# Sexually differentiated philopatry and dispersal:

# A demonstration of the Baldwin effect and genetic drift

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## Abstract

*This describes a computer simulation that demonstrated the Sewall Wright effect, or genetic drift, in artificial Hominids. It spanned the interdisciplinary intersection of ontogenetic evolution, sexually differentiated philopatry and dispersal, attitude bias, and cognitive dissonance. The simulation involved an individual-based model with biomimetic, Hominin-inspired agents possessing individual artificial chromosomes and occupying a foragable and seasonally modulated terrain. Driven by attitude biased foraging, behavioral phenocopy, and individual cognitive and physiological mechanisms the agents demonstrated socio-spatial fission and fusion, and sexually differentiated philopatric dispersal. Post-experiment results showed that if sexually differentiated philopatry and dispersal were conjoined with attitude biased foraging; the distribution of genetic values within an aggregate and affected population would change.*

## Introduction

An individual-based model was created to explore the question of what happens over long periods of simulated time when situated, biomimetic, Hominin-inspired agents disperse across foragable and seasonally modulated terrain due to sexually differentiated philopatry (Poethke, 2007; Parish, 2006; Praschnik-Buchman, 2006; Sterck, 1997, Wrangham, 1980). Consistent with expectation, under such conditions evidence of the Sewall Wright effect (Wright, 1932), a process also known as genetic drift, emerged over the population of agents each of whom had a single, multi-gene chromosome. However, while the appearance of genetic drift was expected, unexpected evidence of ontogenetic evolution (Baldwin, 1896) in the experimental results have made this is the focus of the current report.

The agents in the model were highly detailed metabolic and reproductively active, Hominin-inspired surrogates. Each agent had its own artificial chromosome containing eleven genes (8-bits per gene) ten of which were independently inheritable, graded, and expressible traits like draught tolerance, temperature sensitivity, robust metabolism, improved fecundity in small-group settings, and a greater or lesser tendency for sexually differentiated philopatric dispersal during the year sexual maturity in the individual was achieved. The agents also carried additional artificial genetic material with them that was not expressed in the population.

**Methods**

The code was based primarily on Darwinian Evolutionary Theory (Darwin, 1859) and Hullian Drive Reduction Theory (Hull, 1943). From Darwin, the principles of genetic inheritance and natural selection were enlisted to provide a plausible basis for the use of the computational techniques of simple genetic algorithms (Goldberg, 1989). From Hull, the paradigm of drive reduction was employed to provide a basis for the formulation of agent behavioral responses in non-cognitive social and all non-social contexts. Agents enjoyed a Moore visibility and movement neighborhood of one. The terrain grid was toroidal.

**Time Base**. The simulation epoch was the day. The model used a lunar month of 28 days and accumulated months at the rate of 13 per 364-day year.

**Terrain Grid**. The water sources on the terrain were probabilistically established at startup time but were runtime-constant. Also at program start, each cell on the grid was assigned one of five types of foragable resource. These foragable resources were updated daily based on an annually modulated, repeating, 364-day long sinusoid that emulated seasonality. The foragable resources supported the caloric needs of each individual agent in the simulation and were symbolically named figs, leaves, monkey (Red Colobus), termites (Lonsdorf, 2005; Backwell, 2001), and tubers. Inspired by Boesch (1991) a probabilistically valued predation term ranging between 0.5-1.5% per year per agent provided an attenuation (or culling) effect on the population.

**Foragable Nutrient Resources.** The caloric values of each of the foregoing foragables were unique, i.e., no two foragables had the same caloric base value. The caloric amounts were defined such that they ranged between a high-end, fully sufficient value capable of supporting the daily caloric needs of an active, mature (older) male Hominin down to a low-end value that would ordinarily be insufficient (Prentice, 2005) to support a medium-aged (non-gestating and non-nursing) female. Thus, the quantity of nutrient bearing foragable available to each agent in the simulation became an independent variable. At the extremes there were two experimental settings: fully sufficient or insufficient, as just defined. Daily, the caloric resource in any particular grid cell was updated (driven) by sinusoid in cyclic fashion from a compile time established (arbitrary) low value to the maximum high-end value defined above. This mechanism put the agents under cyclic environmental circumscription (Carniero, 1970) by simulating a foragable but seasonally modulated terrain within which they could breed at will, forage, migrate, and create/dissolve interacting social assemblies. Moreover, the symbolic names (fig, termite, tuber, etc.) provided a basis for the Baldwinian (ontogenetic evolution) portion of the experiment. Agents were allowed to associate themselves, via symbol, with a preferred food and to develop a related attitude towards that food.

**Agents.** This work used an abstract model of metabolic and bio-reproductive behaviors inspired by empirical values taken from extant, higher-order Hominid prototypes, e.g., Pan and Homo. All experimental data emerged from the emulation of agent overt and covert behaviors. Species within the Hominid prototype are known to demonstrate both types of behavior. Species within the family also have ethologies containing fixed action patterns. Since the proximal teleology of a fixed action pattern may be obscured by its ultimate (evolutionary) origins, the agents had simple but highly detailed behavioral ontologies.

**Simulation start.** For the particular experiment described here, four cohorts of 80 individual agents each were place on the terrain; each cohort being placed in one of four unique grid cells. A cohort was defined to be an aggregate gathering of proximally co-located individuals. Females, once sexually mature, were fertile for the remainder of their lives (Lacreuse, 2008). Mating between agents in a cohort was facilitated but incest was forbidden by rule (Tutin, 1979). The agents were allowed to move about on the terrain grid, experience caloric (Gurven, 2005) and water metabolic costs, and demonstrate a 28-day reproductive cycle with female-specific gestation and nursing metabolic adjustments. Immediately after program start, the Hominid tribe-typical social process of fusion and fission (Lehmann, 2004, Isbell, 1996) was observed.

**Genetics.** Each agent had its own unique, eleven gene (8-bits per gene) chromosome. There were ten inheritable genes embedded in each chromosome with an eleventh 8-bit gene reserved for discrete values like agent sex assignment. At birth, each gene was set with a Gaussian distributed integer between 0 and 255 inclusive, one per gene, each respectively. The rate of genetic mutation during agent reproduction (per agent per generation) was $3.0 \times 10^{-5}$. By comparison, Nachman (2000) states the average mutation rate in humans is, "~$2.5 \times 10^{-8}$ mutations per nucleotide site or 175 mutations per diploid genome per generation" (p. 297).

**Cybernetics.** Hullian drive reduction was used as a mechanism to steer agent behaviors cybernetically (Wiener, 1957). Additionally, inspired by Maslow (1943) and his Hierarchy of Needs, a prioritization scheme provided a transition mechanism between agent cognitive features and agent non-cognitive physiological drives. Thus, agent behaviors were prioritized in the following way: first thirst satisfaction, then foraging success, mating success, small-group maintenance (Hill, 2003; Dunbar, 1998), and finally avoidance of unpleasant environmental (temperature) conditions. In particular, whenever an agent had to select a new foraging opportunity, it would first seek a cell offering both improved foraging probability and one that contained its preferred food. If no such foraging opportunity could be found, the agent would then move to any cell that offered improved foraging compared to the current cell regardless of the presence or absence of its preferred food.

It was here that cognitive dissonance theory (Festinger, 1957) provided the model with another transition mechanism, one that could facilitate the reduction of a drive associated with an uncomfortable cognitive apprehension occurring between some stimulus one and some attitudinally counter-biased stimulus two that was equally capable of reducing the initial drive but was unrecognized or unaccepted. The agents were designed to compensate for psychic conflicts arising between experiential (computed) events in the environment and their own internally regulated attitude regarding those events by means of cognitive dissonance resolution.

**Cognition.** The agents in this experiment emulated two cognitive features typical in Homo; seeming to exist in Pan (Fouts, 1997), and by extension may have been present in extinct Hominin prototypes. Those cognitive features were attitudes and cognitive dissonance. In this experiment, cognitive dissonance occurred when an agent apprehended a nutritionally sufficient but currently non-preferential food from the list of figs, leaves, monkey (Red Colobus), termites, and tubers. It was assumed that repeated successful contact with a non-preferred food could potentially lead to a positive adjustment of attitude bias and a food preference reassignment relative to the non-preferred food. Each agent began simulated juvenile "life" with a food

preference transmitted to it by its mother at the time of weaning. Subsequent to weaning, agents then became individually responsible for their own attitude bias and preference adjustment.

In juvenile and adult agents food preference could be changed when a threshold sum representing an attitude bias was exceeded. That threshold was implemented as the sum of days the current (non-preferred) food was recognized and found to be nutritionally sufficient. In this experiment the preference reassignment threshold was an independent experimental variable. There were five possible independent variable threshold values: 1-day, 1, 5, 10, and 15-years. When the experimental threshold was exceeded, a new foragable preference was assigned. Simply, each consecutive day that a non-preferred food provided sufficient caloric intake, the attitude bias variable was incremented. If the same food failed to meet agent nutritional requirements, the attitude variable was decremented. Figures 1 through 4 show their respective preference threshold values and the foragable constraints under which male or female philopatry (and opposite sex dispersal) took place. Data quantify the resulting population size-dynamic that accrued over a one thousand year period under each of the independent variables shown.

## Results

Results are presented as plots of populations for 1,000 years of simulated time with different conditions and five-value preference threshold testing.
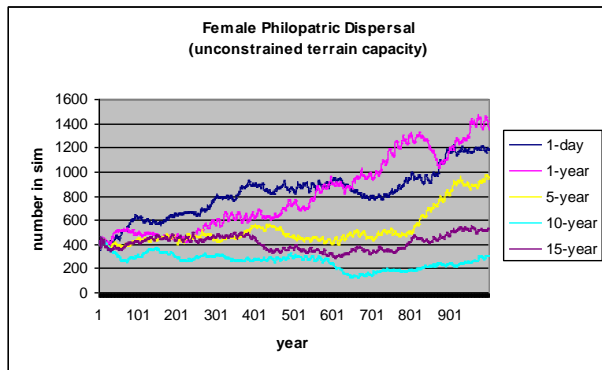


Figure 1 Unconstrained foragable resources, males exhibit philopatry, females disperse.
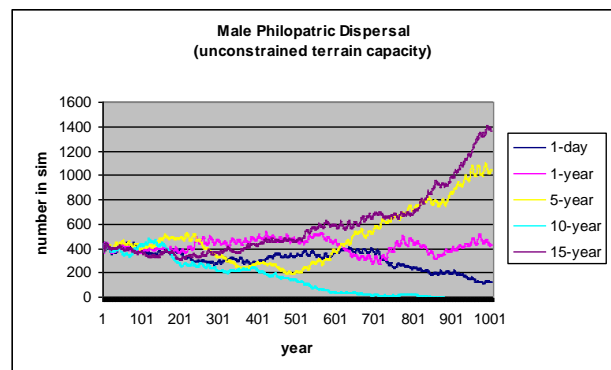


Figure 2 Unconstrained foragable resources, females exhibit philopatry, males disperse.
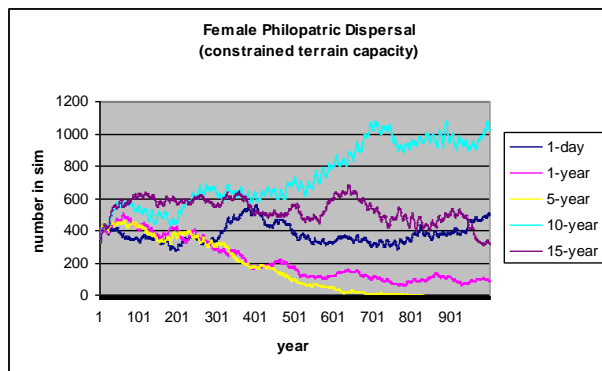


Figure 3 Constrained foraging resources, males exhibit philopatry, females disperse.
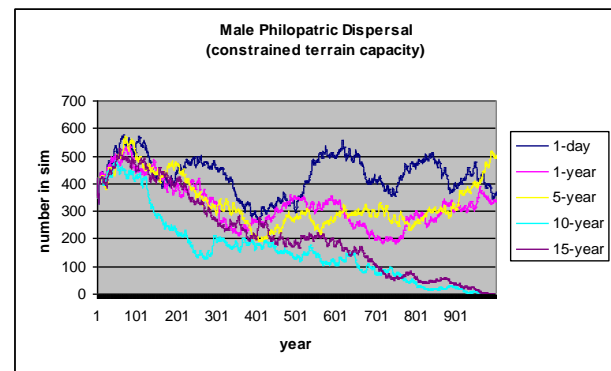


Figure 4 Constrained foraging resources, females exhibit philopatry, males disperse.

Figures 5 through 7 show the results of simulated ontogenetic evolution driven by the confluence of the cognitive processes of attitude and cognitive dissonance, and female philopatric dispersal (males stable females disperse). Shown pair-wise are comparisons between identical populations of agents, i.e., those that were started with the same random number seed.

Figure 5 shows the folded Gaussian distribution of Gene 7 values within the population on day 1. The population in Figure 5 had a preference change threshold set to 1-day. If using the same number seed all starting conditions for any threshold value were mathematically identical whether set to a 1-day, 1, 5, 10, or 15-years level. The 1-day variant is shown for simplicity.
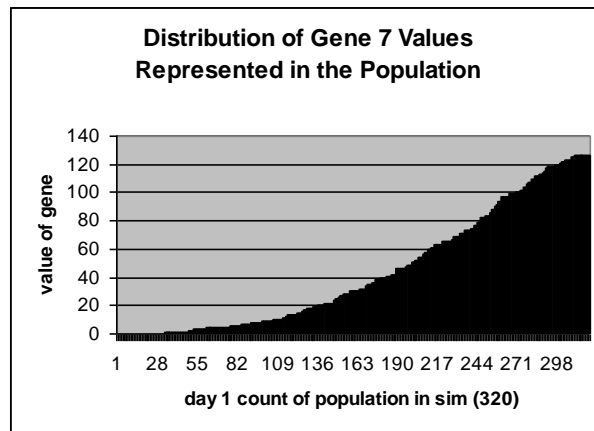


Figure 5 All agent genes values were Normally distributed at start.  This gene is no different.

The populations described above continue in Figures 6 and 7. Figures 6 and 7 reflect the accrued changes in Gene 7 values distributed throughout the same population by year 1000. The population in Figure 6 had a preference change threshold set to 1-day and the population in Figure 7 had a preference change threshold set to 15-years.
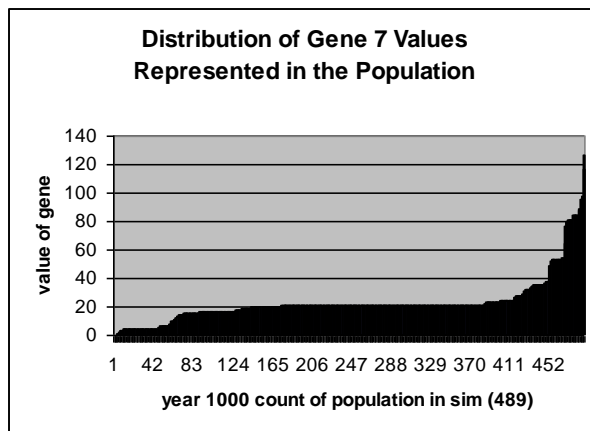




Figure 6 Distribution of values in Gene 7 with preference change threshold set to 1-day.
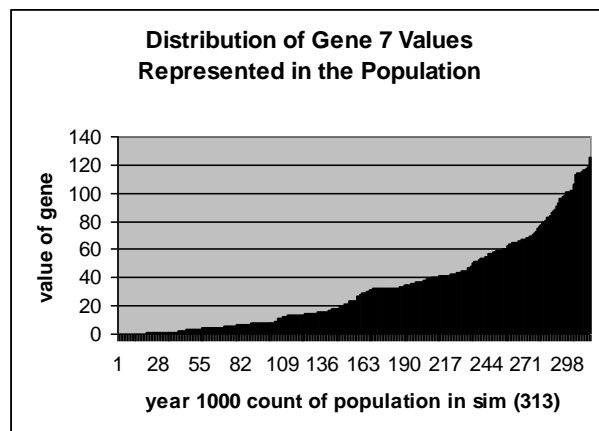
Figure 7 Distribution of values in Gene 7 with preference change threshold set to 15-years

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In Figure 6, the year is now 1000 and the population has 489 members. The distribution is no longer Gaussian and it is highly skewed. In Figure 7, the population has 313 members and the year is 1000. The distribution still resembles the original Gaussian form but is now distinctly inverted and starting to show the beginnings of a heavy tail. Genetic drift in the aggregate population genome appears to be evident.

## Discussion

Plainly, the experiment undertaken here would hold great interest in a natural setting with living, primate specimens. Unfortunately, such an analysis seems impossible with a single living species. However, with a computational model it is completely feasible to pursue that exact experimental end. For example, not only can a population with dispersal drives, i.e., male versus female philopatry together with opposite sex dispersal be simulated, but a control group can be created having identical pseudo-Hominid dynamics without any dispersal tendencies.

Although several researchers have built models and described structures relating to Hominid social, physiological, and ecological considerations (Griffith, 2010; Gros, 2008; Jannsen, 2007) even in the context of the Baldwin effect (Suzuki, 2010), none have examined the confluence of ontogenetic evolution, socio-spatial ecology, agent physiology, psychological constructs like attitude and cognitive dissonance, and the overall combined effects of these components on population genetic drift (the Sewell Wright effect). Why such a computer model was not been created before this may have to do with the unwieldy character of any sufficiently complicated systems model.

All of the experimental runs described here took place on a 100 x 100 cell terrain grid. Overall, there were 180 such experiments made. This report conveys the results of only the first 20. Each of the runs reported here held one random number seed constant and varied only the independent variables. Each random number seed produced 30 results: 10 each for male philopatry, 10 for female, and 10 for a population without dispersal drives whatsoever.

For completeness, the same experimental method was executed 5 more times using other random number seeds to produce those 180 experiments. A total of 6 seeds were used counting the current value (1681107723981969484). The other simulations (those having sexually differentiated philopatric dispersal) produced quantitatively different results but with qualitatively similar properties. (Data not shown.)

## Summary

This computer simulation has demonstrated artificial genetic drift in a community of artificial Hominids at the confluence of ontogenetic evolution, attitude adjustment, and cognitive dissonance. The simulation involved an individual-based model with biomimetic, Hominin-inspired agents possessing individual artificial chromosomes. The simulated terrain the agents occupied was foragable and seasonally modulated. The agents demonstrated attitude biased foraging, individual cognitive and physiological mechanisms, socio-spatial fission and fusion, and sexually differentiated philopatric dispersal. Overall the results suggest that sexually

differentiated dispersal, when explicitly conjoined with attitude bias and an associated foraging preference reassignment, can create correlated and emergent changes in the distribution of genetic values within the artificial genome of an aggregate, virtual population.

**References**

Baldwin, J. (1896). A new factor in evolution. *American Naturalist*. 30. 441-451, 536-553.

Backwell, L., & d'Errico, F. (2001). Evidence of termite foraging by Swartkrans early hominids. *Proceeding of the National Academies of Science*. 98(4). 1358-1363.

Boesch, C. (1991). The effects of leopard predation on grouping patterns in forest chimpanzees. *Behaviour*. 117. 220-236.

Carniero, R. (1970). A Theory of the Origin of the State. *Science*. 169. 733-738.

Darwin, C. (1859). *On the origin of species by natural selection, or the preservation of favoured races in the struggle for life*. London, England: John Murray.

Dunbar, R. (1998). The Social Brain Hypothesis. *Evolutionary Anthropology*. 6. 178–190.

Festinger, L. (1957). *A theory of cognitive dissonance*. Stanford, CA: Stanford University.

Fouts, R. (1997). *Next of kin: What chimpanzees have taught me about who we are*. New York: William Morrow and Company.

Goldberg, D. (1989). *Genetic algorithms: In search optimization & machine learning*. Reading, MA: Addison Wesley Longman, Inc.

Griffith, C., Long, B., & Sept, J. (2010). HOMINIDS: An agent-based spatial simulation model to evaluate behavioral patterns of early Pleistocene hominids. Ecological Modelling. 221(5). 738-760.

Gros, A., Hovestadt, T., & Poethke, H. (2008). Evolution of sex-biased dispersal: The role of sex-specific dispersal costs, demographic stochasticity, and inbreeding. Ecological Modelling. 219. 226–233.

Gurven, M., & Walker, R. (2006). Energetic demand of multiple dependents and the evolution of slow human growth. *Proceedings of the Royal Society* [Biology]. 273. 835–841.

Hill, R., & Dunbar, R. (2003). Social Network Size in Humans. *Human Nature*, 14(1), 53-72.

Hull, C. (1943). *Principles of Behavior*. New York: Appleton-Century-Crofts.

Isbell, L., & Young, T. (1996). The evolution of bipedalism in hominids and reduced group size in chimpanzees: Alternative responses to decreasing resource availability. Journal of Human Evolution. 30. 389–397.

Janssen, M., Sept, J., & Griffith, C. (2007). Hominids foraging in a complex landscape: Could *Homo ergaster* and *Australopithecus boisei* meet their calorie requirements? In Takahashi, S., Sallach, D., & and Rouchier, J. (Eds.), *Advancing Social Simulation*. Springer Publishing. 307-318.

Lacreuse, A., Chennareddi, L., Gould, K., Hawkes, K., Wijayawardana, S., Chen, J., Easley, K., & Herndon, J., (2008). Menstrual cycles continue into advanced old age in the common chimpanzee (Pan troglodytes). Biology of Reproduction. 79. 407–412.

Lehmann, J., & Boesch, C. (2004). To fission or to fusion: Effects of community size on wild chimpanzee (Pan troglodytes verus) social organisation. Behavioral Ecology and Sociobiology. 56. 207–217.

Lonsdorf, E. (2005). Sex differences in the development of termite fishing skills in the wild chimpanzees, *Pan troglodytes schweinfurthii*, of Gombe National Park, Tanzania. *Animal Behavior*. 70. 673–683.

Maslow, A. (1943). Theory of Human Motivation. *Psychological Review*. 50. 370-396.

Nachman, M. & Crowell, S. (2000). Estimate of the mutation rate per nucleotide in humans. *Genetics*. 156. 297–304.

Parish, A., & De Waal, F. (2000). The other "closest living relative": How bonobos (Pan paniscus) challenge traditional assumptions about females, dominance, intra- and intersexual dominance, and hominid evolution. In LeCroy, D. & Moller, M. (Eds.), *Annals of the New York Academy of Sciences: Evolutionary perspectives on human reproductive behavior*. 907. 97–113. New York: New York Academy of Sciences.

Poethke, H., Pfenning, B., & Hovestadt, T. (2007). The relative contributions of individual and kin-selection in the evolution of density-dependent dispersal rates. Evolutionary Ecology Research. 9. 41–50.

Praschnik-Buchman, D. (2000). Female Reproductive Strategies as Social Organizers. In LeCroy, D. & Moller, M. (Eds.), *Annals of the New York Academy of Sciences: Evolutionary perspectives on human reproductive behavior*. 907. 191-195. New York: New York Academy of Sciences.

Prentice, A. (2005). Starvation in humans: Evolutionary background and contemporary implications. *Mechanisms of Ageing and Development*. 126. 976–981.

Sterck, E., Watts, D., & van Schaik, C. (1997). The evolution of female social relationships in nonhuman primates. *Behavioral Ecology and Sociobiology*. 41. 291-309.

Suzuki, R., & Arita, T. (2010). Effects of temporal locality of ecological processes on coevolution of learning and niche construction. *Proceedings of Artificial Life XII (ALIFEXII)*. 471-477.

Tutin, C. (1979). Mating Patterns and Reproductive Strategies in a Community of Wild Chimpanzee (*Pan troglodytes schweinfirthii*). *Behavioral Ecology and Sociobiology*. 6. 29-38.

Wiener, N. (1957). *Cybernetics: Or control and communication in the animal and the machine*. New York: Wiley.

Wrangham, R. (1980). An Ecological Model of Female-Bonded Primate Groups. *Behaviour*. 75(3/4). 262-300.

Wright, S. (1932). The roles of mutation, inbreeding, crossbreeding and selection in evolution. *Proceedings of the 6th International Congress on Genetics*. 1: 356–366.