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## **A Group Selection Model of Territorial War, Xenophobia and Altruism in Humans and other Primates**

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### **Abstract**

A theoretical model of wars over group territories shows that behavioural traits like cooperative warfare, justice, altruism and outsider exclusion may have coevolved in higher primates and prehistoric man. The conditions for territorial war to be an effective mechanism of group selection are discussed. These conditions may have been present in tribal societies in prehistoric times but not in modern times. The geographic evolution of territories is illustrated with computer simulations.

Altruism means unselfishness. Altruism can be defined in evolutionary theory as a behavioural trait that increases the genetic fitness of others but decreases the fitness of the actor, who is called altruist. This is a very controversial issue in evolutionary biology because the principle of "the survival of the fittest" would predict that altruism is eliminated by natural selection.

Altruistic behaviour is nevertheless widespread in human societies. The almost universal readiness to help strangers in need and the widespread support for charity organizations is evidence that altruism is indeed a human trait. A number of possible theoretical explanations have been proposed. The most important explanations are the following theories:

- **Group selection.** A group of altruists is more likely to survive in hard times than a group of egoists. The egoists may be eliminated by extinction of entire groups (tribes) or even species.
- **Reciprocal selection.** It may be profitable for one individual to help another if it can be expected that the favour is later returned. This mechanism has been extensively studied in game theory, where it is known as the prisoner's dilemma. The theory involves many complications such as the probability of meeting again, cheating, and the possibilities of detecting cheating.
- **Kin selection.** Natural selection will promote any behaviour that leads to the production of more copies of the gene that codes for this behaviour. This includes the helping of others who share the same gene. A gene for helping one's siblings will spread if the fitness gain to the sibling is more than double the cost to the helper, because full siblings have a 50% probability of sharing the same gene. Helping distant relatives is less likely to be promoted by kin selection because they have a low probability of sharing the same gene.

- Cultural reward and punishment. Altruists are rewarded with a good reputation, which may confer various social advantages that increase their genetic fitness. Egoists may be punished as criminals.
- Cultural selection. Cultural and religious norms that command their adherers to help others are likely to spread by cultural selection. It is easy to observe that charity is often connected with religion, but there is no evidence that atheists are less altruistic than devoutly religious persons.

All of these theories probably contain part of the explanation why altruism is widespread among humans. Group selection is the theory that can explain the most examples of altruistic behaviour, but also the most controversial theory.

Various mathematical models have shown that the individual selection for egoism will be stronger than the group selection for altruism in almost all cases (Boorman and Levitt, 1980). However, this theory is in sharp contrast to actual observations of a number of animal species. Best known are the social insects, such as ants, bees and termites, where a large number of workers contribute to the survival of the group without ever reproducing themselves. Similar phenomena have been observed in an increasing number of animal species, including social shrimps (Duffy *et. al.*, 2000) and the naked mole rat (Sherman *et. al.*, 1991).

The marked discrepancy between theory and observation has led me to a refinement of group selection models. It turns out that the mathematical models rely on a number of simplifications, approximations and assumptions in order to make the models mathematically tractable. This problem can be overcome by computer simulation studies. Monte Carlo simulation techniques make it possible to study models that are too complex for mathematical analysis. My simulation studies have shown that the simplifications used in mathematical analysis seriously distort the results, and that group selection can indeed be a strong force in evolution under certain conditions.

The classical models of group selection are based on geographic boundaries between groups. Most well-known is the island-model where each group lives on its own island and migration between the islands is rare (Boorman and Levitt, 1980). This model is not very realistic and it lacks a plausible explanation why groups are selectively extinguished.

I have therefore proposed a new model where groups are separated by behavioural boundaries rather than geographic boundaries. Each group has its own territory and avoids contact with neighbour groups. Group selection takes place by the mechanism of territorial warfare. A group with many brave and self-sacrificing warriors will be capable of capturing territory from neighbour groups that have more egoistic members. The egoist group will lose territory and gradually perish from lack of subsistence means. The altruist group will grow and prosper until it gets so big that it splits up in two groups. The process can then continue (Fog, 2001). A snapshot of an ongoing simulation is shown in figure 1.

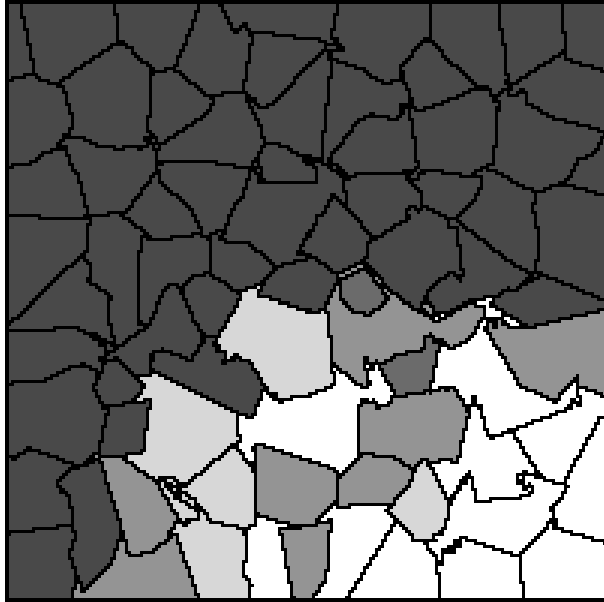


Fig. 1. Simulated evolution of group territories.  
Lighter colours = groups with higher fraction of altruists.

Computer simulations of the group territoriality model (Fog, 2000) show that this mechanism is likely to lead to fixation of the altruism gene when the following conditions are met:

- The rate of migration or interbreeding between neighbour groups is small ( $< 10\%$  per generation)
- The group size is limited ( $< 1000$  members)
- Few or no members of defeated groups survive
- The altruism gene has a stronger positive effect on group fitness than the negative effect on individual fitness
- The fitness of a group is a near-linear function of the fraction of phenotypic altruists in the group

The pattern of group conflict behaviour that has been observed among chimpanzees in the wild (Goodall 1986) suggests that the conditions for group selection to be effective might be satisfied for these primates. My theory is that the same holds true for prehistoric man. The model of fights over group territories does indeed resemble our image of tribal warfare in prehistoric time. If the above conditions were met in prehistoric time then it is possible that this mechanism has had an important influence on human evolution.

It must be emphasized that this applies to prehistoric hunter-gatherer societies only. The first three of the above conditions are obviously not met in modern human societies and most historic cultures. It is therefore certain that any group selection mechanism that may have influenced human evolution in the past is no longer in effect.

The reason why I, as a natural scientist, present this theory at an archaeology conference is that the archaeological record may provide material that is useful for testing this model of group territoriality. A number of predictions can be made from my model, and some of these predictions can be tested against archaeological evidence. The predictions that are most relevant to archaeology can be summarized as follows:

- A strong sense of group identity should be visible in clothing, body decoration and art. These symbols of group identity should be distinct from those of neighbouring tribes.
- Tribal war should have been ubiquitous wherever there were no strong geographic boundaries preventing access to neighbour territory.
- There should be a strong cooperation within the group and a division of labour between warriors, providers, child caretakers, political and cultural (ceremonial) leaders, etc. The theory cannot say whether this division of labour is organized around gender, age or some other criteria. It is possible that everybody in the group contributes to warfare in the most critical situations.
- There may have been a well-organized justice system involving rewards for bravery in battle and punishment for defection and disloyalty.
- Defeated groups suffer a very unkind fate, and few members of a defeated group survive, if any. All members of a defeated group should either die in battle, be massacred, or die as fugitives without a territory. We can expect to find evidence of massacres including women and children.
- The victorious group can be expected to destroy any religious artefacts that the defeated group has used for seeking protection from spirits or other supernatural beings.

I regret to say that this is not a theory that paints a flattering picture of our past. It is an incredible paradox that altruism and charity cannot have evolved without merciless cruelty!

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