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A reinforcement learning model for grooming up the hierarchy in primates

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Primates spend a considerable amount of time grooming each other. Grooming is regularly found to be traded reciprocally (for grooming) or for rank-related benefits in the presence of food competition. It has been suggested that if food sources are clustered and monopolizable, then lower-ranked individuals will groom higher-ranked ones in order to be tolerated on food patches. This leads to grooming being directed up the hierarchy. However, the conditions where this is expected to occur are based on verbal reasoning alone, and no quantitative analysis of the conditions favouring grooming up the hierarchy appear in the literature. Here, we develop a quantitative model investigating when food competition can result in grooming up the hierarchy. Individuals are assumed to take actions pertaining to whom to groom, where to feed and whom to tolerate on food patches. By allowing individuals to choose actions according to reinforcement learning, we delineate conditions where groups of individuals will express reciprocal grooming and grooming up the hierarchy depending on environmental conditions (e.g. quality, number of food patches). In particular, we show that conditions of intense food competition may lead to less grooming up the hierarchy. The predictions of our model could guide future comparative studies and meta-analyses investigating social relationships in primates.

Primates spend a significant proportion of their daily time budget grooming other individuals: picking through fur to remove ectoparasites and clean the skin (social grooming, hereafter grooming; Dunbar, 1991). This observation may come as no surprise since being groomed is beneficial due to the removal of ectoparasites (Tanaka & Takefushi, 1993). Furthermore, grooming has an important social function, where social bonds between individuals are reinforced through the act of grooming. It has been argued that grooming behaviour has evolved because of these benefits (Dunbar, 1991). However, there can also be costs associated with giving grooming. These come in the form of opportunity costs (not being able to use the time or energy for other activities), such as reduced vigilance (Barrett & Henzi, 2006; Maestripieri, 1993). Thus, grooming behaviour can potentially be exploited, whereby within a pair of individuals only one makes the investment to groom and the other reaps the benefit without reciprocating. Understanding the causal proximate and ultimate factors influencing individual grooming decisions is a long-standing goal in primatology (Schino, 2001; Seyfarth, 1980).

Grooming can be thought of as a commodity that can be traded, where individuals give grooming in order to receive something back. If grooming is solely traded for grooming, then pairs of individuals are expected to trade equal amounts of grooming. Numerous studies do indeed report a so-called time matching of grooming between individuals (Barrett, Henzi, Weingrill, Lycett, & Hill, 1999; Leinfelder, de Vries, Deleu, & Nelissen, 2001; Pazol & Cords, 2005; Rowell, Wilson, & Cords, 1991). Here, the individuals in a dyad are found to spend an approximately equal amount of time grooming each other, either within a single grooming bout or over a longer period of time. However, primate troops are nearly always characterized by a dominance hierarchy, and grooming interactions occur between individuals of different ranks. In a significant proportion of studies, grooming is observed to be directed up the hierarchy, that is, higher-ranked individuals receive more grooming than lower-ranked ones. Hence, grooming decisions are likely to depend on factors other than just the exchange of grooming. In other words, grooming of high-ranked by low-ranked individuals is likely to be traded for benefits other than grooming

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(Roubová, Konečná, Šmilauer, & Wallner, 2015; Seyfarth, 1980; Ventura, Majolo, Koyama, Hardie, & Schino, 2006; Wei et al., 2012).

What are the benefits that can explain grooming up the hierarchy? The socioecological model of primatology is concerned with the causes and consequences of food competition and its effect on social relationships (Kappeler & van Schaik, 2002). Within this framework it is argued that under conditions where individuals compete over food resources low-ranked individuals may trade grooming for nongrooming benefits provided by high-ranked ones (Kappeler & van Schaik, 2002; van Schaik, 1989; Sterck, Watts, & van Schaik, 1997). If food sources (or patches) are clumped and monopolizable, then individuals are expected to defend food sources or attempt to displace one another from them. Here, coalitions may be formed between individuals, either to defend a food source or to displace others from it. Then, low-ranking individuals may groom higher-ranking individuals to gain coalitionary support in agonistic interactions (Carne, Wiper, & Semple, 2011; Schino, 2007; Seyfarth & Cheney, 1984; Seyfarth, 1980). Experimental evidence for grooming being traded for coalitionary support can be found in baboons, *Papio hamadryas*, and vervet monkeys, *Chlorocebus pygerythrus* (Borgeaud & Bshary, 2015; Cheney, Moscovice, Heesen, Mundry, & Seyfarth, 2010). Owing to the trading of grooming by low-ranked individuals for such support from high-ranked individuals, on average grooming should be directed up the hierarchy.

Grooming can also be traded for increased tolerance (reduced aggression) for a low-ranked individual by a high-ranked one on a food source (Henzi & Barrett, 1999). This relies on broadly the same ecological conditions as the grooming under the coalitionary support hypothesis. If food sources are monopolizable then, instead of attempting to displace a higher-ranked individual, the low-ranked individual may groom the higher-ranked one in order to be tolerated by that individual on the food source. Like the coalitionary support hypothesis, there is empirical evidence showing that grooming for tolerance occurs (Carne et al., 2011; Tiddi, Aureli, Polizzi di Sorrentino, Janson, & Schino, 2011; Ventura et al., 2006; Xia, Garber, Sun, Zhu, & Sun, 2012). Furthermore, while most primate studies rely on correlational data, it has been shown experimentally that vervet monkeys trade grooming for short-term tolerance (Borgeaud & Bshary, 2015).

There thus exists ample empirical support that grooming may be directed up the hierarchy, when it is traded for either coalitionary support or tolerance. However, the conditions under which this is expected to occur are mainly based on verbal models (van Schaik, 1989; Sterck et al., 1997; Wrangham, 1980), and there are few quantitative predictions as to the conditions under which grooming will be directed up the hierarchy and those grooming patterns that will be associated with it (which individuals receive extra grooming; Dunbar, 2002). One of the few models investigating grooming up the hierarchy is Seyfarth's (1977) model. In this quantitative model individuals make grooming decisions based on the 'attractiveness' of potential recipients. The attractiveness of an individual as grooming partner depends on the rank of that individual, since rank influences the likelihood of successfully supporting the focal individual in an agonistic interaction, and thus the highest-ranked individual is the most attractive grooming partner. The model managed to replicate two features that are typically found in various primate species: high-ranking individuals receive more grooming than low-ranking ones and individuals of adjacent rank groom each other more than expected by chance alone (Seyfarth, 1977). In an extension of this model, various types of competition for grooming access were investigated (Sambrook, Whiten, & Strum, 1995). However, both models explicitly assumed that high-ranked individuals are attractive grooming partners, and thus the grooming decisions are not linked directly to the intensity of food competition itself. It would thus be relevant to have a quantitative model that links endogenous grooming decisions to the mode of food competition and that could determine conditions under which grooming up the hierarchy occurs as an equilibrium behaviour.

Here, we present a reinforcement learning (individual-based) model in which a group of individuals have grooming and feeding interactions, whose payoff consequences ('rewards') affect grooming, feeding and tolerance decisions. This allows us to determine conditions under which food competition can lead to grooming being directed up the hierarchy under the grooming for tolerance hypothesis. Although grooming occurs frequently between kin, a meta-analysis demonstrated a significant effect of grooming reciprocity among nonkin (Schino & Aureli, 2008). Since our main interest here is the effect of food competition, we assume that individuals in the model are unrelated. However, we further assume that individuals spend their entire life together, which corresponds to the philopatric sex, and this typically means the females in primates (Pusey & Packer, 1987). The main questions that we address with this model are: (1) can food competition result in grooming up the hierarchy as an equilibrium behaviour when individuals decide whom to groom, where to feed and whom to evict, dynamically according to payoffs, (2) what kind of grooming patterns are expected if grooming is directed up the hierarchy (e.g. do all individuals groom the alpha individual, or do they mostly groom one rank up the hierarchy), and (3) to what extent does the strength of competition (due to the number of patches or the aggressiveness of individuals) modulate grooming up the hierarchy?

THE MODEL

The Biological Setting

We consider a group of N individuals ranked in a stable, linear dominance hierarchy where individual $i \in \{1, 2, ..., N\}$ has a unique rank $r_i = i \in \{1, 2, ..., N\}$. Individual $i = 1$ is the lowest-ranked and $i = N$ is the highest-ranked or alpha individual. Individuals within this group interact with each other for T discrete time steps, which can be thought of as the number of interactions on a daily basis, monthly basis, yearly basis, etc. Each interaction time step $t = 1, 2, ..., T$ is characterized by four sequential behavioural stages: grooming, food patch selection, aggressive interactions and feeding, which occur in this order and that we now detail.

Stage 1: Grooming

Each individual either selects an individual that it grooms or it grooms no one. The set of actions available to individual i in this

Table 1
List of model parameters

Parameter	Equations	Meaning
c	6	Cost of grooming
b	6, 10	Benefit of being groomed
γ	6	Change in motivation when not grooming
λ	4, 8	Exploration rate
δ	5, 9, 10	Discount factor
β	11	Regulate probability of engaging in a contest
ε	10	Impact of eviction
d	1, 7	Dominance gradient
q_0	3	Reference patch quality
m	2	Interference
N		Group size
N_P		Number of patches