Modelling Primate Social Order: Ultimate and Proximate Explanations

Hagen Lehmann and Joanna J. Bryson

Artificial models of natural Intelligence, University of Bath,United Kingdom
H.Lehmann@bath.ac.uk, J.J.Bryson@bath.ac.uk

Abstract. For many species of primates, arguably including humans, social behaviour can be characterised along an axis usually described as running from egalitarian to despotic. Despotic societies are characterised by a strict hierarchy with very few aggressive interactions, but where aggression occurs it is typically violent and usually unilateral from dominant to subordinate. Egalitarian societies have less well-defined hierarchies; frequent, bilateral, but less violent aggression, and a large repertoire of reconciliation behaviours. In this paper we describe our approach to understanding the selective pressures that results in these different social organisations. Our technique focuses on agent-based modelling of the closely related species in the genus *macaca*. To simplify the problem we have split the models into ultimate and proximate causes, using two different ABM tools for the two different problems. This is work in progress — here we explain our approach, and describe preliminary results from the ultimate cause model.

1 Introduction

Social behaviour is at the core of much of human action, including our motivation and reasoning [6, 10]. Thus understanding ourselves as individuals and as societies requires understanding the bases of our social interaction. For many primate species social behaviour has been characterised along an axis usually described as running from *egalitarian* to *despotic* [17, 22]. Despotic societies are characterised by a strict hierarchy with very few aggressive interactions. Where aggression occurs, however, it is typically violent and usually unilateral from dominant to subordinate [11]. Egalitarian societies, in contrast, have less well-defined hierarchies with only the top few most-dominant individuals clearly differentiated. They have frequent disputes with bilateral aggressive displays, but with less physical violence. They also display a larger repertoire of conciliatory behaviours than despotic species [7].

In this paper we describe our attempt to better understand why these two forms of social behaviour have emerged. We have reviewed the available biological literature and found the explanations that seem best argued are fairly simple. Despotic species, as a result of their social interactions, tend to spend most of their time spread out — keeping out of harm's way by keeping at arms' length. More egalitarian species on the other hand tend to cluster relatively closely together. We believe the pressure for staying further away from each other is simply feeding pressure — under normal conditions more food resources can be found in a larger feeding range.

The contrasting pressure for maintaining proximity is predation. Most predators that prey on primates do not prey exclusively on this family; thus thwarting predation requires only reducing the probability of predatory success to a level that makes other species more appealing. Being closer together increases the probability that some individual will spot a predator in time for all individuals to escape to in accessable heights. Also, depending on the primate and predator species, if enough primate individuals are present they can actually physically overwhelm potential predators.

In order to find support for this hypothesis as an explanation for this key difference in primate species' social behaviour, we are building models that test its validity. To simplify the modelling problem we have decided to build two different models: an ultimate model, which shows the adaptive utility of the different approaches, and a proximate model, which shows how the features characterising despotic and egalitarian behaviour serve as mechanisms for achieving the ultimate 'goals', that is, the adaptive configuration suited for the various environments. This is work in progress — here we explain our approach, and describe the first results from the ultimate cause model. We begin, however, by providing additional background details on the system to be modelled.

2 Categories in Primate Behaviour

Individuals in primate groups influence each others behaviour through their social interactions. They inhibit or reinforce each others' tendency to perform a variety of social acts [21].

The simplest form of an aggressive interaction between two individuals can be described as a sequence of aggressive behaviours followed by either an aggressive or submissive response from the addressed individual. The initial aggressive behaviour is usually composed of threats. These signals can be more or less pronounced and physical. In all species, the initial aggression is directed usually from a dominant individual to a subordinate. Submissive behaviour often contains reconciliatory actions. For both the aggressive and the submissive behaviour each species has a repertoire of possible actions [19]. Choice amongst these actions (e.g. between a bite, a slap, or a growl) usually expresses the seriousness of the executor in its intentions. The reaction to an act of aggression depends highly on the risk of getting injured in an ensuing fight. For weaker individuals in a high-risk situation it is therefore better to submit than to counter attack [4, 9].

One way to operationalize the different social strategies observed in primate species is to define a dominance gradient. The *dominance gradient* is a measure for the distance between animals in their social group's hierarchy. The further apart the individuals are from each other, the more despotic their social style is. The easier it is for the subdominant individual to retaliate, given the action repertoire of the species, the less steep the dominance gradient in this species is. Conversely the higher the intensity of aggressive interactions in a species is (that means as more difficult the expression of submissive reactions), the steeper is the dominance gradient in this species [17].

As a result of these factors, in socially stable situations with a steep dominance gradient, highly intensive aggressive social interactions should be sparse, since they would lead to severe injuries and would therefore be a poor strategy. Mothers in such societies should be very restrictive of their children's actions in order to limit their interactions with other individuals to prevent them from harm [20]. The observable structure of such intolerant groups will therefore show fewer interactions between individuals and a greater spacial distance between them.

In more egalitarian-structured societies the social gradient is less steep. This allows individuals to be more challenging towards each other. As a result, more interactions between individuals can be observed and the average distances between them is smaller. Aggressive behaviours amongst members of the group occurs more frequently than in despotic societies, but the intensity is much lower [21]. Also there is much more likely to be some form of reconciliation behaviour right after an aggression. The variety of reconciliation behaviours enables the individuals to show gradiations of submissive reactions. This enables the group to stay close together.

3 Existing Models

The best known existent model of primate social behaviour is by Hemelrijk [13, 14, e.g.]. Her model uses a simple set of social interactions based on spatial locations. Hemelrijk's model consists of a small group of primates having dominance interactions. It assumes that every dominance interaction results in shifts in the agent's dominance rank. The amount of shift is determined partially by the expectedness of the outcome, and partially by the violence of the interaction. The violence of the interaction is determined entirely by the species of the primate — thus for Hemelrijk, level of violence is the key explanation for the difference in social organisations.

Hemelrijk measures two things to validate her model and compare it to real primate species: the steepness of the dominance hierarchy and the average centrality of each agent. *Centrality* here means the extent to which dominant agents tend to be in the middle of the group. It has been observed in the wild that dominants tend towards this position, and it has been hypothesized that this is a safer position due to pressures of predation. Hemelrijk's model shows that a fairly simple algorithm keeps the dominants central *and* drives despotic species' dominance hierarchy to be much steeper than egalitarians.

In previous work, we have successfully replicated Hemelrijk's model, and presented a critique on its main result concerning the difference between despotic and egalitarian species [2, 15]. We showed that her model both predicts and depends on frequent "upsets", where subordinate agents beat dominant ones in fights. Such results almost never occur in real life; even in egalitarian-structured groups, low ranking individuals very seldom replace high ranking ones. Hemelrijk's model predicts frequent and permant shifts in ranks of individuals, which again are not seen in nature. The dominance system in most primate groups is extremely stable. For females of many species, it is effectively even hereditary, depending on a mother's rank and a daughter's birth order.

These discrepancies between the model and the actual field data justify the construction of a new and potentially more complicated model of primate social behaviour, so long as it provides a better match to the data. We decided to program a model which takes the stable group structure into consideration and focuses on the interaction between agents and the environment as well as on the interactions amongst the agents.

4 Modelling Approach: Ultimate and Proximate Causes

In ethology the causes for behaviour in animals are categorised as ultimate and proximate causes. In our approach to modelling the evolution of social behaviour in non-human primates, we have chosen to use this distinction in order to simplify the modelling problem through decomposition. This approach gives us significant benefits in terms of computational efficiency, since detailed mechanisms are not needed in models at evolutionary time scales. The ultimate / proximate distinction also allows us to be able to better differentiate and describe the mechanisms involved in the process, and thus achieve better scientific and communicative clarity.

The ultimate cause can be described as the explanation of an animal's behaviour based on evolution — why this specific trait has been favoured by natural selection. The question in our case is what are the environmental pressures that force non-human primates to organise in groups and evolve the variety of social strategies we see in dealing with the tensions resulting from a gregarious lifestyle.

The proximate cause can be described as the explanation of an animal's behaviour based on trigger stimuli and internal mechanisms. In other words, the proximate explanation tells us exactly *what* is happening in the individual, while the ultimate cause tells us *why*. For example, reproduction has the ultimate purpose of propagating the species, but individual reproductive behaviour is not generally motivated by considerations of progeny. In the present case, proximate mechanisms are those that explain how and when macaques interact with each other — when and with what motivation they fight or affiliate.

We are developing two different models to illustrate the mechanisms in these two different categories. In this paper we will focus on the ultimate cause for the evolution of their social behaviour.

4.1 Ultimate cause

The ultimate cause for the evolution of a gregarious life style and the social strategies connected to it is the interaction between predation pressure and food availability. Predation pressure acts as an adhesive force, or what [18] called *attraction*. It forces individuals to organise in groups to increase their safety and is thought to be the original reason why animals are gregarious. In savannah-living primates like the yellow baboon (*papio cynocephalus*) females tend to be surrounded by as many other group members as possible to increase their safety. High-ranking dominant females are observed to be most of the time in the centre of the group [5]. The main predator for most old-world primate species are leopards. Although the actual killing of an animal is very hard to observe in the field, since the observer itself is a major disrupting factor in the stalking process of the hunter, the number of individuals getting killed by a predator can be estimated by the decrease in group size and it can be said that hunts happen frequently [25].

The likelihood of falling victim to a predator decreases with the number of individuals in a group [12]. This is true for almost all of the terrestrial living primates.

Restricted food access is the force that drives individuals apart from each other, or what Reynolds calls *repulsion*. Limited resources mean that individuals have to search in different places for food or compete for the food in the same place. Food and energy lead to strength, long life and reproductive capacity.

5 The Model

Here we use NetLogo to program our ultimate model. NetLogo is a multi-agent modeling language that evolved from StarLogo. It enables us to give instructions to independent "agents" and monitor their behaviour in different environmental settings [24].

The model consists of two groups of agents with different interaction patterns. One group has an egalitarian structure, the other despotic interaction patterns. For this ultimate model, all this amounts to is that the egalitarian animals tend to stay nearer to each other than the despotic ones do. In both groups the agents interact with each other in the same environmental setting and are exposed to the same pressures. We monitor the number of the individuals in the groups. We then use this parameter to determine which group is better adjusted for which environmental settings. The pressures the groups are exposed to are food availability and predation. The agents interact only with agents of their own group.

5.1 Behaviour description

The behaviour of each group is defined by a set of different parameters. The agents move around randomly to simulate exploration behaviour. Every agent has an energy level which is reduced after every step the agent makes. If the agent moves over a food patch its energy level is restored by a certain value. This simulates feeding behaviour. If the energy level of an agent goes below a certain level, the agent will start to search for food and move to the food patch closest to it.

The interactions between agents depend on three variables. Each agent has a maximum view. If it does not "see" any of if its group members within this range, it will move towards the closest agent it can see. If an agent "sees" other agents of its own group within a certain distance called near view, it moves randomly around or searches for food. If the agent finds another agent within its personal space a dominance interaction is started.

Dominance interactions depend on a fixed dominance value assigned each agent when it first comes into the simulation. The values determine the agents' position within the hierarchy of the group. High values stand for high dominance and low values for a lower rank position. During a dominance interaction, the more dominant individual displaces the subordinate animal and chases it away from its current position.

Agents can die and be born. An agent dies, if its energy level drops down to 0 or if it is killed by a predator. A predefined percentage of the entire population of agents is killed at regular time intervals. We define this as the predation rate. I order to identify which primates are prey, we calculate the distance of every single agent to the centre

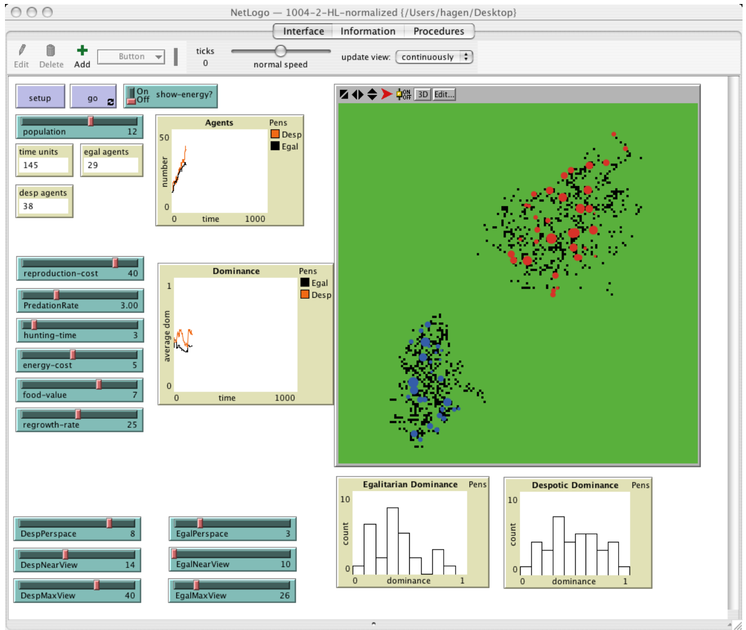

Fig. 1. Screenshot of the model running in NetLogo

of its group. We do this for both populations separately. The agents which are furthest away from the centre of their group are then “killed” by the predator.

Agents give birth asexually when their energy level reaches a certain value. The offspring then inherits a dominance value normal distributed with a standrad variation of 7 around the dominance value of its parent.

We also regulate the food distribution via the regrowth rate of the foodpatches. Once an agent has “eaten” a food patch it stays empty for a certain amount of time before the food grows back again.

5.2 Experimental setup and results

Our hypothesis is that predation pressure has a bigger effect on despotic societies and limited food resources have a bigger effect on egalitarian groups. This should be due to the effect that only the outermost individuals of the population are killed by predators and the regrowth rate has more impact on areas with a higher concentration of agents.

We also assume that the predation has a stronger influence on group structure then food distribution. Besides the constraints of the group dynamics and their travel speed, there are no restriction on where individuals move to, but there is a constant predation pressure killing a percentage of the overall primate population frequently. Notice though that both species are in the same simulation, so one may be predated more than the other.

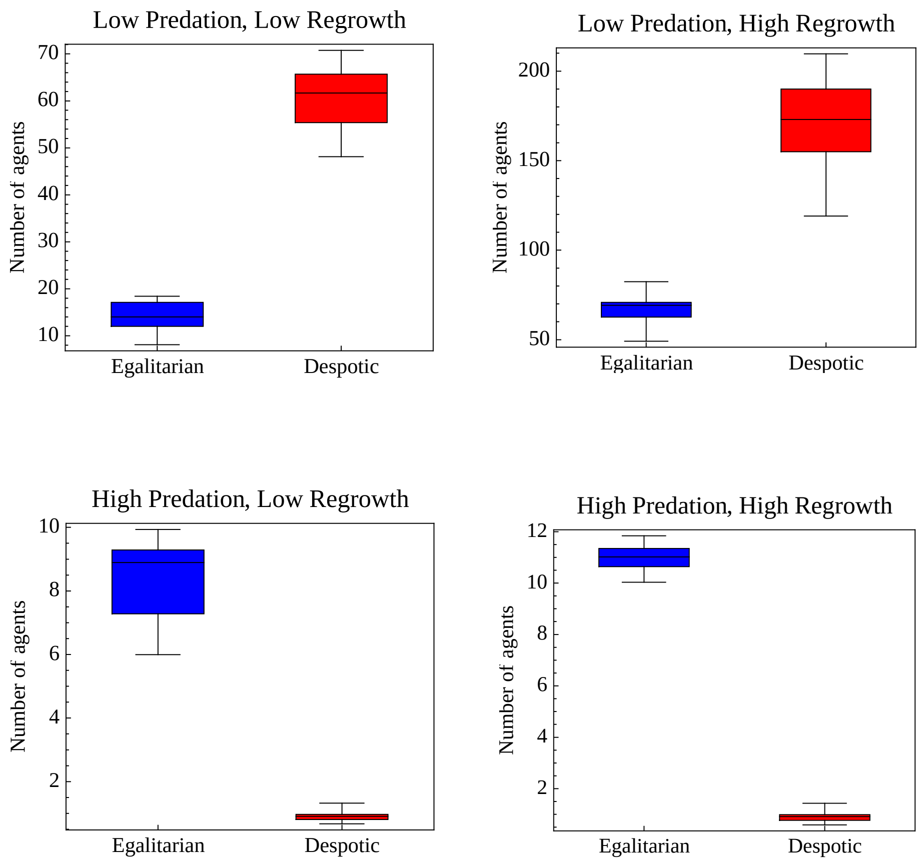

Fig. 2. Preliminary results from our model of the ultimate purpose of the despotic / egalitarian axis. We hypothesize that the distance between animals is the main selective pressure on which social order is present in a population. The model confirms that being more egalitarian (that is, nearer to troopmates) is more of an advantage in the face of predation, but otherwise a disadvantage due to food competition.

We did a series of 80 experimental runs under different settings. We used four different conditions to see how the average number of agents sustained by the environment changed.

In the first condition the environment consists of high predation pressure and low regrowth rate. We then run the experiment with low predation pressure and high regrowth rate. The other two conditions are low predation pressure and low regrowth rate and high predation pressure and high regrowth rate. Each condition was run 20 times. Since this is work in progress we are only able to present preliminary results. But these seem to confirm our hypotheses.

Our results show that the despotic agents did better in conditions with low predation rate and egalitarian agents did better with high predation rate. This supports our first hypothesis. They also show that a high regrowth rate amplified the reproductive success of the group, if the group was already successful. This supports our second hypothesis.

6 Conclusions and Future Work

Our results suggest that it is less adaptive to have a despotic social structure (or at least to live far apart from one another) in environments with high predation pressure, and that the reverse is true for low predation risk. They also suggest that it is more effective for the survival of the group to be despotic in situation with restricted food access and low predation pressure. Predation affects both groups in the same way, but has a stronger effect on the despotic agents, because their social structure leads to larger distances between the individual agents. This results in higher predation on despotic agents and therefore on higher numbers of egalitarian agents in conditions with high predation pressure. However, without this pressure, the despotic group is able to use the give food resources more effectively. This findings support the theory of how ultimate causes shape the nature of interaction in gregarious animals arguments and therefore the arguments of [8, 16, 23, e.g].

Of course our ultimate model says nothing directly about why egalitarian species engage in more reconciliation behaviour, or why despotic species fight less frequently. Now that we have established the hypothesis that distance between troop members may be the ultimate cause of differences in primate social organisation, we are now engaged in examining the proximate causes of this distance. This will involve more detailed modelling of individual behaviour, such as determining the violence of an initial interaction and how to respond to an assault. For this we are currently using another modelling tool, MASON, which we have extended to support a simplified description of complex agent behaviour [1, 3]. The tool set as well as the model are now work in progress.

References

[1] Brom, C., Gemrot, J., Bída, M., Burkert, O., Partington, S. J., and Bryson, J. J. (2006). Posh tools for game agent development by students and non-programmers.

In Mehdi, Q., Mtenzi, F., Duggan, B., and McAtamney, H., editors, *The Nineth International Computer Games Conference: AI, Mobile, Educational and Serious Games*, pages 126–133. University of Wolverhampton.

[2] Bryson, J. J., Ando, Y., and Lehmann, H. (2007). Agent-based modelling as scientific method: a case study analysing primate social behaviour. *Philosophical Transactions of the Royal Society, B — Biology*, 362(1485). in press.

[3] Bryson, J. J., Caulfield, T. J., and Drugowitsch, J. (2006). Integrating life-like action selection into cycle-based agent simulation environments. In North, M., Sallach, D. L., and Macal, C., editors, *Proceedings of Agent 2005: Generative Social Processes, Models, and Mechanisms*, pages 67–82, Chicago. Argonne National Laboratory.

[4] Chapais, B. (2001). Primate nepotism: What is the explanatory value of kin selection. *International Journal of Primatology*, 22:203–229.

[5] Collins, D. (1984). Spatial pattern in a troop of yellow baboons(papio cynocephalus) in tanzania. *Animal Behaviour*, 32:536–553.

[6] Cosmides, L. and Tooby, J. (1992). Cognitive adaptations for social exchange. In Barkow, J. H., Cosmides, L., and Tooby, J., editors, *The Adapted Mind*, pages 163–228. Oxford University Press.

[7] de Waal, F. B. M. and Johanowicz, D. L. (1993). Modification of reconciliation behavior through social experience: An experiment with two macaque species. *Child Development*, 64:897–908.

[8] Dunbar, R. (1988). *Primate social Systems*. Croom Helm, Beckenham.

[9] Dunbar, R. (1991). Functional significance of social grooming in primates. *Folia Primatol*, 57:121–131.

[10] Dunbar, R. I. M. (1995). Neocortex size and group size in primates: A test of the hypothesis. *Journal of Human Evolution*, 28:287–296.

[11] Flack, J. C. and de Waal, F. B. M. (2004). Dominance style, social power, and conflict management in macaque societies: A conceptual framework. In Thierry, B., Singh, M., and Kaumanns, W., editors, *Macaque Societies: A Model for the Study of Social Organization*, pages 157–181. Cambridge University Press.

[12] Hamilton, W. D. (1971). Geometry for the selfish herd. *Journal of Theoretical Biology*, 31:295–311.

[13] Hemelrijk, C. K. (1999). An individual-oriented model on the emergence of despotic and egalitarian societies. *Proceedings of the Royal Society: Biological Sciences*, 266:361–369.

[14] Hemelrijk, C. K. (2002). Despotic societies, sexual attraction and the emergence of male "tolerance": An agent based model. *Behaviour*, 139:729–747.

[15] Lehmann, H., Wang, J., and Bryson, J. J. (2005). Tolerance and sexual attraction in despotic societies: A replication and analysis of hemelrijk (2002). In Bryson, J. J., Prescott, T. J., and Seth, A. K., editors, *Modelling Natural Action Selecton: Proceedings of an International Workshop*, Edinburgh. The Society for the Study of Artificial Intelligence and the Simulation of Behaviour (AISB).

[16] Mayr, E. (1961). Cause and effect in biology. *Science*, 134:1501–1506.

[17] Preuschoft, S. and van Schaik, C. P. (2000). Dominance and communication: Conflict management in various social settings. In Aureli, F. and de Waal, F. B. M., editors, *Natural Conflict Resolution*, chapter 6. University of California Press.

[18] Reynolds, C. W. (1987). Flocks, herds, and schools: A distributed behavioral model. *Computer Graphics*, 21(4):25–34.

[19] Thierry, B. (1985). Patterns of agonistic interactions in three species of macaque (*macaca mulatta, m. fascicularis, m. tonkeana*). *Aggressive Behavior*, 11:223–233.

[20] Thierry, B. (2000). Covariation of conflict management patterns across macaque species. In Aureli, F. and de Waal, F. B. M., editors, *Natural Conflict Resolution*, chapter 6, pages 106–128. University of California Press.

[21] Thierry, B. (2006). The macaques: A double-layered social organisation. In Campell, C., Fuentes, A., MacKinnon, K. C., Panger, M., and Bearder, S., editors, *Primates in Perspective*, chapter 13. Oxford University Press.

[22] van Schaik, C. (1989). *Comparative Socio-ecology: The Behavioral Ecology of Humans and other Animals*, chapter The ecology of social relationships amongst female primates, pages 195–218. Oxford: Blackwell.

[23] van Schaik, C. (1996). Social evolution in primates: the role of ecological factors and male behavior. *Proceedings of the British Academy*, 88:9–31.

[24] Wilensky, U. (1999). *NetLogo*. Evanston, IL, USA.

[25] Zuberbühler, K. and Jenny, D. (2002). Leopard predation and primate evolution. *Journal of Human Evolution*, 43(6):873–886.