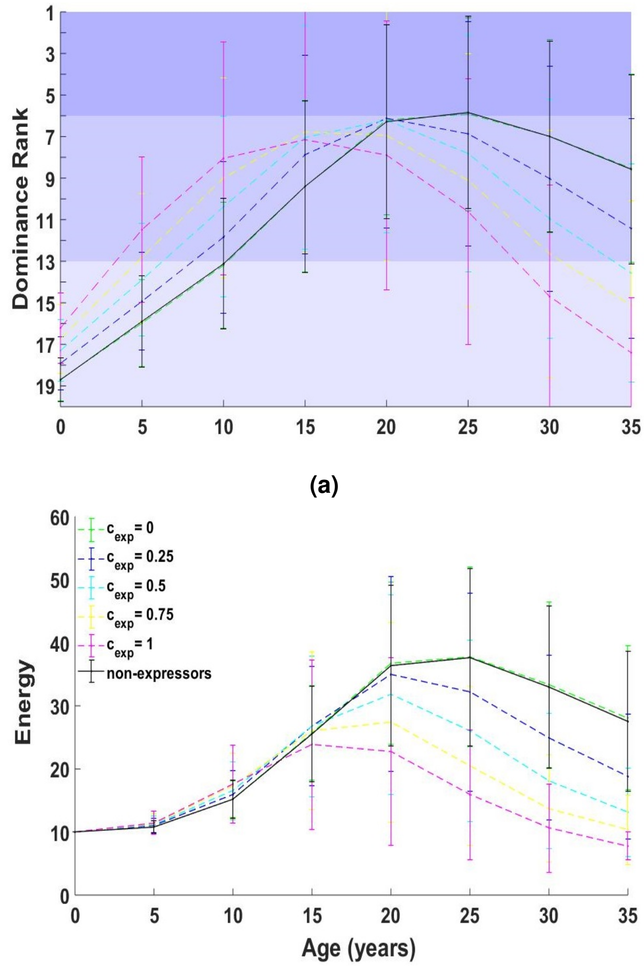
Effect of injuries From Figure 5a, it can be observed that when the frequency of injury was null, the rank of agents kept increasing over their life in a constant way, and most of them were able to become alpha male at the age of 35. In the following figures, it is clear that by increasing the number of injuries per iteration, agents' rank tended to decrease by the end of their life, as they were less able to recover after injury. Moreover, higher frequency of injury resulted in more variability on rank at a certain age. Finally, the top rank obtained during an agent lifespan was achieved earlier when the frequency of injury was higher. As experimental studies indicate that chimpanzees tend to reach their maximum rank around the age of 20-25 [17] and then rank decreases, $n_{injured}$ was settled at 3 injuries per iteration.

Because age limited agents' access to resources, in more dangerous environments it seems that individuals would achieve their top rank by the age of 17-18, when they are not limited



(a) (b)

Figure 7. Evolution of **(a)** dominance rank and **(b)** energy when varying the benefits of showing pain. For this experiment c_{exp} was kept at 0.1, except for the non-expressors community.



(a) (b)

Figure 8. Evolution of **(a)** dominance rank and **(b)** energy when varying the costs of showing pain. For this experiment b_{exp} was kept at 0.1, except for the non-expressors community.

by physical condition (Figure 5d). However, in those environments where injury frequency was relatively low (Figure 5b), agents kept increasing their fitness even when age might have an impact on their physical condition (since the Equation 1 factor takes low values by the age of 20-25). These results suggest that for certain frequency of injury and during a limited period of time, the benefits of being in a high rank (more access to resources) can compensate for the higher chances of injury and the effect of age on their ability to forage.

Effect of social rank Figure 6 shows how increasing disparities in E_{inc} between ranks allowed more agents to reach high ranks during the adult stage. However, in those simulations where $\Delta_{E_{inc}}$ was lower (0.1-0.2), it can be observed how the rank of agents during the juvenile stage was higher than the rank obtained in simulations with greater disparities, but then the majority of agents remained as middle rank during the rest of their life. It is important to note that the shape of the curves changes when increasing $\Delta_{E_{inc}}$ from 0.1 to 0.3 and then remains approximately the same from 0.3 to 0.5. Therefore, $\Delta_{E_{inc}}$ was settled at a default value of 0.3, which was large enough to produce a plausible evolution of rank over the agents' lifespan.

These graphs indicate that when differences between ranks are very low (less hierarchical societies), agents tended to have more stable but lower social ranks during their lifespan. This dynamic arises from the fact that when getting injured, the decrease in rank was more significant in those societies with lower disparities, limiting individuals to achieve higher ranks (as they would have more chances of injury).

Effect of expressing pain As shown in Figure 7a, increasing the benefits of expressing pain had little effect on the evolution of rank. However, the benefits of pain expression had more influence on the evolution of energy. As it was expected, when the benefits were greater, the overall health across the lifespan of individuals increased. Although dominance rank and energy displayed a similar evolution over time, it can be noticed that between 0 and 10 years of age, individuals experienced a little increase in energy whereas rank kept increasing at a constant rate. This fact can be explained by changes in hierarchy membership (in the simulation, agents died and were replaced by others with $E_{initial}$), which is one of the main causes of variation in dominance ranks [10].

From Figure 8, it is clear that increasing costs of showing pain had a greater impact on the evolution of rank and energy compared to the effect that increased benefits had. When increasing the costs of pain by 0.25, the overall health across individuals' lifespan decreased significantly and high ranks were maintained for shorter periods. Moreover, higher ranks at the juvenile stage were found in those simulations in which the costs of expressing pain were higher (Figure 8a). Higher costs determined more injuries in the population, and consequently lower overall health in the community (Figure 8b). As a result, the initial health of agents relative to the other members was higher in populations where expressing pain was more costly, and higher ranks were therefore reached earlier in individuals' lifespan.

Conclusions and future work The agent-based model developed has enabled to explore the role of injury and emerging dynamics within the context of hierarchical communities of chimpanzees. Some of the results obtained with the simulations correlate with behaviours seen experimentally. It has been found that in those environments where injury is more frequent, individuals achieved their maximum rank earlier than in less dangerous environments. Moreover, the results obtained when individuals expressed pain suggested that in hierarchical communities the benefits of expressing pain when there is pro-social behaviour have less impact than the possible costs of being challenged when detected as vulnerable by predators or conspecifics. This finding is consistent with experimental studies where captive primates masked the signs of pain [18, 8]. Therefore, it is suggested that in hierarchical communities of wild chimpanzees the benefits of grooming and being helped might not offset the costs of expressing pain after injury occurs.

Computational and time limitations of this project leave ample room for further development. In this study, not all the parameters were analysed. Therefore, an accurate sensibility analysis of the parameters used in the model would add robustness to the results obtained. Moreover, by allowing individuals to inherit strategies from their parents and generating communities with both strategies, the final proportions at the equilibrium could be studied as a single and informative output. However, the low number of agents and relatively short life made the inheritance of strategies extremely sensible to randomness in this model. Finally, introducing females in the model would add stability to the proportion of strategies in the community, and their interactions with males might give new insights into post-injury behaviours in chimpanzees.

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