



# A computer simulation to investigate the association between gene-based gifting and pair-bonding in early hominins

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## ABSTRACT

This article describes simulation research based on the Hamiltonian theory of gene-based altruism. It investigates the origin of semipermanent breeding bonds during hominin evolution. The research framework is based on a biologically detailed, ecologically situated, multi-agent microsimulation of emergent sociality. The research question tested is whether semipermanent breeding bonds (an emergent homoplastic social construct) might emerge among primate-like agents as the consequence of a mutation capable of supporting involuntary prosocial behavior. The research protocol compared several, single independent-variable longitudinal studies wherein hundreds of generations of autonomous, initially promiscuous, biologically detailed, hominin-like artificial life software agents were born, allowed to forage, reproduce, and die during experimental intervals lasting several simulated millennia. The temporal setting of the experiment was roughly contemporaneous with, or slightly after the time of, the *Pan-Homo* split. The simulation investigated what would happen if, within a population, a single gene for prosocial behavior (the independent variable in the experiment) was either switched on or switched-off. The null hypothesis predicted that, if the gene was switched off, then semipermanent breeding bonds (the dependent variable) would nonetheless emerge within the population. The results of the simulation rejected this null hypothesis, by showing that semipermanent breeding bonds would reliably emerge among the experimental populations but not among the control groups. Moreover, it was found that, across all experimental settings having constrained population numbers, the portion of each population having no prosocial trait would die out early, whereas the portion with the prosocial trait would survive. Large control populations had no discernible loss. The results of this research imply that, during the early stages of hominin evolution, there might have been a set of initially gene-based, altruistic excess forage-sharing social traits that contributed to the onset of morphological and additional complex social changes characteristic of this group. This work also demonstrates that modern computational technologies can extend our ability to test ‘what if’ hypotheses appropriate to the study of early hominin evolution.

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## 1. Introduction

Over fifty years ago, Hamilton (1963, 1964a, b) proposed a theory about gene-based altruism. This theory posited that if a prosocial mutation came into being, it might be passed on to succeeding generations as the result of explicitly non-cognitive, i.e., unconscious and non-reciprocal, reproductive social interaction. In the intervening fifty years, many researchers and theoreticians have considered the Hamiltonian argument. Often, they instantiated their models as agent-based simulations (e.g., Premo, 2006),

grounded them in game theory (e.g., Grund et al., 2013) and/or considered the argument using quantitative statistics (e.g., Gavrillets, 2012). Each time the argument was considered, the individual researchers had to decide if the hominin population under study needed to have some degree of cognitive capacity to support reciprocal prosocial interaction or if their respective research question could be nuanced such that the research could be run without modeling any explicit hominin cognitive attribute in support of prosocial behaviors. This meant researchers might miss the entire point of the initial Hamiltonian argument when they decided that their theoretical model should incorporate hominin cognitive support for prosocial behavior. The research reported in this paper deals with hominin populations having explicit biologically based

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prosocial behaviors, i.e., non-cognitive, non-reciprocal social interactions. In particular, it will be shown experimentally by means of computer simulation that a population could survive, evolve, and adapt on the basis of pure gene-based altruism.

Recent simulation research in the context of hominin evolution is perhaps best represented by the works of Premo (2006) and Gavrillets (2012). Premo (2006) provided a comprehensive simulation research experiment constructed as an agent-oriented simulation operating within a hybridized game-theoretical framework. His work demonstrated evidence of a strong correlation between gene-based altruism, species adaptive survival, and the distribution of forageables within a simulated environment. While Premo (2006) simulated hominin agents that enjoyed only asexual reproduction and 'lived' within an abstract simulation cycle uncoupled from real-world time, he also created two categories of agents whose simulated alleles expressed for phenotypic altruistic behavior. His first category of agent was one in which he installed a discrete set of cognitively nuanced social behaviors. His second agent category represented a non-cognitive hominin he referred to as a 'null' object. Premo's (2006) 'null' agents provided a control against which his more cognitively rich agents could be compared. These 'null' agents were similar to those in this paper, but only in an abstract sense, since the work reported here greatly narrows and extends the previous work by Premo (2006).

In the category of purely quantitative models, Gavrillets (2012) provided a powerful equation-based exploratory mechanism, based on an integrative computational process whose abstract product was evidence that individual, promiscuous hominins could transition to pair-bonded relationships. However, his research did not use an explicit articulation of time, i.e., his populations were neither born nor did they die, and there was no evolution. Simply, Gavrillets' (2012) model was not temporally coupled to the reproductive cycles of any hominin explicit biology, nor their needs to forage in order to survive. Ultimately, his research did not address the role that time and environment, as stochastic drivers of hominin behavior, must have played in hominin evolution. In contrast, in the present article the theory of gene-based altruism is tested using a highly detailed, temporally grounded, discrete-event, microsimulation technology called a spatial agent-based model (ABM; Grimm et al., 2010). This article describes that simulation research performed, the technology that was used, and discusses the results derived for the understanding of hominin origins and evolution.

### 1.1. Motivation

The original motivating challenge behind the simulation experiment described in this paper was to discover why reciprocal exogamy (a social behavior involving the intentional exchange of mating resources; Chapais, 2008) emerged among the higher primates in general and among *Homo* in particular. Based on this motivation, several non-critical hypotheses (listed in the next section) were formulated to help begin the process of operationalizing the problem space, so that its properties and mechanisms could be translated into computer code. However, the first problem was to find a way to sufficiently constrain the motivating challenge, while still producing plausible research whose experimental method could take advantage of a discrete-event simulation technology called ABM. What was required was to identify the set of necessary and sufficient causal mechanisms (biological, possibly cognitive, social, environmental, etc.) that: 1) could be translated into computer code; 2) would support emergent results, later identifiable as solutions directly related to the motivating challenge; and 3) would not provide any 'hard-coded' solutions in any sense. The descriptive name for the project software ('Clans') was selected based on the

notion that, if the research was successful, then one should expect to see extended family groups (or 'clans') self-organizing within each large and promiscuous experimental population. Logically, such evidence of clan-like social behavior would seem to be a necessary precondition to the emergence of reciprocal exogamy. Unfortunately, evidence of reciprocal exogamy never occurred during the experimental period, likely due to limitations of time and coding resources. However, when evidence of the self-organization of 'family-like' groups (more technically called evidence of semipermanent breeding bonds) began to emerge in the simulation, using only an independent variable gene for altruism, the work of Hamilton (1963, 1964a, b) came to mind. It is this part of the simulation experiment and its results that are described here.

### 1.2. Hypotheses

The central hypothesis operationalized for simulation in Clans was that prosocial, gene-based altruism should lead a simulated population of promiscuous hominin agents to develop emergent, semipermanent breeding bonds. The null hypothesis was that, if the same prosocial gene (for gene-based altruism) was withheld from an identical population, then semipermanent breeding bonds should still emerge. In contrast to the central hypothesis, and not implemented in Clans, were the original motivating challenges. These proposed that "reciprocal exogamy emerged because of innate drives for specific territoriality constrained by [...] bipedal mobility, social altruism and alliance, environmental and social circumscription, and sexually differentiated philopatry" (Rouly, 2015a:83). Philopatry, of course, refers to the tendency of community members of one sex to remain in collocation with conspecifics after sexual maturity is achieved, whereas the opposite sex members of the same community will typically engage in some degree of distal migration into unrelated social groups (Parish and de Waal, 2000). To assist in framing and operationalizing the central hypothesis (as instantiable computer code), two additional hypotheses were adopted: 1) a pristine environment is necessary for the identification of the fundamental principles of small-group social behavior, and 2) an environment having a sufficient absence of cultural confounds but also one having a sufficient fullness of socioenvironmental stimuli is required for a complete understanding of 'emergent' sociality. In this context, the word 'pristine' refers to a setting void of prescriptive culture, social assumption, or other human-constructed artifacts. These latter two 'framing' hypotheses led to the development of the artificial ecology inhabited by the Clans hominin agents.

### 1.3. The simulation technology

Initially, the simulation research had a single purpose: try to understand how *Pan*-like promiscuous individuals might transition into family-unit households and, much later, extended families and clans capable of practicing reciprocal exogamy. However, in hindsight, it seems that little empirical evidence exists about 'why' the Hominini transitioned from being presumably small groups of *Gorilla*-like polygynous and/or possibly *Pan*-like promiscuous individuals into family-units having stable breeding bonds, and much later extended families and clans. It seems reasonable to assume that the transition process was quite slow to develop into fuller social dominance among the early hominin species, even as *Ardipithecus*, *Australopithecus*, or even *Homo* emerged (Lovejoy, 1981; Chapais, 2008).

As a simulation technology, Clans is an example of the computational study of natural life called artificial life (ALife). As it will be shown in the next several paragraphs, ALife is only a few decades old. This science uses computer programs (simulations) to study an

extremely broad range of natural life topics. Historically, this science may have started in a computer program called ‘The Game of Life’ (Conway, 1970), which produced a visual output (a computational side-effect) that resembled ‘living’ cells moving about on a two-dimensional display grid. As the program executed, the cells appeared to self-organize in spatial and relational interaction, and those interactions revealed a probabilistic event course that determined all life, death, movement, and reproductive exchanges among the cells.

At about the same time, but following a slightly different argument and path, Axelrod (1986) was considering the evolution of a set of complex human social behaviors. During the early 1980s he developed software with self-organizing mechanisms that appeared to mimic processes associable with the emergence of social norms. Clans owes a debt to the work of Axelrod (1986), because he demonstrated that informal descriptions of human behavior could be translated into executable code. For example, Axelrod (1986:1098) wrote that, after being ‘seen,’ a “player’s vengefulness” may lead “he or she [to] punish someone who is spotted defecting.” Although we intuitively understand the behavioral description and its implication that a complicated social interaction was involved, it still requires fluency in software coding and design to write the experimental code. However, following Conway (1970) and Axelrod (1986), another early ALife researcher decided to practice “a new discipline that studies ‘natural’ life by attempting to recreate biological phenomena from scratch within computers” (Langton, 1989:1). That is, Langton (1989) tried to emulate biological systems in computer code, and his abstract formalization of a theoretic ALife moved the discipline forward. However, a more tangible result was not produced until Yaeger (1994) extended Axelrod’s (1986) work. Yaeger’s (1994) work included mobile agents that could emulate a primitive visual sense and therefore ‘see’ (detect) objects in the space around themselves. Using their simulated ‘vision,’ the agents could seek out (forageable) food objects. In this sense, the hominin agents in the current simulation, which simulate an ability to see each other and their food objects, owe some debt to Yaeger’s (1994) work.

During the remainder of the 1990s, advances in computational machinery led to an already well-accepted software engineering technique to further mature and to begin to evolve. This established technique was known as object oriented programming (OOP; Martin and Odell, 1998). However, by the late 1990s and early 2000s, a new coding style started to emerge from within the OOP community, which took on primacy in some quarters of ALife research. This new coding technology placed a high value on the ability of the software modeler to incorporate informal descriptions of behavior (both ecological and anthropomorphic) in the executable code of OOP software objects—now referred to as ‘agents.’ This new, ‘improved’ OOP technology became known variously as individual-based modeling (IBM) and/or agent-based modeling (ABM). As IBM and ABM matured, it became obvious there was only a very subtle difference between the two. The difference mostly depended on the emphasis (by degree) between ecologically grounded research and social system research, each respectively.

Researchers like Axtell et al. (2002), Epstein and Axtell (1996), and Kohler et al. (2000) were among the first to use the new ABM and IBM technologies as the foundations of their respective research. In so doing, they materially realized the thesis of the ‘sciences of the artificial’ (Simon, 1996). Moreover, it was entirely because of ABM and IBM technology that the new discipline of computational social science emerged (Cioffi-Revilla, 2010, 2016). Leveraging these new technologies and discipline, Epstein and Axtell (1996) created the simulation ‘Sugar Scape.’ This was a program wherein each mobile, self-organizing agent demonstrated an emergent, independent participation in abstract culture and foraging. The current research

owes a huge debt to Sugar Scape, even though the agents of Sugar Scape were not tasked with surviving for lengthy periods of time or to operate under empirically derived biological constraints. Yet, these researchers (exemplified by Kohler et al., 2000; Axtell et al., 2002) showed that in an ABM, the behavioral relationship of situated agents with regard to their environments, as well as with regard to each other, changed both agent and environment in mathematically complex ways. For example, an ABM can compute the results of time and space-dependent non-linear inter-agent behavior and agent–socioenvironmental interaction not easily achieved by any other means. The simulation reported here owes its existence to all of the foregoing modelers, theorists, and scientists: their concepts, simulations, research, and their free sharing of experimental methodologies. The Clans simulation is an example of a complex, natural-life system modeled and instantiated in executable computer code, and therefore an example of ALife.

#### 1.4. Clans in the context of related research software

Clans began by instantiating in software an abstract model of artificial hominin life and a simulated environment as we imagine it may have existed in the Awash River area of the Afar Depression (Ethiopia), perhaps 3–7 million years ago (Ma). (The environmental model provided its hominin inhabitants with large and small water features and abundant forageable opportunities, including leaves, fruits, roots, fish, small prey monkeys, and termites, to name a few.) Clans set three control (reference) populations in comparative opposition to two types of experimental populations. The experimental design aligned the populations as a set of highly related, longitudinal studies. This made the Clans research an experiment whose methodology the reader may want to contrast with, for example, Premo and Kuhn (2010), Premo (2012), Wren et al. (2014), Shook et al. (2015), Wren and Costopoulos (2015), and Hölzchen et al. (2016). Moreover, its experimental design not only made Clans unique, but the design allowed it to consider simultaneously how hominin biology, ecology, and cognition might have interacted over evolutionary time to produce social behaviors characteristic of modern humans. Because Clans is an agent-based simulation, it can be directly compared with the works of previous researchers (te Boekhorst and Hogeweg, 1994a, b; Hemelrijk, 1999, 2002a, b, c; van der Post and Hogeweg, 2004, 2008, 2009; Hemelrijk et al., 2005, 2007, 2008; Janssen et al., 2005, 2007; Poethke et al., 2007; Puga-Gonzalez et al., 2009; van der Post et al., 2009, 2015; Griffith et al., 2010). However, in contrast to all of these foregoing works, Clans combined a simulation of primates (individual software agents with socioenvironmentally influenced artificial genetics and situated in cohort-centric societies) within a pristine ecology over very long temporal horizons. Each of the above-mentioned works was a simulation of various pieces of primate life, behavior, environment, social interactions, and/or socio-environmental issues, whereas, in contrast, Clans is a combined whole.

## 2. Methods

This section describes the experimental method and the related materials used in the construction of the simulation experiment, which was constructed in two parts: (1) a separable, self-sustaining environment; and (2) a dynamic set of self-constructing and self-organizing, separable, autonomous, software agents. The ecology provided a simulated habitat in which the agents could evolve. The agents, in turn, were parameterizable software objects with simulated biological, genetic, and cognitive properties and mechanisms.

Code development took place on one or more machines equivalent to, or greater than, an Intel Core-2 Quad Q8200 2.33 GHz

Central Processing Unit (CPU) with NVIDIA-based PCI-X graphics acceleration. The simulations reported here took place on a dual Intel Xeon W5590 3.33 GHz i7 CPU with NVIDIA-based adapter graphics acceleration. This was an industrial-grade workstation with an Intel motherboard and 48 GB RAM. Clans needs a very large pool of integer, Boolean, and real-valued random numbers (essentially a source of entropy) to produce reliably descriptive output. The Clans experiment used an external random number generator (RNG), specifically, the TrueRNG2<sup>®</sup>. The Operating Systems used during all development work were from Microsoft and included at various times versions XP, 7, and 8, although Clans itself was written in pure Java. The Java Integrated Development Environment (IDE) used was JGrasp version 2.0.1 Beta 2. The Java compiler was Oracle Java version 1.8.0\_20. All verification tests and simulations were run in the Java Runtime Environment 1.8.0\_20-b26 with client Virtual Machine (VM) build 25.20-b23 mixed mode. All the Windows and Java binary codes for the TrueRNG2<sup>®</sup> Random Number Generator and all the Clans Java (text file) source code Classes required to construct a working instance of the software are freely available by download from the following URL: <http://habitatlab.maelzel.org/pages/code/code.html>.

In the following sections it has been attempted to observe the organization and descriptive nomenclature proposed by the 2010 version of the Overview, Design concepts, and Details (ODD) software description methodology (Grimm et al., 2010). However, the final layout of these sections has been reconfigured to comply with immediate publication requirements.

## 2.1. Overview

The design of the simulation involved a population of detachable, independent, self-replicating, and self-organizing software objects (agents) coded to physiologically and behaviorally imitate *Pan-Homo* 'hybridized' entities. These hybrid agents were then situated in a standalone software object coded to resemble an explicit and forageable, niche habitat. The population and their habitat (a virtual environment) were instantiated with as much empirical realism as possible while still maintaining a simplified system model. The work involved giving the hybrid agents simulated sexually dimorphic biology with features like sex-specific nutrition and water requirements (Portman, 1970; Milton, 1999; AZA TAG, 2010) and primate-based reproductive fertility constraints (Tutin, 1979; Lancaster, 1986). Additionally, each agent enjoyed artificial genetics (an 88-allele chromosome), autonomous terrain mobility, and the capacity to suffer cognitive dissonance (Festinger, 1962) when/if frustrated by unsatisfying foraging options. They demonstrated emergent genetic drift (Wright, 1932) through Baldwinian evolution (Baldwin, 1896) and each one had the need to survive long enough to fulfill its individual obligations to participate in the dynamic maintenance of viable population numbers. For example, the hominin agents had, among many other features: (a) sexually dimorphic (male/female) features, including body mass, drinking water and forage requirement differences, as well as mating partner selection behavioral differences; (b) primate-based reproductive constraints (28-day cycles, 5-day conception interval); (c) decision making features for individual behavioral autonomy, such as self-selection of breeding partner, self-selection of movement on the habitat terrain, and self-selection among forage choices; (d) a set of reactive cognitive features including instinctive capabilities to locate edible forage and find water; (e) an ability to locate conspecifics; (f) an unconscious social-memory function resembling that proposed by Westermarck (1921), which supported incest avoidance; (g) a capability to acquire memories of and then later to recognize uterine kin; and (h) an 11-gene (88-allele) artificial chromosome (one per agent). The

foregoing list is abbreviated here, but is fully described in the sections that follow. Above all else, the agents had to survive lengthy periods of simulated time within their habitat through self-selected and artificial sexual reproduction and natural selection (Darwin, 1859).

## 2.2. Purpose

In response to the Grimm et al. (2010:2763) question "What is the purpose of the model," the purpose of the Clans was to evaluate a set of hypotheses related to the causality of complex sociality and to consider its emergence at the least organized ends. Our suspicion is that those causes may rest in the intimate and affine relationships that evolved within the biology, ethology, and environment of the earliest hominins.

## 2.3. Entities, state variables, and scales

The Clans simulation is built of Java classes and these, in turn, are structured around a set of functional object areas. Those object areas specifically include entities and variables of state and/or behavioral attributes, as well as characteristic temporal and/or spatial representation scales. In all, there were 21 Java source code (text file) classes within the Clans program. [Supplementary Online Material \(SOM\) Figure S1](#) illustrates a Unified Modeling Language (UML) structural diagram of Clans.

Additionally, the Java classes focused on three areas of the underlying system model, each with either a distinct or a supporting functionality within the overall simulation. The functional object areas were: (1) ecology—a multi-threaded, 2.5-D, raster-based, virtual environment simulating a pristine niche ecology; (2) social agents—an autonomous and self-reproducing population of explicit, primate-inspired social agents; and (3) bindings—a loosely coupled set of utility source codes that enabled the simulation of the situated social agents within the virtual environment. Each of the three object areas are discussed below. In each case, as the functional object areas are introduced, the Java classes associated with that entity are also listed.

**Entities** The first functional object area is Ecology. This area provided the hominin Social Agent population with an explicit, 2.5-D ecosystem: a virtual habitat. As an Entity, it was responsible for simulating a grid-based spatial terrain with forageable vegetation and prey, water resources, and an annually varying weather model simulated by localized ambient temperature change. The maximum limits of terrain water availability and forageables production were set by Constant parameter. During runtime, forageables (including water resources) were impacted by Social Agent foraging choices and they were regenerated by land-cover regrowth calculations that depended on the resource (food or water) and the season. Accessory methods were maintained within this object area to provide external callers with data on hominin social group temporal, spatial, and numeric information. These data included information about community dynamics, their assembly, disassembly, and movement about the terrain. This object featured load-time reconfiguration of environmental data and a parallelized, multithreaded approach to run-time ecosystem updating. The specifications of the start-time variables of state for this Entity are reported in [SOM Table S1](#), which is a class-by-class listing of constant parameters shared by each of the Entities in the entire Clans software. By name, the classes that are associated with this functional area are the following: Ecology, ModelConstraints, Flora, Fauna, Climate, Terrain, Groups, Cell, and LifeExperiences.

The second functional object area was Social Agent, which was responsible for providing and maintaining the biological and

behavioral activities of each individual agent instance. As an Entity, it was responsible for the emergent spatial assembly of groups of individuals and their collective behaviors that became the populations under study. In Clans, each individual agent instance was a spatially situated, mobile, adaptive, and independent virtual entity. At 'birth,' a hominin was tightly (exactly) coupled nutritionally and spatially to its 'mother.' However, after weaning, a hominin was free to move about within the habitat until it 'died,' interacting or not with any member of any cohort with whom it may choose to come in contact. A cohort was defined as any group of one or more hominins momentarily occupying one terrain grid-cell (a simulated  $10 \times 10$  m area). Each hominin object had its own small, needs-based drive reduction (Hull, 1943) software control engine. These engines were identical, each to the other, and contained a finite set of overt, behavioral schema responsive to the needs of the agent. They served as the entire animating source for the behavioral ethology of that agent and that agent alone. The Social Agent functional object was responsible for assisting in the 'birth' of hominins, as well as in generating and maintaining agent artificial genetics, aging and death, individual quantities/qualities for weight, hunger, satiety, age and sex, caloric and water requirements differentiation, pregnancy, weight loss or gain, disease, and providing abstract cognitive features (psychosocial and psychospatial) that steered the individuals toward their own, long-term, existential outcomes. Each hominin kept a simple 'daily interaction' memory of itself in relation to all others with whom it shared a cohort since birth. Special memory of the identity of self, the mother of self, the siblings of self, the children of self (if self was a female), and the birth order of those offspring, as well as their sex, was kept. As with *Pan*, a hominin agent had no agnatic memory, i.e., no unique recollection or memory of the 'father' of self or the self as 'father.' After program start, and at 'birth,' all offspring inherited their genetics from their parents through artificial crossover and a mutation. The rate of allele mutation per agent per generation per chromosome was 3 in  $1.0 \times 10^5$ . Consider by contrast that Nachman and Crowell (2000:297) stated the average rate in *Homo* was " $\sim 2.5 \times 10^{-8}$  mutations per nucleotide site or 175 mutations per diploid genome per generation." The specifications of the start-time variables of state for this Entity are reported in SOM Table S1. By name, the classes associated with Social Agents are ModelConstraints, ArtificialGenetics, Biology, Heuristic Algorithmic Learning (HAL), Hominid, HominidKit, SeedGroup, Socioecology, and LifeExperiences.

The third functional object area was Bindings. As an Entity, it was a broad-functioning set of Java assemblies concerned with bringing together the entire Clans program. The Classes in this object provided simulation support, visualizations, and user interface capability, report writing codes necessary to provide social agent birthing (new encapsulated agent object instantiation) and death (removal of expired encapsulated social agent objects from computer memory), and operating system entry and exit points into and onto the Clans program overall. The specifications of the start-time variables of state for this Entity are reported in SOM Table S1. By name, the Classes associated with this area are: Clans, ModelConstraints, Graphical User Interface (GUI), Red-Green-Blue (RGB), TrueRNG, ModelReports, and LifeExperiences. State variables Per the ODD protocol, "a state variable or attribute is a variable that distinguishes an entity from other entities of the same type or category" (Grimm et al., 2010:2763). Beginning with SOM Table S1, the Constant parameters (as variables of state and used to initialize and constrain Clans during runtime) were listed. That list was divided into sections (broken out by Java source code Class text file name), by Constant parameter variable name, by assigned value, and by a short (abbreviated) definition. Lastly, the count of parameters in each Class is shown as a running total. SOM Table S2 presents an alphabetized list of the empirical

authorities used to derive the Constant parameters used in the program, whereas SOM Table S3 lists definitions used to construct the genes associated with each chromosome. In turn, SOM Figure S2 provides and illustrates the hominin agent chromosome.

Scales The temporal (scale) increment used in the Clans simulation was the day. The spatial (scale) unit was a fixed  $10 \times 10$  m cell within a large, torus grid. Those system features relying on these scales are explained in greater detail below.

#### 2.4. Process overview and scheduling

Time was processed by the simulated day. The 'day' was the 'epoch.' This is the defined least interval of one complete cycle over all simulated components. Thus, one calculated days accumulating into weeks (of seven days), months (28-day lunar intervals), and years (13 lunar months or 364 days). The least unit of spatial measurement was a squared  $10 \times 10$  m area. These unit areas were called grid cells, or terrain cells, within the experiment. There were two simulated habitats used in the work. These were constructed as equilateral (square), toroidal terrain grids. One terrain grid simulated  $64 \text{ km}^2$  and the other  $16 \text{ km}^2$ . In both cases, each grid cell corresponded to a pixel on a graphical output display. Any number of hominins could occupy a grid cell and any aggregated social group located on a  $10 \times 10$  m area was referred to as a cohort regardless of its momentary or long-term social interaction. The distance a hominin could move during a day was constrained by Constant parameter, as was the distance the agent could 'sense' within the habitat environment. All distances were built in increments of the spatial unit. Agent sensing and spatial movements were further defined as 'Steps' within extended Moore neighborhoods, i.e., spatial areas surrounding each agent, respectively. For example, if the GroupStep parameter was 30 units, that meant the agent could move anywhere within a contiguous set of cells (the extended Moore neighborhood) whose left or right movement was less than or equal to 30 cells or into any adjacent cell encompassed by that 30-unit limit (see ModelConstraints in SOM Table S1).

Process overview The Clans simulation was a computational process that emulated a natural-life, cybernetic system. Moreover, it was only 'potentially' self-sustaining. The agents, mechanisms, and rules in Clans were advanced temporally but not controlled by any centralized, exogenous process. Process features like instantaneous population membership and momentary land-cover carrying capacities were dynamic. It was possible for any simulated population to 'self-collapse,' operate in a self-sustaining socioenvironmentally steady-state mode, to 'explode' computationally, or to operate anywhere in between. Every experimental outcome was the sole product of endogenous interaction between the components, mechanisms, and rules of the emulated system.

Operationally, a 'self-collapse' was defined as a condition wherein the initial seed-population of hominins (those put into the simulation at start) would die out and the habitat would become vacant of artificial hominin life. The meaning of 'computationally explode' was derived from a similar but opposite computational outcome. If a simulated population became so productive and numerous that the computational machinery simulating the habitat slowed to some arbitrarily slow speed so that its progress could no longer be tolerated by the operator, then the simulation would be declared 'computationally exploded' and stopped. These extreme outcomes did happen during the early course of the experiment as initialization variables were being selected, but neither condition was considered successful.

Scheduling An important part of the experimental method was a demand for each simulation to run for an extended interval of

thousands of simulated years. The phrase ‘enduring time’ was adopted as part of the experimental method to describe this demand.

Yearly the large bodies of water were refilled. In contrast, small bodies of water (known as water basins) were refilled daily. All forageables were regrown daily and all prey resource opportunities (monkey, fish, termites, etc.) were recomputed daily based on Constant parameter limits and all accumulating hominin foraging effects. Forageable resources (figs, roots, leaves, etc.) regrew seasonally based on a periodic sinusoidal cycle. Local temperatures, a surrogate for climate, were reassessed and changed annually. These seasonal environmental and ecological factors were constrained by Constant parameters. Environmental functionalities were multithreaded for computational speed.

All hominin behaviors were incremented by the day but they were not multithreaded. SOM Figure S3 illustrates the behavioral process schedule associated with a day in the life of a hominin agent. These represent the entirety of all possible hominin behavioral trajectories. Two general classes of hominin behavior may be understood. The first type involved direct social interaction. These included behaviors like innate drives toward social assembly, individual alliance motivated by self-perceived stimulus reinforcement, innate mating drives, and of course ‘gifting’ (the non-*quid pro quo* transfer of costly self-gathered forage from self to other at cost to self) can be associated with this type. This latter behavior is innate and prosocial. The second class of hominin behaviors involved subjective, non-social forms of overt motor activities like finding forage and/or water, giving birth, dying, etc.

All the foregoing were incremented by the day and were prioritized according to their placement within an adapted version of the Maslow (1943) hierarchy. Although this daily routine was the same for each agent, no agents shared their daily routines as a part of any centralized plan. The behavioral trajectory of each agent was independent and subject to disruption based on opportunity. The schedule shown in Figure 3 satisfies baby (age 0 to weaning), juvenile (weaned to prepubescent), and adult (sexually mature) members of the hominin population. Males could become sexually mature at 13 years of age and females at 15. In summary, during a day, each individual hominin was responsible for autonomously computing-then-scheduling its own behavioral trajectory because of innate drives, drive-reduction schema, simplified cognitive considerations, autonomous decision making, and socioenvironmental interactions.

## 2.5. Design concepts

The design concept implemented in Clans was our interpretation of the sociotemporal conjecture described in each of several works from Chapais (2008, 2010, 2011, 2013, 2014). His idea of a ‘deep social structure’ in *Homo* was adopted. Its implementation in Clans assumed that the beginnings of human deep social changes could have been among any of the early hominins, such as *Ardipithecus* (Lovejoy, 2009; Lovejoy et al., 2009), *Australopithecus* (Asfaw et al., 1999), or *Homo* (Chapais, 2014). It is because of this interpretation that the Clans temporal conjecture, the research question, and the hypotheses were implemented as they were; and, because of the implementation, the Hamiltonian theory was identified.

**Basic principles** The first principle in Clans was a temporal conjecture. The second was a requirement that any ‘species’ simulated in Clans would need to be validated against the temporally nearer end of *Homo sapiens* phylogeny, while still emulating all empirically knowable aspects of extinct early hominins. (To simplify this, we know about the physical and social character of modern humans, but similar knowledge of the earliest hominins becomes increasingly unknowable the further we go back in time. Thus, the final experimental validity of the model had to remain

consistent with the knowable past [and its absent parameters] and still remain faithful to the entirely knowable present.) The third design principle aligned itself with the two framing hypotheses described earlier.

**Emergence** The simulation produced many emergent socio-behavioral and artificial genetic results. The Results section contains the quantitative emergent results. Qualitative results also emerged. In compliance with ODD (Grimm et al., 2010), they will be quickly summarized here. There was evidence of matrilineal culture transmission, self-organized foraging migrations, incest avoidance based on long-term individual recognition of, and familiarity with, spatially collocated conspecifics, primate-like community fission and fusion (Lehmann and Boesch, 2004), and long-term community-size self-regulation. See Rouly (2015b) and ‘Collectives’ below for a respective accounting of these foregoing.

**Adaptation** According to Grimm et al. (2010:2764), adaption refers to agent “decisions or change behavior in response to changes in themselves or their environment.” In Clans, both the control and the experimental populations had identical environmental opportunities to succeed. Both populations had identical opportunities to acquire cognitive imprinting during development, inherit genetic traits from parent to offspring during simulated ‘births,’ and to express innate social drives common to all members of the species. In the first case (the control), reference populations were genetically incapable of ‘gifting’ excess forage to a conspecific. In the second case (the experimental), some population members were genetically capable of the non-*quid pro quo* ‘gifting’ of excess forage under certain conditions. With only that single genetic exception, the two groups were identical: having equal opportunity for adaptation and adaptive success.

In the experimental populations (those having the genetic capacity for ‘gifting’), their primary adaptive trait was the tendency of the bearer of the ‘social altruism gene’ to ‘gift’ excess food resources. The gene expressed differentially in males and females. In males, ‘gifting’ could occur when the benefactor was a sexually mature adult and the beneficiary an adult female. In females, ‘gifting’ could occur when the benefactor was a sexually mature adult and the beneficiary was the youngest, weaned offspring of the benefactor. In the control, reference populations ‘gifting’ was not possible by Constant parameter genetic exclusion.

One final important note is that all members of both populations (control reference and experimental) had a gene-based trait for alliance. Alliance was defined as the tendency of an individual who had received a beneficiary ‘gift’ to preferentially seek the company of its ‘gifting’ benefactor. The hominin decision to relocate was emulated as a reactive cognitive schema. However, in the control-reference populations, no ‘gifting’ was possible by explicit genetic exclusion. Thus, ‘gifting’ was only possible in the experimental settings and then only per a Gaussian random distribution of the ‘gifting’ gene over the initial starting population in the simulation. The bearer of the ‘gifting’ gene—if it was expressed in the individual and if they received a ‘gift’—would engage in attempts at sociopreferential movement to the location of their most recent benefactor. If the benefactor moved away, then the effort toward alliance would become frustrated. The gene expressed similarly in males and females and it was only the age and sex of the bearer that led to differentiated behavior. In the case of females, during the year she would become sexually mature that female would selectively choose random spatial dispersal over preferential relocation. Then, for the remainder of her ‘life,’ that female would engage in preferential relocation. Males were philopatric; that is, they did not relocate when they became sexually mature. Additionally, if they had the ‘gifting’ gene, they would always give.

**Objectives** There was no objective value in a hominin having or not having the genetic capacity to ‘gift.’ ‘Gifting’ was the independent

variable. Clearly, having the genetic capacity to ‘gift’ precipitated quantifiable changes in the dependent variables of the populations of Clans. However, having the capacity to ‘gift’ (or not having it) was not an objective or goal defined by any measure within the software design.

**Learning** Every hominin was given a set of overt, behavioral schema responsive to the needs-based drive reduction engine that was the animating source of hominin ethology. We have already seen one: the reactive schema for alliance relocation. It would not be accurate to describe these mechanisms as ‘learning’ generally. Rather, the ethology employed was more like the behavioral schema proposed by Tinbergen (1951). In this case, when a hominin encountered a stimulus trigger, a corresponding individual response or fixed action pattern of responses would fire. Configured in this way, hominin agent behavior was heuristics-based, primarily reactive, and was easily fit into a simple, Maslow-inspired (Maslow, 1943) prioritization scheme. Hominin ethology was a light-weight computational product with a minimal cognitive architecture. Hominins had rules and schema for navigating to and approaching upon bodies of water, an ability to reckon over the numeric size of distal cohorts, to seek group affiliations of a preferred size (Boesch, 1991), a preferential relocation and alliance schema to bring self to the location of a benefiting other, a drive to disperse or relocate spatially in the year self became sexually mature (if female), to ‘gift’ if the opportunity (and genetics) presented themselves simultaneously, to relocate self away from a fear-producing stimuli (like the fear of drowning), a raw need-based drive to reduce hunger and one to reduce thirst, and finally a drive-reducing mechanism to move self away from an uncomfortable environment (simulated by elevated or reduced ambient temperature). None of these were learned.

There was, however, one instance of true learning among the hominins. This came about during the resolution of cognitive dissonance and in the context of foraging. Psychologists define cognitive dissonance (Festinger, 1962) to be that discordant mental perception caused when the apprehension of some stimulus one versus some attitudinally counter-biased stimulus two presents an uncomfortable ‘cognitive’ realization to the self that stimulus one is equally capable of reducing stimulus two, but was hitherto unrecognized or unaccepted as being possible. In the case of the simulated hominins, cognitive dissonance and its drive-reducing mechanisms involved a latent circumstance that could potentially occur after a ‘mother’ hominin transferred to her offspring, at weaning (Thompson, 2013), her individual foraging preference. For example, the notion that figs were preferable to leaves, roots, red colobus monkeys, or fish might be conveyed. If that offspring later, as a juvenile or as an adult, was unable to obtain the preferred food to which it had become accustomed, but found itself nonetheless able to reduce its basal drive for sustenance over some period using some other food or prey species, then a condition of cognitive dissonance would develop. In this way, the hominins in Clans were capable of learning and would change their forage preferences over time. Moreover, because of this cognitive feature in the model, quantitative evidence of Baldwinian evolution (Baldwin, 1896) emerged over the long-term genetic record of each simulated population. Similar results to these were reported by Rouly and Kennedy (2011) and will not be repeated here.

**Prediction** Semantically, prediction can be both a result and a process. As discussed in the previous section, the hominin agents in Clans exercised individual control over a potent, reactive ethology. However, they were not predictive. Simply put, prediction as an emulation of “estimating future consequences of decisions” (Grimm et al., 2010:2765) was not part of the Clans system model.

**Sensing** The agents in Clans had six simulated senses and one simple affect. Among the special senses, they had vision, gustation,

olfaction, and a haptic exteroceptive sense of temperature sensitivity. They also had a pair of non-differentiated proprioceptive ‘internal’ senses: hunger and thirst. They could ‘see’ forageable food at a distance and distinguish if that food was of a preferential type. However, they could not tell if the distant location contained more food than their current location. They could ‘see’ their conspecifics at a distance but they could not tell if a distant individual (or individuals) were male or female, nor could they specifically recognize the number of individuals in the distal location. However, they could determine if there were more or fewer individuals in that distal location than within the cohort they currently occupied.

Implicitly, female presentation was occulted in a manner more akin to *Homo* than to *Pan*. In Clans, the reproductive process was simulated by a mechanism that relied on the simulation of female receptivity and gene-based tendency for greater or lesser pheromone production associated with likelihood of presentation (Thornhill et al., 2003). Only when a female was in estrus and ready for mating could the latter (with a possibility of conception) occur. Males did not possess an exteroceptive (visual or olfactory) sense that would inform them if a female was ready to mate. This made ovulation effectively occulted in females. The female was responsible for deciding to mate and with whom. Thus, females had an implied sense of artificial vision sufficient to allow them to recognize the presence of a male conspecific in their cohort and to decide over any suitable mating opportunity. The likelihood of conception was probabilistically computed.

The hominins could sense water at a distance; whether that was by scent or vision is not defined. Moreover, the agents knew if they were sated, hungry, thirsty, or quenched. As stated earlier, the agents had a haptic sense of temperature sensitivity. This sense allowed them to decide if the temperature within the current cohort was to their liking or if they should relocate assuming all other basal drives had been reduced. Because every agent had a cognitive mechanism for remembering its uterine kin, children could recognize their mothers and mothers could recognize not only their offspring, but the birth order of their offspring. In this context, it can be assumed that all agents had some sense of vision and/or olfaction in order to recognize others. Since agents of either sex could identify their most recent ‘gifting’ benefactor at a distance and choose to preferentially relocate to be with that benefactor, it is also implicit that the agents had a sense of vision or possibly olfaction that supported this behavior. Finally, if an agent was in a body of water for more than a day, it would experience the affect ‘fear’ and it would attempt to move to dry land. If the agent could not relocate successfully, then it would die the next day. Although death by predation was simulated, it was not accompanied by any associable ‘fear.’ Death by predation and disease was simulated probabilistically based on empirical evidence (Sterck et al., 1997; Williams et al., 2008) with no associable cognitive or affective component. The hominin agents of Clans ‘lived’ close-to-empirically valid lifespans (35–45 years) that were constrained only by the effects of local events and/or old age.

**Interaction** Hard-coded social interactions were few in Clans. However, some did exist. For example, mothers passed to their offspring a preferred food choice during weaning. This behavior set in play the opportunity for emergent social results that resembled culture-driven migration as genetically related troops overgrazed their habitat over time (Rouly, 2015b). Remember too that ‘gifting’ was a behavior in which adult males and females engaged when they had excess food. Reciprocally, all members of both populations (control, reference and experimental) had a gene-based trait for alliance. Alliance was defined as the tendency of an individual who had received a beneficiary ‘gift’ to preferentially seek the company of its ‘gifting’ benefactor. The hominin decision to relocate was

emulated as a reactive cognitive schema. Additionally, Clans contained a Westermarck function, which is a hypothetical social effect named after its originator, Edvard Westermarck, where recognition-memory of 'others' gained during early life tends to discourage incest (Westermarck, 1921). Interestingly, this function was an antagonist to the formation of semipermanent breeding relationships, since the more often breeding partners occupied the same cohort, the more intense would become their desire to observe Westermarck-like reproductive avoidance. Westermarck (1921) hypothesized that 'familiarity' implicitly contributes to incest avoidance. In Clans, this heuristic operated by the 'self' remembering all 'others' over the course of a lifetime. Beyond these four hard-coded social interactions, agent behaviors were the emergent result of stochastic social opportunity and individual agent decision. It can be restated that, in every experiment, all agent simulated life-events ('births,' 'deaths,' 'mating,' movement, forageables choices, lifespans, etc.) and all sociospatial community outcomes were the emergent results of the interplay between the agent objects, their heuristic rules of behavior, and their environments.

**Stochasticity** Upon the annual increment of their 'birthday,' each hominin agent received a new, noise-generated random number seed (created by the TrueRNG2<sup>®</sup> device) for use in the agents own individual Java factory random number generator (RNG) processes. While the number of such Java factory individual RNG process events was in the thousands per agent taken per year, the levels of entropy produced by reseeding agent's RNG with a noise-generated device value efficiently guaranteed that agent-on-agent and agent-in-environment behaviors were mathematically uncorrelated and stochastic across each simulation run. On the contrary, every simulated day, the environment and its associated subcomponents (e.g., forageables regrowth and prey species availability) were also refreshed by random number sequence regeneration processes. Since it was believed that ecologically grounded systems tend to be somewhat more stable over time, and since the ecology was not the prime focus of the simulation work, it was decided the environment and its subcomponent systems could be efficiently driven by a single-seeded Java factory RNG. This decision improved process latency associated with TrueRNG2<sup>®</sup> random number production.

**Collectives** It has been assumed that those (extinct) primates of interest for this paper existed in long-lived, patrilocal, hierarchical, and collective assemblies. In particular, the processes associated with collective formations of *Pan* involve a highly social and repetitive process of male philopatric (female dispersing) group formation, dissolution, and then reformation along community subgroup (and individual) lines within and between related communities. Moreover, it is possible that extinct early hominin species may have behaved in a similar way. Thus, in this context, 'Collectives' must be considered a complicated subcategory. It is simultaneously a result, an emergent property, and a design feature of the software. However, under no circumstances was the emergence of Collectives a 'hard-coded' result. The emergence of Collectives was a 'permissible' structure, but unforced within the design of the code. However, innate behavioral rules, like male philopatry and female dispersal (both common to the genus *Pan*), were expressed as hard-coded phenotypes. Violent conflict was not simulated. Thus, the tendency for patrilocal sociality was the norm among the mixed sex cohorts. Individuals could freely migrate, forage, breed, and die anywhere within the habitat. The infants in Clans enjoyed mother-offspring behavioral modeling culminating in a transfer of preferred food type at weaning. When an agent became an adolescent (defined as the age after weaning [4–6 years old] and before sexual maturity), they began a life-long practice of herbivorous habituation offset by the potential for carnivory and

punctuated by the dynamic and life-long process of relearning individual food preferences. Later, as the hominin agents exited adolescence and became reproductively viable adults, they continued their demonstration of male-female sexual dimorphism in size, weight, and overt behaviors.

**Observation** Every epoch (day) deceased members of the population were removed from the simulation. When an agent was removed, a complete 'death certificate' was made for that individual. The 'death certificate' contained running data like agent ID, date and location of simulated birth, death, age at weaning, biological mother and father IDs, agent actual weight, caloric and water requirements, preferred prey, cause of death, and several more data points including a complete sample of the genetic material of the agent. Although only used for diagnostic testing and software development verification, a complete listing of each of the siblings belonging to the agent and the birth order of those siblings, assuming there were any, was available. Along with this/these, a listing of all cohort acquaintances and their respective daily interaction accounts were produced (Rouly, 2015b:96). In addition to these recorded data, several running totals were presented at the operator console. Those included the current year, the day in the year, the relative productivity of all currently occupied terrain cells, the number of hominins still alive, the average terrain cell occupancy rate, the totals of births and deaths recorded to date, the average birth rate taken yearly, the running percent total of infant mortality (including probabilistic generated infanticide), recorded incest counts (copied to the operator console in later versions of the code), and the total head count of all agents simulated since program start.

## 2.6. Initialization

The initialization of the Clans experiment required the coordination of spatial layout, start-up populations, agent genetics, and habitat environments to achieve a balance between computational efficiency and results reliability. The process of simulation initialization is now described. SOM Table S4 shows the experimental schedule.

**Start-up populations** There was a start-up population (called a seed group) created new for each simulation experiment. The age, sex, and genetic properties of each seed group member varied probabilistically. However, the exact number of members in the seed group was explicitly defined in the starting configuration of each simulation. Those numbers were either 1000 or 200, depending on the spatial configuration employed. The breakdown of the seed group populations by sex and age was determined using a uniform random distribution. The value of the genes in the chromosome held by each starting agent was determined by Gaussian distribution. Based on this, it is believed that the artificial populations under test were closely related, probabilistically, although they were not identical.

**Habitat carrying capacity** There were two spatial configurations used in the experiments. The first of these involved the uniform random spatial placement of 1000 singleton agents during three control reference and one experimental demonstrator run across 64 km<sup>2</sup> of simulated habitat. The second configuration involved the placement of two groups of 100 agents each at the same two locations over 14 experimental runs, but within a 16 km<sup>2</sup> simulated habitat. Since area differences between the two spatial configurations suggested a population density to habitat carrying capacity confound, a mitigation strategy was devised. The solution was to start proportionately fewer agents in the smaller experimental setting using a simple ratio. This change allowed not only for improved computational efficiency and provided comparable (or slightly improved) habitat carrying capacity, but also placed

additional social stress in the smaller test habitats due to fewer initial seed group test subjects.

### 2.7. Input data

“The model [did] not use input data to represent time-varying processes” (Grimm et al., 2010:2766). This does not mean that the system model did not rely on time-varying processes within its algorithms. It means only that there were no time-varying data series ‘ingested’ by the model at program start or at any other time during program execution.

### 2.8. Submodels

There are two primary submodels upon which the Clans top-level system model rests. These have already been described in the foregoing sections. However, in compliance with ODD (Grimm et al., 2010), they will be quickly summarized one last time.

**Environment** The system model required the instantiation of an ecological submodel devoid of cultural assumption and artifact. Additionally, the ecology had to be capable of plausibly supporting the emulation of artificial hominin life over lengthy periods of simulated time. Clans provided a simplified but detailed ecology that emulated fluctuations in forageable productivity resting on continuous seasonal change and differentiated by inhabitant self-directed foraging.

**Hominins** Artificial hominins were a class of software objects that could simulate self-directed foraging, artificial sexual reproduction, inheritable artificial genetics, and emergent complex social behaviors. A hominin agent possessed a simplified yet explicit set of overt schemas responsive to the needs-based drive reduction engine employed as the animating source of its ethnology.

## 3. Results

In this section, the experimental data derived from the Clans simulation are reported. These data were taken over hominin agents whose individual and group social behaviors, and mating behaviors, were autonomous and temporal-spatially constrained. Baseline social organization among the mixed sex cohorts resembled *Pan*-like promiscuity, male philopatry, and patrilocal sociality. The challenge was to detect, via proxy evidence, indications of increasing social organization through the emergence of ‘family-like’ groupings technically referred to as semipermanent breeding bonds. Beyond individual differences like sex, age, body mass, food preference, etc., the only difference between any individual agent in any control or experimental population was if the agent had the state of its gene-based trait for altruistic ‘gifting’ either switched-on or switched-off. The control populations had no capacity for altruistic ‘gifting,’ because their gene had been switched-off. Agents in the experimental populations had a random chance that their individual genes would be switched-on, thus they might possess the ‘gifting’ trait. Every simulation was begun, given an arbitrary settling period, and then allowed an opportunity to demonstrate operations in enduring time. With a single exception, all simulations ended without operator interruption: the experimental demonstrator experiment (running over 10 kyr) was manually terminated.

### 3.1. Causes of death

Figure 1 illustrates emergent results: evidence of the cost of survival reflected through the causes of death of a population. Figure 1A describes results from a control (reference) population type that ended at 8863 years of days, whereas Figure 1B describes an experimental (altruist) population type ending at 4683 years of

days. Death by starvation and death from thirst changed from a 2:1 ratio (in the reference, control group) to more than 6:1 (in this typical experimental group). Clearly, the effect of ‘gifting’ excess forage, as was the case in the experimental group, had a very real survival cost. While these two histograms do not describe the entire set of Clans populations, they are typical. These histograms should not be interpreted as cumulative over the entire sequence of experiments or average over their respective types, control or experimental.

### 3.2. Large populations

Figure 2 illustrates emergent results: evidence of the steady-state size of the two largest and longest running control (reference) and experimental (demonstrator) simulations. These populations were each started with 1000 randomly placed agents in a 64 km<sup>2</sup> habitat. In these graphs, we can see the final, long-lived, steady-state population numbers, and the concept of ‘settling time’ noise in the initial years of the simulation. The term of art ‘settling time’ is that period where initial start-up parameters in the simulation tend to produce ‘noisy,’ uncorrelated output. It occurs as an agent population becomes adapted to its environment and assumes its own run-time properties. Figure 2A shows the reference-control population without the gene for ‘gifting.’ Figure 2B is an experimental demonstrator population composed of individuals having the gene for ‘gifting.’ Once the two simulations entered into enduring time, population numbers for the Reference-Control population became roughly twice as many as those in the Experimental-Demonstrator, even though the initial startup condition for each simulation was identical. The ‘gifting’ population was able to exist with far fewer members, e.g., on the order of  $\geq 100$  individuals (compare with *Homo ergaster* as suggested in Willems and van Schaik, 2017).

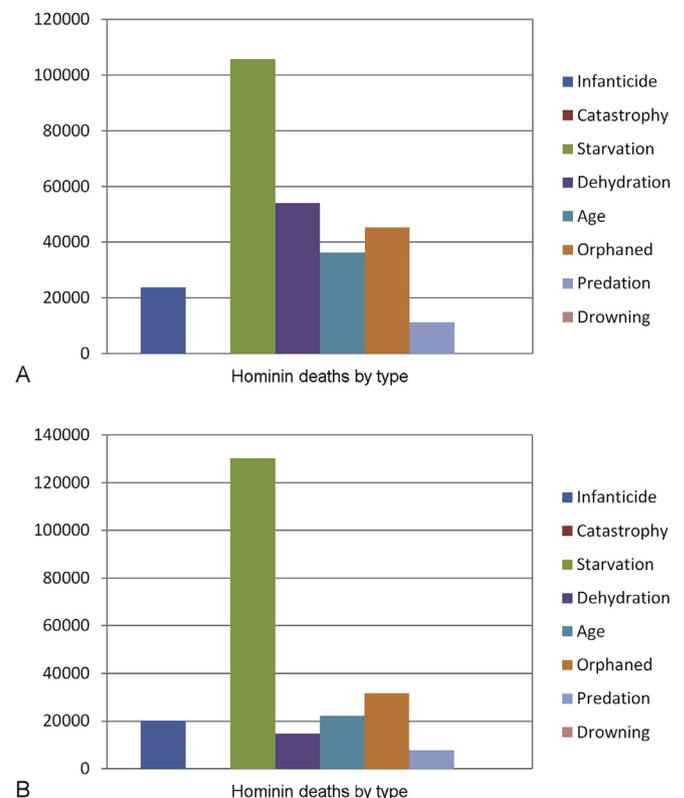
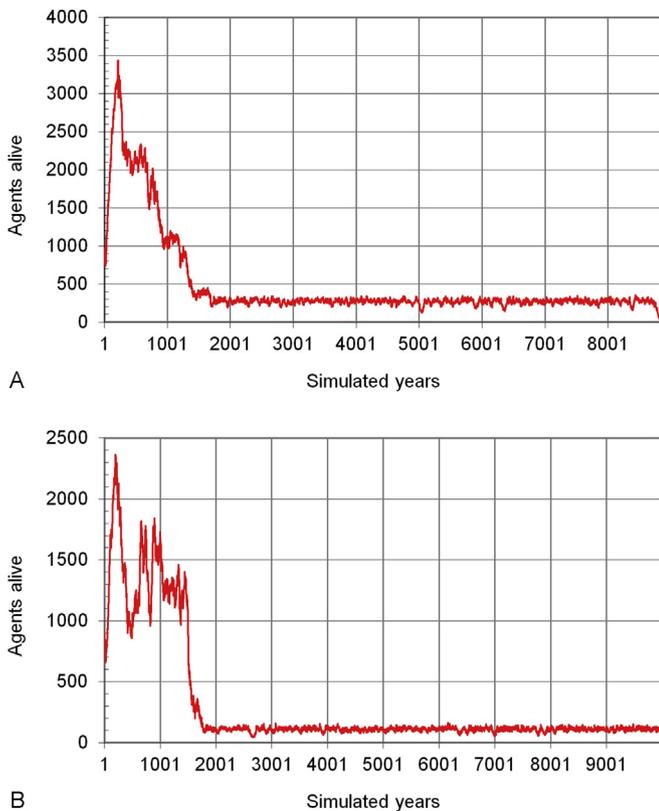


Figure 1. Two examples (A and B) of the cost of survival reflected through the causes of death.



**Figure 2.** Two large populations (A and B) endured with no discernible loss.

### 3.3. Small populations

Figure 3 illustrates emergent results: evidence there was an aggregate phylogenetic consequence for members of a population having a genetic bias ('pro' or 'con') regarding prosocial 'gifting,' or altruism. Effectively, a color-coded line simply indicates that some numbers of couples were alive and repeat mating in the simulation as indicated. The population numbers in these small population groups were size-constrained in comparison to the large population tests above. Here, each test was started as two groups of 100 agents, and not 1000 randomly placed agents. Extreme extinction level consequences were shown to be not only possible, but typical, when operating under population size constraints. Large control populations, on the other hand, had no discernible loss (compare with Fig. 2A). It was experimentally defined that a breeding couple would be called 'permanent' if the couple coproduced four or more ( $n \geq 4$ ) offspring during the lifetime of the female partner. The reasoning came from an interpretation of Tutin (1979:31): female (*Pan*) lifetime offspring production was six or less, with a "maximum of five or six offspring who survive to weaning."

In Figure 3, we see aggregated data for 14 small population experiments. These were the experimental setting results. In the experimental setting simulations, each agent in the initial starting population had a random chance that their individual gene for 'gifting' would be switched-on, i.e., have the Hamiltonian mutation. From then on, the gene was inheritable and subject to mutation. In each simulation, the entire group of agents was allowed to interact undisturbed until every agent died and the simulation ended. Same couple repeat mating was the proxy for the dependent variable.

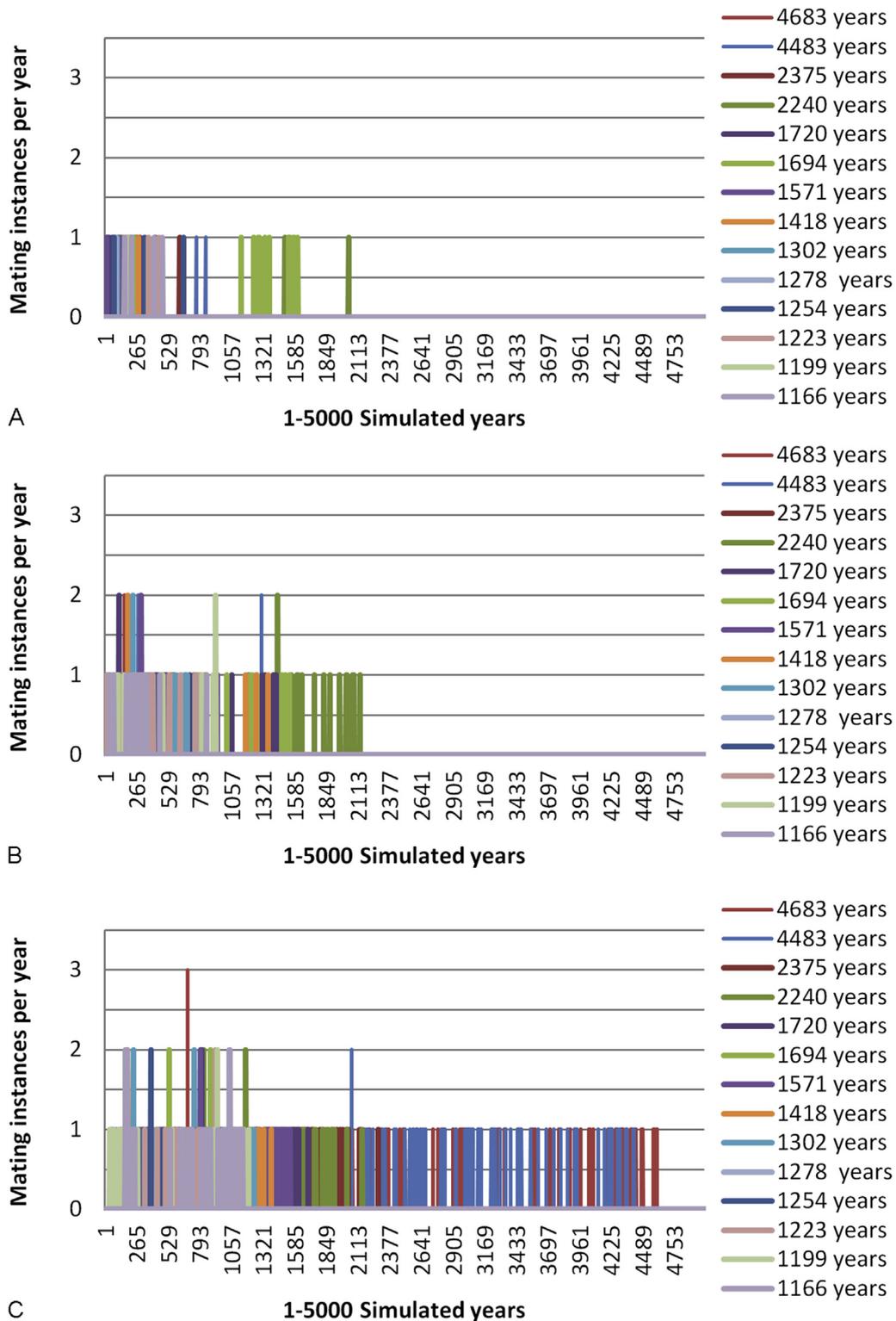
There were three possible genetic endowment configurations in the experimental setting: neither, either, or both mating partners

had an active gene for 'gifting,' each respectively. On the Y-axis in each graph, we see the number of instances that one or more couples accumulated a lifetime total of repeat matings equivalent to four or more. The instance and the count of that repeat mating event is shown by a vertical color-coded line in association with a simulated year (on the X-axis) and in association with the color-coded simulation in which it occurred. Thus, if one couple mated for the fourth or more time, then that repeat mating event was counted and shown on Figure 3 as a level 1 in the simulated year in which it occurred. If two couples repeatedly mated (four or more times), then those two instances would be recorded on the Y-axis as a level 2 in association with the year and the simulation in which they occurred. Similarly, if there were three couples that repeated mating (four or more times), then a 3 would be shown. As previously stated, effectively a color-coded line simply indicates that some numbers of couples were alive and repeated mating in the simulation as indicated. Since all simulations ran out to their natural ends, it can be concluded that in the longest running simulations, e.g., those over 4000 years, agents without an active gene did not survive, whereas those with an active gene did so, because the latter group (those with the gene) was still providing evidence of permanent breeding bonds in even the longest running of the experimental simulations. What the graphs are showing is that, across all experimental populations, the portion of each population having no prosocial trait would die out early, whereas the portion with the prosocial trait would tend to survive.

## 4. Discussion

ABM simulation technology is concerned with demonstrating emergent individual and/or group behavior between agent-actors over a topology of social, logical, spatial, or similar constraints after some interval of agent-agent and agent-environment interaction. As a subclass of ABM technology, a microsimulation is an arbitrary differentiation. A microsimulation is best characterized as an ABM with additional code to support more highly detailed agent activities and the post-processing analysis of the data generated by the more detailed agent interactions. A microsimulation is useful, as in the case of Clans, to examine detailed individual, within-and-between small-group, and/or agent-environment interaction behaviors. In general, an ABM is a powerful demonstrative and diagnostic tool capable of supporting the researcher in theory-building and the exploration of questions unreachable by almost any other means. It achieves this by requiring the designer (the coder) to construct reliable and expressive code that embodies small, falsifiable theories as microlevel rules and data structures. In its best form, a completed ABM will exemplify this phrase: microlevel rules producing macrolevel results. In Clans, a niche habitat theme was used to allow for tight experimental control of all microlevel rules and variables. Once the code was verified and validated, the work became capable of plausibly demonstrating its macrolevel results.

Ultimately, it was not only the Hamiltonian hypothesis that drove the success of the Clans ABM. Several biomechanical observations made by Lovejoy (2009) made a strong impact on the work, and a summarizing social theory developed by Chapais (2011) was also critical to formalizing the experiment and to answering the research question. Lovejoy and coauthors (Lovejoy, 2009; Lovejoy et al., 2009) identified anatomical changes in the fossil record based on *Ardipithecus ramidus*, one of the oldest early hominins. Lovejoy (2009) remarked the anatomical changes in the hands, wrists, feet, canine teeth, and several adaptations related to bipedalism, and speculated that these changes were critical components contributing to, or resulting from, our emerging sociality. Lovejoy (2009) suggested that *Ardipithecus* may have had an



**Figure 3.** The individual simulation experiments are shown by color-code and by the year-length of the simulation run-time. The color-coded years to the right are identical for each panel. A) Neither the male nor the female partner had an active gene for 'gifting.' B) Either the male or the female partner had an active gene for 'gifting.' C) Both male and female partners had an active gene for 'gifting.' The number of mating instances per year is shown on each respective panel's Y-axis. This Y-axis value indicates the number of same partner repetitive mating instances in a particular year for a particular color-coded simulation.

improved hand-carrying ability while erect, while [Chapais \(2011\)](#) similarly argued that the presence of such anatomical changes ('physiological enablers' according to him) might have been precursors to what he referred to as our emergent 'deep social

structure.' For Chapais and Lovejoy, upright walking, newly freed hands, and the reduction of canine size were symptomatic of what were believed to be telltale signs within an accumulating fossil record describing our evolving 'humanity.' These ideas led to

specific, coded structures in the Clans simulation. When the agents had their abilities to gather and carry forage translated into code, their abilities and capacities to acquire excess edible materials were differentiated by their sex. Moreover, when excess forage was given altruistically (in a non-*quid pro quo* fashion between agents, male to female and female to youngest weaned offspring), it was Hamilton's ideas that were being operationalized.

To be clear, Clans did not attempt to simulate a particular hominin species, nor is it a game-theoretic simulation or quantitative, mathematical model trying to determine some evolutionary statistical probability. Rather, Clans asked what few simple things might have caused one of the early members of the hominin tribe to evolve into a creature whose more evolutionarily recent descendants were well-placed to later display a human-like sociality and household forming behaviors. Clans built upon the Hamiltonian argument (Hamilton, 1963, 1964a, b), the hypotheses of Lovejoy (2009) and Chapais (2011), and extended the ABM technology of Epstein and Axtell (1996) to implement an experiment never before tried.

Each simulation had to demonstrate continuous operation over what was called enduring time. This requirement provided simulations lasting minimally hundreds, and preferably thousands, of years of days before results were gathered. There were three reasons for this demand. First, there was a desire to produce a long-term genetic record over all the agents in the simulated populations, in order to support observation of any apparent Sewell Wright effect (or genetic drift). Second, there was a desire to support simulation result validation based on comparisons with empirical evidence from the genus *Pan*. Third, there were issues of population reproductive dynamics with which to contend. For example, the mature female members of the population had 28-day reproductive cycles, during which only five days were given to estrus and reproductive presentation. Then, too, if an offspring was to be 'born,' it was imperative at least that one mature female be collocated with a male and mate; else, there would be no probability of conception. Moreover, if there was a conception, a 252-day gestation term was imposed, further negating the possibility of immediate positive population increase. Finally, during lactation female fertility and receptivity was halted. This further constrained positive population increase until simulated weaning. (infanticide was simulated probabilistically.) Thus, a demand for enduring time allowed individuals and groups enough time to survive as complex, emergent, ever-developing cohorts within their forageable and highly detailed habitat.

This work asked important and explicit questions. For example, what might have been the primary environmental, biological, and sociobehavioral cognitive antecedents present or necessary when the initial emergent foundations of human sociality arose? Fundamentally, Clans suggests that human-like sociality may have begun to arise as a consequence of initial biological (or genetic) components. It is unknown whether that process was invariant to environment or individual-level sociobehavioral cognition, because Clans did not explore those options. However, we know that the hominins of Clans were incapable of computing (cognitively 'deciding') any *quid pro quo* exchange. Thus, after a few males and females, each having a prosocial 'gifting' gene, reproduced, all future generations of similarly endowed hominins (in every experimental population) began to profit by means of what seems like inclusive fitness. Another question asked is: might early hominins have made these transitions during the emergent physiological development of creatures slightly preceding or merely contemporary with *Ardipithecus*, the later *Australopithecus*, or much later during the emergence of *Homo*? For this question, the answer seems far less

knowable. However, one might speculate that the overall process emerged coincident with obvious physiological changes.

This work also invoked deep questions about what role altruism may have played in the structuring of our evolutionary past. Informally, it can be stated that the simplest of the results validating the Clans experimental method was evidence of matrilineal culture transmission, self-organized foraging migrations, incest avoidance similar to the Westermarck effect, primate-like community fission and fusion, and long-term community-size self-regulation.

## 5. Summary and conclusions

Clans attempted to simulate a time in the past when human-like sociality may have begun to emerge during hominin evolution. The simulation instantiated autonomous, biologically grounded software agents situated within a detailed socioenvironment and ecology. The results it produced were inherently inductive, yet grounded in empirical evidence, and they were taken from species-specific physiological and/or psychological first principles. The independent variable was a gene-based trait for the unconscious 'gifting' of excess forage. Our proxy for emergent sociality was evidence that the dependent variable 'permanent breeding bonds' developed not only among the experimental populations, but that it ultimately became the predominant genotype. Initially, our hypothesis was that reciprocal exogamy began to take its first 'social steps' long ago as biology, genetics, reactive drives, and environment interacted to shape mating habits among early hominins. Operationally, the hypothesis took the form of an assumption that the earliest emergent semipermanent breeding bonds (perhaps little more than impromptu, but still affine relations) would emerge out of a *Pan*-like, promiscuous milieu based on no more than the addition of a single gene-based tendency for 'gifting' excess forage. The results revealed that the dependent variable (the social construct of semipermanent breeding bonds) would reliably emerge among the experimental populations, but not among the control groups. Moreover, it was found that, across all experimental settings having constrained population numbers, the portion of each population having no prosocial trait would die out early and the portion with the prosocial trait would survive.

Because of these results, it seems that gene-based 'gifting' behavior could have contributed to the onset of hominin morphological changes associated with the *Pan-Homo* split and/or contributed to the morphological significance of those changes over evolutionary time. This simulation experiment has permitted us to consider one possible explanation for what may have occurred during just a few critical millennia, perhaps 3–7 Ma, when the anatomical features and the newly emerging prosocial behaviors of early hominins were in dynamic reconstruction.

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## Supplementary Online Material

Supplementary online material related to this article can be found at <https://doi.org/10.1016/j.jhevol.2017.11.009>.

## References

- Asfaw, B., White, T.D., Lovejoy, O., Latimer, B., Simpson, S., Suwa, G., 1999. *Australopithecus garhi*: a new species of early hominid from Ethiopia. *Nature* 371, 306–312.
- Axelrod, R., 1986. An evolutionary approach to norms. *Am. Pol. Sci. Rev.* 80, 1095–1111.
- Axtell, R.L., Epstein, J.M., Dean, J.S., Gumerman, G.J., Swedlund, A.C., Harburger, J., Chakravarty, S., Hammond, R., Parker, J., Parker, M., 2002. Population growth and collapse in a multiagent model of the Kayenta Anasazi in Long House Valley. *Proc. Natl. Acad. Sci.* 99, 7275–7279.
- AZA TAG, 2010. Chimpanzee (*Pan troglodytes*) Care Manual. Association of Zoos and Aquariums, Silver Spring.
- Baldwin, J.M., 1896. A new factor in evolution. *Am. Nat.* 30, 441–451.
- Boesch, C., 1991. The effects of leopard predation on grouping patterns in forest chimpanzees. *Behaviour* 117, 220–241.
- Chapais, B., 2008. Primate Kinship. How Pair-Bonding Gave Birth to Human Society. Harvard University Press, Cambridge.
- Chapais, B., 2010. The deep structure of human society: primate origins and evolution. In: Kappeler, P.M., Silk, J. (Eds.), *Mind the Gap*. Springer, Berlin, pp. 19–51.
- Chapais, B., 2011. The deep social structure of humankind. *Science* 331, 1276–1277.
- Chapais, B., 2013. Monogamy, strongly bonded groups, and the evolution of human social structure. *Evol. Anthropol.* 22, 52–65.
- Chapais, B., 2014. Complex kinship patterns as evolutionary constructions, and the origins of sociocultural universals. *Curr. Anthropol.* 55, 751–783.
- Cioffi-Revilla, C., 2010. A methodology for complex social simulations. *J. Artif. Soc. Social Sim.* 13, 7.
- Cioffi-Revilla, C., 2016. Bigger Computational Social Science: Data, Theories, Models, and Simulations—Not Just Big Data. SSRN. <https://ssrn.com/abstract=2784278>.
- Conway, J., 1970. The game of life. *Sci. Am.* 223(4), 4.
- Darwin, C., 1859. On the Origin of Species by Means of Natural Selection, or the Preservation of Favoured Races in the Struggle for Life. John Murray, London.
- Epstein, J.M., Axtell, R., 1996. Growing Artificial Societies: Social Science from the Bottom Up. Brookings Institution Press, Washington, D.C.
- Festinger, L., 1962. A Theory of Cognitive Dissonance. Stanford University Press, Palo Alto.
- Gavrilets, S., 2012. Human origins and the transition from promiscuity to pair-bonding. *Proc. Natl. Acad. Sci.* 109, 9923–9928.
- Griffith, C.S., Long, B.L., Sept, J.M., 2010. Hominids: an agent-based spatial simulation model to evaluate behavioral patterns of early Pleistocene hominids. *Ecol. Model.* 221, 738–760.
- Grimm, V., Berger, U., DeAngelis, D.L., Polhill, J.G., Giske, J., Railsback, S.F., 2010. The ODD protocol: a review and first update. *Ecol. Model.* 221, 2760–2768.
- Grund, T., Waloszek, C., Helbing, D., 2013. How natural selection can create both self-and other-regarding preferences, and networked minds. *Sci. Rep.* 3, 1480.
- Hamilton, W.D., 1963. The evolution of altruistic behavior. *Am. Nat.* 97, 354–356.
- Hamilton, W.D., 1964a. The genetical evolution of social behaviour. I. *J. Theoret. Biol.* 7, 1–16.
- Hamilton, W.D., 1964b. The genetical evolution of social behaviour. II. *J. Theoret. Biol.* 7, 17–52.
- Hemelrijk, C.K., 1999. An individual-orientated model of the emergence of despotic and egalitarian societies. *Proc. Roy. Soc. B* 266, 361–369.
- Hemelrijk, C.K., 2002a. Despotic societies, sexual attraction and the emergence of male “tolerance”: an agent-based model. *Behaviour* 139, 729–747.
- Hemelrijk, C.K., 2002b. Self-organization and natural selection in the evolution of complex despotic societies. *Biol. Bull.* 202, 283–288.
- Hemelrijk, C.K., 2002c. Understanding social behaviour with the help of complexity science. *Ethology* 108, 655–671.
- Hemelrijk, C.K., Wantia, J., Gygas, L., 2005. The construction of dominance order: comparing performance of five methods using an individual-based model. *Behaviour* 142, 1037–1058.
- Hemelrijk, C.K., Puga-Gonzalez, I., Steinhauser, J., 2007. Cooperation, coalition, alliances. In: Henke, W., Tattersall, I. (Eds.), *Handbook of Paleoanthropology*. Springer, Berlin, pp. 1693–1720.
- Hemelrijk, C.K., Wantia, J., Isler, K., 2008. Female dominance over males in primates: self-organisation and sexual dimorphism. *PLoS One* 3, e2678.
- Hölzchen, E., Hertler, C., Timm, I., Lorig, F., 2016. Evaluation of out of Africa hypotheses by means of agent-based modeling. *Quatern. Intl.* 413, 78–90.
- Hull, C., 1943. Principles of Behavior. An Introduction to Behavior Theory. Appleton-Century, Oxford.
- Janssen, M.A., Sept, J.M., Griffith, C.S., 2005. Foraging of *Homo ergaster* and *Australopithecus boisei* in East African environments. In: Takahashi, S., Sallach, D., Rouchier, J. (Eds.), *Advancing Social Simulation: The First World Congress 2007*. Springer, Tokyo, pp. 1–6.
- Janssen, M.A., Sept, J.M., Griffith, C.S., 2007. Hominids foraging in a complex landscape: could *Homo ergaster* and *Australopithecus boisei* meet their calories requirements? In: Takahashi, S., Sallach, D., Rouchier, J. (Eds.), *Advancing Social Simulation: The First World Congress*. Springer, Tokyo, pp. 307–318.
- Kohler, T.A., Kresl, J., Van West, C., Carr, E., Wilshusen, R.H., 2000. Be there then: a modeling approach to settlement determinants and spatial efficiency among late ancestral Pueblo populations of the Mesa Verde region, US Southwest. In: Kohler, T.A., Gumerman, G.J. (Eds.), *Dynamics in Human and Primate Societies: Agent-Based Modeling of Social and Spatial Processes*. Oxford University Press, New York, pp. 145–178.
- Lancaster, J.B., 1986. Human adolescence and reproduction: an evolutionary perspective. In: Lancaster, J.B., Hamburg, B.A. (Eds.), *School-Age Pregnancy and Parenthood*. Biosocial Dimensions. Aldine de Gruyter, Hawthorne, pp. 17–39.
- Langton, C.G., 1989. Artificial life. In: *Proceedings of an Interdisciplinary Workshop on the Synthesis and Simulation of Living Systems (ALIFE 1987)*, Los Alamos. Addison-Wesley, Redwood City, pp. 1–48.
- Lehmann, J., Boesch, C., 2004. To fission or to fusion: effects of community size on wild chimpanzee (*Pan troglodytes verus*) social organisation. *Behav. Ecol. Sociobiol.* 56, 207–216.
- Lovejoy, C.O., 1981. The origin of man. *Science* 211, 341–350.
- Lovejoy, C.O., 2009. Reexamining human origins in light of *Ardipithecus ramidus*. *Science* 326, 74e1–74e8.
- Lovejoy, C.O., Suwa, G., Simpson, S.W., Matternes, J.H., White, T.D., 2009. The great divides: *Ardipithecus ramidus* reveals the postcrania of our last common ancestors with African apes. *Science* 326, 73–106.
- Martin, J., Odell, J., 1998. Object-Oriented Methods. Prentice Hall PTR, Upper Saddle River.
- Maslow, A.H., 1943. A theory of human motivation. *Psychol. Rev.* 50, 370–396.
- Milton, K., 1999. Nutritional characteristics of wild primate foods: do the diets of our closest living relative have a lesson for us? *Nutrition* 15, 488–498.
- Nachman, M.W., Crowell, S.L., 2000. Estimate of the mutation rate per nucleotide in humans. *Genetics* 156, 297–304.
- Parish, A.R., de Waal, F.B.M., 2000. The other “closest living relative”: how bonobos (*Pan paniscus*) challenge traditional assumptions about females, dominance, intra- and intersexual interactions, and hominid evolution. *Ann. N.Y. Acad. Sci.* 4, 97–113.
- Poethke, H.J., Pfenning, B., Hovestadt, T., 2007. The relative contribution of individual and kin selection to the evolution of density-dependent dispersal rates. *Evol. Ecol. Res.* 9, 41–50.
- Portman, O.W., 1970. Nutritional requirements (NRC) of nonhuman primates. In: Harris, R. (Ed.), *Feeding and Nutrition of Nonhuman Primates*. Academic Press, New York, pp. 87–115.
- Premo, L., 2006. Patchiness and prosociality: Modeling the evolution and archaeology of Plio-Pleistocene hominin food sharing. Ph.D. Dissertation, The University of Arizona.
- Premo, L., 2012. Local extinctions, connectedness, and cultural evolution in structured populations. *Adv. Complex Syst.* 15, 1150002.
- Premo, L., Kuhn, S., 2010. Modeling effects of local extinctions on culture change and diversity in the Paleolithic. *PLoS One* 5, e15582.
- Puga-Gonzalez, I., Hildenbrandt, H., Hemelrijk, C.K., 2009. Emergent patterns of social affiliation in primates, a model. *PLoS Comput. Biol.* 5, e1000630.
- Rouly, O.C., 2015a. At the root of sociality: working towards emergent, permanent, social affines. In: Andrews, P., Caves, L., Doursat, R., Hickinbotham, S., Polack, F., Stepney, S., Taylor, T., Timmis, J. (Eds.), *Proceedings of the European Conference on Artificial Life*. MIT Press, Cambridge, pp. 82–89.
- Rouly, O.C., 2015b. Towards Emergent Social Complexity. Ph.D. Dissertation, George Mason University.
- Rouly, O.C., Kennedy, W.G., 2011. Sexually differentiated philopatry and dispersal: a demonstration of the Baldwin effect and genetic drift. In: *Proceedings of the Computational Social Science Society of America*, Santa Fe (9–12 Oct. 2011), pp. 9–12.
- Shook, E., Wren, C., Marean, C., Potts, A., Franklin, J., Engelbrecht, F., O’Neal, D., Janssen, M., Fisher, E., Hill, K., Esler, K., Cowling, R., Scheiter, S., Moncrieff, G., 2015. Paleoscape model of coastal South Africa during modern human origins: progress in scaling and coupling climate, vegetation, and agent-based models on XSEDE. In: 4th Annual Conference on Extreme Science and Engineering Discovery Environment, XSEDE 2015 — St. Louis, United States. ACM International Conference Proceeding Series, 2015-July. Association for Computing Machinery, St. Louis, 8 pp.
- Simon, H.A., 1996. *The Sciences of the Artificial*. MIT Press, Cambridge.
- Sterck, E.H.M., Watts, D.P., van Schaik, C.P., 1997. The evolution of female social relationships in nonhuman primates. *Behav. Ecol. Sociobiol.* 41, 291–309.
- te Boekhorst, I.J.A., Hogeweg, P., 1994a. Effect of tree size on travel band formation in orangutans: data analysis suggested by a model study. In: Brooks, R., Maes, P. (Eds.), *Artificial Life IV*. MIT Press, Cambridge, pp. 115–134.
- te Boekhorst, I.J.A., Hogeweg, P., 1994b. Self-structuring in artificial “chimps” offers new hypotheses for male grouping in chimpanzees. *Behaviour* 130, 239–252.
- Thompson, M.E., 2013. Reproductive ecology of female chimpanzees. *Am. J. Primatol.* 75, 222–237.
- Thornhill, R., Gangestad, S.W., Miller, R., Scheyd, G., McCollough, J.K., Franklin, M., 2003. Major histocompatibility complex genes, symmetry, and body scent attractiveness in men and women. *Behav. Ecol.* 14, 668–678.
- Tinbergen, N., 1951. *The Study of Instinct*. Oxford University Press, New York.
- Tutin, C.E., 1979. Mating patterns and reproductive strategies in a community of wild chimpanzees (*Pan troglodytes schweinfurthii*). *Behav. Ecol. Sociobiol.* 6, 29–38.
- van der Post, D.J., Hogeweg, P., 2004. Learning what to eat: studying inter-relations between learning, grouping, and environmental conditions in an artificial world. In: Sloat, P.M.A., Chopard, B., Hoekstra, A.G. (Eds.), *Cellular Automata*. 6th International Conference on Cellular Automata for Research and Industry, ACR 2004, Amsterdam, The Netherlands, October 25–28, 2004. *Proceedings*. Springer-Verlag, Berlin, pp. 492–501.
- van der Post, D.J., Hogeweg, P., 2008. Diet traditions and cumulative cultural processes as side-effects of grouping. *Anim. Behav.* 75, 133–144.

- van der Post, D.J., Hogeweg, P., 2009. Cultural inheritance and diversification of diet in variable environments. *Anim. Behav.* 78, 155–166.
- van der Post, D.J., Ursem, B., Hogeweg, P., 2009. Resource distributions affect social learning on multiple timescales. *Behav. Ecol. Sociobiol.* 63, 1643–1658.
- van der Post, D.J., Verbrugge, R., Hemelrijk, C.K., 2015. The evolution of different forms of sociality: behavioral mechanisms and eco-evolutionary feedback. *PLoS One* 10, e0117027.
- Westermarck, E., 1921. *The History of Human Marriage*. Macmillan, New York.
- Willems, E.P., van Schaik, C.P., 2017. The social organization of *Homo ergaster*: inferences from anti-predator responses in extant primates. *J. Hum. Evol.* 109, 11–21.
- Williams, J.M., Lonsdorf, E.V., Wilson, M.L., Schumacher-Stankey, J., Goodall, J., Pusey, A.E., 2008. Causes of death in the Kasekela chimpanzees of Gombe National Park, Tanzania. *Am. J. Primatol.* 70, 766–777.
- Wren, C., Xue, J., Costopoulos, A., Burke, A., 2014. The role of spatial foresight in models of hominin dispersal. *J. Hum. Evol.* 69, 70–78.
- Wren, C.D., Costopoulos, A., 2015. Does environmental knowledge inhibit hominin dispersal? *Hum. Biol.* 87, 205–223.
- Wright, S., 1932. The roles of mutation, inbreeding, crossbreeding, and selection in evolution. In: *Proceedings of the Sixth International Congress of Genetics*. Ithaca, pp. 356–366.
- Yaeger, L., 1994. Computational genetics, physiology, metabolism, neural systems, learning, vision, and behavior or Poly World: life in a new context. In: Langton, C. (Ed.), *Santa Fe Institute Studies in the Sciences of Complexity Proceedings*, vol. 17. Addison-Wesley Publishing, Boston, p. 263.