

# Apes in the Anthropocene: The impacts of global change on parochial cooperation and intergroup aggression in *Pan troglodytes*

Noah Atkin

*University of Cambridge*

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## Abstract

Parochial cooperation in chimpanzees is supported by social structures which encourage repeated interactions that can build trust between individuals, which consequently allows chimpanzees to cooperate with non-kin individuals on territory patrols, resource defence and lethal raids. As climate change impacts food and water availability across sites, groups that are able to maintain close in-group relations are predicted to have a competitive advantage during increasingly important inter-group conflicts over limited resources. However the impact of changing ecological conditions on group cohesion is unexplored across most sites, despite the significant observed differences in intergroup violence between chimpanzee populations being hypothesised, in part, to be due to differing ecological conditions. This project aims to examine the impact of food & water availability and predictability on chimpanzee intra-group cohesion and inter-group aggression, and to estimate the impacts climate change will have on these behaviours under current emissions pathways. I ultimately hope to explain how global change drives intergroup conflict, the impact of resource limitation on intra-group cohesion and explore the limits of parochial altruism under extreme environmental conditions.

## Research Background

The Anthropocene extinction threatens to make all non-human great ape species extinct in the wild by the end of the century [2]. Great apes are particularly vulnerable to Anthropogenic threats due to their slow life history, long inter-birth intervals, and low population densities [16]. Habitat destruction, climate change, pollution and the synergistic effects between all of these have already enormously reduced great ape ranges worldwide, and the impacts are predicted to worsen for all great ape species over time [2, 16, 9, 10] .

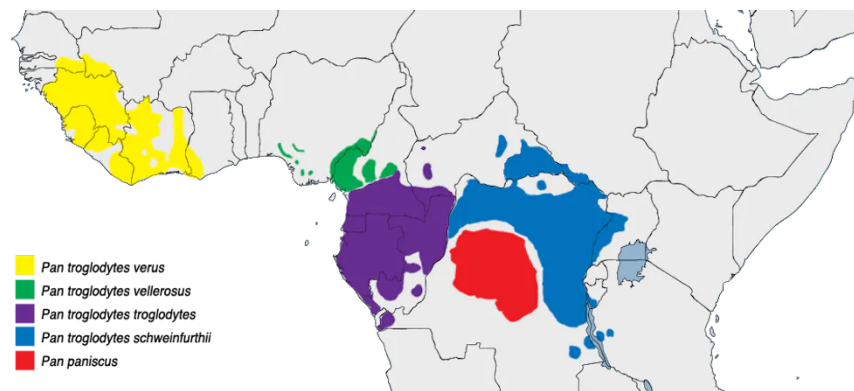
While in the 20th century land use change was the largest driver of great ape extinction, by 2070 climate change is predicted to become the largest driver of extinction in great ape populations, due

to existing habitat fragmentation, and poor thermoregulation limiting dispersal abilities [9]. Under current emissions, Carvalho et al. predict a 94 percent loss of great ape habitat in Africa by 2050. Even under RCP 2.6, a 85% decrease in great ape range sizes is predicted in just 3 decades time. These enormous reductions are due to human population changes, which land use change in existing ranges and future potential areas (outside of protected areas), and climate change, which impacts the viability of existing ranges and increases human demand for existing land currently containing great ape populations [2].

Climate change, of course, does not just affect wild animals. Climate change has dramatic impact on water availability, soil viability, disease emergence and phenological mismatch - all of which causes human mass migration, increases illegal logging, hunting and demand for bush meat [13, 9, 1, 20]. As the century goes on humanity itself will become synergistic stressor to the all of the factors affecting range size in great apes worldwide [2].

As the total land suitable for great ape habitation becomes smaller due to the above factors, the ecological constraints model predicts existing populations will be forced into competition over limited resources and increasingly come into contact with other groups - especially as decreased productivity of the land increases the required range size needed to support the same population size [19, 9].

On a species level, the effect of global change on great ape populations is well described, and on an individual level the impacts of reduced water availability and habitat on fitness is understood [2, 16, 9]. What is less understood currently is the impact these changes will have on communities, and the relationships between them.



**Figure 1:** Distribution of *Pan* species across the African continent. *Pan paniscus* is geographically separated from the other species by the Congo river.

This project aims to examine the role global change will have on *Pan* habitats and the communities that reside in them, with a specific focus on how coming reductions in food, water and total viable habitat size affect *Pan* species behaviour in 2 intrinsically linked areas:

### Intra-group dynamics

The ubiquity of intra-group cooperation in *Pan* species is well studied, particularly in chimpanzees where cooperative behaviour between non-kin individuals is seen on a group level (collective hunt-

ing and territory defence) all the way down to a dyadic level [12]. Groups work together via a model of parochial cooperation, which is the tendency for individuals within a group to favour the in-group over the out-group [11]. This trait spreads as larger groups' tendency towards cooperation have competitive advantage in inter-group conflicts where the out-group is less co-operative. Hence, parochial cooperation is paramount to effective resource and territory defence, however maintaining the social bonds and groups necessary for this cohesion may become strained under rising temperatures and reduced water availability.

An example of how seasonal variation can significantly impact chimpanzee social structures has been seen in western chimpanzees at Fongoli. Fongoli, in southeastern Senegal, is the hottest and driest site where habituated chimpanzees are studied, and during the 7 month long dry season all but 2 water sources dry up [22]. Soaring temperatures results in chimpanzees spending most of their activities budgets resting, which may impact non-kin social bonding behaviour used to maintain social ties [18]. Despite this, chimpanzees at Fongoli are significantly more cohesive than chimpanzees studied elsewhere, with an average party size of 15. When the party size is taken in the context of the community size, Fongoli chimpanzees also form significantly larger parties. Fongoli chimpanzees exhibit an average party size of close to 50% of their community size, compared to the average of 15% seen at other sites [14]. This cohesion does not make the group to immune to intra-group violence however as the group has been recorded killing the previous alpha male for approaching females in oestrus [15]. Whether these social structures are changing as temperatures continue to rise and water availability becomes lower generally has not been explored, however increasing group size and/or territory size would be expected under the ecological constraints model.

Under current emissions pathways, one of the predicted impacts across sub-Saharan Africa is increases in dry season length and shorter, more intense rainy seasons [8]. As a result, dry season patterns will start to resemble the more extreme conditions in West Africa - examining which social behaviours are conserved year round in highly seasonal areas, and how activity budgets change in response to extreme conditions can shed light on how chimpanzees communities across Africa will adapt to limited resources.

Additionally how decreased water availability and predictability impacts food availability has not been explored. Increased seasonality in food availability in chimpanzees has been associated with increased levels on infanticide and decreased female sociality [6], which can impact group cohesion and increase the likelihood of intra-group conflict. This has not currently been explored due to the requirement for systematic and methodical collection of data on food availability, predictability and seasonality across sites [11].

Ultimately in the face of ongoing climate catastrophe the chimpanzee communities that are able to maintain group cohesion, size and number of males will be more successful compared to others, and this success will be based on strategies used to reduce infanticide and intra-group conflict. Whether other chimpanzee communities' social structures will start to resemble those seen in more resource limited areas such as Fongoli is an area of debate, and would require projections of how current supplies of water and food will become limited in existing areas.

## Intergroup violence

Compared to all species, chimpanzees show high levels of territoriality however levels of inter-group violence vary across chimpanzee populations [7]. Inter-group conflict is regular and ex-

pressed mostly as vocal exchanges, which can escalate to chasing and attacking the out-group, occasionally ending in lethal violence [21]. Some chimpanzee communities also conduct lethal raids on other groups, killing males and juveniles [7].

Population density is correlated with the frequency of inter-group conflict in chimpanzee species. West African chimpanzees (*Pan troglodytes verus*) are the most sparsely populated, and fewer intergroup killings are observed in this sub-species compared to all others we have data on [23]. Notably for 2 studied west African populations (at Bompusa and Bossou), no intergroup killing has been observed at all, suggested to be due to comparatively large home ranges and reduced border patrols [11]. In stark comparison to east African chimpanzee species (*Pan troglodytes schweinfurthii*), where the ecology of their habitats can support much population densities and interaction rates increase accordingly [24].

The intensity of intergroup conflict also varies between *Pan* species, sub-species and study sites, notably the lethality of intergroup encounters. Killing is most common in eastern chimpanzees and least common in bonobos where no lethal intergroup encounters have been recorded [4]. Previous studies have shown lethality of intergroup encounters generally increases with population density, and the number of adult males in the attacking community; while the most common victims are adult males and unweaned infants [7, 17, 24]. Previous levels of lethal aggression in *Pan* show little correlation with human impacts, such as habitat disturbance and provisioning, but are instead better described by an adaptive hypothesis that killing is a means to eliminate rivals when the costs of killing are low [24].

Nonetheless it has also been suggested that habituation to humans gives some chimpanzee groups a competitive advantage during inter-group conflict, as fear of humans can interrupt cooperative responses to inter-group raiding [11]. This is particularly important going forward as increasing habitat fragmentation will expose more communities to humans, and possibly provide competitive advantage to communities bordering human habitats or have been previously habituated. However the impact of this has not yet been explored.

It has been hypothesised that differences in ecological conditions drives observed differences in aggression both between *Pan* species and between communities within species. Increased food predictability and availability reduces intra-group conflict, allows for greater party sizes and reduces differences in territory value. As the balance of power is more equal between the communities, the risk of intergroup violence is reduced as both groups have little to gain. However global change will increase the demand for valuable resources, such as water, as well decreasing the predictability or availability of the supply [2]. If there is link between ecological conditions and inter-group conflict levels, global change is likely to impact lethal raid frequency across populations.

In addition, we may also see increases in the frequency of inter-group encounters globally, changes to frequency of aggressive intrusions, or defensive behaviours such as border patrols. We may also see the role that reduced food availability has on group size. When less food is available per patch, we may see more fission and smaller parties, which may provide advantages within the home range, but increasing the risk of attack to these smaller groups while on the periphery of home ranges (as conflict is more likely to escalate when there is large asymmetry in opposing group sizes).

This has currently not been examined as it requires systematic analysis of food availability, water availability, distribution and predictability between multiple field sites [11].

## Key questions

The key questions, as yet unexplored from the above data are:

- What impact does resource availability, predictability and seasonality have on intra-group cohesion in *Pan* species? (e.g. is there an emerging trend towards larger chimpanzee groups as seen in Fongoli?)
- What impact does food availability, predictability and seasonality have on levels of inter-group lethality in *Pan* species?
- Is asymmetry in home range resource availability a key driver of inter-group lethality in *Pan* species?

This PhD aims to answer the above questions, in doing so predicting how wide scale climate disruption and global change will impact levels of lethality between and within *Pan* groups, ultimately shedding light on how early Hominid communities may have coped with large scale disruption to food and water supplies.

## Methods

This study will focus on the observed behavioural impacts of climate change on western chimpanzees, as multiple long term field sites are set up to observe their behaviour in a variety of habitats, and their latitude makes the seasonal effects of a changing climate more pronounced and easier to observe. After the behavioural adaptations to a changing climate have been broadly described, I will move onto projecting which environmental changes are likely to impact behaviour in other sub-species and make a series of predictions as to how specific climate impacts will affect chimpanzee intra-group cohesion and inter-group conflict in other areas.

### Trends in western African chimpanzee social interactions

Due to their latitude, west African chimpanzees are predicted to feel impacts of climate change, including shorter rainy seasons and longer, more intense dry seasons sooner than central and east African chimpanzee communities - making them an ideal model to study changing social interactions within and between communities. Additionally, IPCC modelling suggests coming large temperature increases in Gabon, where a central chimpanzee study site is located (Loango), making it the ideal location to start testing predictions of social changes caused by changes to climate [8].

The project will first examine seasonal trends in chimpanzee social behaviour at Fongoli, examining in particular the prioritisation of non-kin social grooming behaviour over other activities while under metabolic stress. It will also examine how the frequency, and lethality of intergroup conflict varies by season to examine whether particularly extreme climatic events drive conflict during the dry season over limited resources, or whether lethal raids are conducted during the wet season where the individual costs of conflict are marginally lower.

I will also examine the availability and predictability of water sources across studied communities home ranges by taking extensive temperature readings across sites and estimating water source volume over time. From there I can predict the impact of rising temperatures on water availability during the dry seasons and predict when communities will start to experience metabolic stress. In

addition the impact of water availability and rainfall patterns have on food availability, which in some regions may be the limiting resource. Ultimately, this data will be able to draw conclusions on the relationship between inter-group conflict and seasonality and increased temperature over time. I will then model how temperatures and range shifts will impact total available range of chimpanzees in this area, and extrapolate trends in intergroup conflict and intra-group behaviours to 2050.

From there I will test these predictions using the long term behavioural and climatic datasets at Taï and Loango. At each site, rainfall, phenological and behavioural datasets have been recorded for many years, which in combination with my freshwater volumetric measurements and analysis of behavioural patterns will allow us to examine how these affects vary (and remain the same) between sites. Each habitat has a unique ecological environment, and so while in Fongoli the dry season is an extreme period of limitation for all resources, this is more complicated at other sites. For example at Taï, the dry season is the period when food availability increases, and the rainy season is when food availability becomes limited - testing the hypotheses here will allow us to see whether food or water availability has a bigger impact on chimpanzee behaviour and intergroup conflict. Similarly, I will then model temperatures and range shifts will impact total available range of chimpanzees in this area, and extrapolate trends in intergroup conflict and intra-group behaviours to 2050.

To project water availability in the future, I will need to examine weather variations in multiple western field sites over time and see which easily measurable environmental conditions correlate with lower water availability (e.g maximum daily temperature, minimum daily temperature, number of consecutive hours over 40°C, etc.). At Fongoli and Taï rainfall measurement have already been taken historically which will allow us to Then using projections of climate change under various emissions pathways, examine how these will impact the number of water sources in these communities to predict when changes to social structures will start to be observed. I can also examine the relationship between food availability with water availability to examine how changes to rainfall will impact food availability in the future. Global trends towards shorter, more intense rainy seasons may cause phenological shifts in fruiting trees that depend on rainfall and temperature.

## **West African chimpanzee study sites**

### **Taï Chimpanzee Project**

The Taï chimpanzee project is located in Cote d'Ivoire following 4 chimpanzee communities for over 40 years. The current relevant research focuses are long term demographic changes, intercommunity interactions and social bonds & cooperation. The communities live in an evergreen rainforest habitat, with 2 wet seasons (March-June; September-October) and 2 dry seasons (July-August; November-February) [5]. Cote d'Ivoire is being severely afflicted by climate change - the mean average temperature over the past 5 years is more than 0.2°C hotter than it was the preceding 5 years, and the standard deviation in average rainfall has increased 5% in the same time [3].

### **Fongoli Savanna Chimpanzee Project**

The Fongoli Savanna Chimpanzee project is located in Senegal, and is the northernmost study site of wild chimpanzees in the world. Since 2001, the project has been studying a community of 35 semi-habituated individuals, collecting behavioural data. There is one long dry season (November–April) and a short wet season (June–September), with May and October being transitional months when some rain may fall. Maximum temperatures at Fongoli exceed 40°C during the late dry season (Pruetz 2007), and chimpanzees are reduced to between two and four permanent water sources available during the peak of the dry season. Rainfall before 2010 averaged less than 1,000 mm annually, but between 2010 and 2015 rainfall has become more erratic, with some wet years of >1,000 mm and some very dry years.

### **Central African chimpanzee study sites**

#### **Loango Chimpanzee Project**

This study site was established in 2005 in Loango National Park, Gabon. The Loango community is bordered by 5 other chimpanzee communities. The area consists of a mosaic of rivers, swamps, coastal forests, mangroves, savannahs, and secondary and mature forests. Temperatures range between 18 and 32 °C, with the mean minimum and maximum temperatures being 22.7 °C and 27.8 °C, respectively. There is a long rainy season between October and April, interrupted by a short dry season between December and January. The long dry season usually lasts from May to September (Head et al. 2011).

### **Time schedule for data collection, analysis and thesis**

#### **Year 1**

The first year will consist of an extensive literature review of chimpanzee sociality and inter-group conflict with a focus on western chimpanzee communities. During this first year I will begin analysis of Fongoli behavioural data to examine long term trends in sociality and conflict, particularly in relation to rising temperature to establish predictions for other field sites.

I will travel to Fongoli at the start of the dry season to set up multiple temperature monitors across the site, as well as measuring total water availability across the season. One month into the rainy season I'll return to the U.K. to analyse what has been collected, in combination with the historical datasets. The newly collected data, predictions of future water availability and predicted impacts on intergroup conflict and intra-group cohesion will form the basis of the first year report.

#### **Years 2 & 3**

The second and third years will involve testing whether the observed predictions in Fongoli hold true for other field sites, environments and subspecies. This will require examination of the long term behavioural data sets at other field sites, based on current climate projections I believe the most appropriate field sites to examine would be Taï and Loango, however this may be subject to change based on the literature review. As 2022 and 2023 are both predicted to be in the top 5

hottest recorded years on record, I hope we will be able to observe the emerging trends in these communities regarding resource availability, intra-group cohesion and inter-group conflict.

## Broader implications and future goals

Under current emissions pathways, global temperatures are set to increase by at least an average of 2.7°C [8]. While changes in range shifts have already been modelled, the impact of these drastic changes on community structure is currently not studied. Examining how these impact great ape communities can shed light into social strategies that helped early Hominid communities survive natural disasters, and can provide insight into how providing access to more water and food resources to wild chimpanzee communities in times of extreme drought can mitigate inter-group conflicts as well as aiding their survival. Ultimately, this project aims to explore the impacts of Anthropogenic climate change on warfare, social structures in chimpanzees, but the methodology can be applied to many different social species, including all great apes; and will fundamentally change our understanding of the impacts unchecked climate change will have on our closest relatives.

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