

# A Multilevel Selection Model of the Co-evolution of Cooperation and Inter-group Conflict, Climate Change, and Pastoralist Conflict in East Africa

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## Abstract

This study presents a multilevel selection simulation of the co-evolution of cooperation and intergroup conflict in a continuously varying environment. The model is inspired by the pastoralist societies of the arid and semi-arid regions of East Africa, relying upon a two-resource ecology—one uniformly distributed (pasture) and the other clustered (well water). A varying climate model drives a dynamically productive ecology, allowing the examination of the consequences of acute shortages occurring when the carrying capacity of an area temporarily falls below population-levels. In sum, I find extensive support for the hypothesis that cooperation and intergroup conflict are co-evolved, and discover several insights into the relationship. Specifically, I find that resource scarcity promotes cooperation, and the effect is most-pronounced when resources are clustered; not coincidentally, this is when in-group cooperation is most likely to yield advantages in gaining and security them. Consistent with this, the tactical advantage of altruism in warfare appears to generate additional selection pressures on cooperation, even if that altruism implies increased individual mortality. Additionally, I find that human socio-cognitive advancements—specifically the ability to engage in concerted violence—lends itself more to conflict over clustered than heterogenous resources. Finally, I discuss implications of this research for contemporary issues in human security. In particular, my findings emphasize the role of identities as mechanisms for cooperation, both as means for resolving collective action problems within a group, but also as vehicles shaped by and for intergroup conflict. I consider the possibility that potential climate change-induced resource scarcities during this century could result in increased sub-national instability and conflict, even while international conflict may be decreasing.

**Keywords:** Multilevel selection; evolution; cooperation; conflict; ecological change

## Introduction

This study employs multi-agent based simulation in order to establish a theoretical basis for linking individual-level challenges from the environment to group behavior. The key theoretical insight is that cooperation in groups is a primary adaptation humans evolved in order to overcome environmental challenges, including competition from other groups. In other words, this model asks whether the presence of intergroup competition can shift the evolutionary rewards to individuals with a propensity to engage in individually-costly, but group-strengthening behavior.

The substantive context of the simulation design is abstracted from the arid and semi-arid regions of east Africa, generally encompassing the Great Rift Valley region of northern Kenya in the west and the Mander triangle on the east, where the borders of Kenya, Ethiopia, and Somalia meet. While constituting relatively small portions of national populations, nomadic pastoralists occupy large swatches of these countries marginally hospitable territories, including 70% of Kenya (Fratkin 2001). Pastoralists make their living moving herds of animals in search of pasture and water, subsisting on the products of their animals. Though they may occasionally supplement their diets by trading with farmers and fishing, their diets generally consist of milk, meat, and blood tapped from their living animals. Also according to Fratkin (2001), tribesmen of the Boran and Turkana tribes—fairly representative of others in the region—have on average 3.5 to 3.7 tropical livestock units *per person* (a TLU is a standardized unit of livestock by design irrespective of composition, usually based upon comparisons of species' *metabolic weights* (Heady 1975)).

Studying this region offers several advantages. Of the world's total population of pastoralist and agro-pastoralists, Africa is home for roughly one-half, or some 23 million people (Galaty, Johnson et al. 1990). Substantial evidence suggests that degradation of the environment from various sources, including climate change, has already contributed to an increase in violence (Parenti 2011; Hendrix and Salehyan 2012; Suliman 1993; Raleigh and Kniveton 2012; Buhaug and Rød 2006; Kuznar and Sedlmeyer 2005). Over the last three decades, both temperatures and the frequency of droughts have increased near and around the horn of east Africa, with prolonged drought occurring every 5-6 years, most recently in 2000-2001, 2005-2006, 2008-2009, 2010-2011, and 2015, with all signs pointing to another devastating year in 2017 (Fratkin 2001; IFRC 2011; NIDIS 2015; Halake N.d.; Network N.d.).

At the same time regional governments lack the capacity or reach to adequately mitigate these challenges, or at least to ensure security in the fall out. To the extent that government policy has reached the arid regions of northern Kenya, northern Uganda, and southern Ethiopia, it has largely done so with the support of western international organizations. Such efforts, however well-intentioned, have in too many cases made an already bad situation worse (Parenti 2011; Fratkin 2001). In 1968, ecologist Garrett Hardin published his seminal piece in *Science* The Tragedy of the Commons, in which he argues that commonly shared resources are inevitably depleted by rational individuals; thus, natural resources should be either regulated or privatized in order to ensure good stewardship. With this in mind, well-intentioned western aid organizations made grim predictions of the sustainability of pastoralist societies and encouraged local governments to implement land use reforms. East African pastoralists found their large, communally shared lands increasingly fragmented by expanding farming operations, private ranches, wheat estates and game parks (Fratkin

2001). One of the advantages of the pastoral economy is that it is viable on marginal land which is too dry for permanent cultivation. The introduction of more intensive agricultural practices has in many cases produced only short-term gains in productivity that are cut short by soil exhaustion (Parenti 2011). According to Swift (1991), land degradation has not been halted and has sometimes increased, livestock productivity has not grown although economic inequality has, and vulnerability to food insecurity and loss of tenure rights has increased. Moreover, since Hardin's seminal paper, anthropologists and others, including Nobel Memorial Prize in Economics laureate Elinor Ostrom (1990), have documented the rich array of customary institutions regulating resource use in African pastoral societies.

Traditionally, these groups have relied upon kinship ties to cooperatively breed their animals and defend them. The institution of "livestock raiding", in which large groups of pastoralist tribesmen gather in order to conduct raids on other tribes for the purpose of stealing livestock, has existed since at least the 19th century when it was first observed by the British (Fukui and Turton 1979; Parenti 2011). Raiding is believed to accomplish several social, economic, and strategic purposes. Among them, raiding can replenish stocks following the dry season during which a tribe can lose half of their livestock, which can be especially important if a bachelor tribesman is intending to amass a dowry for marriage (Parenti 2011). Mathew and Boyd (2011) observe raiding to be an individually costly activity producing collective goods for the tribe including deterrence and increased access to grazing areas and water holes. Accordingly, they observe participation in raids to be backed by cultural norms and various forms of social punishment of free-riding. For example, participation is a rite of passage into adulthood. Though this practice is deeply rooted in the cultures and pasts of these peoples, the combination of a changing climate, land fragmentation, degradation and competing farmers appears to be driving increased frequency and severity of raiding (Parenti 2011; Suliman 1993).

East Africa is highly diverse ethnically, with an ethnic fractionalization Index score of 72 out of 100, making it one of the most highly fractionalized places in the world (Elbadawi and Sambanis 2000). Raiding is done in order to replenish stocks following the dry season when they are likely to lose half of their livestock before they can be brought to market. In general, the preferred strategy to overcome the high mortality rate—bringing the largest number of animals to market or to otherwise profit from—is to pursue larger, if more sickly herds, rather than attempting to lower mortality by concentrating resources on fewer animals (Fratkin 2001). Stolen livestock can also make an impressive dowry and be invaluable for a young man seeking marriage. The combination of increasingly frequent and severe drought, land fragmentation, degradation and competing farmers has caused a dramatic uptick in raiding (Parenti 2011; Suliman 1996). Complicating matters further, the legacy of the Cold War has left the region awash in small arms, rendering raids not only more frequent, but substantially more deadly.

Several studies have productively applied agent simulation to the question of pastoralist conflict. Motivated by genocide in Darfur, Kuznar and Sedlmeyer (2005) model how individuals respond to environmental and material challenges, and in turn attempt to describe a process by which collective action (i.e., intergroup violence) can emerge from individual motives. The authors create an intricate model, including detailed and realistically defined geography, agriculture, agent and livestock metabolisms, demography, and a rudimentary trading economy. They find that drought can lead to sustained violent conflict and a break-

down of intertribal relations in terms of mutually beneficial activities, such as trade. Kennedy et al. (2010) use the MASON agent-based modeling environment to test a conflict model of nomadic herding with data-driven seasonal cycles. They find greater scarcity favors a strategy of domination by a single group. (Hailegiorgis et al. 2010) more richly model Mendera triangle region of east Africa, focusing on the tensions that can emerge between groups over utilization of common grazing land. MacOpiyo, Stuth and Wu (2006) develop the Pastoral Livestock Model (PLMMO), which simulates pastoralist foraging and movement patterns across geographic information systems (GIS) based raster landscape

## Theory

The proposed model is a computational, multi-agent based simulation of the evolution of tribalism, or intra-group cooperation/inter-group conflict. The design is based on two core design principles: 1) multi-level selection, and 2) realistic (i.e., ‘material’) competition for scarce resources agents need to survive.

Multi-level selection is an extension of traditional evolutionary theory and may be employed to mathematically explain the evolution of cooperation from within the counter-intuitive, competitive-yet-cooperative, dynamics of social living (Wilson and Wilson 2007). Evolutionary game-theoretic models have been extensively used to model the proliferation (or elimination) of behavioral strategies in well-mixed populations in the say way population genetics models the proliferation of genetic traits (Nowak 2006; Gintis 2005; Dugatkin and Reeve 2000). In fact, recent advances in evolutionary psychology and biopolitics suggest many social behaviors have foundations in our genome (Fowler, Baker and Dawes 2008; Fowler, Dawes and Christakis 2009; Dawes and Fowler 2009; Alford, Funk and Hibbing 2005).<sup>1</sup> One relevant feature of human societies, however, is that individuals are both competing and cooperating with each other in the context of social groups, which are themselves in competition with each other. Early social darwinists speculated that the same evolutionary dynamics affecting individuals are played out at the group-level, reasoning that groups which are most inwardly-patriotic and cooperative would possess an advantage over rival groups in the competition for the resources they need to survive and grow (Spencer 1904; Bannister 2010; Weikart 1993). Accordingly, Nature would “select” for these groups to displace those groups lacking their patriotic fervor. This (all too frequently misappropriated) conception of evolution, however, is fundamentally mistaken because it neglects the fact that individuals within those groups will be in competition with each other and therefore under

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<sup>1</sup>It is important to keep in mind that ‘genes’ may also be understood as strategies; ‘population genetics’ may therefore be thought of as a praxis for keeping track of strategies in a large population. Whether these strategies are coded chemically as DNA or in some cognitive capacity is not as important as how they are transferred, or replicated, within the population. The primary mechanism through which strategies are transferred between individuals is *heredity*. Individual agents possess an attribute, *c*, which disposes a particular strategy. To the degree those individuals live longer, more prosperous lives than other individuals exhibiting alternative strategies, there will be progressively more individuals in the population exhibiting attribute *c*. In other words, while the details of the replication algorithm employed bear the closest resemblance to genetic evolution by natural selection, the critical issue is that successful strategies will proliferate faster than unsuccessful strategies.

selective pressure to “defect”, or shirk their “patriotic submission” to the collective interests. For this reason, historical conceptions of so-called “group selection” are invalid from a Darwinian point of view.

Still, it is difficult to ignore the penetrating insight Darwin’s own declaration from the *The Decent of Man* (1871),

*“[A] tribe including many members who, from possessing in high degree the spirit of patriotism, fidelity, obedience, courage, and sympathy, were always ready to aid one another, and to sacrifice themselves for the common good, would be victorious over most other tribes, and this would be natural selection.”*

Multi-level selection has emerged as a re-rendering of this notion in a way that does not violate the principle of individual-level selection, while at the same time incorporating inputs from higher-orders of competition (i.e., intergroup competition) (Nowak 2006; Wilson and Wilson 2007). Sidanius and Kurzban (2003) define a “group” as “any set of individuals that have a fitness impact on one another”. This definition does not assume any degree of genetic relatedness between individuals within a group and neither does the proposed model. According to multilevel group selection theory, nature can be said to select for an entire group if, despite some relative fitness inequality between internal phenotypes, members of all phenotypes are on the whole more successful in passing on their genes than individuals belonging to other groups. As the authors explained, this is not “an alternative to the genetic view of ... selection,” but rather is “simply another way of keeping track of genes’ success by looking at their relative replication rates within and between groups”

More technically, the model presented here consists of a population of  $N$  agents randomly distributed across a two-dimensional plane. Each grid cell has a host of properties including an amount of *grass* and *water* (if a well is present), which are replenished according to a dynamically-modeled climate cycle. Agents may be thematically thought of as pastoralist nomads, wandering (prospecting) the grid in search of grass and water to sustain their herds. Ensuring their herds are neither too *hungry* nor too *thirsty*, agents maximize their herds’ *health* and in turn the rate at which their herd grows.

For agents, the size of their herd is of critical importance because it affects their likelihood of reproductive success, as well as the size of the “dowry”, or the endowment herd with which their offspring begin their own journeys. Importantly, agents are also characterized by a tribal affiliation. While the agents think and act on their own, their actions have an impact on their tribe, the cumulative effects of which can indirectly affect them. Agents not only interact with the environment but also with each other when they find themselves co-located. Accordingly, each agent possesses a heritable behavioral strategy  $c \in [0, 1]$  corresponding to a propensity to cooperate with their fellow tribesmen.

Like real societies, agents are independent actors nested inside higher-order units of aggregation. The attributes of tribes are constituted from aggregations of actions their members take. A tribe’s attributes, however, may have an indirect impact on what its members are able to do in the future. A key tribal attribute is its *cohesion*. Cohesion is calculated as the average proportion of resources agents contribute in public games with their fellows, or the mean propensity to cooperate of a tribe’s members. The cohesion of an agent’s tribe can impact them in several ways, enabling them to cooperatively drive away competing tribes from valuable resources. The efficiency with which greater levels

of cohesion confer advantage in battle is determined by a parameter  $L$ , representing the Lanchester law exponent, developed by military theorist Frederick Lanchester (Lanchester 1956), which mathematically describes the advantage in combat power enjoyed by a force able to coordinate their behavior over an equally-sized force unable to do so. According to Linear Law, the combat power of a force which is unable to concentrate their offensive capabilities grows linearly with their number; i.e. an exponent equal to 1. The combat power of forces which are able to concentrate their fire, however, is presumed to increase with the square of their number, or an exponent of 2. Other benefits of proximity to tribemembers include cooperative breeding benefits and the ability to use local resources more efficiently by cooperating.

These theoretical perspective suggest several empirical implications, which shall be the focus of the computational model.

*Hypothesis 1:* Bellicosity and cooperation exert independent, reciprocal effects on each other. While the costs of violent conflict will fall disproportionately on cooperators, thus generating negative selection pressures on cooperation, the opportunities greater within-group cooperation creates for individuals in groups to promote their selfish interests through intergroup conflict will drive increased bellicosity. Accordingly, since cooperation will yield critical advantages in combat, cooperation will still persist despite the direct fitness costs to cooperators.

*Hypothesis 2:* Differential effects of clustered verses homogenously distributed resources. While warfare may drive the emergence of cooperation, this relationship is likely subject to be inconstant across various competitive contexts, in particular the shape and character of the resources over which violent conflicts are waged.

*Hypothesis 3:* The ability to coordinate violent action contours these relationships. Human cooperation is defined not only by the *quantity* but the *quality* of collective action. In the traditional, game-theoretic model of cooperation we measure an individual willingness to forego certain benefits—or place some benefits at risk—in order to resolve some collective problem depending on others’ similar decisions. This model is used to describe potentially cooperative interactions between everything from prisoners’ in jail cells to microorganisms (Zinser and Kolter 2004). Yet cognitively complex, cultural beings such as humans are able to structure, or link their individuals actions in concert that generate benefits of cooperation exponentially rather than linearly. In some circumstances, this ability will offer unique advantages, contouring the evolution of human cooperation.

## Model

The main challenge associated with hypotheses concerning evolutionary processes is that evolution can be virtually impossible to observe in the world. One of the most powerful tools available to us is multi-agent simulation (MAS). MAS is a quasi-empirical methodology, in which data are “collected” from a simulated world operating according to the physics (or rules) the researcher specifies. Simulations allow us to view the world that would exist if our

models were correct and complete. In other words, they allow us a glimpse at what the world would look like if it worked the way we suppose it does. Simulation can play an important role in the scientific process because it allows us to rigorously examine the implications of our assumptions in ways that, for reasons of inherent complexity and our susceptibility to biased reasoning, would just be too much to expect from a human mind. Quoting Epstein (1999), the canonical agent-based experiment is as follows:

*“Situating an initial population of autonomous heterogeneous agents in a relevant spatial environment; allow them to interact according to simple local rules and thereby generate—or ‘grow’—the macroscopic regularity from the bottom up.”*

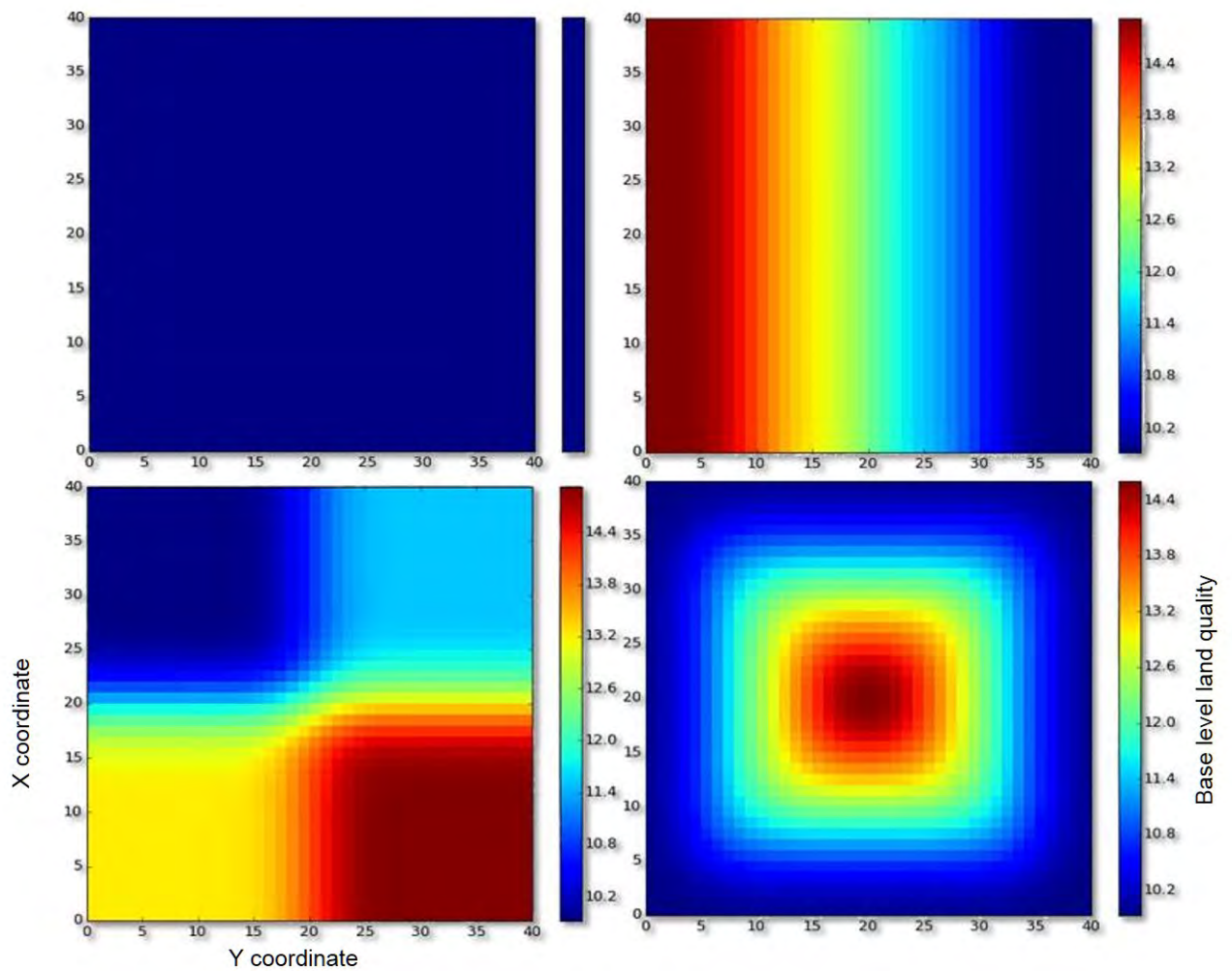
The proposed model is a computational, multi-agent based simulation of the co-evolution of intragroup cooperation intergroup competition, which I call *tribalism*. In sum, this simulation is designed to test the hypothesis that realistic conflict over resources could have played a role in the evolution of tribalism as an organizing principle of human cooperation.

### Simulation Design

The simulation takes place on a two-dimensional spatial grid of dimension  $S \times S$  with boundaries. Each grid cell has a host of properties including an amount of *pasture* and *water*. For the amount of water to be greater than 0, there must be a *well*, which occurs randomly at some frequency  $wf$  at the onset of the simulation. *Precipitation* causes pasture to grow and wells to fill with water. Since both pasture and well water are determined by rainfall, it might seem like a simpler approach to reduce to only a single resource. Research from biology and behavior ecology suggests the way in which resources are distributed over a foraging area (e.g., uniformly or clustered) could potentially impact the dynamics of cooperation (Senft et al. 1987; Waser 1988; Sterck, Watts and van Schaik 1997; Koenig 2002; King et al. 2008; Wittig and Boesch 2003). For example, social animals like buffalo and gelada baboons who graze off of uniformly distributed resources of comparatively low-nutritive value may live in very large communities consisting of hundreds of animals. The level of coordination between them, however, is limited. This particular form of cooperation might be less suited in a situation where resources are distributed in clumps, or clusters of comparatively high-nutritive value. Clustered resources may favor a kind of sociality that enables a number of individuals to cooperatively defend or assault a location. This is a model of the evolution of tribalism under pastoralism—an economic modality demanding both widely distributed and clustered resources. A two resource system, therefore, allows modeling of the distribution of resources, without sacrificing the pastoralist character of the model.

Both the maximum density of pasture as well as rate of growth are determined by the cell’s *land quality*. The distribution of land quality is determined at the start of the simulation according to user selection from four possible conditions. 1) Uniform: The default setting is for all land to be of equal quality; 2) Striped: Land quality is greatest at the left of the grid and decreases in quality gradually in a linear fashion to the right; 3) Radial gradient: Land quality is greatest at the center of the grid and decreases with the radial distance from the center point; 4) Quadral: At is highest in one corner, lowest in one corner, medium-high in one corner, and medium-low in one corner. Quality converges at the center point according to a Gaussian smoothing algorithm. Well depth (well capacity) is affected by land quality, but not rate of fill (see Figure 1).

Figure 1: Spatial distribution of land quality: Uniform (top-left), linearly decreasing gradient (top-right), quadral categories (bottom-left), and radially decreasing (bottom-right)





The amount of precipitation is determined by a climate model. The basic climate model is determined by a sine wave function establishing four “seasons” defined by the peak (summer), trough (winter), and the inflection points (equinoxes). Seasonality acts as a periodic deviation from a base rate  $br$  of precipitation. At peak, precipitation is equal to the base rate plus  $\frac{br}{ex}$ , where  $ex$  is a seasonal extremity parameter. When  $ex = 2$ , peak precipitation is  $1.5br$  and  $.5br$  at the trough. The actual amount of precipitation will also be affected by exogenously determined “anomalous” weather patterns including extended periods of drought or excess. The frequency, severity, and duration of weather anomalies are parameter controlled.

## Agents and Tribes

### Agent Attributes

Agents may be thematically thought of as pastoralist nomads, wandering (prospecting) the grid in search of pasture and water to sustain their herds. Ensuring their herds are neither too *hungry* nor too *thirsty*, agents maximize their herds’ *health* and in turn the rate at which their herd grows. At any given time a herd’s hunger is  $f$  is in  $[0, 1]$ , where a value of 0 indicates that the animal is perfectly starved and a value of 1 indicates it is perfectly satisfied nutritionally. Similarly, thirst  $w$  is in  $[0, 1]$  where 0 is perfect dehydration. The quantity of food or water an agent’s herds demand is equal to the number of animals in the herd multiplied by  $f$  and  $w$ , respectively.

**Herd hunger:**  $f \in [0, 1]$

**Herd thirst:**  $w \in [0, 1]$

**Herd health:**  $\frac{Herdhunger + Herdthirst}{2}$

**Demanded food:**  $f * Herdsize$

**Demanded water:**  $w * Herdsize$

For agents, the size of their herd is of critical importance because it affects their likelihood of reproductive success, as well as the size of the “dowry”, or the endowment herd with which their offspring begin their own journeys. Importantly, agents are also characterized by a tribal affiliation. While the agents think and act on their own, their actions have an impact on their tribe, the cumulative effects of which can indirectly affect them. This will be explained in greater detail below.

### Behavioral Strategy

Agents not only interact with the environment but also with each other, should they find themselves co-located. Accordingly, each agent possesses a heritable behavioral strategy  $c \in [0, 1]$  corresponding to a propensity to cooperate with their fellow tribesmen.

### Prospecting

In each time period  $t$ , agents survey the environment of the cell they currently occupy as well as the 8 surrounding cells. A multinomial probability distribution is then assigned over the set of tiles based on the expected utilities associated with each. Utilities are in terms of

expected health outcomes for an agents' herds, as determined by each cell's ability to satisfy the nutrition and hydration its animals require. In order to generate the set of expected utilities, the agent imagines itself moving to (or staying in) each of the 9 cells and how any interactions with other agents located there are likely to go. They take into account the tribal affiliation of the occupants, whether interactions are likely to be cooperative or conflictual, and if conflictual how well off they are likely to emerge from the conflict. There are three possible cases:

**Agent will occupy cell alone:** They will be free to consume whatever resources their herds demand, and leave what remains (if any).

**Agent will occupy cell with fellow tribesmen only:** Resources within the cell are initially distributed equally across the  $n$  co-located tribesmen, which becomes each individual's endowment  $g$  in a standard public goods game (PGG). For the PGG, each tribesman's contribution, or effort, level is determined according to their propensity to cooperate  $c \in U[0, 1]$ . The sum of collected proceeds are multiplied by a benefit of cooperation  $b \in U[1, 10]$ , redivided evenly across the participants, such that agent  $i$ 's payoff is described by:

$$\Pi_i = \frac{1}{n} \sum_n^i b g c_i \quad (1)$$

After the game is complete and each agent has received their payoff, they each individually feed their herds.

**Agent will occupy cell with at least one out-tribesmen** When agents from multiple tribes are present, the agent imagines two scenarios: A) peaceful coexistence or B) conflict. In the case of peaceful existence, all available resources are distributed equally to all tribesmen from all tribesmen. All agents participate in PGGs with their own tribesmen, but not with members from other tribes. However, if the agent determines that his tribe (or another tribe) is likely to fight for the entire share of the available resources, they will generate an expected payout, which is the product of their possible payoff if their tribe hoarded all of the resources available and the tribe's probability of victory in battle.

In so doing, agents generate a vector of expected utilities  $VU$  from the 9 cells. However, the actual value of the cell will also be affected by its proximity to water, and agents must take this into account. Accordingly, the agent also generates a corresponding vector of weights  $VW$  based on each cell's "water value". The formula for water value is as follows:

$$VW_{cell} = Thirst \sum_{well} \frac{(q_{well}/n_{well})}{d_{well}^2} \quad (2)$$

Where  $q$  is quantity of water available,  $n$  is number agents present, and  $d$  is the distance to the well. It is assumed that the utility of a well decreases with the inverse square of the distance since the water value of a cell should be disproportionately determined by water

resources close by. The journey to reach distant wells will require substantial energy, as well as time during which the availability of the resource could change. The agent's thirst value is included because water increases in value with thirst, potentially making distant, but unoccupied, wells more attractive. This formula looks unnecessarily complicated but all it is a weighted average between how much water the agent is likely to receive if it is only split with his tribe versus if it is split with everyone, where the weights are the relative proportions of cohesiveness between the two tribes. The values are also standardized so that weights are in  $[0, 1]$ .

The vector defining the multinomial probability distribution over each of the 9 cells is therefore,

$$VN_{cell} = \frac{VU_{cell}VN_{cell}}{\sum VU_{cell}VN_{cell}} \quad (3)$$

A random draw from this distribution determines an agent's location in each subsequent time period.

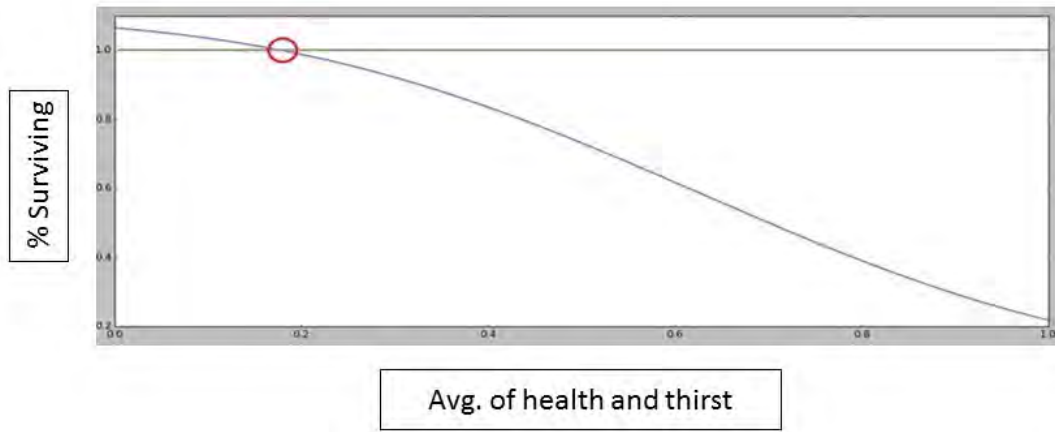
### Metabolism

Every time period, the hunger of an agent's herds increases by  $u$  and their thirst increases by  $h$ . The longer they go without food or water, the more likely it will be that they die. The rate of herd exhaustion is calculated according to a survivor function of the form:

$$\%Surviving_{agent'sherd} = 1 + tolerance - e^{-[1.5-(u_i h_i)^3]} \quad (4)$$

Where *tolerance* is a global variable determining how long an agent's herds may go without food or water before it begins to incur losses. Figure 2 depicts the functional form with  $tolerance = .1$ .

Figure 2: Percent of an agent's herds surviving by average of herd health and thirst



Like the real world, agents are independent actors nested inside higher-order units of aggregation. The attributes of tribes are constituted from aggregations of actions their members take. A tribe's attributes, however, may have an indirect impact on what its members are able to do in the future. A key tribal attribute is its *cohesion*. Cohesion is

calculated as the average proportion of resources agents contribute in public games with their fellows, or the mean propensity to cooperate of a tribe's members, as in:

$$TribeA's cohesion = \frac{1}{n_A} \sum_{n_A}^i c_{A_i} \quad (5)$$

The cohesion of an agent's tribe can impact them in several ways.

### Inter-tribal conflict

Strong, cohesive tribes have an advantage over other tribes in that where resources might have to be shared globally, they may "fight" for the right to harvest a resource exclusively. This means that the resource shares per agent within the tile will be larger since they are only shared amongst the members of the victorious tribes. This may result in weaker, less cohesive tribes actually avoiding coming into contact with cohesive tribes.

When there are members of two or more tribes located on a single cell, they may either "share" the resources or "fight" for them. Sharing resources means that they all just take their share, which they will use as their endowment  $g$  to play with in a public goods game if any fellow tribesmen are present. This decision to fight or share is made "collectively" by the tribesmen of each tribe. If the "average tribesmen" is better off fighting, then the tribe fights. If one tribe in any dyad of tribes decides to fight, then they will fight. A tribe decides to fight when:

$$EU(fight) > EU(share) \quad (6)$$

such that

$$EU(fight) = FH_{AllResourcesGained} * Pr(victory) + FH_{NoResourcesGained} * [1 - Pr(victory)] \quad (7)$$

where FH is the expected health of an agent's herd and  $Pr(victory)$  is determined by each sides' relative fighting power  $pow$ , or

$$Pr(victory_A) = \frac{pow(Tribe_A)}{pow(Tribe_A) + pow(Tribe_B)} \quad (8)$$

A tribes fighting power  $pow$  is determined by

$$pow(Tribe_A) = \left( \frac{C_A S_A}{D_{Axy}} \right)^L \quad (9)$$

where

$C_A$  = TribeA's cohesion  $S_A$  = TribeA's size  $D_{Axy}$  = Average distance of TribeA's members to cell  $(x, y)$ .  $L$  = Lanchester Law of Combat (linear or square law)

The  $L$  parameter, or the Lanchester law, comes from World War I era military theorist Frederick Lanchester's Laws of Combat (Lanchester 1956). Among these are the *Linear Law* for ancient combat and the *Square Law* of modern combat. For ancient combat in particular phalanx formations of soldiers with spears or swords were pressed into one another and

essentially only able to fight one man to a man. Thus, a side’s fighting potential may be said to increase linearly with the number of soldiers. However, under so-called “modern” conditions with ranged weapons or in other cases where targeting may be concentrated power is said to increase with the square of the number of units. In a recent issue of the *Journal of Evolution and Human Behavior*, Johnson and MacKay (2014) detail how human ancestral warfare is best characterized by the Square Law, suggesting a mechanism by which human evolution was potentially adapted to it. In practical usage, it is common for analysts to use an intermediary exponent like 1.5 because it is assumed that combat will be a mixed bag of linear and square elements.

### Death in combat

While agents do not directly figure into their cost-benefit calculations whether or not to go to war, i.e., to fight for a larger portion of a cell’s resources, this decision could come back to haunt them—win or lose. An agent’s (per time period) probability of meeting a violent death is determined according to the function:

$$Pr(\text{violentdeath}_i) = 1 - Y^{b_{i,tribe} v_{i,tribe} c_i} \quad (10)$$

where  $Y$  is a global parameter defining a base lethality, or probability of surviving a battle. This base probability is compounded with every battle the agent participates in, however, it is necessary to take into account that not every battle is the same and not every agent fights with the same level of commitment. Accordingly the number of battles an agent participates in  $b$  is weighted by his tribe’s average probability of victory  $v$  and the agent’s level of cooperation  $c$ . Thus, an agent is more likely to die when his tribe fights with generally poorer odds of victory and if he fights with greater heroism.

### Reproduction and cooperative breeding

A basic premise of multi-level selection is that while some inter-group competition exists, mate selection is primarily an intra-group process. In this model agents’ likelihood of reproducing is a function of their standing within their own tribe, as determined by the size of their herds. The probability of reproduction in time  $t$  is given by:

$$Pr(\text{Reproduce}_i) = \text{MateScore}_i * (\text{BirthRate}_{base} + \text{CooperativeBreeding}_{bonus}) \quad (11)$$

where

$$\text{MateScore}_i = \left( \frac{n_{i,tribe} - \text{rank}_i}{n_{i,tribe}} \right) \text{MateCompetitionSeverity} \quad (12)$$

and

$$\text{CooperativeBreeding}_{bonus} = \text{BirthRate}_{base} * \text{Cohesion}_{i,tribe} * \text{EffectSize}_{base} \quad (13)$$

In plain language, within each tribe all tribesmen are arranged in reverse order according to the size of their herds. This is their raw rank which is normalized by the total number of tribesmen in order to get their percentile rank score. I include one additional parameter, the *mate competition severity factor* (MSF), which allows me to control the “intensity” of

mate competition. When MSF is 1, then mate score decreases linearly with rank. At MSF = 2, mating potential decreases exponentially with rank. This value is compounded by the global parameter, natural birth rate. However, cooperative breeding practices may actually enable a tribe to achieve a birth rate greater than the “natural rate”. Thus, this rate is increased by the *cooperative breeding bonus*, which is equal to the natural birth rate times the level of a tribe’s cohesion, multiplied by an additional global parameter moderating this bonus effect. If the bonus effect is 0, then there is no cooperative breeding bonus. When the bonus effect is 1, the effective birth rate of a perfectly cohesive tribe (cohesion = 1) will be exactly 2 times the natural rate.

The final result is a value bounded  $[0, 1]$  unique to every agent, which is treated as a probability of reproduction. All agents in all tribes have a chance to reproduce, but the size of probability is determined only in comparison to fellow tribesmen. The most cooperative tribes get a bonus to birth rate because I assume that cooperative breeding practices enable them to have more babies.

When an agent reproduces, the offspring emerges as a fully formed ‘adult’ agent and inherits a number of its parent’s herd equal to the endowment factor  $e$  times its herd size. Therefore, the size of the new agent’s initial endowment is proportional to the economic success of the parent. This ensures that even though poorer tribes, *ceteris paribus*, are equally likely to produce offspring as wealthier ones, the offspring of wealthier tribes are going to have a better chance at survival since they are able to provide their offspring with larger number of herds.

## Other modeling factors

### Migration

In order to account for gene transfer between groups, every round agent’s probabilistically migrate to another tribe (change tribal affiliation) according to a probability  $m$ . This is a global variable, with a default value of 5% chance of migrating within a 20 time step period, or 0.025% per time period. The reader should note that in terms of the program coding, when an agent “migrates” the only thing that happens is its tribal identification changes. The agent is not “transported” anywhere. Whether the agent subsequently proceeds in the direction of its new fellows is “up to them”, i.e., it is an emergent outcome of the simulation.

### Mutation

Every round agents will ‘mutate’ with probability  $mu$ . In practical terms, this means that mutating agents’ propensity to cooperate with their tribesmen  $c$  is redrawn randomly from the initial distribution  $U[0, 1]$ .

### Tribe splitting and dissolution

If a tribe’s membership exceeds  $Kmax$ , a tribe will fission into two tribes.  $\frac{Kmax}{2}$  agents will be selected at random to form a new tribe. If a tribe’s membership drops to 0 it is considered dissolved and removed from the simulation.

## Data

In order to examine the implications of this model I employ Monte Carlo simulation methods in which the simulation is repeated many times with randomized parameterization. Though the simulation was initialized 5 million times, in most instances of the simulation the parameterization resulted in an environment so severe that all agents died out. In such cases, the simulation is terminated and reinitialized with a new set of parameter values. Of the total intializations, agents survived through 10,000 time periods in 18,235 cases.

For the present study, the two outcomes I am most interested in are the prevalence of cooperation and the frequency of conflict. In order to assess their respective relationships to the environment and to each other I model them together in a system of two simultaneous equations, which I estimate using a *Three-stage Least Squares* (3SLS) estimator (Zellner and Theil 1962). Like a Two-stage Least Square estimator, the 3SLS allows flexible instrumentation to deal with endogeneity, but has the additional advantage of taking into account covariances in the disturbances across all equations in the system, which are estimated simultaneously.

Table 1 presents the summary of statistics of major input and output parameters of the simulation from all 18,235 that completed 10,000 time periods. Output parameters represent their mean values over the final 500 time periods of each simulation.

Table 1: Summary statistics of simulation parameters

<i>Variable</i>	<i>Mean</i>	<i>Std. Dev.</i>	<i>Min</i>	<i>Max</i>
Cooperation	0.1847141	0.1531976	0.0013043	0.8739958
Bellicosity	137.4163	276.8788	0	5095.258
Well Frequency	0.1558435	0.0340359	0.0503255	0.1999972
Tribe Size	46.3003	15.81839	14.14812	171.47
Lanchester exponent	1.50174	0.288359	1.00015	1.999945
Lethality	-0.8879937	0.0492882	-0.9699934	-0.8000007
Climate Extremity	-3.122743	1.721739	-9.998944	-0.5002133
Ben. Of Cooperation	5.55125	2.58469	1.000998	9.999235
Food Consump. Rate	0.1416963	0.0683087	0.050007	0.299972
Water Consump. Rate	0.071524	0.0216772	0.0500003	0.2943195
Pasture Supply	32.34214	21.17949	2.398146	154.444
Water Supply	8.286654	4.93927	0.0063582	34.8098
Total Population	452.4641	434.4378	18.838	4401.54
Num. of tribes	10.02291	9.824588	1	135.462
Deprivation Tolerance	0.0325794	0.0157388	-0.0425311	0.0499992
Heterogenous Land Quality	0.7448314	0.4359679	0	1
Base resource level	6.839155	2.328807	2	10
Mate competition severity	1.500336	0.2889427	1.00001	1.999991
Birth rate	0.1261561	0.0413152	0.0500027	0.1999803
Dowry price	0.3117289	0.1125224	0.1000039	0.499936
Mutation rate	0.005528	0.0026052	0.001	0.0099991

## Cooperation and Conflict

### Linear 3SLS model

Table 2 presents the results of the linear 3SLS statistical model. As predicted, bellicosity and cooperation exhibit independent, direct effects on each other. Interestingly, they are in opposite directions suggesting that in real-world scenarios the existence of an equilibrium, which is likely conditioned on other environmental factors. Fighting more, *ceteris paribus*, implies dying more. The most patriotic, altruistically self-sacrificing warriors will in turn die with the greatest frequency. Accordingly, it makes sense that war frequency should negatively impact cooperation, assuming cooperation is a heritable trait. A one standard deviation increase in bellicosity corresponded to a roughly 6% decrease in average cooperation propensity (coef. = 0.0002,  $p < 0.001$ ), but cooperation increases bellicosity (across full range of cooperation increasing bellicosity by roughly 1.1 standard deviations) (coef. = 312.57,  $p < 0.001$ ). Neither of these appear to be especially large effects. However, they are likely to be conditional on other factors, which I will explore below.

Disentangling this endogenous relationship requires some careful consideration of interactions between these variables and others. Before I get into that, it will be worthwhile to note certain covariates exert substantively significant direct influences on the evolution of cooperation. Food consumption (coef. = 0.39,  $p < 0.001$ ) and water consumption (coef. = 1.51,  $p < 0.001$ ) rates are large; i.e. the amount of food and water an agents' flocks must consume per time period in order to maintain their health. Across the range of these variables, they predict increases as large as 10% and 38% increases, respectively, in cooperation propensity. The value of the Lanchester law exponent—moving from the linear to Square Law—is significant and in the expected direction, though is substantively small. Not surprisingly, the coefficient on average group size is negative. This is consistent with the general rule that collective action becomes increasingly difficult to maintain as group size increases dating back to Olson (1965). At extreme values, tribe size can decrease cooperation by as much as 45%. The lethality of combat is deleterious to cooperation. Across the range of values (death rates ranging from .03 to .2), the disproportionately high costs of war to cooperators results in a roughly 19% decrease in cooperation. This finding is consistent with Smirnov et al. (2007) and Bowles (2006) who have sought to explain the evolution of cooperation in the presence of these fitness costs to cooperators, appealing to “reproductive leveling” (fitness compensation in the form of privileged access to resources or mates) as a means to evolutionarily compensate individuals for selfless acts. This model, however, contains no such feature. Lastly, well frequency had a smaller but still statistically and substantively significant effect on cooperation (coef. = -.0159,  $p < 0.001$ ), increasing it by as much as 4% across its range.



Table 2: 3SLS Regression models

	Model 1	Model 2	Model 3	Model 4	Model 5
<b>Cooperation</b>					
		<i>Linear Coefficients</i>			
Bellicosity	-0.0001916 *	-0.0283924 *	-0.3016453 *	-0.1055387 *	-0.0192543 *
Well Frequency	-0.1598231 *	-0.3419344 *	-0.3907673 *	-62.92157 *	0.1884651 *
Avg Tribe Size	-0.0025964 *	-0.0023883 *	-0.0026026 *	-0.0028679 *	-0.0028985 *
Lanchester law Exp.	0.0163147 *	0.0158732 *	-27.14922 *	-6.892977 *	-1.073351 *
Comb. Lethality	-1.104605 *	3.80929 *	47.25372 *	-0.6575278 *	-0.7332182 *
Extremity	0.004444 *	0.0067219 *	0.0079874 *	0.0067469 *	0.003731 *
Benefit of Cooperation	0.0034511 *	0.0001113	0.0044335 *	0.0031196 *	0.0013573
Food Consume Rate	0.3856683 *	0.5222945 *	0.4823486 *	0.3624232 *	0.4684784 *
Water Consume Rate	1.508136 *	1.966714 *	1.877947 *	1.459068 *	1.770576 *
Pasture Supply	-0.0002917 *	-0.0004165 *	-0.0004782 *	0.0000181	-0.045206 *
Water Supply	-0.0031271 *	-0.0024195 *	-0.0021336	-0.0006494 *	-0.0092163 *
Bellicosity X Lethality		-0.0318423 *	-0.338862 *		
Bellicosity X Lanchester			0.192971 *	0.0681493 *	0.0123246 *
Lethality X Lanchester			-30.61859 *		
Bellicos. X Lethality X Lanchester			0.2168651 *		
Bellicosity X Well Freq.				0.6076453 *	
Well Freq. X Lanchester				40.5145 *	
Bellicosity X Well Freq. X Lanch				-0.3927359 *	
Bellicosity X Pasture					0.0006367 *
Pasture X Lanchester					0.0295386 *
Bellicos. X Pasture X Lanchester					-0.0004075 *
<b>Bellicosity</b>					
Cooperation	312.573 *	974.4989 *	968.5222 *	986.8632 *	982.3893 *
Well Frequency	-349.9694 *	-346.7327 *	-339.9257 *	-336.7854 *	-336.8731 *
Total Population	0.5777615 *	0.7287894 *	0.7218265 *	0.7250537 *	0.7300267 *
Num. of tribes	2.593114 *	-0.3971266	-0.1177563	-0.1627317	-0.4480178
Food Consume Rate	-112.798 *	-369.5733 *	-370.8859 *	-379.5061 *	-377.5913 *
Water Consume Rate	532.8729 *	-272.9589 *	-283.7822 *	-314.9988 *	-312.1801 *
Pasture Supply	0.3168496 *	0.5028026 *	0.4962433 *	0.5047963 *	0.5173243 *
Water Supply	2.038975 *	4.729805 *	4.719678 *	4.805368 *	4.806898 *
Deprivation Tolerance	-346.9066 *	-466.7897 *	-376.3076 *	-347.5686 *	-381.3265 *
Heterogenous Land Quality	41.5084 *	51.64724 *	53.76962 *	53.74318 *	49.93671 *

Significance levels \* : 95% confidence interval does not include 0.

On the bellicosity equation, the largest, most important driver of conflict was population density, or the overall number of agents in the simulation (coef. = 0.57,  $p < 0.001$ ). Though the number of violent conflicts per time period reached values as high as 5000, roughly 90% of had values under 350. A 1 standard deviation increase in population (434 agents) corresponded to an increase of roughly 252 conflicts per period. Interestingly, the number of tribes present had less of an effect that expected. While one would expect the overall fractiousness of the population to result in a large increase conflict, the coefficient is relatively small (coef = 2.60,  $p < 0.001$ ). A one standard deviation increase (9.82 tribes) predicts an increase of only 25.5 violent conflicts per period. Taking these last to estimates together, it would appear that the size of the population relative to the space available matters more for substantially more than the constitution of the population. Dummy categories for the 3 categories of heterogeneity (striped, radial, and quadral), all were significantly different from zero, but not significantly different from each other. Accordingly, in the final specification of the model I simply, using only a single dummy variable as an indicator of heterogeneity. Conflict was more common when land quality was heterogenous. However, the size of the effect was smaller than expected (coef. = 41.50,  $p < 0.001$ ), implying an increase of roughly 41 conflicts per period (about .15 standard deviations).

The overall supply of pasture and water positive predicts conflict, though their effect sizes are not substantively significant. The consumption rates of pasture and water have opposite signs (coef. of pasture = -113,  $p < 0.001$ ; coef. of water = 533,  $p < 0.001$ ). While neither of these effects is substantively large, it is an intriguing result which will have to be analyzed more deeply in subsequent analysis. The coefficient on deprivation tolerance (coef. = -347,  $p < 0.001$ ) is negative, implying a connection between violent resource conflict and the immediacy of the belligerents' need for those resources. That being said, the coefficient is not substantively significant. Across its entire range, from least tolerant to most tolerant, the predicted amount of violent conflict increases by only 30 per time period, or about a tenth of a standard deviation. Still, this is consistent with the hypothesis that war will increase when the contested resources are needed imminently for survival.

### **Multiplicative models**

In order to tease out the complexities of the relationship between cooperation and bellicosity, it is necessary to consider its potential dependencies on other variables. In Model 1, we observe that bellicosity exerts a mean, direct effect of the propensity of agents too cooperate with each other of roughly -6% per standard deviation. While statistically and substantively significant, this seems smaller than one would likely expect given the disproportionate sacrifice (often the ultimate sacrifice) cooperators make on behalf of their tribes during times of war. Accordingly, Models 2 and 3 (Table 2) assess a set of factors which may both reduce the burden of warfare to cooperators. Model 2 includes a two-way interaction term between bellicosity and combat lethality. Figure 3 presents the marginal effects of bellicosity on the evolution of cooperation at varying levels of combat lethality. The downward slope of the interaction crosses zero, suggesting that when combat fatalities are rare, the advantages tribes can realize through initiating conflict with other tribes easily outweighs the risks to their most altruistic members. In fact, the coefficient is roughly an order of magnitude larger than the direct, negative effect predicting an increase of 77% in cooperation propensity (across one standard deviation of bellicosity) when combat lethality approaches zero. Alternatively,

when combat lethality is highest the effect is the opposite, decreasing cooperation by roughly the same amount. Intuitively, this makes sense because in the former case cooperative tribes receive the benefits generated by their altruistic tribesmen, benefiting everyone, including the altruists, while not placing the altruists at an adaptive disadvantage with regard to their more selfish fellows. When that cost is fully realized, however, intergroup conflict cannot be an explanation for the evolution of cooperation.

But what this analysis fails to take into account is the character of the advantage cooperation yields to the cooperative tribe. Figure 4 depicts the marginal effect of bellicosity on cooperation at levels of lethality, but also how this relationship changes as a function of the Lanchester law exponent (i.e., the three-way interaction). The above two-way model seems to typify the relationship when agents possess no ability to coordinate their attacks, essentially each fighting independently. In such tribes, the gains from cooperation in combat are likely realized in the form of larger tribes, since under the Linear Law a tribe's fighting power increases linearly with number and greater cooperation generally will enable more efficient usage of resources and larger tribes. Accordingly, this positive effect evaporates under the Square Law (*Lanchesterlawexponent* = 2). Under the Square Law, however, the advantage cooperation brings directly to the battlefield the most important influencer of the relationship between bellicosity and cooperation. When tribes can coordinate their actions on the battlefield *and* warfare is constant and pervasive, tribes stand together or die together in warfare. Because the coefficient is negative at low lethality and under the Square Law, these data suggest that the advantage cooperation yields by allowing larger tribes is wiped out entirely; even larger but uncooperative tribes are helplessly slaughtered by tribes whose strength grows exponentially.

Figure 3: Bellicosity drives the evolution of cooperation when lethality is low.

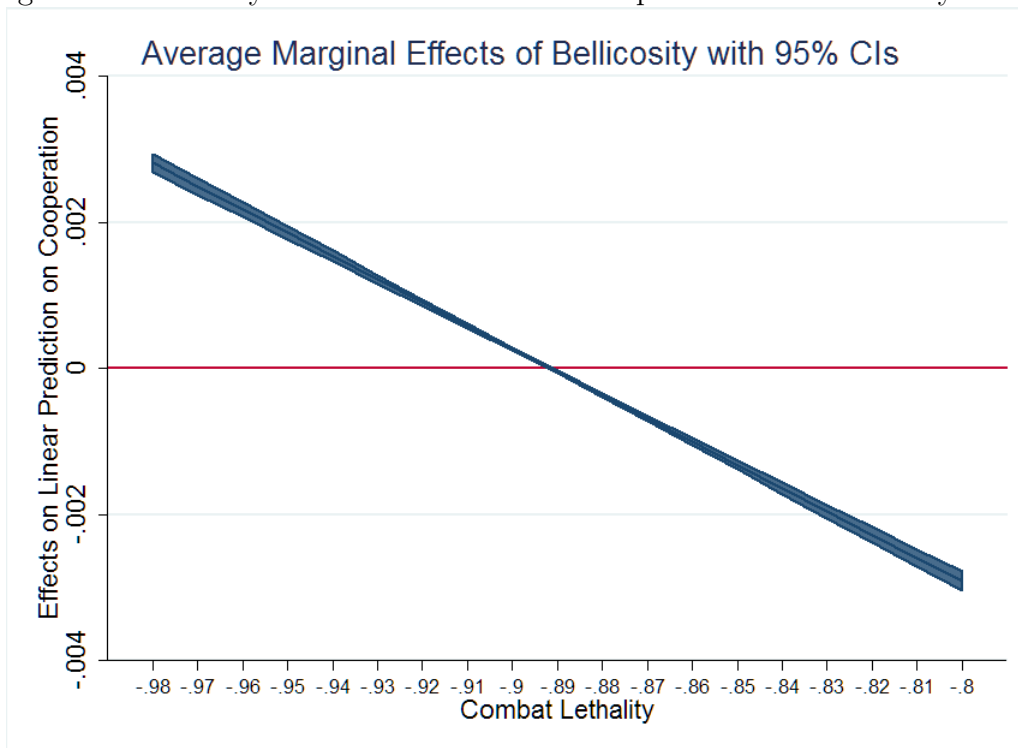
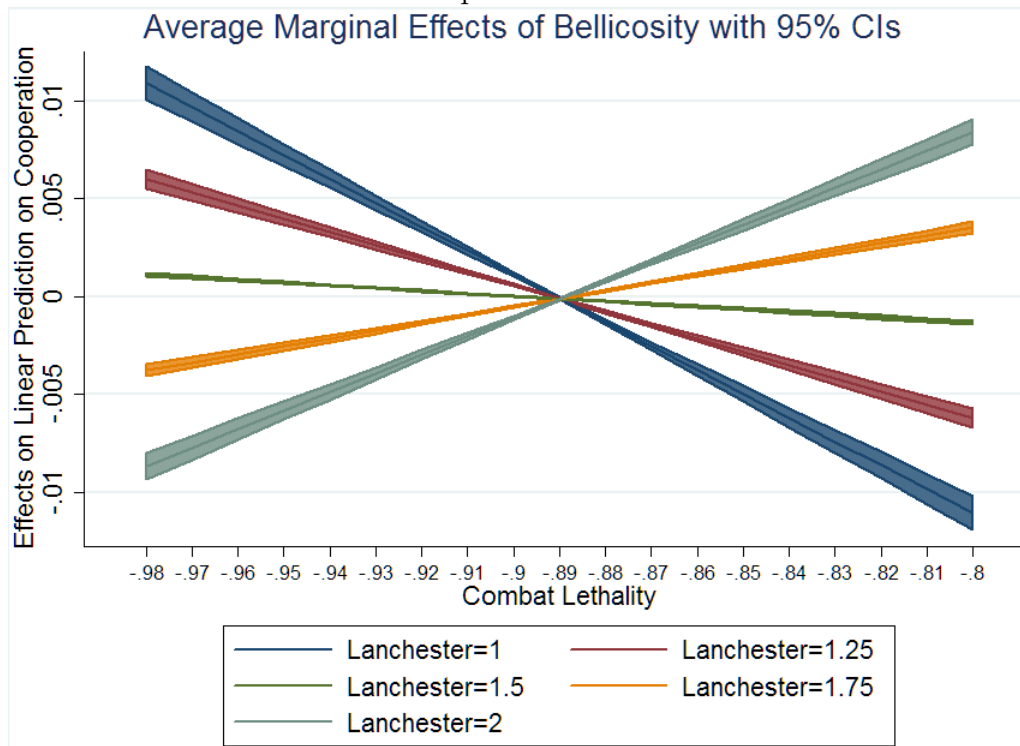


Figure 4: Conditional effect of lethality is inverted when agents can coordinate their attacks. The more lethal combat is, the more important tactical coordination is the relationship between the evolution of warfare and cooperation.



If the above analysis assesses the conditionality of the relationship between bellicosity and cooperation from a “supply-side” perspective (i.e., by taking into account the costs and forms of cooperation supplied), another way to look at it may be the “demand-side” of the equation. Accordingly, Models 4 and 5 consider the character of the resources (clustered vs. heterogonously distributed, respectively) which are subject to violent contestation. Figure 5 depicts the two-way interaction of bellicosity and the Lanchester law exponent as a function of well frequency (hence, also a three-way interaction). Functionally, the well frequency parameter determines the average distance between wells, implying that as the well frequency increases the resource becomes increasingly homogenous, or de-clustered. At  $wf = 0.17$ , the probability of there being at least one well within 9 tiles surrounding (or underneath) a given agent is approximately 81%, and a 47% chance of there being more than one. For comparison, at  $wf = 0.05$  there will be a well within the base 9 tiles 37% of the time and more than one about 7% of the time. Hypotheses 2 states that when resources are clustered, the ability to engage in concerted action to secure those resources will be paramount. Consistent with this hypothesis, when resources are most clustered ( $wf = 0.05$ ) the Lanchester law exponent fully moderates the marginal effect of bellicosity on the evolution of cooperation. In other words, when resources are clustered and tribes can employ concerted, violent action to take and monopolize those resources the frequency of warfare was an evolutionary driver of cooperation. Note that as  $wf$  increases and the resource is de-clustered, the marginal effect of bellicosity on cooperation approaches zero. In this regard, the effect is “fully moderated”.

Setting the question of heterogeneity aside, what are the implications of changes in the

*quantity* of resources independent of their distribution? Model 5 presents the results of a three-way interaction between bellicosity, Lanchester law exponent, and pasture availability. This measure is essentially “how much is there?” as opposed to “where is it?”. Figure 6 depicts this three-way interactive prediction of cooperation. Interestingly, we observe a mirrored, opposite relationship for quantity of resources compared to resource clustering. When food is scarce, the ability to organize and coordinate in battle yields no changes in the marginal effect of bellicosity on the evolution of cooperation. The clearest explanation for this is that when resources are inadequate to sustain tribespeople living in close proximity to one another the tactical advantage coordination cannot overcome that gained by superior numbers. Accordingly, under the Linear Law (when agents cannot coordinate on the battlefield), the primacy of superior numbers drives cooperation as a means for more efficiently allocating resources and achieving higher relative densities than a tribe’s adversaries. At the bottom right quadrant of the figure, we see significant, negative coefficients under circumstances of high food availability and the Square Law of Combat. In this case, the advantage of absolute numbers in combat diminishes, but so does the reward:risk ratio of going to war over an abundant resource which can be had easily going elsewhere. Cooperators in a tribe are subject to rapidly diminishing returns on their altruistic investment in their fellows, and thus we see negative selection on cooperation.

Figure 5: When resources are more sparsely clustered, the ability to coordinate in battle makes warfare a good deal for cooperators.

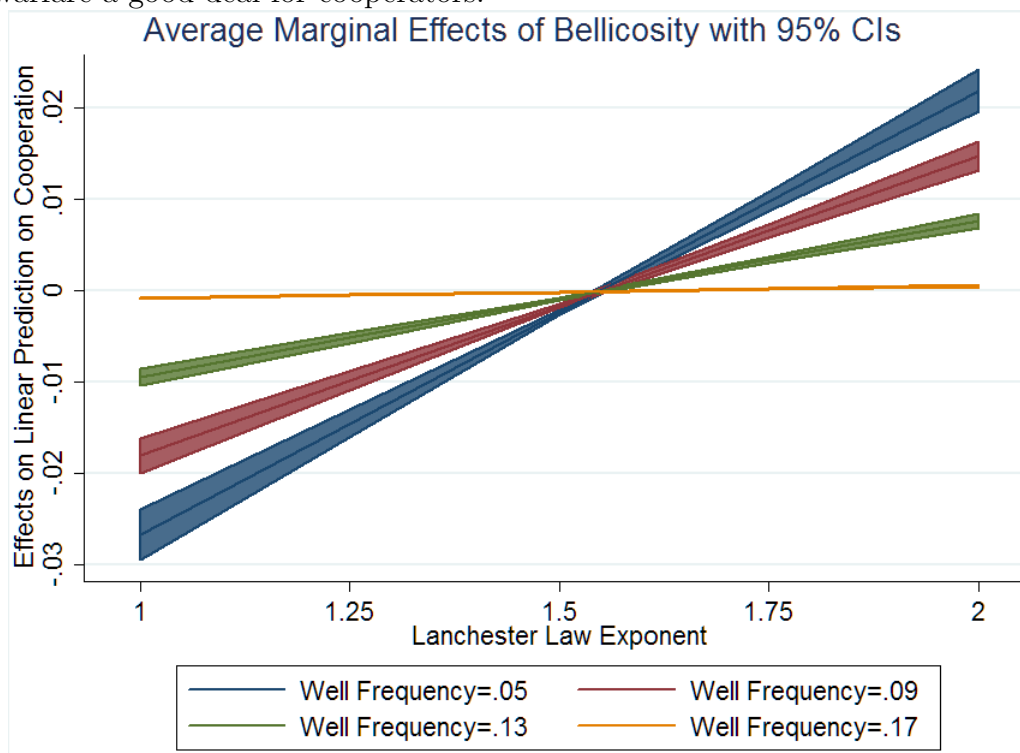
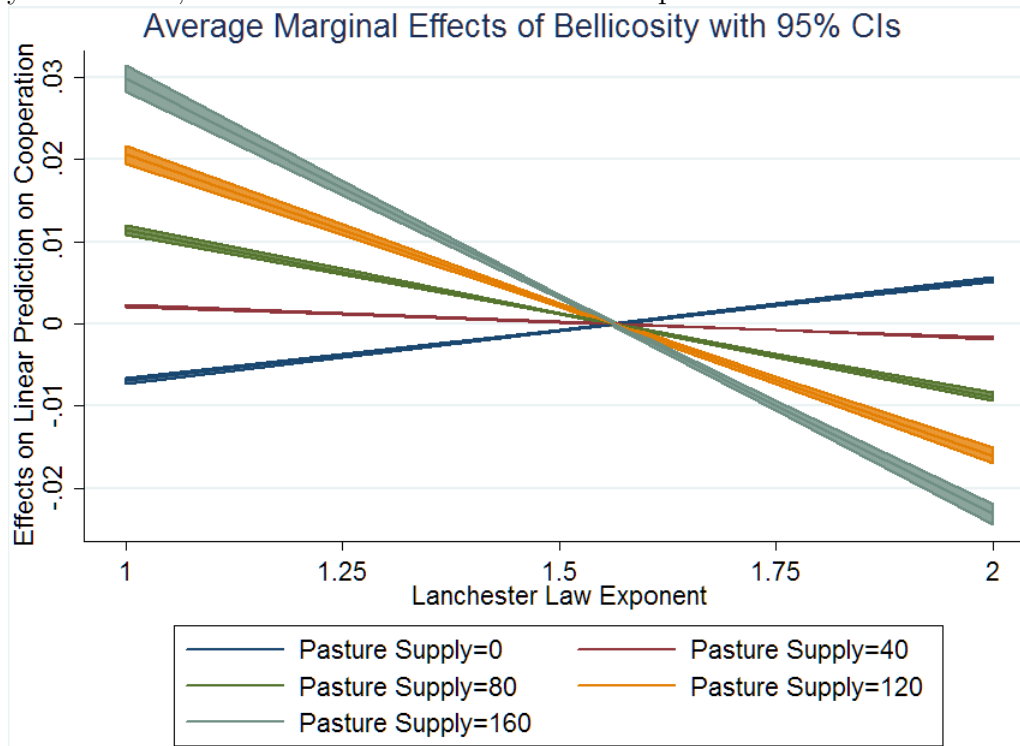


Figure 6: When victory in war is determined by absolute numbers rather than the ability to tactically coordinate, abundance drives conflict and cooperation rather than scarcity.



## Discussion

This study modeled the co-evolution of cooperation and tribalism under pastoralism. While pastoralism may not perfectly characterize the hunter-gatherer environment in which humans evolved in, it is a perennial pre-agrarian economic modality and inspires or more focused, simplified meditation on the moderating effects of environment on the evolution of cooperation. Rather than rule out the implications of a pastoralist model on human evolution, we should take these findings and apply them to formulate new hypotheses about hunter-gatherer modalities plausibly more characteristic of the deep human past.

Taken as a whole, this study concludes that the quintessential human trait of cooperation can be explained by multi-level selection. This is evident in several ways. First, consistent with *Hypothesis 1*, bellicosity and cooperation exert independent, reciprocal effects on each other. Importantly, increased within-group cooperation drove increases in bellicosity. While bellicosity—on average—undermined cooperation, conditional factors can alter the returns to cooperation on warfare for even the most altruistic, self-sacrificing agents. These results suggest that warfare was a prevalent and key feature of human evolution with interesting implications for human socio-cognitive development, as demonstrated by the conditional effects of the ability to engage in organized violence. These capabilities were most potently expressed when resources were clustered, consistent with *Hypothesis 2*. While I expected a stronger relationship between warfare and cooperation in the clustered case, it was surprising to discover this effect was reversed when resources were homogenously distributed, but also depending on the quality of cooperation (*Hypothesis 3*). For widely distributed resources, it

was the condition of the Linear Law of Combat that showed the greatest, positive influence of bellicosity on cooperation. This is intriguing because it suggests distinct mechanisms underlying the evolution of cooperation among different species facing different socio-ecological challenges. In the case of animals grazing on abundant pastures, the dynamics of intergroup conflict appear to be determined by maximizing the size of “herds”, squeezing more and more animals onto smaller spaces and simply pushing competing herds aside with greater absolute mass. For such beasts, greater abundance of resources seems to drive conflict more than scarcity. Alternatively, in the case of more sparse and clustered resources, resource conflict favors smaller, more tactically cooperating tribes where victory is determined more by guile and maneuver, and that is us. Insofar as team sports are, in a sense, a dramatic reenactment of primordial tribal contests, it is intriguing to speculate on what the team sports of a race evolved from pasture grazing creatures. Rather than emphasizing greater teamwork, the contest would likely turn on which side was able to muster the greater numbers on their side of the field.

Another interesting finding was that while cooperators bare disproportionate costs of violent conflict, which in the most lethal cases can exert powerful negative selection on cooperation, circumstances that can reduce lethality will quickly turn the coefficient. In other words, anywhere warfare can be made less punishing to cooperators will potentially change relationship, positively increasing effect of warfare on cooperation. Perhaps not coincidentally, the lethality of so-called tribal raiding in among the Turkana tribes has not historically been high. Rather, lethality has increased only recently with the widespread introduction of inexpensive and pervasive small arms; in particular, Soviet-made AK-47s left in the region following the numerous Cold War proxy wars (Parenti 2011). This also seems to elucidate Wrangham’s “Imbalance-of-Power Hypothesis” (Wrangham 1999), of intergroup warfare among chimpanzees, which states that violent conflict is only likely to occur in the presence of significant power imbalances where the cost to the attacking side is minimal. However, when evenly matched conflicts between chimpanzee groups is largely comparative demonstrations of force, with each side screaming at each other and beating the ground until one side yields.

So what implications do these findings have for the dynamics of future conflicts which may be, in part, caused by ongoing climate change and climate disruption? Resources scarcity is likely to increase the amount individuals rely upon their tribes—or other sources of identity—to collectively manage scarce resources, though increased fractionalization does not necessarily imply increased bellicosity. When competing groups have opportunities to resolve disputes through non-violent means (i.e., through more institutional, legalistic arenas for intergroup conflict), they will use them. The recent surge in so-called “identity politics” may be an expression of this. However, even institutional means for factional conflict resolution may be inadequate to prevent violence when the resources at contest meet one or both of the following conditions: 1) The resources are immediately needed for the survival of a desperate group, and 2) the character of the resource is such that it may be “monopolized” by one group able to “lock out” others. This second condition has particular implications for how we plan to respond to climate change-induced scarcities rather than the direct effect of the scarcities themselves. Specifically, these analyses suggest that international aid agencies may inadvertently increase the risk of violent intergroup conflict among target-populations if their distribution protocol results in “clustered” distribution channels. For example, large

and regular shipments of aid to a single location may inspire “turf wars” between rivaling factions, to the victor going control of the aid and its distribution. When aid agencies are directing aid through state institutions, they should be wary of the factional character of local politics. In cases where elected offices are largely ethnic or tribal contests, channeling aid through a government body charged with local distribution may heighten the stakes of electoral outcomes, potentially rendering a defeat which is unacceptable to the losers.

## References

- Alford, John R, Carolyn L Funk and John R Hibbing. 2005. “Are political orientations genetically transmitted?” *American political science review* 99(02):153–167.
- Bannister, Robert. 2010. *Social Darwinism: Science and myth in Anglo-American social thought*. Temple University Press.
- Bowles, Samuel. 2006. “Group competition, reproductive leveling, and the evolution of human altruism.” *science* 314(5805):1569–1572.
- Buhaug, Halvard and Jan Ketil Rød. 2006. “Local determinants of African civil wars, 1970–2001.” *Political Geography* 25(3):315–335.
- Darwin, Charles. 1871. *The descent of man*. Digireads. com Publishing.
- Dawes, Christopher T and James H Fowler. 2009. “Partisanship, voting, and the dopamine D2 receptor gene.” *The Journal of Politics* 71(3):1157–1171.
- Dugatkin, Lee Alan and Hudson Kern Reeve. 2000. *Game theory and animal behavior*. Oxford University Press.
- Fowler, James H, Christopher T Dawes and Nicholas A Christakis. 2009. “Model of genetic variation in human social networks.” *Proceedings of the National Academy of Sciences* 106(6):1720–1724.
- Fowler, James H, Laura A Baker and Christopher T Dawes. 2008. “Genetic variation in political participation.” *American Political Science Review* 102(02):233–248.
- Fratkin, Elliot. 2001. “East African pastoralism in transition: Maasai, Boran, and Rendille cases.” *African Studies Review* pp. 1–25.
- Galaty, J.G., D.L. Johnson et al. 1990. *The world of pastoralism: herding systems in comparative perspective*. Guilford Press.
- Gintis, Herbert. 2005. *Moral sentiments and material interests: The foundations of cooperation in economic life*. Vol. 6 MIT press.



- Hailegiorgis, Atesmachew B, William G Kennedy, GC Balan, Jeffrey K Bassett and T Gulden. 2010. An agent based model of climate change and conflict among pastoralists in east Africa. In *Proceedings of the 2010 International Congress on Environmental Modelling and Software*.
- Halake, Sora. N.d. “La Nina Threatens to Bring Drought to East Africa.” . Forthcoming.
- Hardin, Garrett. 1968. “The tragedy of the commons.” *Science* 162(3859):1243–1248.
- Heady, Harold F. 1975. *Rangeland management*. McGraw-Hill New York.
- Hendrix, Cullen S and Idean Salehyan. 2012. “Climate change, rainfall, and social conflict in Africa.” *Journal of Peace Research* 49(1):35–50.
- IFRC. 2011. Drought in the Horn of Africa: Preventing the Next Disaster. Technical report International Federation of Red Cross and Red Crescent Societies.
- Johnson, Dominic DP and Niall J MacKay. 2014. “Fight the power: Lanchester’s laws of combat in human evolution.” *Evolution and Human Behavior* .
- Kennedy, William G, Atesmachew B Hailegiorgis, Mark Rouleau, Jeffrey K Bassett, Mark Coletti, Gabriel C Balan and Tim Gulden. 2010. An agent-based model of conflict in East Africa and the effect of watering holes. In *Proceedings of the 19th Conference on Behavior Representation in Modeling and Simulation (BRiMS)*.
- King, Andrew J, Caitlin Douglas, Elise Huchard, Nick JB Isaac and Guy Cowlshaw. 2008. “Dominance and affiliation mediate despotism in a social primate.” *Current Biology* 18(23):1833–1838.
- Koenig, Andreas. 2002. “Competition for resources and its behavioral consequences among female primates.” *International Journal of Primatology* 23(4):759–783.
- Kuznar, L.A. and R. Sedlmeyer. 2005. “Collective violence in darfur: An agent-based model of pastoral nomad/sedentary peasant interaction.”.
- Lanchester, Frederick William. 1956. “Mathematics in warfare.” *The world of mathematics* 4:2138–2157.
- MacOpiyo, Laban, Jerry Stuth and Jianjia Wu. 2006. Use of GIS and Agent-Based Modeling to Simulate Pastoralist Mobility in the Rangelands of East Africa. In *GSDI-9 Conference Proceedings*.
- Mathew, Sarah and Robert Boyd. 2011. “Punishment sustains large-scale cooperation in prestate warfare.” *Proceedings of the National Academy of Sciences* 108(28):11375–11380.
- Network, Famine Early Warning Systems. N.d. “Special Report: Persistent drought in Somalia leads to major food security crisis.” . Forthcoming.
- NIDIS. 2015. “Global Drought Information System.”.  
**URL:** <http://www.drought.gov/gdm/current-conditions>

- Nowak, Martin A. 2006. "Five rules for the evolution of cooperation." *science* 314(5805):1560–1563.
- Olson, Mancur. 1965. *The logic of collective action: Public goods and the theory of group*. Harvard University Press Cambridge.
- Parenti, C. 2011. *Tropic of chaos: climate change and the new geography of violence*. Nation Books.
- Raleigh, Clionadh and Dominic Kniveton. 2012. "Come rain or shine: An analysis of conflict and climate variability in East Africa." *Journal of Peace Research* 49(1):51–64.
- Senft, RL, MB Coughenour, DW Bailey, LR Rittenhouse, OE Sala and DM Swift. 1987. "Large herbivore foraging and ecological hierarchies." *BioScience* 37(11):789–795.
- Sidanius, Jim and Kurzban, Robert. 2003. Evolutionary Approaches to Political Psychology. In *Oxford handbook of political psychology*, ed. Robert Ed Sears, David O and Huddy, Leonie Ed and Jervis.
- Smirnov, Oleg, Holly Arrow, Douglas Kennett and John Orbell. 2007. "Ancestral war and the evolutionary origins of heroism." *Journal of Politics* 69(4):927–940.
- Spencer, Herbert. 1904. *A system of synthetic philosophy*. Vol. 1 William & Norgate.
- Sterck, Elisabeth HM, David P Watts and Carel P van Schaik. 1997. "The evolution of female social relationships in nonhuman primates." *Behavioral ecology and sociobiology* 41(5):291–309.
- Suliman, M. 1993. "Civil war in the Sudan. From ethnic to ecological conflict." *Ecologist* 23(3):104–109.
- Waser, Peter M. 1988. "Resources, philopatry, and social interactions among mammals." *The ecology of social behavior* pp. 109–130.
- Weikart, Richard. 1993. "The Origins of Social Darwinism in Germany, 1859-1895." *Journal of the History of Ideas* 54(3):469–488.
- Wilson, David Sloan and Edward O Wilson. 2007. "Rethinking the theoretical foundation of sociobiology." *The Quarterly review of biology* 82(4):327–348.
- Wittig, Roman M and Christophe Boesch. 2003. "Food competition and linear dominance hierarchy among female chimpanzees of the Tai National Park." *International Journal of Primatology* 24(4):847–867.
- Wrangham, Richard W. 1999. "Evolution of coalitionary killing." *American Journal of Physical Anthropology* 110(S29):1–30.
- Zellner, Arnold and Henri Theil. 1962. "Three-stage least squares: simultaneous estimation of simultaneous equations." *Econometrica: Journal of the Econometric Society* pp. 54–78.

Zinser, Erik R and Roberto Kolter. 2004. "Escherichia coli evolution during stationary phase." *Research in microbiology* 155(5):328-336.