Experiences with Computer Simulations of Primate Populations

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Abstract

For decades, computer simulations have held advantages over mathematical models of primate populations. Primates are highly social animals, often living in groups with complex, hierarchical, dynamic structures. However, particulars of primate group structures and dynamics vary considerably among species. Age, sex and kinship relationships often provide bases for behavioral organizational features seen in primate groups. As a result, numerous interconnections appear to exist between demographic, genetic and behavioral processes in primate populations.   The complexity known to exist in primate populations is difficult to model mathematically. However, simulations that model individual life histories and use syntax-like data structures borrowed from abstract language theory have proven adaptable and effective. Several generations of primate population simulation libraries using these approaches have been written in FORTH, C and Python languages.   The current Python language system, named CRITTRZ, makes heavy use of object-oriented architecture and incorporates a run-time interface to a geographic information system, for representation of landscapes occupied by simulated populations.   This system is designed to support basic scientific research and planning decisions by conservation biologists. Recent applications of the current system have allowed a detailed examination of interplays between demographic circumstances of simulated populations, group subdivision processes and gene distributions among groups. This system adds support for modeling infectious disease transmission and multiple species in the same environment. This work has required extended shifts of focus between considering results from field studies, contemplating formal models that would best portray events seen in the field, implementing software and conducting simulations. The author has found that results of primate population simulations often include unanticipated findings that lead to further investigations and give the process an ongoing exploratory character. One goal of the author is to apply approaches developed for modeling primate populations to populations of non-primate species. It will be interesting to see to what extent formal structures that have been useful in representing primate group organizations remain useful when applied to populations of other kinds of mammals.

Introduction

My talk today is about computer modeling of primate populations. Some of the work dates back several decades. Some of it is underway today.

During the 1970's, I did research on gene frequency dynamics of mammalian populations. I mainly studied monkey populations. Research subjects included savanna baboons in Kenya and an introduced rhesus monkey population on the island of Cayo Santiago, Puerto Rico. I was interested mostly in 'microevolution' - the evolution, primarily by stochastic processes, of gene distributions in social groups that lived fairly near to each other. Understanding microevolution seemed a necessary element in understanding how species vary over time and space. Some of this work also drew the attention of sociobiologists, who were interested in how kinship relations might affect the evolution of altruism and other kinds of behaviors.   My research involved capturing monkeys, collecting blood samples, analyzing their blood protein genotypes in the laboratory and then analyzing how demographic events and social behaviors affected gene distributions and changes over time.
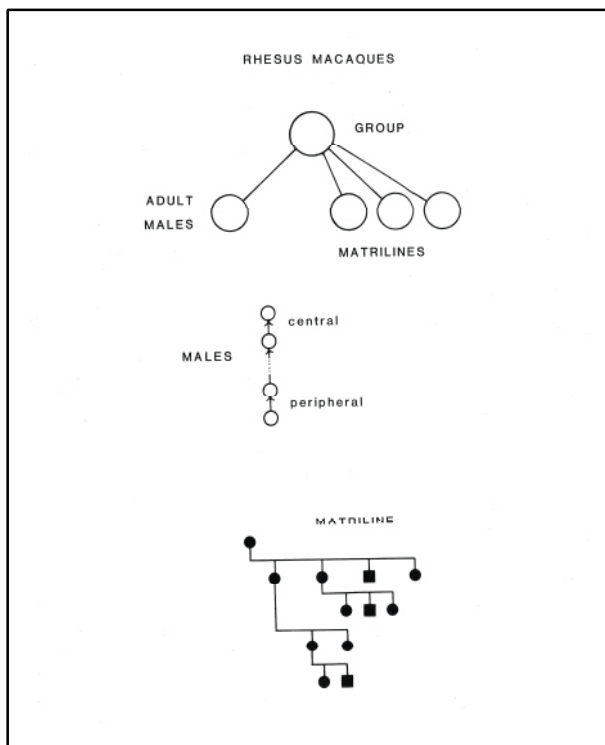

Figure 1. Rhesus group structure.   From T. Olivier, 1984, *J. Social Biol. Struct.* **7**, 61-73.

At Cayo Santiago, the monkeys lived in groups containing a few dozen to over a hundred individuals. Animals were tattooed for individual identification and group memberships were

censused regularly.   Detailed demographic and behavioral research by Donald Sade and colleagues (Sade, 1965; Sade et al 1977) showed that the rhesus males, upon reaching adulthood, ordinarily emigrated from the groups in which they were born. As adults, males migrated between social groups. Males residing in each group organized into linear dominance hierarchies and bred with females residing there. Females, in contrast, usually remained in the groups in which they were born. They organized into matrilines, groups of adult females related by descent through females and their immature offspring of both sexes. Matrilineal memberships affected many behaviors of females - members of a matriline often remained in spatial proximity and intervened on behalf of each other in fights.
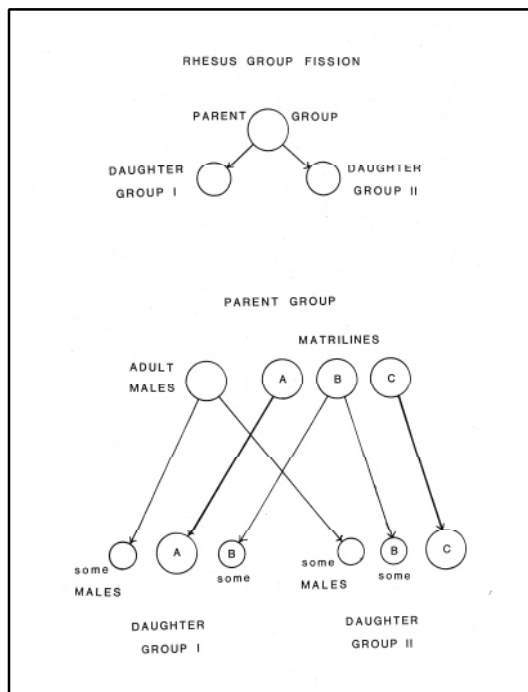

Figure 2. Rhesus group fission.   From T. Olivier, 1984, *J. Social Biol. Struct.* **7**, 61-73

Large groups sometimes fissioned into two, with members of the same matriline usually joining the same fission-product group. However, large matrilines sometimes divided along sublineages at group fissioning, with sublineages joining different fission product groups. Small groups sometimes fused. Savanna baboons lived in societies similar to those of rhesus monkeys, though data were less detailed.

We found linkages between the complex social processes and gene frequency dynamics of these groups.   For example, genetic differences between matrilines in a group generally were greater than genetic differences between groups. Genetic differences between fission product groups generally were much greater than expected from a random allocation of genes in the original group among fission product groups.   Simulations and mathematical analyses showed that observed differences matched well with greater differences expected when groups of related animals

(matrilines) joined the same fission product group (Olivier et al, 1981; Buettner-Janusch et al, 1983). This effect is known as the lineal effect and was first discovered in human populations.
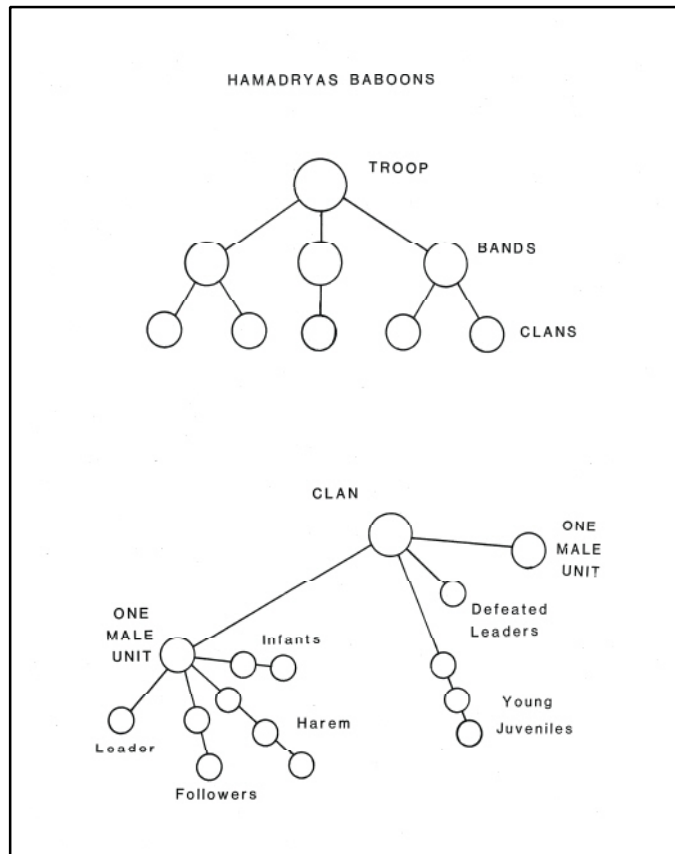

Figure 3. Hamadryas baboon troop.   From T. Olivier, 1984, *J. Social Biol. Struct.* **7**, 61-73

And now for something different, namely hamadryas baboons. These monkeys are closely related to the savanna baboons I studied in Kenya (in fact interbreeding can occur) but their social systems are very different. Pioneering research into hamadryas baboon behavior was done in Ethiopia in the 1960's and 1970's by Hans Kummer and his colleagues (Kummer, 1968, 1971).

Hamadryas baboons lived in arid areas and slept at night on rocky cliffs and outcrops. All animals that slept together at night formed a troop. A single troop could contain several hundred animals. During the day, group members subdivided into bands. Bands dispersed to forage. Their memberships were relatively stable.

Bands further subdivided into clans, which displayed a quite distinct internal structure.   In clans, some males (leaders) maintained near-exclusive access to mating over group females (the harem). Males moved during their lives through a series of distinct statuses, with different roles attached to each (infant, juvenile, follower, leader, defeater leader). Male memberships of clans were stable. Females migrated, sometimes between harems, sometimes between clans and sometimes between bands.

Whereas migration in rhesus monkey and savanna baboon groups was an all or none phenomenon, migration in hamadryas baboons was by graded steps in a multi-level social space. Rhesus groups seemed completely outbred but behavioral observations of hamadryas troops implied they were inbred. Though I had never done empirical research on hamadryas baboons, I thought it would be extremely interesting to model genetic consequences of their social system.

Modeling System with Syntax-Like Data Structures and Operators

At that time, population genetics contained many mathematical models for subdivided populations. However, mathematical models typically assumed that subpopulations were of fixed size, with little or no internal structure and no group fissioning or fusing. How could you examine the genetic consequences of different primate social structures using models that ignored those structures?

From experience, I knew that computer simulations were capable of modeling complex group structures and dynamics that field researchers had been finding. However, all was not excellent. I tried modeling hamadryas baboon troops using Pascal. I realized quickly that static, single level data structures such as arrays (which were so widely used in examples in computer textbooks) were poorly suited to modeling multi-level, dynamic structures seen in primate groups. Prospects for code reuse in models of different species also seemed low. I needed to develop a computer simulation system designed to facilitate modeling of primate populations.

My aims for the system were:

1. simulate individual life cycles
2. maintain individual kinship links
3. use kinship relations in process decisions
4. data structures usable for varied groups
5. eventually model spatial effects
6. system useful for exploring questions from field research on primates

Accomplishing the first two seemed straightforward but the path to the third wasn't obvious at all. With training in anthropology, I was aware that kinship analysts in social anthropology represented the different, elaborate kinship systems of traditional human societies using discrete, graphical structures that portrayed naturally in a digital computer. On looking into formal language theory I realized that things resembling language parse trees and grammatical production rules were useful for portraying primate group structures and transformations. Syntactically structured character strings easily represented group structures in simulations. Text patterns or templates for normal group structures could be specified and used to check correctness of structures of simulated groups using abstract machines much like the finite automata that appear in formal language discussions.

I was surprised and encouraged by much of this, in roughly equal parts. In the early 1980's, I began building primate simulation libraries drawing on some of these notions. I want to show you some of their common elements.

Animal Key Strings

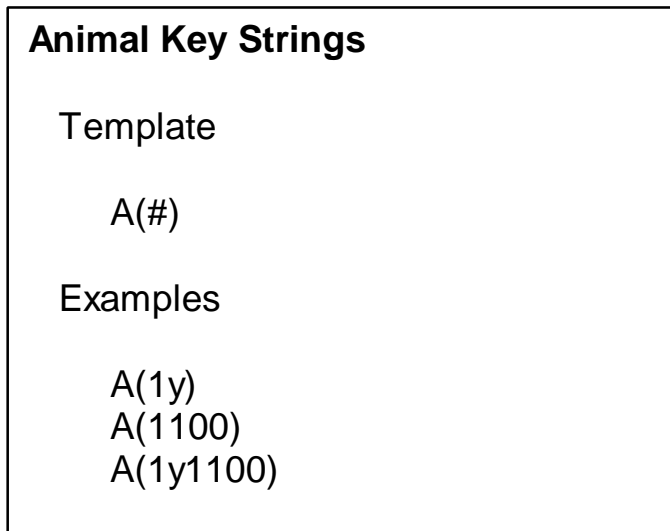Template

A(#)

Examples

A(1y)
A(1100)
A(1y1100)

Figure 4. Animal template, example key strings.

All group data structures were represented using syntactically structured character strings I called 'key strings'.   A key string began with a label or key character that identifies its population element type. The label character is followed by data fields contained between bounds markers. Nested key strings are used to represent multilevel group structures. I used the FORTH language to develop a prototype modeling system that ran on an Apple II computer and with it constructed simulations of a simply subdivided population resembling the 'island model' of population genetics and small rhesus monkey population containing several groups.
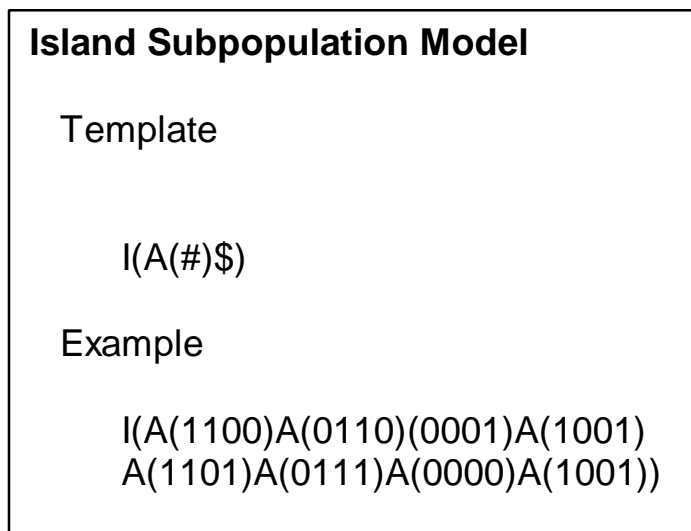
Island Subpopulation Model

Template

I(A(#)$)

Example

I(A(1100)A(0110)(0001)A(1001)
A(1101)A(0111)A(0000)A(1001))

Figure. 5. Island model template and example.

Rhesus Group

Template

G(H(A(#)$)N(M(A(#)$)$))

Example

G(H(A(y)A(y)A(y)A(y))
N(M(A(x)A(x)A(y)A(x)A(x))
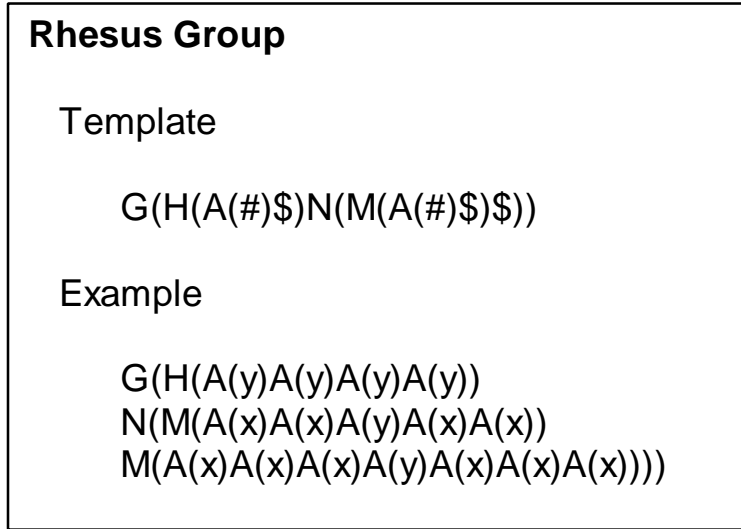M(A(x)A(x)A(x)A(y)A(x)A(x)A(x))))

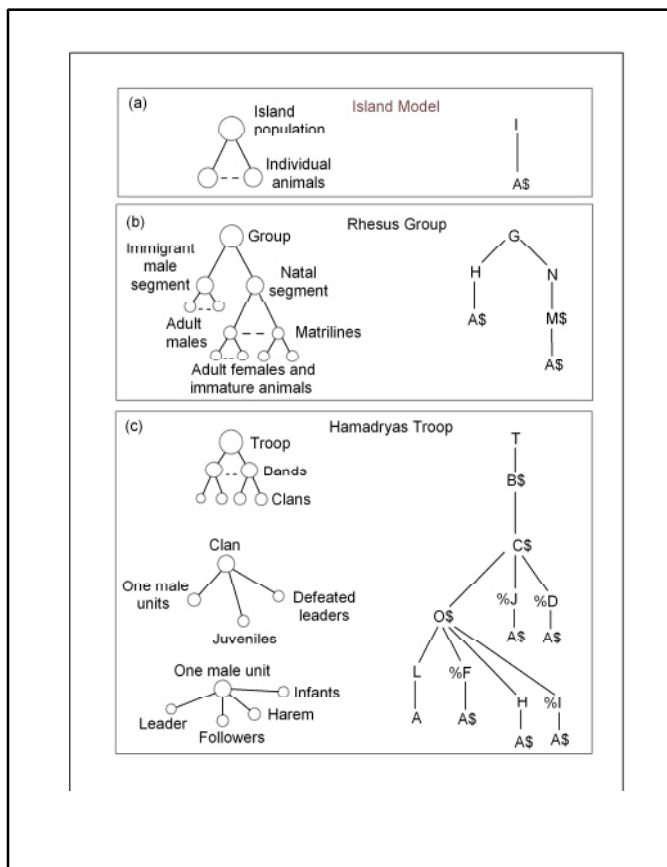Figure 6. Rhesus group template and example

Figure 7. Group structures and templates represented in tree structures.   After T. Olivier, 1985, *J. Theor. Biol*. **115**, 539-549.

Simulated populations were stepped through a series of discrete time periods. In each time period, biological events in the population being modeled were simulated. Changes in group structures, whether by births, deaths, migration, group fissions or fusions, were accomplished by key string insertion, delete and move operations. With the regular structure of key strings, a small number of subroutines were able to accomplish a wide range of group structural changes. For example, one subroutine that randomly allocated high-level substrings of a key string was used to subdivide adult male and natal segments into fission product group adult male and natal segments. However, in the first case, allocated substring were those representing adult males, in the second substrings represented matrilines.

Following the FORTH prototype system, I developed a more complete system in C. This system ran initially on a CP/M microcomputer, and later more powerful systems. In many ways, the inputs resembled state data we had used to analyze the Cayo Santiago rhesus monkey populations; output resembled the kinds of things we geneticists had been concerned with in the same population. This C library supported individual identification numbers, separate tables of individual ages, sexes, genotypes and maternal kinship links. Input text files used key strings to specify starting population group numbers, matriline structures and internal memberships. This text file also specified age and sex specific birth and death rates and other parameter values needed for decision-making in simulations of biological events.

Using the C system, I simulated model populations resembling real rhesus monkey and savanna baboon populations I had studied and happily found gene distributions in simulated populations much like those found in real ones. I also was able to look into things like the influence of population growth rates on rates of group fissions, fusions and matriline extinctions.
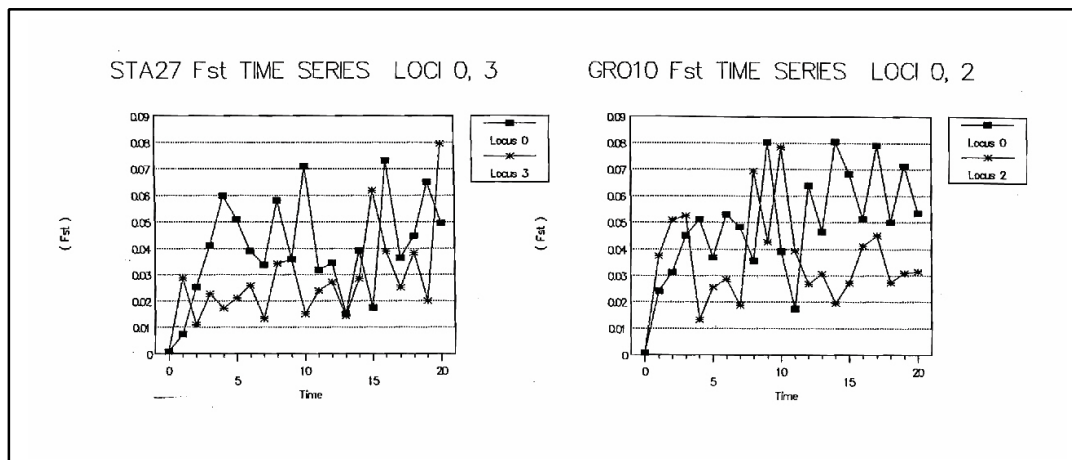

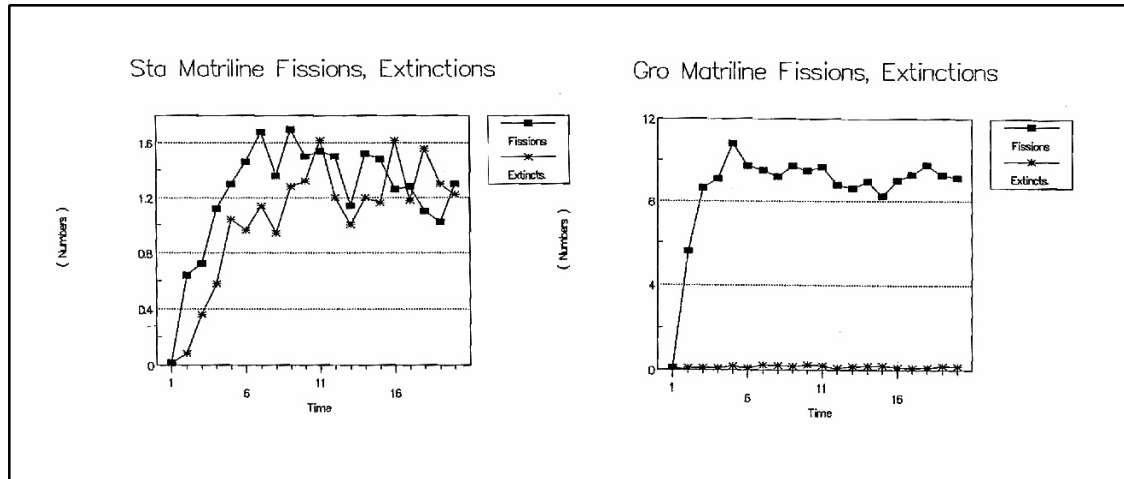Figure 8. C system modeling of genetic differentiation variations.

Figure 9. C system modeling of matriline fissions, extinctions.

I was very pleased with the performance of the C system. However, submissions of papers based on this work were rejected for publication. Reviewers complained I spent too much time discussing models and computers and not enough time on topics of biological substance.

Around 1990, I put work on these models aside, but then returned in 2002.   By then I had become involved with conservation biology and realized that the sorts of primate simulations I had done years before were applicable to understanding population processes in the small, local populations that were common targets of conservation efforts.   Additionally, I heard about, bought and read Stephen Wolfram's *A New Kind of Science*. One of the things I took away from this reading was a sense that simulations were receiving the breadth of acceptance and appreciation as scientific tools that they warranted. With so much better software and hardware then available, the opportunities were too much to resist. I set to work on yet another monkey modeling system known as CRITTRZ and sent Stephen Wolfram a few of my old reprints.

CRITTRZ features include:

1. GIS interface for modeling landscape, spatial effects
2. module for modeling infectious disease transmission
3. ability to model large populations
4. ability to model multiple, possibly interacting, species
5. detailed process logging for recording scenarios

The system I began developing in 2002 shares many broad, logical features with earlier ones but extends the modeling capabilities of its predecessors. The new system includes a run-time interface to a geographic information system, so that influences of space and habitat variations on population processes can be examined. We know that social interactions and population spatial distributions can influence infectious disease transmission. CRITTRZ contains a module for modeling of infectious disease transmission. On contemporary hardware, populations of more than 10000 individuals and more than 100 subpopulations are comfortably simulated. Multiple, possibly

interacting, populations of different species, can be simulated at one time. Detailed logging of population structures and events is supported.

CRITTRZ is written in Python, with much use of object-oriented architecture. CRITTRZ is available under an open source license. Five test versions have been released.

I have presented several reports on monkey population simulations at Society for Conservation Biology meetings. Here is a slide from one illustrating connections between social group fission and fusion sizes, demographic circumstances and genetic differentiation between groups.
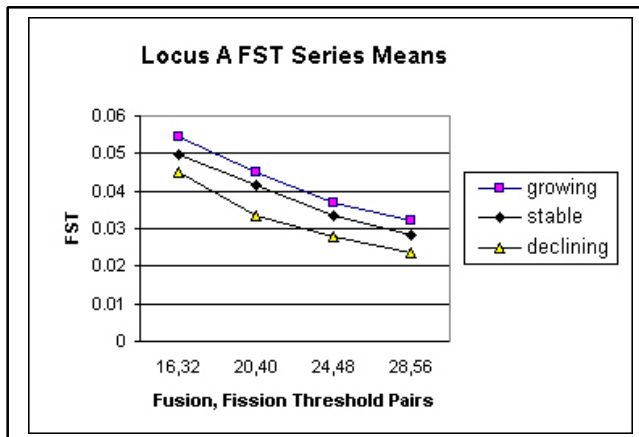

Figure 10. Relationships between group fusion, fission size thresholds, demographic circumstances and genetic differentiation levels. Modified from T. Olivier, 2004. Report presented at the annual meeting of the Society for Conservation Biology.

After four years of focusing on software development, I am looking forward soon to more time reading field studies of animal populations and building models with CRITTRZ of processes that seem interesting and worth further exploration.

One seductive difficulty with computer models is that we can always add pieces to a model to closer approximate the complex behaviors of some real system. Sometimes this is fine. However, the end result is that with time, models can become more and more complex and less and less general. NKS notes that very simple underlying processes may generate phenomena that are perceptually complex.

The structures seen in rhesus and baboon groups emerge from associative decisions of individuals. Surely, the rules by which animals decide their social bonds cannot be too complex. The modeling systems I've talked about today have opportunistically borrowed pieces from various formalisms. I suspect more tailored and systematic approaches to portraying groups based on algebraic structures or cellular automata could be developed. I will guess that simulations so built would be simpler and more general than current comparable models.

Conferences such as this one demonstrate the expanded influence and acceptance of computer modeling as a scientific tool. I was pleased to receive an invitation to speak at this conference. I thank you for allowing me to talk to you today about computer monkey models.

For more information on CRITTRZ, visit www.greencreekparadigms.com/CRITTRZ.htm.

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