INTERACTIONS BETWEEN SOCIAL, GENETIC AND DEMOGRAHIC PROCESSES IN SIMULATED MONKEY POPULATIONS

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ABSTRACT

This study illustrates use of a computer simulation system built to permit modeling by conservationists of a range of processes in spatially and socially subdivided populations. The study examines relationships between social, demographic and genetic processes in simulated populations with subpopulations similar to multi-male groups found in many cercopithecine monkey species. Groups in model populations contain immigrant adult males and natal animal segments composed of matrilines. Groups may fission, partly along matrilines, and they may fuse. The models simulate individual life histories and maintain age, sex, genotype and pedigree information on simulated individuals. Parameters allow control of various aspects of group fission and fusion processes. Analyses in this study compare group compositions, dynamics and gene distributions in simulation series where age-specific birth and survival rates are set to set to produce expectations of population size stability, growth and decline. The modeling system employed here is written in Python using a strongly object-oriented architecture. Application of the software to modeling other mammalian species is discussed. The system includes a run-time link to a geographic information system. Applications of the system to modeling infectious disease spread and site-specific conservation planning are considered.

INTRODUCTION

CRITTRZ is a population simulation library built to support modeling of demographic, genetic and infectious disease processes in animal populations divided by space or social groupings. CRITTRZ simulates individual life histories in detail. Keyed data structures store information on local subpopulation or group structures (Olivier, 1985, 2003a). These data structures were developed initially to address challenges in the modeling of complex, dynamic groups of some Old World monkey populations (Olivier, 1984) but they should be well suited to modeling groups of other taxa of large, social mammals.

CRITTRZ is written in Python and uses strongly object-oriented architecture. The library includes a run-time link to the Idrisi GIS (Clark Labs, 2003). An initial test version (Ver. 0.7.0) was released in June 2004 under an open-source license. The home page (www.greencreekparadigms.com/CRITTRZ.htm) provides links for documentation, downloading and reports on earlier development versions of the system (Olivier 2003a, 2003b).

The library includes several modules for modeling cercopithecine monkey populations divided into multi-male social groups. Species exhibiting this form of population organization include savanna baboons and rhesus monkeys. Groups in model populations contain immigrant adult males and natal animal segments composed of matrilines. Matrilines consist of adult females related by maternal descent and immature offspring of both sexes. Figure 1 illustrates the structure of one simulated group using the indented text block form of keyed structure. In this figure, "G,124", "H,124" and "N,124" are unique identifiers in the system for the group and its adult male and natal segments, respectively. Letter and number pairs beginning with "A" identify individuals belonging to group elements. In the current study, CRITTRZ identifies matrilines on an as need basis from the kinship link data maintained for each simulated population.

Fig. 1 Example Simulated Group Structure

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G,124
  H,124
    A,19470 A,19848 A,19652 A,19572 A,19899 A,19782 A,20413
  N,124
    A,20628 A,20630 A,20629 A,20633 A,20632 A,20631 A,20360 A,20636
    A,20635 A,20634 A,20637 A,20638 A,20366 A,20640 A,20639 A,20641
    A,20368 A,20367 A,20069 A,20643 A,20642 A,19458 A,20645 A,20644
    A,20372
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Model groups may fission when large, partly along matrilines, and they may fuse with other groups when small. Males ordinarily leave their natal groups when they reach adulthood. Males may change groups from time to time when adult. The present model includes only social subdivision with no spatial domain effects. In this model, male migration is semi-random, with immigration into groups more likely when adult female to male ratios are high. The models maintain age, sex, genotype and pedigree information on simulated individuals. Parameters allow control of various aspects of survival, reproduction, migration, group fission and fusion processes.

Sizes of cercopithecine multi-male groups vary greatly between species and populations. In model populations, size thresholds initiate group fusion and fission processes and heavily influence mean group sizes. Random processes that produces gene frequency differentiation may act most strongly within small subpopulations. This report examines whether gene frequency differentiation levels among model cercopitehcine multi-male groups vary inversely with group fusion and fission threshold values (and thus, mean group sizes).

In growing populations, the elevated frequency of group fissions may add to gene frequency differentiation levels. In declining populations, the elevated frequency of group fusions may reduce differentiation levels. This report also examines whether genetic differentiation levels are highest in growing populations, least in declining and intermediate in stable populations.

More broadly, this study provides a test application of CRITTRZ as it continues in development.

METHODS

Twelve simulation series of CRITTRZ cercopithecine multi-male populations were conducted. In these models, individuals could live a maximum of five time periods. Each series consisted of 30 simulations run for 50 time periods. In four run series, age-specific birth and survival rates were set to set to produce expectations of population size stability. In four series, demographic rates were set to create expected growth of about 3 percent per simulated period. In four series, demographic rates were set to produce a similar rate of decline. In the four run series with each demographic condition, each of the following four fusion, fission size threshold value pairs were employed by one and only one run series: a) 16,32 b) 20, 40 c) 24, 48 d) 28, 56. In all run series, other conditions were identical. An output population file from a previous exploratory simulation provided the initial population for all simulations. This population contained 631 individuals divided into 18 social groups. Simulated individuals possessed two independent autosomal genetic loci that were polymorphic in the population. CRITTRZ log files were used to record temporal variations in population sizes, group numbers, FST gene frequency differentiation levels and group fusion and fission events.

RESULTS

Mean terminal population sizes for run series with different demographic conditions were a) stable, 597.4 b) declining, 127.8 c) growing 2575.3. Over all run series, terminal population sizes ranged from 29 to 4445. The terminal number of groups in runs ranged from 1 to 160.

Table 1 presents terminal mean group sizes for each simulation run series. Mean group sizes are consistent for each fusion, fission threshold pair, whether the simulation series is in the stable, declining or growing category. These results indicate that the model is conserving group sizes over the course of extensive variations of population sizes.

Table 1
Mean Group Sizes at Simulation Terminations
In Twelve Simulation Run Series

	(16,32)	(20,40)	(24,48)	(28,56)
Stable	22.9	28.4	34.0	40.3
Declining	22.8	29.3	33.8	40.8
Growing	22.9	28.4	34.0	39.7

*Columns tabulate results by fusion, fission threshold pairs. Rows list results by demographic conditions.*

Table 2 presents ratios of group fusions to fissions in various run series. Events were tallied over the last 40 time periods in each simulation, to reduce influences of initial conditions on ratios. Here, fusion to fission ratios are similar across demographic circumstances, whatever the threshold settings.

Table 2
Group Fusion/Fission Ratios
In Twelve Simulation Run Series

|	(16,32)	(20, 40)	(24,48)	(28,56)
Stable	1.00	.973	1.00	.992
Declining	1.23	1.40	1.35	1.37
Growing	.784	.760	.742	.742

Columns tabulate results by fusion, fission threshold pairs. Rows list results by demographic conditions.

Figure 2 illustrates variations over time of FST values in one simulation run with the stable demographic regimen and 20, 40 as fusion and fission threshold values. Values fluctuate over short sequences of time periods, with the values for the A and B loci sometimes moving similarly, but sometime shifting with differences in direction and size.

Fig. 2 FST Variations over Time in One Simulation
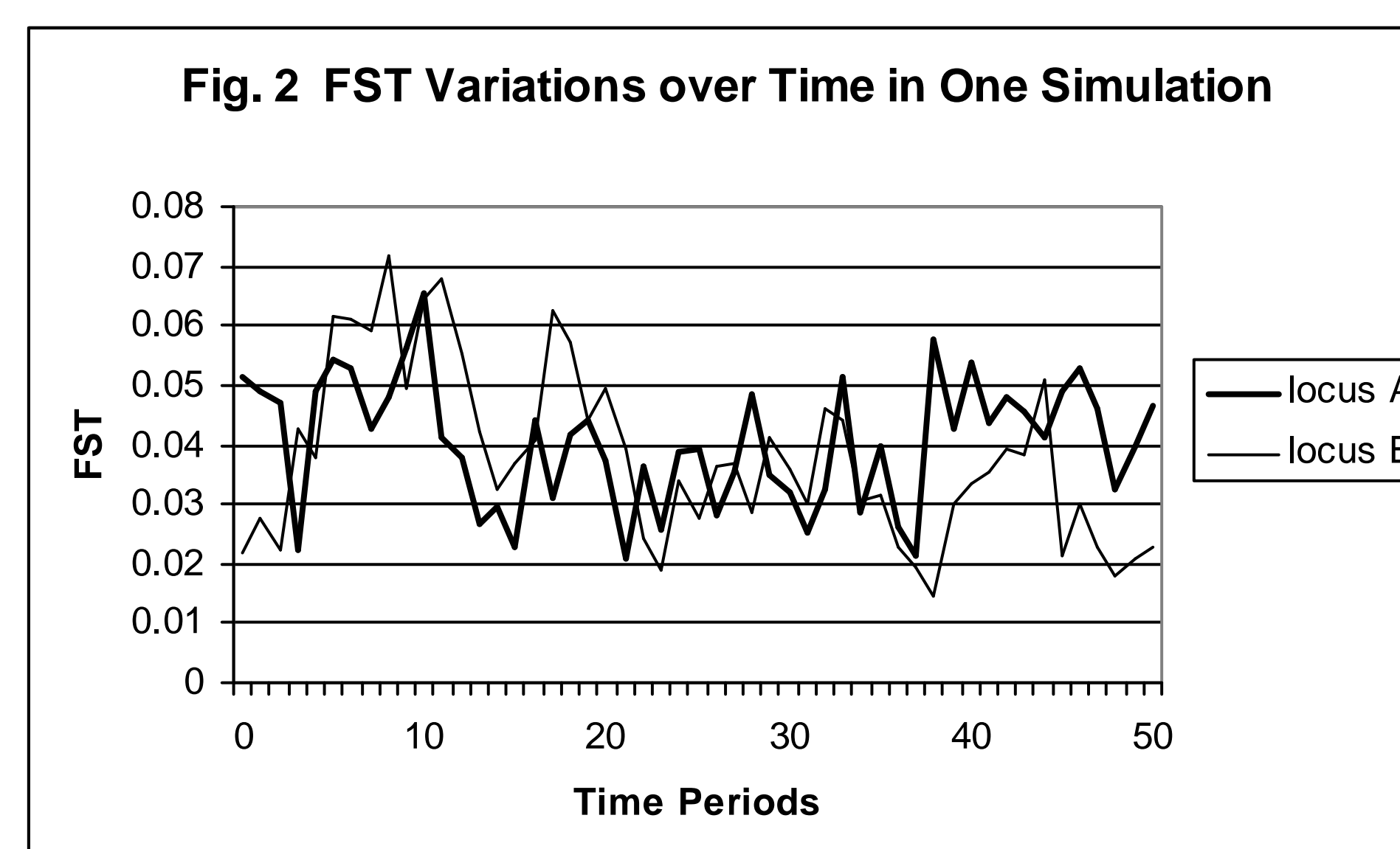
Figures 3a and 3b plot mean FST values for the twelve run series for both genetic loci. The horizontal axis represents fusion and fission threshold categories. Points with matching demographic circumstances are symbolized similarly and connected by lines. FST values are calculated over the last 40 time periods in each simulation to reduce

influences of initial conditions on FST values. Graphs for the two loci are quite similar. For all fission threshold values, FST values are highest for the growing population series, intermediate for the stable and the lowest for the declining. In addition, declines in FST values are evident as one proceeds from lower to higher fusion and fission thresholds (and larger mean group sizes). These graphs suggest that demographic circumstances and fusion, fission size thresholds influence gene frequency differentiation levels in model monkey groups.

Fig. 3a Locus A FST Series Means

Fig. 3b Locus B FST Series Means
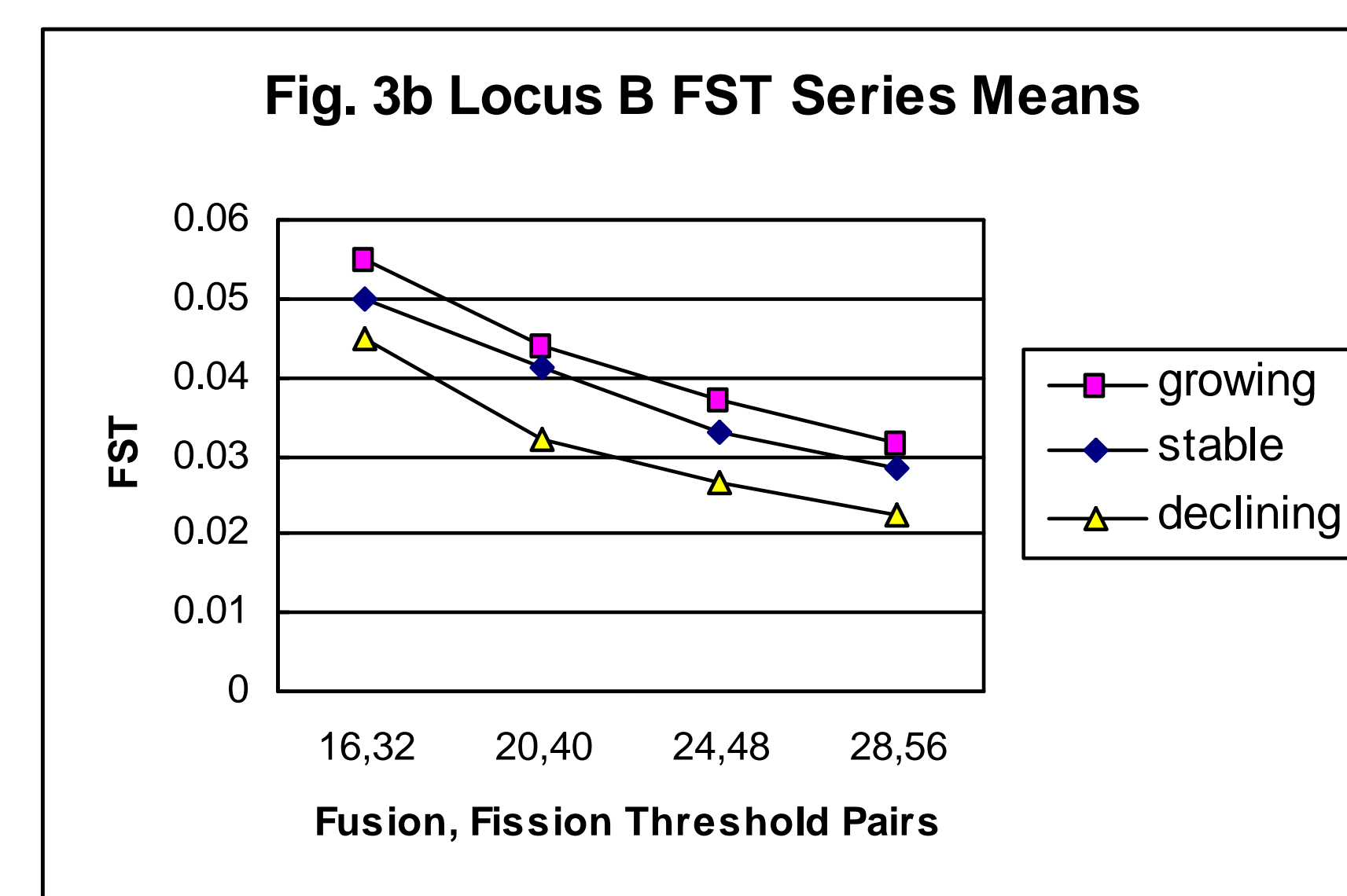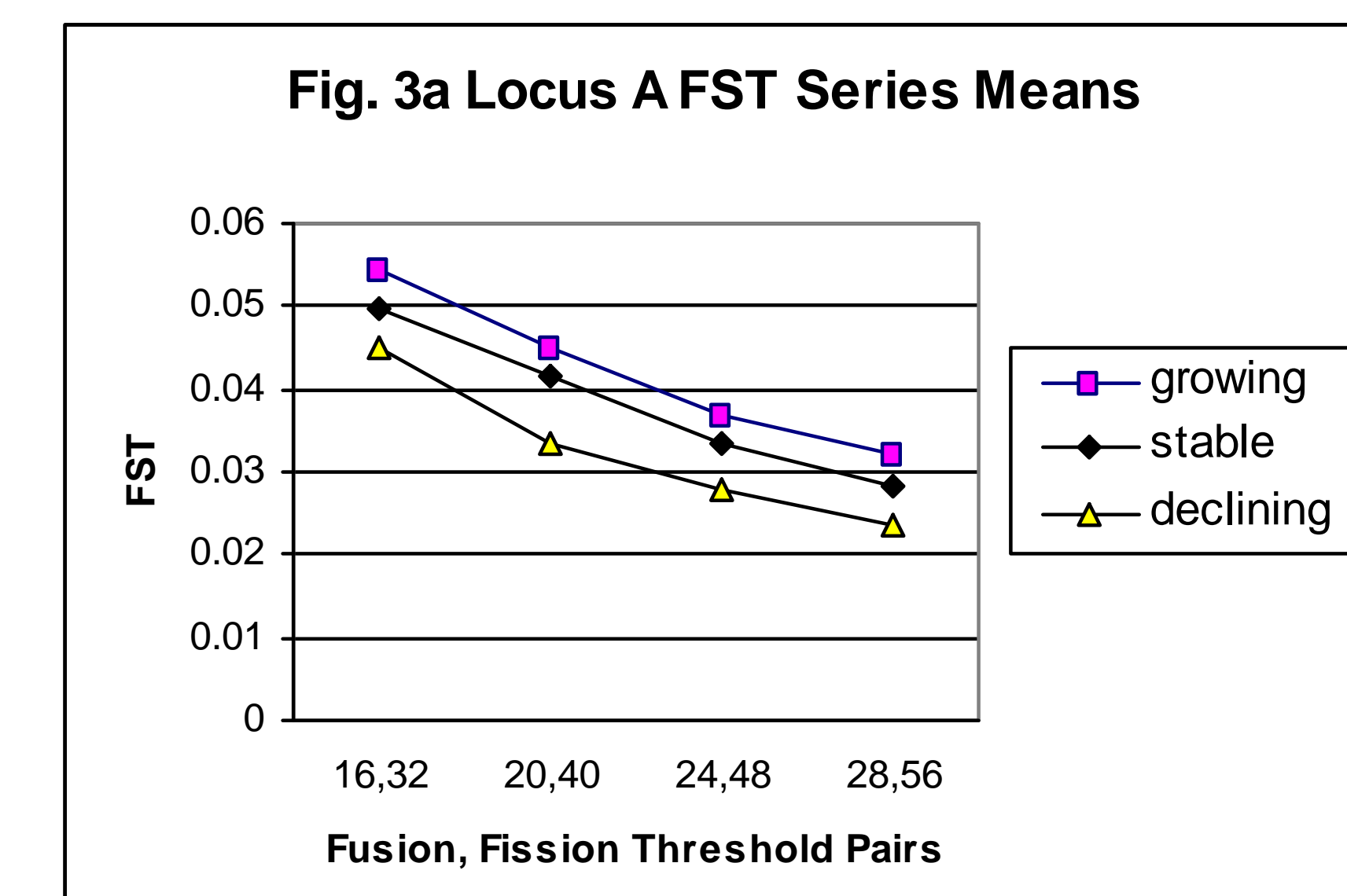
DISCUSSION

These simulations show that the CRITTRZ library can be applied to exploring a range of processes in model populations with features resembling those of some Old World monkeys. More simulations with variations in CRITTRZ parameters held constant here are planned.

In object-oriented software development, specialized classes of objects are derived from more general classes. In CRITTRZ, classes specialized for modeling cercopithecine multi-male groups are derived from more general classes for modeling populations with simpler structures and processes. The same strategy could be applied to create models of other mammalian species (candidates include African lions, wild sheep and many other primates).

Transmission of infectious diseases often involves direct contact between population members. With its detailed representation of social group structures and individual life histories CRITTRZ models embody much information on relationships between population members, relationships that are likely to influence paths of disease transmission. The current release includes a module for simplified modeling of sexually transmitted diseases. CRITTRZ is designed to support modeling of interacting populations of more than one species. Modeling of interspecific disease transmission (for example between wild ungulates and domestic livestock) should be feasible.

In coming months, the author intends to extend the GIS interface, to support examination of interactions between population processes and landscape features. The GIS interface permits use of real world data layers to represent landscapes on which model populations exist. With its focus on simulation of individual life histories and group dynamics, the level of abstraction employed by CRITTRZ corresponds approximately to that employed in many ethological and ecological field studies of large mammals. For these reasons, CRITTRZ seems suited to modeling scenarios in site-specific mammalian populations of interest to conservation planners.

Additional test releases of CRITTRZ are planned for later in 2004. Release of Version 1.0 is scheduled for the first quarter of 2005.

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