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# **Emergent patterns of affiliative behaviour in group-living lemurs**

**By**

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## Abstract

Many patterns of affiliative behaviour have been described for lemurs, such as grooming reciprocation, grooming up the hierarchy and grooming others of similar rank. The patterns have been suggested to emerge due to specific cognitive processes in these animals such as recordkeeping of acts given and received, selective attractions towards dominants or similar ranked individuals. However, as more parsimonious alternative, these patterns can be shown to emerge from interactions among individuals and their environment rather than from cognition. In present paper, we investigated the patterns of affiliative behaviour of two species of lemurs that vary in their degree of despotism – *Lemur catta* and *Eulemur rufifrons*. We then used an agent-based model based on concepts of self-organization to generate the patterns observed in these two species of lemurs. In our model, called LemGroWorld, individuals tend to group, forage for food, and may perform a dominance interaction when competing for food or space. The outcome of winning or losing in these dominance interactions is self-reinforcing. If individuals think they will be defeated, they consider grooming the opponent. Our model was able to generate patterns similar to many affiliative patterns observed in the empirical data. When the distribution of food is changed from uniform to patchy, the rate of grooming increased and the proportion of mutual grooming bouts decreased. Thus, by merely changing the distribution of food the patterns in the model changed from those resembling less despotic lemurs to those resembling more despotic ones. Patterns in our model emerged through local interactions and rule of thumb, rather than the specific cognitive processes that are usually thought to underlie these patterns. Therefore, in order to increase our understanding of affiliative behaviour of lemurs, our model can be used as a null model that indicates what patterns might be expected in the absence of the usual cognitive rules.

## Introduction

Grooming behaviour is one of the most common affiliative behaviour observed in group-living primates (Schino et al., 1988). It has been suggested to provide benefits to the recipient in the form of improved hygiene (Hutchins & Barash, 1976), and reduction of tension (Schino et al., 1988). The market theory (Barrett et al., 1999; Noë & Hammerstein, 1995) explains that grooming represents a service in a biological marketplace, where it can either be exchange for itself (reciprocation) – for its own intrinsic benefits, or it can be exchanged for other services (interchange) – agonistic support (Schino, 2007), tolerance (Berman & Kapsalis, 1996), food (de Waal, 1997) or mating (Gumert, 2007). Studies on female chacma baboons suggested that the decision to reciprocate or exchange grooming is dependent on the degree of competition in the social group (Barrett et al., 1999). In despotic societies where dominance gradient is steeper (Vehrencamp, 1983), grooming was largely exchanged for other services. Here lower ranking individuals were more likely to direct grooming up the hierarchy, in exchange for support or tolerance from

dominants (Henazi & Barrett, 1999). Conversely, in egalitarian societies where dominance gradients are shallow (Vehrencamp, 1983), grooming was predominantly reciprocal. Since individuals that are closer in rank cannot exchange anything other than grooming (Barrett et al., 1999).

Although the market theory explains many of the patterns of affiliative behaviour that have been observed in primates, it also poses several problems. Firstly, the anthropocentric view of the biological marketplace can lead to over/under estimation of the cognitive ability of these animals (Barrett et al., 2007). Secondly, many specific cognitive processes have been suggested to explain the various affiliative patterns. In order to exchange grooming, individuals must keep records of given and received behaviour (de Waal & Luttrell, 1988), and then use their knowledge of the rank of others to decide how it exchanges grooming (reciprocate or interchange). Further, individuals are supposed to be selectively attracted towards dominants or others of similar rank (Seyfarth, 1977, 1981). Although, primates are intelligent (Seed & Tomasello, 2010), it is hard to imagine that they intentionally combine all these cognitive considerations in their distribution of grooming. As a more parsimonious alternative, patterns of complex behaviour can emerge from simple rules with fewer cognitive processes (Camazine et al., 2003; Hemelrijk, 2002; Puga-Gonzalez et al., 2009).

Recent studies using complexity science have demonstrated that complex patterns of social behaviour may emerge by self-organization, due to interactions among individuals and their environment (Hemelrijk, 2002; Hemelrijk et al., 2017). This has been demonstrated in the case of affiliative behaviour by the GrooFiWorld model (Puga-Gonzalez et al., 2009). The model ignores many of the specific cognitive assumptions that have been made for primates such as recordkeeping, selective attractions towards specific individuals, and tendency to exchange). Individuals in the model tend to group and can recognise the rank of others. Upon meeting other individuals may perform dominance interactions, the outcome of which are self-reinforcing. This implies that winning increases the chances of victory in subsequent fights, while losing increases the chance of defeat in subsequent fights (Hsu & Wolf, 1999). Lastly, individuals are sensitive to the risk of losing a fight, and so groom when they expect to be defeated. Using the rule for grooming from the fear of defeat, the model was able to generate many patterns of affiliative behaviour such as grooming reciprocation (without recordkeeping), grooming up the hierarchy (without interchange for grooming) and grooming of similar rank (without selective attraction towards dominants or similar ranked individuals). Additionally, by changing the intensity of aggression, affiliative patterns in the model changed from those resembling egalitarian macaques to those resembling despotic macaques.

In our study we investigate the patterns of affiliative behaviour of group-living lemurs. Grooming interactions in lemurs are more intimate and highly reciprocal, compared to anthropoids (Barton, 1987). However, they show some of the same patterns such as grooming reciprocation, grooming up the hierarchy, and grooming others of similar rank (Nakamichi & Koyama, 1997; Port et al., 2009). Thus, in this

study we first examined the patterns of affiliative for two species of lemurs – *Lemur catta* (Ring-tailed lemur) and *Eulemur rufifrons* (Red-fronted lemur) (Norscia & Palagi, 2015). For this purpose, we used observational data from multiple groups for each species. We then used an agent-based model to study how the patterns of affiliative behaviour of lemurs can emerge by self-organisation.

Our model is an extension to the LemurWorld model (Hielkema, n.d.). We decided to use this model as it has previously been used to demonstrate the emergence female dominance in lemurs, and can produce patterns of aggression and dominance that resemble that of despotic and egalitarian lemurs. Individuals in this model tend to group, they forage for food when they have less energy, and fight to secure their food. Female dominance in the model emerges as females lose energy at a faster rate than males. This is done to replicate the higher energetic investments in females during reproduction (Dunham, 2008). In the model, individuals are hungrier put more effort into fights. As females lose energy at a higher rate than males, they tend to forage more and put more effort into fights for food. This causes females to win more, and become dominant over males. Further, the two dominance styles (despotic and egalitarian) emerge from differences in the distribution of food due to the inter-relationship among group cohesion, aggression rate and counter-aggression. When food is distributed in patches, individuals are closer and interact more often. While in uniform distribution of food, individuals are spread out and interact less often. When individuals interact more, they have a higher chance of fighting over food (or higher rates of aggression). Higher rate of aggression causes stronger hierarchical differentiation due to the winner loser effect (Hsu & Wolf, 1999) . Since females win more as they put more effort into fights, they tend to become dominant over more males. Thus, the degree of female dominance increases with increase in rate of aggression. Finally, in a steeper hierarchy dominance of individuals differs more, and so there are fewer undecided fights (fights in which neither individual display submissive behaviour).

In our new model called LemGroWorld, individuals have an additional option for grooming. When an individual encounters another individual in its proximity, it must decide whether to fight or to groom. Like the GrooFiWorld model, a fight is only initiated when the individual expects to win. Although if it thinks that it will lose it decides to groom the opponent. Once groomed the opponent decides based on its own risk of losing whether to groom back (mutual) or to leave (unidirectional). Based on these rules we predict that – 1) due to stronger group cohesion individuals groom more frequently, 2) when dominance of individuals differs more (steeper hierarchy), they tend to groom uni-directionally rather than mutually. Conversely, when individuals are closer in rank, they tend to groom mutually rather than uni-directionally.

In order to assess our model's ability to generate patterns affiliative behaviour of empirical data, we compared the patterns from the two food distributions to that of the two species of lemurs (Ring-tailed lemurs and Red-fronted lemur). We first examined if the model was able to produce the same patterns as observed in the

empirical data, namely- grooming rate, grooming reciprocation (within bout for mutual grooming and over-time for uni-directional grooming), grooming-up the hierarchy and grooming others of similar rank . Next, we investigated if the model could replicate the variation in affiliative behaviour with the change in dominance style. Lastly, we test our predictions regarding the interrelationship among cohesion, aggression rate, counter-aggression (proportion of undecided fights), grooming rate, grooming reciprocation (proportion of mutual grooming)

## Methods

### Collection of empirical data

We used data on two species of lemurs- Ring-tailed lemur (*Lemur catta*) and Red-fronted lemur (*Eulemur rufifrons*), which were provided to us by Prof.Dr.Peter Kappeler and Dr.Claudia Fitchel from the German Primate Center, Göttingen, Germany (Table 1). The data was collected using continuous focal observations of agonistic and affiliative behaviours in adult lemurs. During focal observations, the focal individual was followed and its interactions with other group members. To ensure that all individuals within each group were observed for similar amount of time, individuals were selected for observation by a rotation system. Focal observations of individuals from a group were recorded for three hours in the morning and in the afternoon. The focal observations per individual per day lasted 30 mins. During these observations, agonistic and affiliative interactions were recorded by noting the identity and behaviour of the individuals that were interacting.

Agonistic behaviour was defined as exchange of aggression, submission, or both. Aggressive behaviours included chasing, grabbing, lunging, biting, or displacing the opponent. Submissive behaviours included submissive vocalizations or fleeing. Interactions in which one individual displayed submissive behaviour to the other were recorded as 'decided' (AS) indicating that there was a clear winner and loser. This also included interactions in which submissive behaviour was evoked without any aggressive act, also known as spontaneous submission (OS). Interactions in which no individual displayed submissive behaviour were classified as 'undecided' fights, as there was no clear winner. This included cases where aggression was responded to with counter aggression (AA) or a neutral behaviour (AO). For all definitions refer to the full ethogram by Pereira and Kappeler (1997).

Grooming behaviour involved either one individual grooming the other (uni-directional) or both individuals grooming each other (mutual). A grooming bout was defined to begin when one individual initiated the grooming episode, and ended when one individual left. In case both individuals continued to remain in social contact, the bout was considered to have ended if they did not groom for 5 minutes.

**Table 1: Data collection per species, for each group: field site, groups name and size**

| Species           | Field site      | Groups | # Adults in group | Observation time per individual (hours) |
|-------------------|-----------------|--------|-------------------|---|
| Ring-tailed lemur | Berenty Reserve | C1     | 10                | 24 – 25                                 |
|                   |                 | C2A    | 9                 | 12.5 – 15                               |
|                   |                 | YF     | 8                 | 24 – 25                                 |
| Red-fronted lemur | Kirindy forest  | A      | 12                | 5 – 7                                   |
|                   |                 | B      | 5                 | 6.5 – 7.5                               |
|                   |                 | F      | 11                | 6 – 6.5                                 |
|                   |                 | J      | 7                 | 5.5 – 6.5                               |

### Model description

Our model is an extension of the LemurWorld model, coded in NetLogo (Wilensky, 1999). We call this new model LemGroWorld, since it includes rules for grooming in addition to the rules for grouping, foraging, and fighting that were present in the original model (for default parameters see Table 2).

The LemGroWorld model simulates a world of 100 x 100 patches with a continuous border, presenting individuals with the freedom to move in all directions. All individuals have a field of view of angle (*vision*) and maximum distance of perception (*maxview*). Further, all individuals start with the same initial energy (*init-energy*) and elo-rating (*elo*). Energy is lost after each activation (*EnergyRateAll*), and after fighting (*EnergyRateDominance*) or grooming (*EnergyRateGroom*) interactions. In addition to this female lose extra energy (*EnergyRateFemale*), to resemble the energetic costs of reproduction. The elo-rating gets updated based on the outcomes of fights (win or loss), and the amount of increase/decrease is given by a scaling factor (*step-elo*) and the difference in elo-rating of the two interacting individuals.

When the simulation is initialised, individuals get randomly placed in a circle, around the centre of the world. Their energy and elo-rating are set to initial values. When the simulation is started, individuals are activated one at a time, in a specific order, to perform a behaviour. All individuals are activated for a minimum of 20 times every day. In order to avoid any bias caused by the order in which individuals get activated, this order of activation is changed every 20 days.

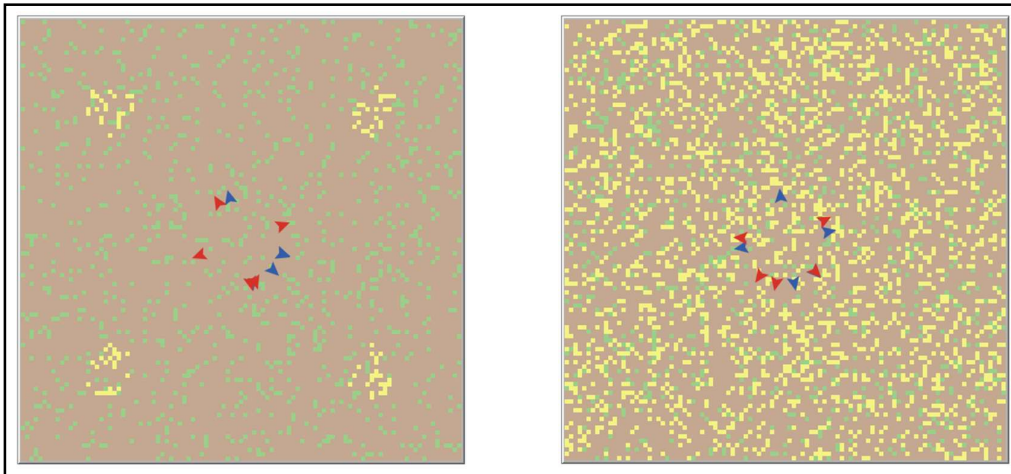
Table 2: Parameters used in the LemGroWorld model along with a brief description of each parameter.

| Parameter                   | Description   | Value |
|-----------------------------|---|-------|
| Food                        |   |       |
| <i>fruit-abundance</i>      | Initial abundance of 'fruit' items                    | 2000  |
| <i>leaves-abundance</i>     | Initial abundance of 'leaves' items                   | 4000  |
| <i>fruit-quality</i>        | Energy of fruit                                       | 80    |
| <i>leaves-quality</i>       | Energy of leaves                                      | 30    |
| <i>fruit-handling-time</i>  | Activations needed to eat fruit                       | 3     |
| <i>leaves-handling-time</i> | Activations needed to eat leaves                      | 3     |
| <i>pref-fruit</i>           | Probability of finding fruit first                    | 0.8   |
| <i>pref-leaves</i>          | Probability of finding leaves first                   | 0.2   |
| Agents                      |   |       |
| <i>population</i>           | Population size                                       | 10    |
| <i>perspace</i>             | Personal space  | 1     |
| <i>nearview</i>             | Near view distance                                    | 15    |
| <i>maxview</i>              | max view distance                                     | 75    |
| <i>vision</i>               | Angle of vision                                       | 120   |
| <i>searchangle</i>          | Turning angle to find others                          | 90    |
| <i>fleeangle</i>            | Turning angle to flee                                 | 180   |
| <i>dodgeangle</i>           | Turning angle to dodge fight                          | 180   |
| Energy                      |   |       |
| <i>init-energy</i>          | Initial energy of agents                              | 600   |
| <i>saturation</i>           | Energy at which agents do not need food               | 1000  |
| <i>hungry</i>               | Energy at which agents get hungry                     | 600   |
| <i>starving</i>             | Energy at which agents are starving                   | 300   |
| <i>EnergyRateAll</i>        | Energy lost after every activation                    | 1     |
| <i>EnergyRateFemales</i>    | Additional energy lost by females at every activation | 1     |
| <i>EnergyRateDominance</i>  | Energy lost after dominance interaction               | 1     |
| <i>EnergyRateGroom</i>      | Energy lost after grooming interaction                | 0.5   |
| Dominance                   |   |       |
| <i>elo</i>                  | elo-rating (initial value = 1000)                     |       |
| <i>step-elo</i>             | Scaling factor for elo-rating                         | 50    |

## Food

In the model, there are two types of food items – fruits and leaves. Although fruits give more energy (*fruit-energy* > *leaves-energy*), leaves are more abundant (*fruit-abundance* < *leaves-abundance*) and require less activations for consumption (*fruit-handling-time* > *leaves-handling-time*). Leaves are randomly distributed over the world, but the distribution of fruits can be changed from uniform (randomly scattered over the world), to patchy (clustered in patches) (see Fig1). Lastly, food items disappear after being consumed, and get reinitialised to initial abundance and distribution at the beginning of each year.





**Figure 1: Different fruit distributions in the model. (Left) Uniform distribution of fruit. Fruits are randomly distributed. (Right) Patchy distribution of fruit. Fruits are clumped in specific spots. Yellow dots indicate fruits, and green dots indicate leaves. The red arrows are females, and the blue arrows are males.**

### Foraging

Individuals have an increased chance of foraging once their energy drops below *hungry*. While foraging it first searches for its preferred food –fruit ( $pref-leaves < pref-fruit$ ) at its current location. If no fruit is available at its current location, it extends its search to the *nearview*. If it does not find any fruits in its *nearview*, it starts looking for leaves.

When the energy falls below *starving*, individuals prioritize foraging. They try to search for any food available at their current patch, and if current patch is empty it searches in the *nearview*. If it still does not find any food, it will turn an angle and continue its search for food in different direction, in the next activation.

When an individual finds food while foraging, it will move towards the food and claim it. Once the food has been claimed, the individual looks in its *perspace* to check for other individuals that might contest for the claimed food. Note, if more than one individual is present in its *perspace* the closest one is considered. If someone is present, the individual that has claimed the food decides if it should initiate a fight. If no one is present, it can eat the claimed food.

The consumption of claimed food requires a set number of activations (*handling-time*). At each activation, the individual will check its *perspace* before proceeding to eat a portion of the food. With each portion the individual gets a fraction of the total energy of the food item.

### Grouping

When an individual is not *starving* and does not see anyone near-by (in *nearview*) it does a grouping behaviour. It searches for others in its *maxview*. Once it spots other individuals (or individual), it will move in their average direction. If it is unable to spot anyone, it turns over a *searchangle*.

## Fighting

Fights may occur either over claimed food – when one individual has claimed food and another individual is in its *perspace*, or over space – when an individual which is not hungry but has another individual in its *perspace*.

In both the cases, the activated individual ( $i$ ) has a mental battle against the individual in its *perspace* ( $j$ ), where  $i$  assesses its chances of winning ( $P_i$ ) against  $j$ . It does this by comparing its elo-rating to that of the opponent.

$$P_i = \frac{1}{1 + e^{-0.01 * (Elo_i - Elo_j)}},$$
$$P_j = 1 - P_i$$

If  $P_i$  is greater than a random number between 0 and 1. Individual  $i$  thinks that it can win the fight and thus, proceeds to initiate the fight. On the other hand, if  $P_i$  is less than a random number between 0 and 1. Individual  $i$  thinks it will lose the fight and so it will groom the opponent.

Once individual  $i$  has completed its mental battle, its opponent also has mental battle to decide if it should fight back. It does so by assessing its own probability of winning against  $i$ . If  $P_j$  is greater than a random number between 0 and 1, individual  $j$  thinks that it can win the fight. This leads to an undecided fight, where there is no clear winner. As a result, elo-rating is retained and no energy is lost.

However, if  $P_j$  is less than a random number between 0 and 1, individual  $j$  thinks it will lose and so a real fight occurs. The probability of winning this fight ( $p$ ) is decided based on the elo-rating of both individuals, and the effort that they put into the fight. Effort is inversely proportional to the energy, as hungrier individuals put more efforts into fights.

$$p_i = \frac{1}{1 + e^{-0.01 * (Elo_i * Effort_i - Elo_j * Effort_j)}}$$

If the  $p_i$  is greater than a random number between 0 and 1, individual  $i$  wins ( $w_i = 1$ ) the fight, otherwise it loses ( $w_i = 0$ ). After the outcome of the fight has been decided, the dominance values are updated. The winner has its dominance value increased, and the loser has its dominance value decreased. The change in dominance value is dependent on the difference in the dominance values of the two individuals. When an individual wins against someone with higher dominance than itself, its dominance values increase more than what it would have if it won against a less dominant opponent.

$$elo_i = elo_i + (w_i + p_i) * step-elo,$$

$$elo_j = elo_j + (w_j + p_j) * step-elo$$

After dominance values are updated, both individuals lose energy (*EnergyRateDominance*) and the loser of the fight turns a *fleeangle* and flees from the winner. The winner remains in its position. If the fight was over food and the initiator (individual *i*) is the winner, it will eat the claimed food.

### **Grooming**

When individual *i* loses its mental battle and *j* wins its mental battle, *i* grooms *j* in a uni-directional grooming bout. However, if both *i* and *j* lose their mental battles, they groom each other in a mutual grooming bout. Following any grooming bout, both individuals turn away from one another. Individuals that performed grooming lose energy (*EnergyRateGroom*) and elo-rating of both individuals remain unchanged.

### **Parameterization of model**

We ran our model with the default parameters described for LemurWorld (Hielkema, n.d). Additional parameters regarding grooming (*EnergyRateGroom*) were tuned so that the model could replicate patterns of aggression and dominance that were demonstrated in LemurWorld.

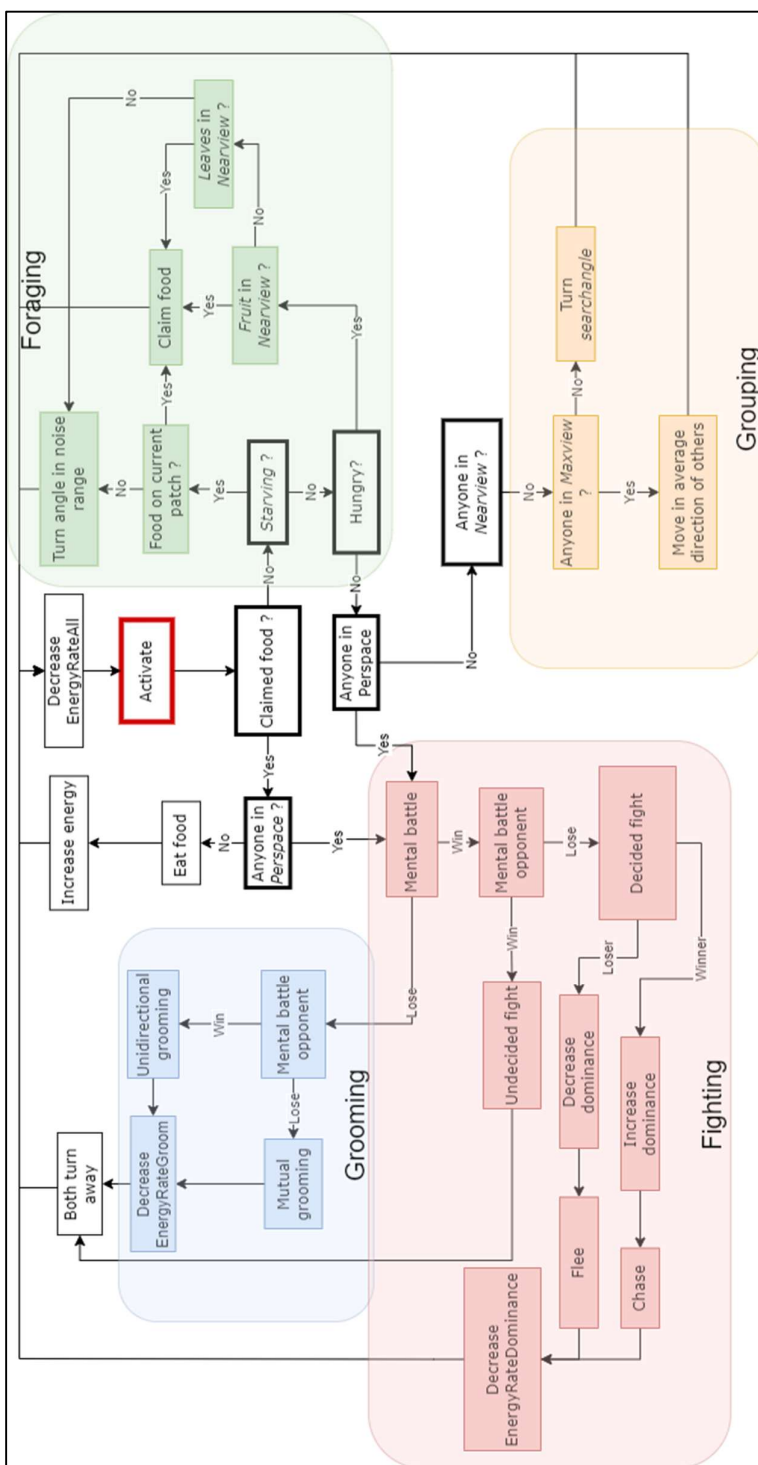


Figure 1: Flowchart describing the LemGroWorld model. Once activated (red), the individual can perform a behaviour. It first checks if it had claimed food in the previous activation. If it did claim food, it will eat it. In case, there is anyone nearby that might want to contest for the claimed food both will have a mental battle leading to a real fight, undecided fight, mutual grooming bout, or uni-directional grooming bout. If no food was claimed in previous activation, it will then have decide based on its current energy level whether it should forage or group

## Collection of model data

We ran the model 40 times for both patchy and uniform fruit distributions, using the parameters listed in Table 1 (for more details check Table 3). Each run lasted for 7 years, and each year consisted of 365 days. Data was collected only from the final year. Dominance interactions from transition periods was omitted to avoid any bias (Puga-Gonzalez et al., 2009). The data from each run included dyad specific counts of fights won, decided interaction, undecided interactions, uni-directional grooming bouts and mutual grooming bouts, as well as the identity of the actor and receiver in each of these interactions.

**Table 3: Data collection for each fruit distribution: number of runs, group size, sex ratio, and number of activations.**

| Fruit distribution | # Run | Group size | Sex ratio | Number of activations per individuals |
|--------------------|-------|------------|-----------|---------------------------------------|
| Patchy             | 40    | 10         | 1:1       | 20                                    |
| Uniform            | 40    | 10         | 1:1       | 20                                    |

## Analysis of empirical and model data

### Dominance

The dominance hierarchy was derived from counts of fights won. For this we used the average dominance index (ADI; Hemelrijk, Wantia and Gygax, 2005). The average dominance index is the average percentage with which an individual wins in interactions with each of its group members, excluding the ones with which it did not interact. The ADI values were then used to assign ordinal ranks to all individuals. The degree of female dominance over males was estimated using the female dominance index (FDI; Hemelrijk, Wantia and Isler, 2008). This gives the average proportion of males over which females dominant.

The proportion of undecided fights was used as a measure of steepness of the hierarchy (Seex et al., 2022). A higher proportion of undecided fights indicates that the species is more egalitarian. We calculated the proportion of undecided fights for each group, as the number of undecided fights (both individuals show aggression, but there is no clear winner) divided by the total number of interactions (decided and undecided fights).

### Agonistic interactions and group cohesion

We calculated the average rate of aggression for each group, as the sum of decided and undecided agonistic interactions initiated per individual per day. The group cohesion was measure using the nearest-neighbour distance. This was calculated as the distance of each individual to its closest neighbour, measured every day and averaged over the year.

## **Grooming**

For each dyad combination we calculated the frequency of grooming given by one individual to its grooming partner, and the frequency of grooming that it received in return. We made these calculations separately for uni-directional and mutual grooming. Further, for the empirical data we converted the counts into rates of grooming given/received per hour.

Since mutual grooming is inherently reciprocal (both individuals groom each other in a single grooming bout), we used the proportion of mutual grooming as measure of grooming reciprocation. It was calculated as the number of mutual grooming bouts divided by total number of grooming interactions (mutual and uni-directional).

## **Statistical Analyses**

Statistical analysis was conducted in R (version 4.1.2) (R Core Team, 2021) and RStudio (RStudio Team, 2022). Graphs were created using *ggplot2* (Wickham, 2016) and *ggpubr* (Kassambara, 2020) packages in Rstudio. We used Wilcoxon Rank-Sum test for the comparison of mean using the stats package (R Core Team, 2021). We Generalized linear mixed effect models were fitted using *glmmTMB* package (Brooks et al., 2017), and distribution of model was then selected based on corrected AIC (AICc; small-sample corrected Akaike Information Criterion) comparison using *bbmle* package (Bolker & R Development Core Team, 2022). Goodness of fit of the models were measured using simulated residuals from the *DHARMA* package (Hartig, 2022).

We made separate GLMMs for each species (for empirical data) and fruit distribution (for model data) , and for the two types of grooming (mutual and uni-directional) using dyad specific counts from empirical and model data. In the models, we first investigated whether grooming was reciprocated indirectly between bouts, by examining the dependence of counts grooming given on the counts of grooming received. We also investigated if grooming was distributed up/down the hierarchy, by examining the effect of receiver rank on the counts of grooming given. Lastly, we investigated if grooming was directed towards individuals of similar ranking, by examining the effect of rank difference on the counts of grooming given. Note that the model for mutual grooming did not test for grooming reciprocation since mutual grooming is inherently reciprocal.

### **GLMMs for the empirical data**

We decided to fit Zero-Inflated Negative-Binomial mixed models with the unit of analysis being each actor (groomer)-receiver (groomee) dyad (check Table 4). Since not all individuals interacted with one another, we had zero counts in our data. The total counts of grooming given per individual was used as the response variable, and the counts of grooming received per individual per hour, rank of receiver and the absolute difference in rank of partners as the predictor variables. The identity of actor, receiver, unique dyad id, and the group id as random effects as this controls for nonindependence of data. To account for the variation in observation time, we decided to specify the observation time as an offset.

**Table 4: Details of GLMMs for empirical data: distribution of response variable, fixed effects, interaction variable, random effects, offset and number of actor-receiver dyads.**

| Grooming type   | Response distribution           | Response variable                   | Fixed effects  | Random effects                           | Offset           | Number of actor-receiver dyads |
|-----------------|---------------------------------|-------------------------------------|--|--|------------------|--------------------------------|
| Uni-directional | Zero-inflated Negative binomial | Grooming given by actor to receiver | Grooming received by actor from receiver per hour, Receiver rank, Absolute rank difference | Group id, Actor id, Receiver id, Dyad id | Observation time | 218                            |
| Mutual          | Zero-inflated Poisson           | Grooming given by actor to receiver | Grooming received by actor from receiver per hour, Receiver rank, Absolute rank difference | Group id, Actor id, Receiver id, Dyad id | Observation time | 316                            |

#### GLMMs for the model data

Again, due to large number of zero counts we fit Zero-Inflated Negative-Binomial mixed models, using the actor-receiver dyads as the unit of analysis. The total counts of grooming given per individual as the response variable, and the total counts of grooming received per individual, rank of receiver and the absolute difference in rank of partners as the predictor variables. The identity of actor, receiver, unique dyad id, and the group id as random effects as this controls for nonindependence of data.

**Table 5: GLMMs for model data: distribution of response variable, fixed effects, interactions variable, random effects, offset and number of actor-receiver dyads.**

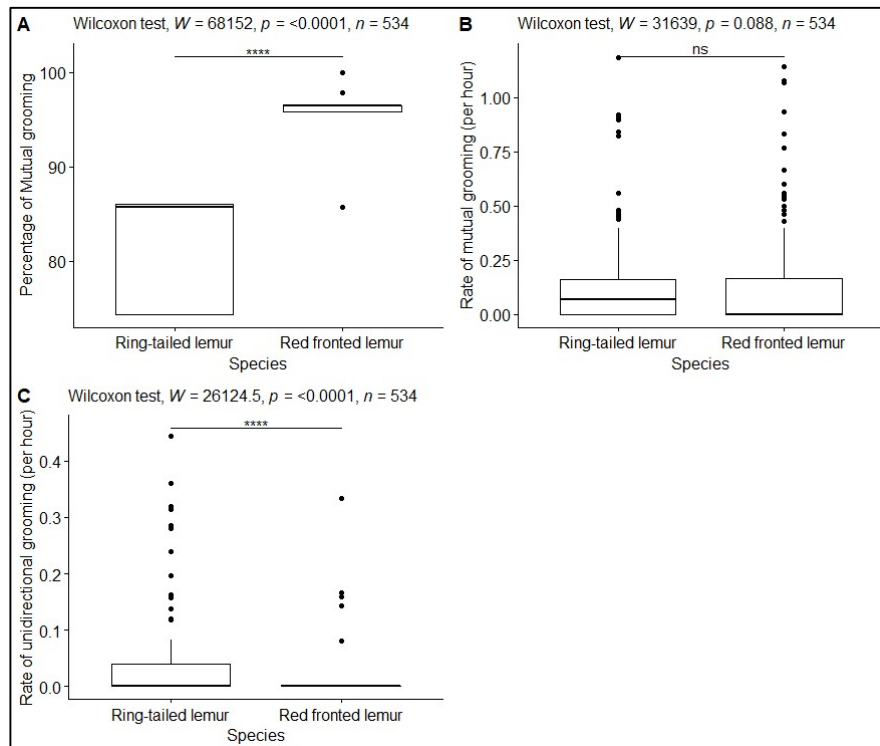
| Grooming type   | Response distribution       | Response variable                   | Fixed effects   | Random effects                           | Offset | Number of actor-receiver dyads |
|-----------------|-----------------------------|-------------------------------------|---|--|--------|--------------------------------|
| Uni-directional | Truncated Negative binomial | Grooming given by actor to receiver | Grooming received by actor from receiver, Receiver rank, Absolute rank difference | Group id, Actor id, Receiver id, Dyad id | -      | 3600                           |

|        |                             |                                     |   |  |   |      |
|--------|-----------------------------|-------------------------------------|---|--|---|------|
| Mutual | Truncated negative binomial | Grooming given by actor to receiver | Grooming received by actor from receiver, Receiver rank, Absolute rank difference | Group id, Actor id, Receiver id, Dyad id | - | 3600 |
|--------|-----------------------------|-------------------------------------|---|--|---|------|

## Results

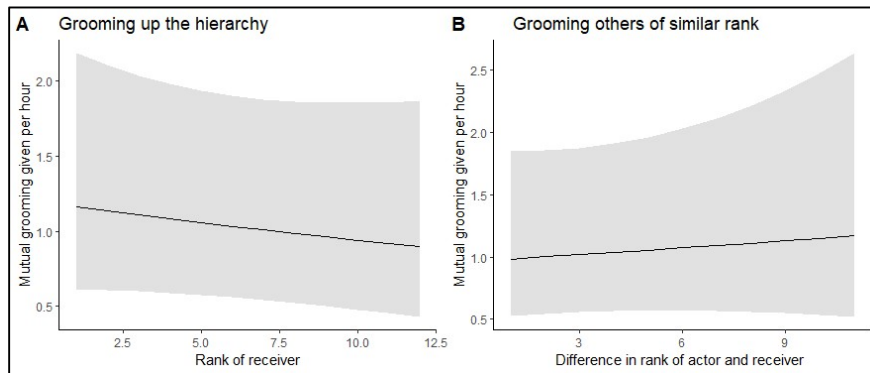
### Patterns of grooming in empirical data

Red-fronted lemurs almost exclusively perform mutual grooming (Fig 2.A). The distribution of this grooming was only weakly affected by rank of receiver, and the difference in ranks of both individuals (Fig 3.A, B). Alternatively, grooming in ring-tailed lemurs was largely, but not exclusively mutual (Fig 2.A). Ring-tailed lemurs performed uni-directional more frequently than red-fronted lemurs (Fig 2.B, C). Besides, uni-directional grooming was not reciprocated over time (Fig 4.A), instead it was directed up the hierarchy and towards individuals of similar rank (Fig 4.B, C). On the other hand, mutual grooming in ring-tailed lemurs was more frequently only directed towards others of similar rank (Fig 5.B).

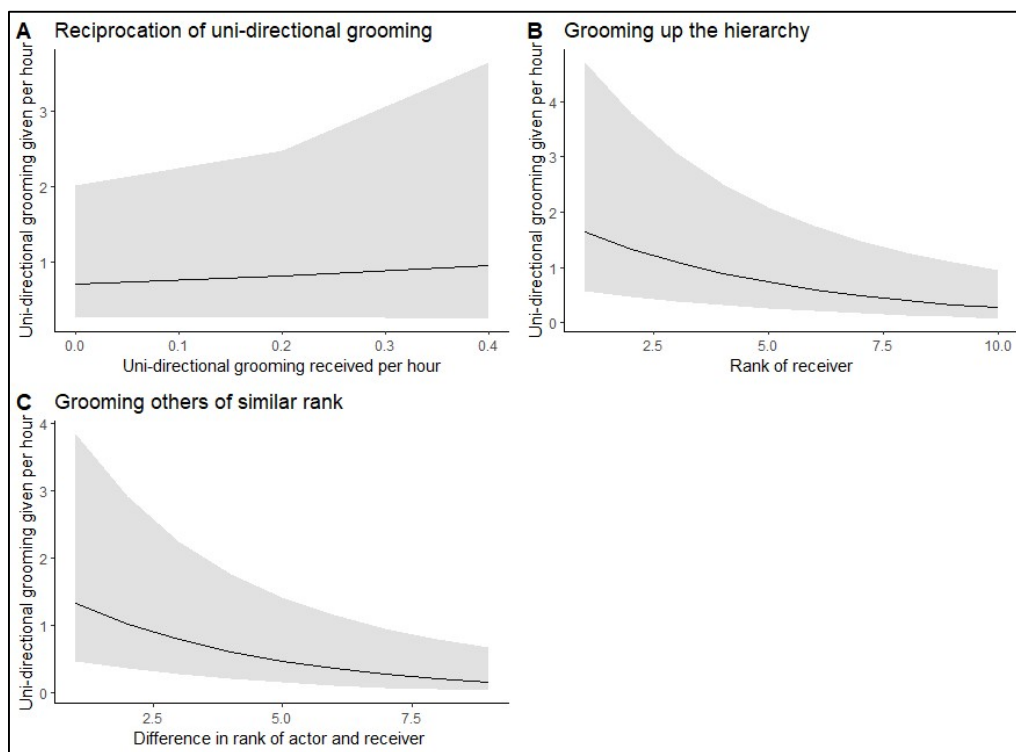


**Figure 2: Comparing patterns of grooming behaviour between despotic (ring-tailed lemur) and egalitarian (red-fronted lemur) species. (A) Percentage of grooming bout that were mutual. (B) Average rate of mutual grooming bouts initiated per hour. (C) Average rate of uni-directional grooming bouts initiated per hour.**

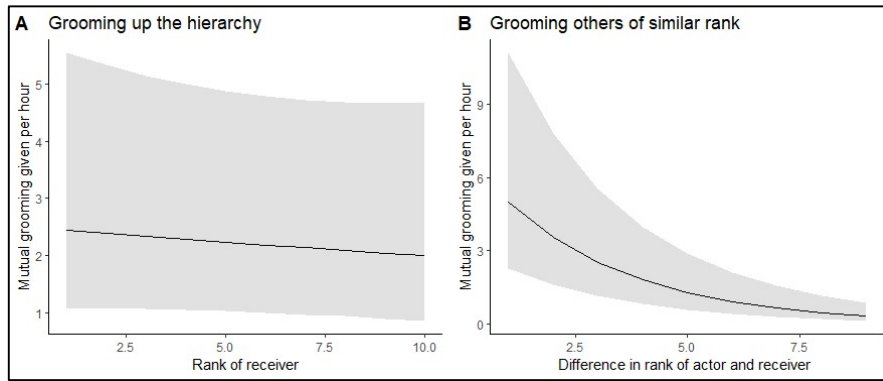




**Figure 3: Results of GLMMs of mutual grooming in red-fronted lemurs, investigating (A) effect of receiver rank on the rate of mutual grooming received per hour (Grooming up the hierarchy), (B) effect of rank difference on the rate of mutual grooming given per hour (Grooming others of similar rank). The lines are fitted on the raw data with zero-inflated negative binomial mixed models which used each actor-receiver dyad as the unit of analysis, and the shaded areas represent 95% confidence intervals.**



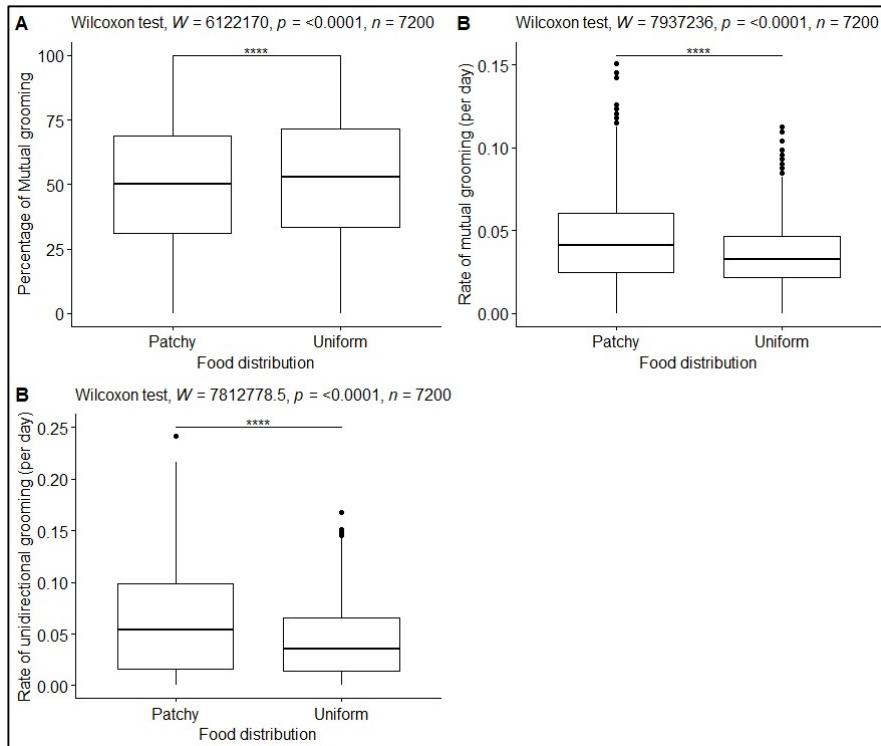
**Figure 4: Results of GLMMs of uni-directional grooming in ring-tailed lemurs, investigating (A) rate of uni-directional grooming received on the rate of uni-directional grooming given (Grooming reciprocation over time), (B) receiver rank on the rate of uni-directional grooming received per hour (Grooming up the hierarchy), (C) rank difference on the rate of uni-directional grooming given per hour (Grooming others of similar rank). The lines are fitted on the raw data with zero-inflated negative binomial mixed models which used each actor-receiver dyad as the unit of analysis, and the shaded areas represent 95% confidence intervals.**



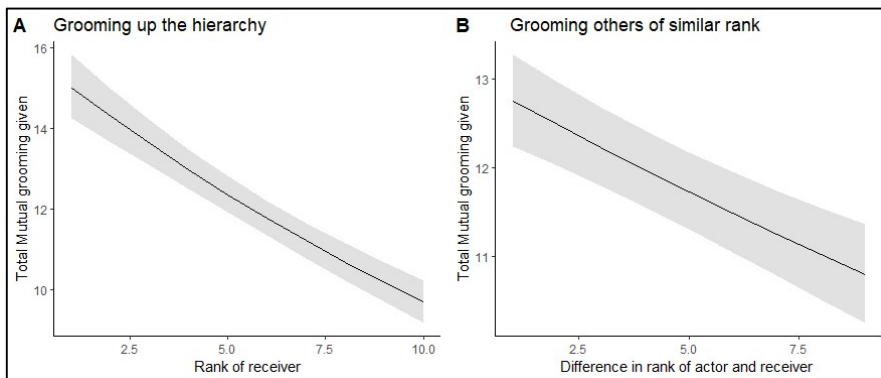
**Figure 5: Results of GLMMs of mutual grooming in ring-tailed lemurs, investigating (A) effect of receiver rank on the rate of mutual grooming received per hour (Grooming up the hierarchy), (B) effect of rank difference on the rate of mutual grooming given per hour (Grooming others of similar rank). The lines are fitted on the raw data with zero-inflated negative binomial mixed models which used each actor-receiver dyad as the unit of analysis, and the shaded areas represent 95% confidence intervals.**

### Patterns of grooming in model data

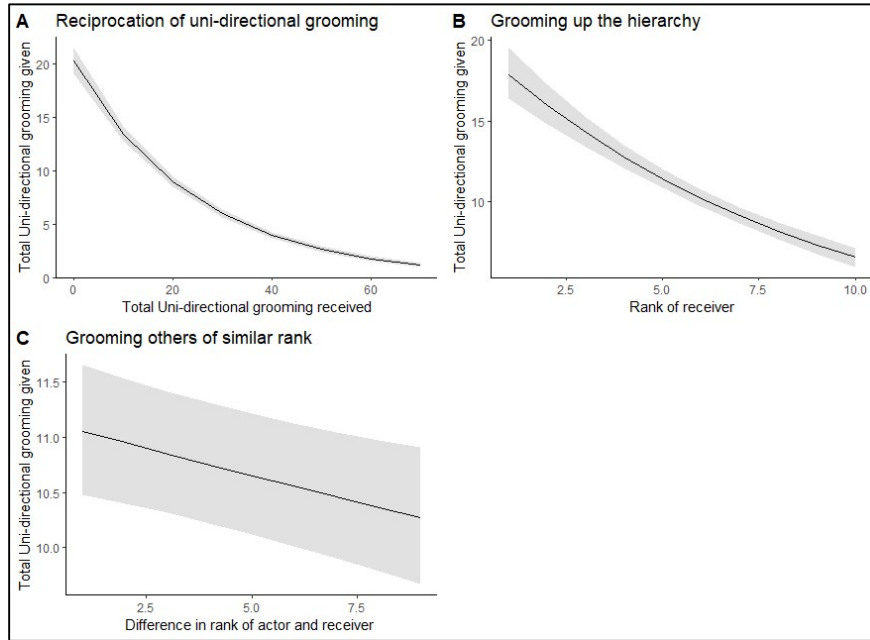
When the fruit distribution was set to uniform, individuals performed mutual grooming more often (Fig 6.A). The mutual grooming was more often directed towards dominants and towards others of similar rank (Fig 7.A, B). Uni-directional grooming also followed the same pattern, it was directed up the hierarchy and towards others of similar rank (Fig 8.M9,10). When fruit was distributed in patches, relatively lower proportion of grooming was mutual compared to uniform fruit distribution (Fig 2.M(A)). However, individuals groomed (uni-directionally and mutually) more often in patchy fruit distribution (Fig 2.M(B, C)). In patchy fruit distribution, both forms grooming followed the same patterns as was observed in uniform fruit distribution, uni-directional grooming and mutual grooming were directed up the hierarchy and towards individuals of similar rank.



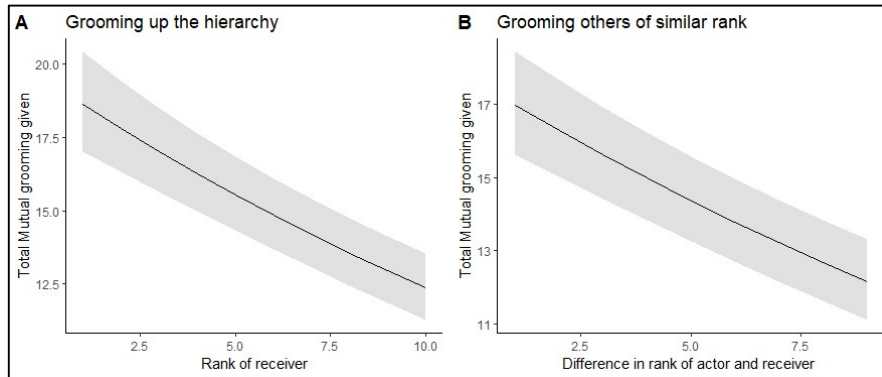
**Figure 6: Comparing patterns of grooming behaviour between patchy and uniform fruit distribution. (A) Percentage of grooming bout that were mutual. (B) Average rate of mutual grooming bouts initiated per day. (C) Average rate of uni-directional grooming bouts initiated per day.**



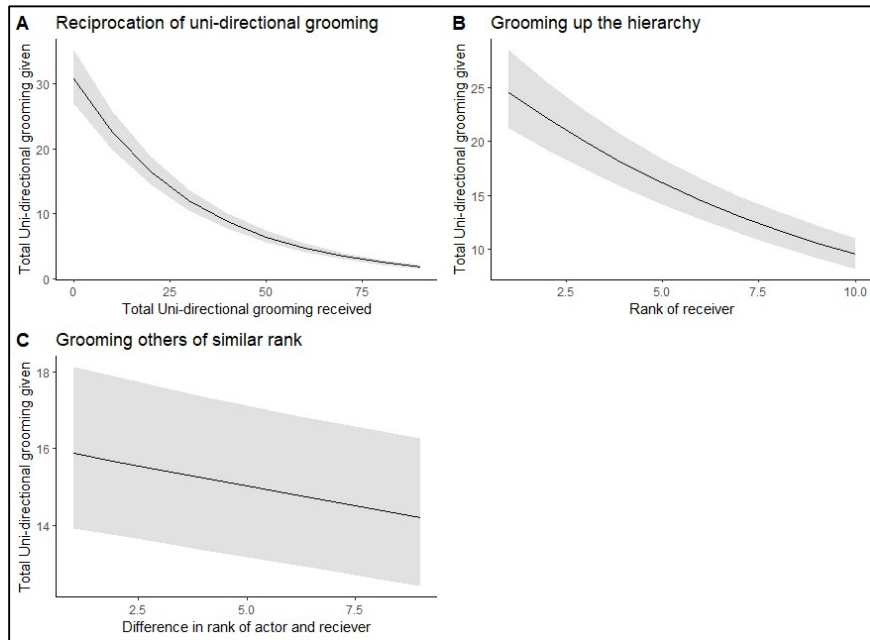
**Figure 7: Results of GLMMs of mutual grooming in uniform fruit distribution, investigating (A) effect of receiver rank on the rate of mutual grooming received per hour (Grooming up the hierarchy), (B) effect of rank difference on the rate of mutual grooming given per hour (Grooming others of similar rank). The lines are fitted on the raw data with zero-inflated negative binomial mixed models which used each actor-receiver dyad as the unit of analysis, and the shaded areas represent 95% confidence intervals.**



**Figure 8: Results of GLMMs of uni-directional grooming in uniform fruit distribution, investigating (A) rate of uni-directional grooming received on the rate of uni-directional grooming given (Grooming reciprocation over time), (B) receiver rank on the rate of uni-directional grooming received per hour (Grooming up the hierarchy), (C) rank difference on the rate of uni-directional grooming given per hour (Grooming others of similar rank). The lines are fitted on the raw data with zero-inflated negative binomial mixed models which used each actor-receiver dyad as the unit of analysis, and the shaded areas represent 95% confidence intervals.**



**Figure 9: Results of GLMMs of mutual grooming in patchy fruit distribution, investigating (A) effect of receiver rank on the rate of mutual grooming received per hour (Grooming up the hierarchy), (B) effect of rank difference on the rate of mutual grooming given per hour (Grooming others of similar rank). The lines are fitted on the raw data with zero-inflated negative binomial mixed models which used each actor-receiver dyad as the unit of analysis, and the shaded areas represent 95% confidence intervals.**



**Figure 10: Results of GLMMs of uni-directional grooming in patchy fruit distribution, investigating (A) rate of uni-directional grooming received on the rate of uni-directional grooming given (Grooming reciprocation over time), (B) receiver rank on the rate of uni-directional grooming received per hour (Grooming up the hierarchy), (C) rank difference on the rate of uni-directional grooming given per hour (Grooming others of similar rank). The lines are fitted on the raw data with zero-inflated negative binomial mixed models which used each actor-receiver dyad as the unit of analysis, and the shaded areas represent 95% confidence intervals.**

### Comparison of model and empirical data.

When fruits were distributed in uniformly, the patterns resembled that red-fronted lemurs. Larger proportion of grooming was mutual (Fig 2.A; 6.A). When fruits were distributed in patches, the patterns resembled that of ring-tailed lemurs. Larger proportion of grooming was mutual, although it was relatively lower than that found in uniform fruit distribution (Fig 2.A; 6.A). Further, both forms of grooming more frequently (Fig 2.B, C; 6.B, C), and were more often directed up the hierarchy and towards individuals of similar rank (Fig 4.B, C; 10.B, C).

## **Discussion**

In this study, we show that many patterns of affiliative behaviour of group-living lemurs can be explained to emerge by self-organization. Our model generates many patterns similar to those found in the empirical data. By changing the fruit distribution from uniform to patchy, affiliative patterns in the model change from those resembling egalitarian lemurs to those resembling despotic lemurs. Individuals in the model ignore several cognitive considerations that have been used to explain these patterns. The only cognitive assumptions we make in the model are that individuals tend to group, they can recognise rank of others, the decision to initiate fights is sensitive to risks of being defeated, and grooming is induced by the expectation of being defeated. This follows the view that individuals groom in order to reduce aggression directed towards them (Silk, 1982). Patterns such as grooming up the hierarchy and grooming others of similar rank occurred without the intention of receiving support in exchange, or attraction towards higher ranking or similar ranked partners.

### **Causation of patterns in the model**

The patterns of affiliative behaviour emerge due to the interrelationship between cohesion, rate of aggression, rate of grooming and grooming reciprocation (more specifically mutual grooming). In line with our first prediction, stronger cohesion led to higher rate of grooming in patchy fruit distribution. In the model, when individuals meet each other at close proximity, they decide whether to fight or groom. Thus, in patchy fruit distribution where individuals are closer together, they initiate more fight or grooming.

In regards to our second predictions, mutual grooming was performed more frequently in uniform fruit distribution due to weaker hierarchical differentiation, while uni-directional grooming was performed more frequently in patchy fruit distributions due to stronger hierarchical differentiation. In the model, grooming is only induced by the expectation of being defeated. Uni-directional grooming occurs when only the initiator expects to be defeated, while mutual grooming occurs when both the initiator and its opponent expect to be defeated. Thus, individuals are more likely to groom mutually when they are closer in rank, and groom uni-directionally when they differ in rank. Therefore, in uniform fruit distribution where hierarchy is weakly differentiated (lower rate of aggression caused by weaker cohesion) individuals are closer in rank, and so are more likely to perform mutual grooming. On the other hand, in patchy fruit distribution individuals are less likely to perform mutual grooming (and more likely to perform uni-directional grooming) as they differ in rank.

### **Shortcomings of model**

Many of the patterns generated by the model resembled those found in empirical data, however, there were few deviations. Firstly, grooming in lemurs is highly reciprocal (Barton, 1987), and we also found this to be the case in our empirical data. But, mutual grooming in both fruit distributions did not occur as frequently.

According to our predictions, individuals that are closer in rank are more likely to groom each other mutually. However, we do not know if individuals that are closer in rank are more likely to also interact with one another. In the GrooFiWorld model, aggression leads to the formation of a spatial structure with sub-ordinates at the periphery and dominants at the centre (Hemelrijk et al., 2017; Puga-Gonzalez et al., 2009). This means that individuals that are closer in rank are also more likely to interact with one another. Since, formation of such social-spatial structures has not been extensively studied in lemurs, therefore, they have not been studied in the models (current and previous) either. Thus, future empirical studies focussing on discerning patterns in the spatial organization in lemurs might provide more insights.

Secondly, in both empirical and model data we found evidence that uni-directional grooming was directed up the hierarchy and towards others of similar rank. Although, based on self-organization we could not explain why both patterns occur simultaneously. In ring-tailed lemurs, dominant males monopolize most of the male-female interactions and also frequently get groomed by sub-ordinated (Kappeler, 1993). Therefore, looking at patterns at individual level rather than populations level could help in generating a hypothesis regarding the simultaneous occurrence of both these patterns.

Lastly, the affiliative patterns of mutual grooming in the model did not resemble that of red-fronted lemurs. Since, red-fronted lemurs almost exclusively perform mutual grooming it was unlikely that any patterns could be observed. Studies on this species generally used duration of grooming rather than count/rates for quantifying grooming (Port et al., 2009). Therefore, including time for grooming in the model could be more informative.

### **Future recommendations**

Although the LemGroWorld model was able to produce many patterns of the empirical data, it is hard to determine the accuracy of its predictions. Firstly, lemurs differ in their degree of despotism (or steepness of hierarchy) (Norscia & Palagi, 2015). It is therefore essential that we also test the model against multiple species that represent different degrees of despotism. This not only allows us to investigate how affiliative patterns change with the degree of despotism (stronger hierarchical differentiation, it also allows us to test if our model predictions can be generalized to all lemurs or if they are specific to the species in the current study.

Secondly, our study was solely focussed on- grooming reciprocation, grooming up the hierarchy and grooming others of similar rank. The GrooFiWorld model also explored patterns of conciliatory behaviour such as reconciliation after fight by grooming between former opponents (Puga-Gonzalez et al., 2009). Reconciliation among former opponents has also been observed in different species of lemurs. Further, the patterns reconciliation differ between species ((Kappeler, 1993), which have resulted in different explanations for emergence of these patterns (Norscia &

Palagi, 2010; Palagi & Norscia, 2015). Therefore, investigating reconciliation within our model may provide an integrative explanation (based on self-organization) for the emergence of these patterns and its variation between species.

Lastly, in lemurs inter- and intra-sexual relationships have been shown to affect the agonistic and affiliative behaviour of lemurs. Grooming by subordinates is directed up the hierarchy towards dominants. In the case of ring-tailed lemurs, males which are sub-ordinate groom dominant males and females which are typically more dominant over males (Kappeler, 1993; Nakamichi & Koyama, 1997). While in red-fronted lemurs, grooming is directed by sub-ordinated males and females towards dominant males and females, unlike ring-tailed lemurs, grooming was observed in all dyads ((Kappeler, 1993; Port et al., 2009). Therefore, effect of sex on grooming should be investigated within our model.

### **Conclusion**

We have shown that patterns of affiliative behaviour typical of despotic and egalitarian lemurs can emerge by self-organization, without the use of specific cognitive assumptions. These patterns emerge from individuals grooming out of fear of defeat and the interrelationships between the traits of aggression and affiliation. Because our model produces many behavioural patterns found in real lemurs, we suggest that it can be used as a null model that indicates what patterns can be expected in the absence of the usual cognitive rules that used to explain these patterns of affiliation.



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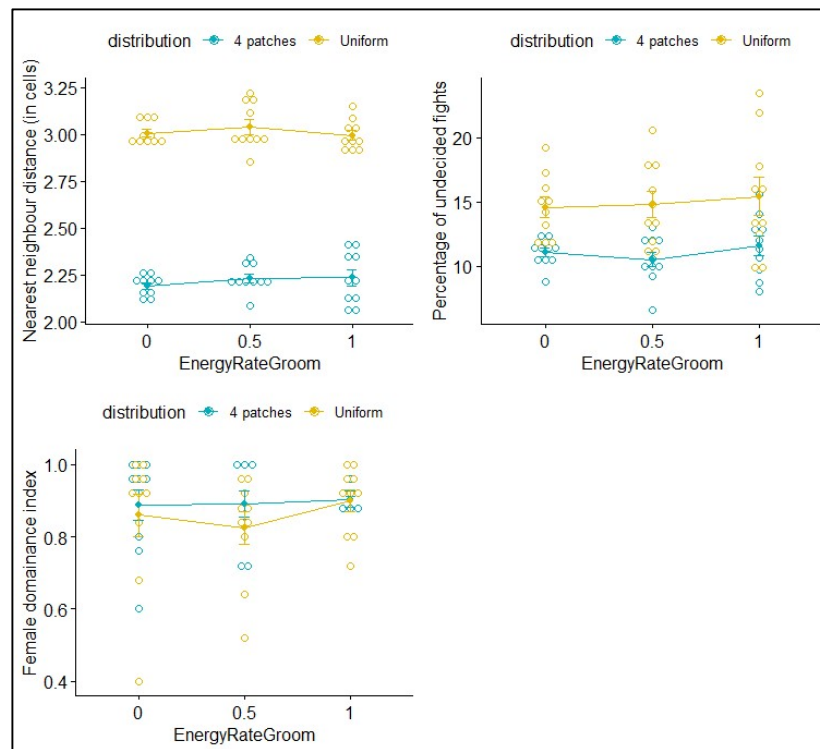
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## Appendix

### Tuning grooming parameter

In the LemGroWorld model, the parameter- *EnergyRateGroom* determines how much energy an individual loses when it grooms. We tuned this parameter so that we could produce the same interrelationship of traits – cohesion, steepness and degree of female dominance described in LemurWorld. We chose parameter values to lie between 0 (no energy required for grooming) and 1 (energy required for grooming), we used three values – 0, 0.5 and 1. In order to investigate the effect of energy of lost by grooming on each of these traits, Friedman test, followed by pairwise Wilcoxon rank sum test were performed (see Supplementary material).



**Figure 8: Investigating variation in traits between patchy and uniform fruit distribution for different values for energy lost after grooming (*EnergyRateGroom*). (A) Nearest neighbour distance as measure of group cohesion against value of energy lost after grooming. (B) Percentage of undecided fights as a measure of hierarchical steepness against value of energy lost after grooming. (C) Female dominance index (using internal elo-rating) as a measure of the degree of female dominance over males against the value of energy lost after grooming.**

The different values of the parameter did not show any statistically significant effect any of the traits. The plots that we have presented support this statement (Fig 8.A, B, C), although, there was an exception in the case of degree female dominance. When *EnergyRateGroom* is 1, the degree of female dominance is greater in uniform rather than patchy distribution. Therefore, based on the evidence we decided to - 1) Assign energy for grooming as this resembles natural scenario, 2) We decided to set grooming to 0.5, as the model was able to reproduce all the patterns of LemurWorld for this value.

## Results from GLMMs

**Table 6: Results from GLMMs for Model and Empirical data**

| Model 1: Uni-directional grooming in Patchy fruit distribution [N = 3600, R2m = 0.50, R2c = 0.90]  |   |                          |
|--|---|--------------------------|
| Response   | Predictor                               | $\beta$ ( $\pm$ S.E)     |
| Total Uni-directional grooming given   | Total Uni-directional grooming received | -0.031*** ( $\pm$ 0.001) |
|  | Rank of receiver                        | -0.105*** ( $\pm$ 0.008) |
|  | Absolute difference in rank of partners | -0.014*** ( $\pm$ 0.003) |
| Model 2: Uni-directional grooming in Uniform fruit distribution [N = 3600, R2m = 0.55, R2c = 0.87] |   |                          |
| Response   | Predictor                               | $\beta$ ( $\pm$ S.E)     |
| Total Uni-directional grooming given   | Total Uni-directional grooming received | -0.041*** ( $\pm$ 0.001) |
|  | Rank of receiver                        | -0.112*** ( $\pm$ 0.008) |
|  | Absolute difference in rank of partners | -0.009** ( $\pm$ 0.003)  |
| Model 3: Mutual grooming in Patchy fruit distribution [N = 3600, R2m = 0.58, R2c = 0.49]           |   |                          |
| Response   | Predictor                               | $\beta$ ( $\pm$ S.E)     |
| Total Mutual grooming given  | Rank of receiver                        | -0.046*** ( $\pm$ 0.005) |
|  | Absolute difference in rank of partners | -0.042*** ( $\pm$ 0.004) |
| Model 4: Mutual grooming in Uniform fruit distribution [N = 3600, R2m = 0.07, R2c = 0.42]          |   |                          |
| Response   | Predictor                               | $\beta$ ( $\pm$ S.E)     |
| Total Mutual grooming given  | Rank of receiver                        | -0.049*** ( $\pm$ 0.004) |
|  | Absolute difference in rank of partners | -0.021*** ( $\pm$ 0.003) |
| Model 5: Uni-directional grooming in Ring-tailed lemur [N = 218, R2m = 0.16, R2c = 0.34]           |   |                          |
| Response   | Predictor                               | $\beta$ ( $\pm$ S.E)     |
| Total Uni-directional grooming given   | Total Uni-directional grooming received | 0.740 ( $\pm$ 1.217)     |
|  | Rank of receiver                        | -0.201*** ( $\pm$ 0.055) |
|  | Absolute difference in rank of partners | -0.260*** ( $\pm$ 0.073) |
| Model 6: Uni-directional grooming in Red-fronted lemur [N = 316, R2m = N.A, R2c = N.A]             |   |                          |
| Response   | Predictor                               | $\beta$ ( $\pm$ S.E)     |
| Total Uni-directional grooming given   | Total Uni-directional grooming received | -                        |
|  | Rank of receiver                        | -                        |
|  | Absolute difference in rank of partners | -                        |
| Model 7: Mutual grooming in Ring-tailed lemur [N = 218, R2m = 0.16, R2c = 0.30]                    |   |                          |
| Response   | Predictor                               | $\beta$ ( $\pm$ S.E)     |
| Total Mutual grooming given  | Rank of receiver                        | -0.022 ( $\pm$ 0.033)    |
|  | Absolute difference in rank of partners | -0.338*** ( $\pm$ 0.045) |
| Model 8: Mutual grooming in Red-fronted lemur [N = 316, R2m = 0.003, R2c = 0.18]                   |   |                          |
| Response   | Predictor                               | $\beta$ ( $\pm$ S.E)     |
| Total Mutual grooming given  | Rank of receiver                        | -0.021 ( $\pm$ 0.027)    |
|  | Absolute difference in rank of partners | 0.015 ( $\pm$ 0.036)     |

