

Hierarchical societies of primates: Comments on love, war and cultures

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Another way to look at culture is to study the evolution of social systems and distribution of power in animals and, ultimately, their manifestation in human institutions. More precisely, by looking at the repartition of power across individuals we can order societies as ranging from more egalitarian to more despotic. The variation of distribution of power among human beings nevertheless appears to be relatively limited when compared to what is found in nature. To appreciate a considerable variation in humans, in fact, we need to dig into our past and compare ancient cultures to unravel the ever-changing human rank structure. In animals, instead, we have the opportunity to find a greater range of variation in the organisation of power across different phylogenetic groups at any one time. Looking at how societies are structured in our closest relatives, in particular the primates, provides excellent opportunity that also helps us better to understand the differences within our own species.

The distribution of power in primates does not only depend on the species we are looking at, but to a lesser degree also on the varying ecological conditions that characterise different populations of the same species. [Boehm \(1999\)](#) provides a comprehensive account of the variation of the social systems ranging from more egalitarian to more despotic in both human and some non-human primates. In addition, several models exist aimed at explaining the socioecology of primates living in a group and feeding together ([Sterck et al. 1997](#); [van Schaik 1989](#); [Thierry 2008](#); [Koenig and](#)

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Borries 2009). These models attempt to explain why we witness a repartition in rank in nature, looking at the distribution of food resources in the environment as its causing basis. Phenomena of within group competition may arise among group members when living in territories with limited and patchy food resources, as opposed to groups with large and evenly scattered nourishment. In particular, contest competition takes place when the resources can be accessed by multiple individuals and they can be monopolised. Under these conditions, an order for accessing food needs to be established, even when food sharing is the strategy preferentially adopted. In short, rank differences are then exploited in favour of the dominants, and this society can be described as generally 'despotic'. Ugo Pagano in his paper provides an excellent example, comparing the sexual and social structure of human with gorilla societies.

The biological market theory (Noë and Hammerstein 1995) is used in biology to explain the occurrence of phenomena such as mutualism and cooperation. It is of concern here since the distribution of power can be better understood, I believe, if framed within a more general framework of exchange and bartering of social 'favours'. As it was already pointed out in this journal in relation to cultural group selection (Landa 2009), the biological market theory is equivalent to the Neo-classical Walrasian theory of exchange in human markets (see also Bowles and Hammerstein 2003). Within a social market, individuals choose their partners so as to maximize their payoff from mutual trading. This partner choice, when successfully achieved, should yield the most profitable outcome as measured by a gain in profit from the cooperative social exchange. Profit is shown by the number and quality of commodities received as compared to those offered. It follows that competition to join with the best partners induces the value of attractive partners to increase resulting in a fluctuation of rank.

Behavioural commodities that can be traded in the order of primates are, for instance, grooming (fur cleaning) given or received in exchange of tolerance, mating and infant handling (Barrett et al. 1999; Henzi and Barrett 2002; Gumert 2007). Grooming is a behaviour that primates and some other animals like to receive; it has turned out to be a commodity that can be exchanged depending on favourable circumstances. The access to valuable commodities may differentiate in a market, leading to a fluctuation in price of such commodities depending on their availability during their 'trading'.

To an extent similar to what can possibly be done at a comparative level, that is comparing different species living in different habitats, today in primatology we need evidence at an empirical level if we go beyond simpler correlation effects. Experiments should be put in place to test how the structure of groups can possibly change depending on the type of goods at stake and their repartition across group members.

As Pagano points out for human societies, individuals acquire power and status through accumulating wealth. As I will try to explain, this holds true also with other primates. With this order we have experimental evidence coming only from the laboratory (cognitive studies) and usually with a limited number of individuals interacting and trading goods (usually food types). Yet again, the evidence that is needed today for the study of the modifications involved in the repartition of power must come from naturally occurring animal populations. The most common criticism that can be addressed to studies done in captivity relates to the behaviours displayed by provisioned animals. Assumptions from these behaviours can, at times, hinder deductions

coming from more natural behaviours found in wild individuals. Exceptions to this lack of information are: (1) a study looking at the biological market in vervet monkeys (Fruteau et al. 2009), and (2) another study I made with the same species and focussing specifically on cooperative behaviour (Pansini 2011). Both studies induced non-invasive modifications at a social level in the animal subjects.

As also Pagano points out, people acquire power and status by accumulating wealth; monkeys can also acquire power by mean of accumulation of social favours. It was then the point of these field experiments with vervet monkeys to try to modify the power of only certain individuals of a social group to allow the rest to have access to food resources. In general terms, through these experiments we attempted to combine microeconomics theories with evolutionary biology. Being the value of a commodity governed by supply and demand, the price of a commodity was expected to increase when its demand rose.

Fruteau et al. (2009) chose two low-ranking vervet females as food providers by giving only to these two individuals the opportunity to supply the other group members with fruit. The expectation of the researcher was that such a setup would influence the way grooming (the currency they can use) was exchanged between these food providers and the other group members. Grooming distribution was eventually recorded to differ in terms of time each partner invested in grooming, toward an eventual benefit in favour to the food provider individuals. These results can be generalised in terms of power, since the relative social power of the providers increased in the group.

In order to extend this line of experimentation further, I studied cooperative behaviour in this same species of vervet monkeys (Pansini 2011). The purpose was still to measure the exchange of behavioural commodities carried out by different trading classes of individuals. I induced the monkeys to stand in front of small feeders, operate them and, as an ultimate step, share food. During a training phase the feeders could be accessed by one or more individuals that were assigned to two distinct classes of different size (future cooperators). In each group, a smaller class was comprised of those two individuals who became used to have access to feeders of black colour. These two individuals of the smaller class were assigned and chosen in such a way as to be representative of the other larger class and the entire group (in particular I chose this smaller class to comprise one dominant and one subordinate individual). This class distinction was made to generate predictions linked to the biological market theory. Due to the law of supply and demand the monkeys of the smaller cooperation class ($N = 2$) were expected to gain a privileged status compared to the rest of the group members. During the cooperation phase the feeders were joint, one black and one white together. The individuals could access food as long as at least one monkey from each cooperator class was standing in front of the machines trying to operate them. The individuals were free to associate in many desired combinations giving the system the opportunity to work not only with dyadic combinations, but also in the presence of multiple partners. This design allowed the monkeys to interact at the food source and combine also as possibly predicted by the matching market hypothesis (Sotomayor 2004).

By inducing the monkeys to share food at close distance I offered the monkeys the opportunity to redistribute goods autonomously. This situation is similar to the one seen in humans who need to access wealth that can be accumulated. Pagano

emphasises that it is during the move from hunter and gathers societies to agriculture and, later, to industrial societies that human power becomes unequally distributed and castes of different social power are established. In this field experiment though, the monkeys' individual ranks were already well established before the experiment. The opportunity offered to the subjects was nevertheless that of handling new and sharable food resources. The matching market design in particular allowed scoring whether dominants preferred cooperating with other dominants or rather subordinate individuals. Eventually, what was found was that dominants preferred cooperating with other dominant, and subordinates with other subordinate, individuals. These results can be interpreted according to the socioecological models that attempt to investigate whether primates conform to types of societies with egalitarian or more despotic attributes. With this perspective in mind, we can understand why, in the course of the experiment, the three groups of vervets moved to a temporary and relatively more despotic state. Eventually, the individuals of the smaller class, being in short supply as cooperators, became rewarded by the high demand of the larger class, as scored by an increase in affiliative behaviour (e.g. grooming) directed towards them.

These experiments well portray some of the more general arguments Pagano addresses in his paper. Although examples of warfare in primates are still lacking [with the exception of [Mitani et al. \(2010\)](#)], we can for now focus on primates' 'economics' to ponder the distribution of power and the way it originated in our more recent ancestors.

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