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The Demographic Stability of Small Human Populations

1. Introduction

To an anthropologist, questions of historical demography are more than inquiries into particular temporal events; they are investigations into basic human biology and the evolution of human culture. It is important that we be able not only to describe the births and deaths of a specific set of observed individuals, but that we describe the rates of birth and death which prevail in the population over a long time period.

We have two basic kinds of data. There are aged skeletal series from large burial sites, and there are censuses from living primitive populations. The former give us direct information from past populations, and the latter give us information from living populations generally assumed to be representative of cultures during the long period of human evolution. Hence, both sources are used to reconstruct human demographic evolution.

Most populations of these types are small ones which are not literate and do not keep records sufficient for demographic analysis. We generally have but a single census (or aged skeletal series) and only minor scraps of other information. There is almost never any actual data on age-specific rates of mortality, yet these rates are the fundamental parameters of demography and must be known.

With standard theoretical approaches, it has been shown that the age distribution of small groups is unstable from year to year, and may be unreliable as a source from which to determine age-specific death rates (e.g., Moore, Swedlund & Armelagos, 1975; Angel, 1969). It is also known that populations are so subject to extinction, due to statistical fluctuations in births and deaths, that they are too transitory and unstable for useful study (this is based on statistical theory, which can be found in Bartlett, 1960; Pielou, 1969; Keyfitz, 1968). If this is true, then we must avoid the use of typical anthropological data, and are to a great extent prevented from gaining a reasonable knowledge of past demographic patterns.

The mathematical models on which these assertions are based use fixed age-specific birth and death rates. Yet there is a wealth of biological and anthropological information to show that these vital processes of a population vary according to population size or density in a negative-feedback way. A population which becomes crowded suffers higher mortality and lowered fertility, and one which is uncrowded enjoys higher fertility and lower mortality. These facts must be incorporated into a realistic demographic model.

In this paper we use a density-dependent demographic model to answer two questions: How much extinction pressure exists for small populations over moderate time periods? How representative of the underlying demographic patterns is a census from such a population? For populations which survive to be observed, we shall show that stochastic fluctuations in the vital rates generally do not disturb the census greatly from that produced by a comparable deterministic population.

As anthropology usually relies on a census rather than direct observation of the vital rates, we will be examining the relationship between stochastic fluctuations in the vital rates and their reflection in the census. A census close to its underlying deterministic form is one from which vital rates that are close to their underlying average values may be obtained.

2. Methods

We have used a stochastic (Monte Carlo) simulation of a density-dependent demographic process which is a modification of the standard fixed-rate projection derived first by Lewis (1942) and Leslie (1945, 1948). In the standard model, the age-specific birth and death rates are all constant over time; we have made them dependent on the size and composition of the population at any particular time; details of the method are given in the Appendix.

If the census at time t is divided into m age classes, we represent the number of individuals in age class i by $n(i, t)$, and treat the entire census as an m-element vector $N(t)$. We use the notation t for time, but really we are speaking of the number of iteration steps from some beginning population $N(0)$, each iteration representing the length of time included in each age class.

An individual at age i has a probability $P(i)$ of surviving to the next age class and a probability $F(i)$ of producing an offspring of the same sex. If these vital rates are fixed, then it has long been known that, no matter what the starting population, the population will approach a fixed age distribution (proportions in the m age classes) and a size which grows at a fixed rate, λ, determined by the set of vital rates $P(i)$ and $F(i)$. Although mathematically convenient, such a model allows fractions of individuals to survive or to be born and hence is somewhat approximate.

It is known (e.g. Keyfitz, 1968) that if λ is small, that is, if the population's intrinsic growth rate is close to zero, then most small populations will eventually become extinct, due solely to the statistical aspects of birth and death. At some time enough individuals will die, or will not reproduce, merely due to chance, that the population will diminish and disappear. The rate at which this occurs depends on the value of λ. An example will be given below.

Real vital rates are not constant. The wealth of studies on animal behavior which are now available show that territoriality, aggression, sexual selection, crowding and its nutritional and hormonal concomitants, and perhaps most of social behavior directly affect the vital rates of the population. These behavioral processes generally operate to keep the population close to some equilibrium composition. Primitive populations are no exception to this pattern, and while there are exceptional circumstances, it is more realistic to model them with negative-feedback in their vital rates than it is to use the standard fixed-rate model.

By assuming that the effect of other individuals in the population on the survival or fertility of a given individual is proportional to the frequency with which encounters

between them occur (other assumptions will lead to similar results), we can specify a form for the age-specific vital rates which has the desired negative-feedback properties. The time dependent, age-specific vital rates are expressed as follows:

$$P(i, t) = P_i e^{-\Sigma b_{ij} n_j},$$

$$F(i, t) = F_i e^{-\Sigma a_{ij} n_j} \qquad (1)$$

where b_{ij} and a_{ij} are the damping effects of encounters of individuals in age class i with those in age class j, and where P_i and F_i are the density-independent, or maximal, vital rates for age class i. The exponential term is a damping factor with a value between 0 and 1, and hence expresses the fraction of the maximal vital rate which applies to a population with composition $N(t)$. The damping coefficients a_{ij} and b_{ij} represent the pattern by which crowding is reflected on the vital rates, and for various types of feedback we merely must specify the relative values of these coefficients. To produce a population with any specific total size, one merely needs to adjust all of the coefficients by an easily-computed constant factor.

These density-dependent vital rates will produce a deterministic equilibrium in which growth eventually comes to zero. The model contains too many parameters to be of empirical use, but it is easy to simplify things by assuming simple patterns in the damping coefficients, by which realistic ecologically-stable populations may be modeled.

The stochastic element in birth and death processes must now be included to make the model more realistic. We do this by Monte Carlo methods. At any time t, we know the population composition $N(t)$, and using equations (1), we compute $P(i, t)$ and $F(i, t)$. Then for each individual in the population, we determine the chance of reproducing by drawing a random number between 0 and 1. If less than $F(i, t)$, we place an infant in the first age class at the next time $(n(0, t + 1))$. By drawing another random number we determine from $P(i, t)$ if the same individual survives to be a member of age class $i + 1$ at time $t + 1$. We do this for all individuals alive at time t, and the entire process is carried out for 100 iterations (until $t = 100$). We have used 5 age classes for illustrative purposes, but any number can be used; if human fertility ceases at age 50, this simulation can be visualized as covering 1000 years.

The properties of this model are such that the results of any single run for a set of starting conditions $(N(0), P(i, 0), F(i, 0))$ depend on the specific random numbers drawn. To understand the general properties of the system the same starting conditions must be replicated several times with different random numbers. We tried many cases with 100 replicates and found that the essential demographic properties are revealed by as few as 25 replicates. Since the computing costs are considerable, the results which are given below are based on 25 replicates.

We are interested in the representativeness of a single census. To look at this, we must compare the results of our simulation with the population which would be produced deterministically, that is, with the population representing the underlying average vital rates, free of the statistical fluctuations whose magnitude we are investigating. For all of the demographic patterns to be examined, we have iterated the deterministic model 1000 times, so that we know the equilibrium population $N(*)$ (see Appendix) to many decimal places of accuracy.

We have devised two indices to gauge the degree to which a population $N(t)$ is a

reflection of the equilibrium $N(*)$. We need these to determine how well a small population, experiencing statistical fluctuations, represents its underlying equilibrium structure. The first measure, the Index of Numerical Convergence, P, is merely the population size at equilibrium, minus that at time t, divided by the equilibrium size. It is simply the fractional deviation of the actual population from the equilibrium.

The second measure, the Index of Angular Convergence, ϕ, is the angle between the population vector (we treat $N(t)$ as an m-dimensional vector) at time t and that at equilibrium. This is computed from the standard formula for the cosine of the angle between two m-dimensional vectors (e.g. see Schwartz et al., 1960). An angle of 20 degrees or less is, we feel, a close similarity between two age distributions for the small populations in which anthropologists are interested.

We need to know not only the deviation from equilibrium at any time (and the average of these deviations over all replications of the stochastic model), but also some measure of the variability of these deviations. Since we know the population toward which the model tends, we have computed the variance of these error measures about the equilibrium. In the case of the angular measure, we compute only positive values. Since the population oscillates around the equilibrium $N(*)$ in m-space, negative values would have little meaning. Since all values of ϕ are positive (or absolute values), the mean value of ϕ is not expected to be zero. These two indices tell us the degree of representativeness of a census in terms of population size and age composition, which relates to the usefulness of censuses from living populations. Many of us are interested in working with skeletal series since these are our only source of direct knowledge of man's demographic past. We cannot expect to estimate population size directly from the total number of such skeletons, since the length of time of deposition is critical (other methods of inference may be used to deal with this under some circumstances; see Ubelaker, 1974), but we can use the age distribution to determine whether a skeletal series is a fair representation of the demographic processes which produced it. This is done by determining a stationary age distribution from the skeletons (see Weiss, 1973) and by computing of a Graves Index G, which is merely the angle between the actual and the expected age distribution vectors (a measure comparable to ϕ for cemetery populations). This gauges the degree of reliability with which survivorship rates and a life table can be reconstructed from the data. The "actual" age distribution results from our stochastic simulation and the expected distribution is $N(*)$. The graves index indicates the reliability *of the complete cemetery* at any time t, relative to the start of deposition. Errors caused by incomplete sampling must be considered as a separate question which generally must be answered separately for each case. Complete cemeteries may occasionally be available (e.g. Ubelaker, 1974).

3. Results

The demographic properties of a population with density-dependent vital rates are functions of the value of λ, the growth rate intrinsic to the *undamped* vital rates, and of the damping coefficients (a_{ij} and b_{ij}). The damping coefficients determine the magnitude of the feedback effects at any particular population size. The growth rate λ determines how fast the population would grow if the damping term were equal to 1 (zero damping coefficients), and hence the population were determined only by the maximal vital rates P_i and F_i. The undamped growth rate determines what can be thought of as the resiliency of the population. In a population where λ is close to 1, there is very little

potential growth, even in an ideal, undamped environment. If the population becomes overcrowded, the damping coefficients can cause it to rapidly return to its equilibrium composition, but if it becomes rarefied for any reason, its maximum growth rate, by which it returns toward equilibrium, is small. Thus, a stochastic model of such a population should show the maximum degree to which extinction pressure exists. It is easy to show that for a population with a low undamped growth potential, the equilibrium age distribution is very close to that of a fixed-rate model, no matter what the relative values of the damping coefficients. On the other hand, a population with large λ has more marked response to perturbation from equilibrium and the particular pattern of the damping coefficients can have a profound effect on the equilibrium age distribution.

We model three types of population here, to illustrate the range of possibilities. Based on the value of undamped growth, λ, they are populations with high growth potential ($\lambda = 1.95$), medium growth potential ($\lambda = 1.51$), and low growth potential ($\lambda = 1.002$). We have simplified things by setting all undamped vital rates (P_i and F_i) equal, but this does not affect the gist of our results.

To test the effect of equilibrium population size on stochastic stability of the census, we simulate populations with $N(*) = 50$ and 100 individuals. The degree of stability of any stochastic process will increase with larger size, so if these populations produce reliable censuses, so will larger ones.

We use three types of density feedback, to isolate effects which can occur. In the first, only fertility rates respond to crowding, with survival rates unaffected ($b_{ij} = 0$, $a_{ij} = c$). We use the same value for all of the fertility damping coefficients to simplify our results, but we can show that this causes no loss of generality of important information. This pattern may be thought of as a damping only on infant survival rates. It is similar to the feedback now found in industrial nations, which rely largely on fertility control. The second type of feedback is that in which fertility is not damped, but all survival rates are damped; here again, we use a constant damping coefficient ($a_{ij} = 0$, $b_{ij} = c$); crowding affects the survival rate of every segment in the population. The third damping regime we study is one in which only post-infant survivals are damped ($a_{ij} = b_{0j} = 0$; $b_{ij} = c$, $i \neq 0$). Damping of infant survival is a common and effective means of population regulation, but is covered by the first (fertility damping) case. This third pattern tests the effectiveness of damping on the rest of the population instead.

In all, we test 9 populations, using combinations of the types just enumerated; Table 1 gives the details of these models. In addition to these density-dependent cases, we have simulated case number 1b, with no density dependent damping. This is a fixed-rate model for a population of size 50 with virtually zero growth. Such a population should be as sensitive to demographic fluctuation as any we are testing with the density model, and further, since $\lambda \approx 1$, the expected age distribution is like that of cases 3, 6, and 9, and provides a standard of reference. Table 2 gives the equilibrium age distributions of all 9 cases.

The undamped case is shown on the last lines of Table 6. Twenty-five replicates of 100 iterations were run (unless extinction occurred before $t = 100$). The starting population, $N(0)$, was the equilibrium population, rounded to the nearest whole individuals in each class. The means of the three indices of convergence and their variance are given for 3 steps in the simulations to show the progress of the populations over time. The variance is computed for the first 25 populations which survived to the time given.

Table 1   **Cases run**

Case no.	$N(*)$	F_i, P_i all i	Damping type	Damping coefficients		
				a_{ij} all i,j	b_{0j} all j	b_{ij} $i \geq 1$; all j
1	50	0·99	all fertility	0·0316	0	0
2	50	0·75	all fertility	0·01655	0	0
3	50	0·51	all fertility	0·0001	0	0
4	50	0·99	all survivorship	0	0·01332	0·01332
5	50	0·75	all survivorship	0	0·0077654	0·0077654
6	50	0·51	all survivorship	0	0·0000546	0·0000546
7	50	0·99	post-infant survivorship	0	0	0·0919
8	50	0·75	post-infant survivorship	0	0	0·02192
9	50	0·51	post-infant survivorship	0	0	0·000118
1a	100	0·99	all fertility	0·0158	0	0
2a	100	0·75	all fertility	0·002875	0	0
3a	100	0·51	all fertility	$0·4895 \times 10^{-4}$	0	0
4a	100	0·99	all survivorship	0	0·00666	0·00666
5a	100	0·75	all survivorship	0	0·00388	0·00388
6a	100	0·51	all survivorship	0	$0·2627 \times 10^{-4}$	$0·2627 \times 10^{-4}$
7a	100	0·99	post-infant survivorship	0	0	0·04595
8a	100	0·75	post-infant survivorship	0	0	0·01096
9a	100	0·51	post-infant survivorship	0	0	$0·56945 \times 10^{-4}$
1b	50	0·51	no damping	0	0	0

$N(*)$ = equilibrium population size. Cases for $0·99 = F_{ij}P_i$ are *high growth* type ($\lambda = 1·95$), 0·75 is *medium growth* ($\lambda = 1·51$), and 0·51 is *low growth* potential ($\lambda = 1·002$). Case 1b has $\lambda = 1$.

a_{ij} are damping coefficients for fertility, b_{0j} are damping coefficients for infant survival, b_{ij} ($i \geq 1$) are post-infant survival damping coefficients.

It is clear that the threat of extinction, and demographic instability, are significant for a population of 50 with approximately zero growth. Seven of 25 populations reached extinction before 100 iterations. The population size is within 10 percent of its equilibrium value for about 30 iterations, although with high variability; by the end of 100 iterations, however, we can only expect numeric convergence to 80 percent, and a variation so large that any single population can have virtually any size deviation. We cannot have confidence in an observed census size. The age distribution is generally within 10° to 12° of the equilibrium, but its variance is considerable (see below). The graves

Table 2   **Equilibrium age distributions* of cases run**

Case no.	Age class				
	1	2	3	4	5
1	0·204	0·202	0·200	0·198	0·196
2	0·328	0·246	0·184	0·138	0·104
3	0·508	0·258	0·132	0·067	0·034
4	0·509	0·259	0·132	0·067	0·034
5	0·509	0·259	0·132	0·067	0·034
6	0·509	0·259	0·132	0·067	0·034
7	0·990	0·010	0·0001	0·000001	0·00000001
8	0·750	0·188	0·047	0·012	0·003
9	0·510	0·259	0·131	0·066	0·034

* This is independent of equilibrium population size; values rounded to nearest 0·1%.

index shows that the net results of stochastic fluctuations have very little effect on the age distribution which can be reconstructed from a complete burial series; compensating fluctuations are sufficient to guarantee virtually perfect accuracy. This shows that without density damping, one has cause for suspicion of a single census taken from a small anthropological population. Smaller populations than 50 will have considerably more problems, unless several tribal subpopulations can be aggregated.

The results for the fertility damping cases are listed in Table 3. The numeric indices become more variable as the growth rate (λ) decreases. For $\lambda = 1 \cdot 002$, the population size is highly variable among replicates. In all cases, the variance is less for $N(*) = 100$ than for $N(*) = 50$, as expected. The angular index ϕ presents the opposite tendency. As λ decreases, so does the average value of ϕ, as well as its variance. This is due to the fact that the equilibrium age distribution becomes progressively steeper as λ is decreased. This narrows the range of achievable age-distributions, and reduced $\phi(t)$. The graves index G follows the same pattern as the numeric index P. The reason for this is not entirely clear.

The results for general survival damping are shown in Table 4. The numeric index P is more variable for small λ, as before. Neither the angular index ϕ nor the graves index G is responsive to growth rate, since the equilibrium age distribution is the same in all cases. As before, the variance of all measures decreases as $N(*)$ increases from 50 to 100.

The results for post-infant survival damping are shown in Table 5. Again, the numeric index P varies more for low growth than for high growth populations. This time, both the angular index ϕ and the graves index G become more variable as λ is decreased, since the age distribution becomes progressively flatter as λ is decreased. Again, large populations are less variable than small ones, as precited.

In general, low growth-low damping populations are most variable. One may compare such cases with the zero growth (no damping) case, as is shown in Table 6. As can be seen, cases 3, 6, 9 and 1b are essentially interchangeable, as far as the indices are concerned. The zero growth case (1b) experiences more frequent extinctions, but for those populations surviving, there is little to choose among them, as predicted.

The important point is that density damping and high growth potential are counteracting pressures which maintain the population close to the equilibrium structure. For populations of size 100, this stability is quite pronounced, and only low growth cases are quite unstable. For populations of larger size, stability should be considerable.

Because we have only computed age distribution convergence in terms of positive angles, it being rather academic whether the angle between two m-dimensional vectors is positive or negative, it is somewhat difficult to appraise the variance of angular convergence. This is in most cases about equal to the square of the mean of $\bar{\phi}$. Since the populations average $\bar{\phi}$ degrees out of equilibrium and also have mean square deviations of $\bar{\phi}^2$, this implies that most angular deviations are very close to the mean error in magnitude. Although the direction of the angle would actually change as the population oscillates about its equilibrium (i.e. if we computed the sign of the angle, keeping $N(*)$ as the reference vector), the magnitude of the error changes little. The population's age distribution may be thought of as moving in a tightly-constrained cone about the equilibrium vector, generally being $\bar{\phi}$ degrees out of equilibrium. Most populations will be very close to that degree of error. This is as close as we can come to specifying confidence limits for the angular convergence measures.

6

Table 3   Simulation results, fertility damping

Case no.	N(*)	(λ)	Numeric index P			Angular index ϕ			Graves index G		
			20	50	100	20	50	100	20	50	100
1	50	(1·95)									
		mean	−0·008	0·0168	−0·0208	15·6	14·5	12·4	0·3	0·2	0·1
		variance	0·0161	0·0094	0·0094	264	216	165	0·1	0·05	0·02
1a	100	(1·95)									
		mean	0·0028	0·0400	0·0020	10·4	10·4	10·5	0·2	0·2	0·1
		variance	0·0043	0·0050	0·0048	117	126	123	0·08	0·03	0·01
2	50	(1·51)									
		mean	−0·0184	−0·0056	0·0096	11·2	13·8	11·8	1·4	0·9	0·8
		variance	0·0247	0·0232	0·0208	136	208	160	2·2	0·9	0·7
2a	100	(1·51)									
		mean	−0·0064	−0·0124	0·0084	8·9	8·9	7·5	0·8	0·6	0·5
		variance	0·0074	0·0076	0·0142	92	91	61	0·8	0·4	0·3
3**	50	(1·002)									
		mean	0·1032	0·1056	−0·0616	7·0	8·5	10·7	1·3	0·8	0·6
		variance	0·1667	0·3300	0·4346	61	95	158	1·9	0·7	0·5
3a	100	(1·002)									
		mean	−0·0352	−0·0324	−0·0492	5·2	6·7	7·1	0·9	0·7	0·4
		variance	0·1295	0·2251	0·4010	31	47	89	1·2	0·6	0·2

** Lost 4 replicates at iterates 51, 58, 84, 8.

Table 4   Simulation results, survival damping

Case no.	$N(*)$	(λ)	Numeric Index P			Angular index ϕ			Graves index G		
			20	50	100	20	50	100	20	50	100
4	50	(1·95)									
		mean	0·0144	−0·0072	0·0000	8·2	8·3	7·7	1·2	0·8	0·6
		variance	0·0072	0·0084	0·0140	82	80	68	1·6	0·7	0·4
4a	100	(1·95)									
		mean	−0·0016	−0·0124	−0·0448	5·6	5·8	6·0	0·9	0·5	0·4
		variance	0·0045	0·0059	0·0073	35	36	45	0·9	0·3	0·2
5	50	(1·51)									
		mean	0·0136	−0·0160	−0·0096	8·4	8·9	8·5	1·3	0·8	0·5
		variance	0·0087	0·0168	0·0153	81	87	84	2·0	0·7	0·3
5a	100	(1·51)									
		mean	−0·0232	0·0168	−0·0088	5·6	5·0	5·5	0·9	0·5	0·4
		variance	0·0075	0·0092	0·0058	36	28	35	1·1	0·3	0·2
6**	50	(1·002)									
		mean	0·0288	0·1488	0·2080	7·8	9·0	10·9	1·2	0·8	0·6
		variance	0·1540	0·4472	0·8296	75	101	182	1·5	0·6	0·4
6a†	100	(1·002)									
		mean	0·0536	0·0908	−0·1100	5·5	5·2	6·2	0·9	0·6	0·4
		variance	0·1145	0·1404	0·2357	35	31	46	1·2	0·4	0·2

** Lost 4 replicates at iterates 80, 74, 53.
† Lost 1 replicate at iterate 84.

Table 5 Simulation results, post-infant survival damping

Case no.	N(*)	(λ)		Numeric index P			Angular index φ			Graves index G	
				20	50	100	20	50	100	20	50	100
7	50	(1·95)	mean	−0·0032	0·0168	0·0144	0·7	0·8	0·7	0·1	0·1	0·1
			variance	0·0032	0·0021	0·0040	0·7	0·8	0·7	0·03	0·02	0·01
7a	100	(1·95)	mean	−0·0024	0·0204	−0·0088	0·4	0·4	0·5	0·1	0·1	0·1
			variance	0·0029	0·0032	0·0019	0·3	0·4	0·4	0·01	0·004	0·003
8	50	(1·51)	mean	−0·0248	0·0192	0·0328	4·8	4·3	4·2	0·9	0·5	0·4
			variance	0·0121	0·0198	0·0241	29	23	27	1·0	0·4	0·2
8a	100	(1·51)	mean	0·0036	−0·0108	−0·0152	3·1	3·3	3·1	0·6	0·3	0·3
			variance	0·0103	0·0053	0·0105	12	13	11	0·4	0·1	0·1
9**	50	(1·002)	mean	−0·0584	0·1864	−0·0744	8·4	7·7	10·7	1·4	0·8	0·6
			variance	0·0176	0·3420	0·3108	91	75	170	2·1	0·9	0·4
9a†	100	(1·002)	mean	−0·0051	−0·0139	−0·0871	5·8	5·8	7·9	0·9	0·6	0·4
			variance	0·0679	0·1303	0·2846	41	40	157	1·0	0·4	0·3

** Lost 1 replicate at iterate 48.
† Lost 1 replicate at iterate 93.

Table 6 Simulation results, populations with little growth

Case no.	$N(*)$	(λ)	Numeric index P			Angular index ϕ			Graves index G		
			20	50	100	20	50	100	20	50	100
3**	50	(1·002)									
		mean	0·1032	0·1056	−0·0616	7·0	8·5	10·7	1·3	0·8	0·6
		variance	0·1667	0·3300	0·4346	61	95	158	1·9	0·7	0·5
6†	100	(1·002)									
		mean	0·0288	0·1488	0·2080	7·8	9·0	10·9	1·2	0·8	0·6
		variance	0·1540	0·4472	0·8296	75	101	182	1·5	0·6	0·4
9‡	50	(1·002)									
		mean	−0·0584	0·1864	−0·0744	8·4	7·7	10·7	1·4	0·8	0·6
		variance	−0·0176	0·3420	0·3108	91	75	170	2·1	0·9	0·4
1b§	100	(1·002)									
		mean	0·0496	0·2504	0·1864	8·8	9·0	11·9	1·3	0·7	0·6
		variance	0·2188	0·6677	1·1039	112	123	290	1·9	0·7	0·4

** Lost 4 replicates at iterates 51, 58, 84, 8.
† Lost 1 replicate at iterate 84.
‡ Lost 1 replicate at iterate 48.
§ Lost 7 replicates at iterates 86, 69, 78, 73, 59, 40, 74.

In general, feedback based on fertility damping is slower-acting than that based on mortality, since disequilibrium effects in production of new individuals can only be introduced by way of age class 1, whence they must "age" their way along the census vector. This is why, with zero-growth fertility rates at present, the United States must still grow for several decades to come. With mortality damping, the survivorship of those left alive can decrease to restore population faster toward equilibrium. Hence with fertility-damping feedback, reaction is slower and errors are somewhat larger. With post-infant survival damping, feedback is fast, since infants are produced in large numbers from undamped reproduction, per parent, and mortality can cull these parents at all age classes when the population is crowded, and can allow them to survive—and hence reproduce—better when population size is down. Real situations will have combinations of these density reactions, of course, and will generally converge very rapidly and maintain close equilibrium. The pure damping strategies we have used merely illustrate their different effects when applied in isolation.

4. Discussion

We have found that a population with low growth potential is an unreliable source for single-census-based demographic statistics, because stochastic aspects of vital processes cannot be overcome by density-dependence. Populations with greater growth potential are demographically reliable to levels of accuracy to which anthropologists can aspire. Extinction is rare over a period of many generations, and the age distribution is not likely to deviate too far from its equilibrium form. Complete burial series are almost totally unaffected by stochastic processes. All of these results confirm the preliminary nonstochastic study by Weiss (1975) along these lines, where it was shown that even epidemics, wars, and so on, do not necessarily distort the age distribution for very long time periods.

These conclusions must be qualified to stress that (a) one must not attempt to reconstruct equilibrium vital rates from a census when there is evidence that systematic disruptions have recently occurred, (b) the basic demographic patterns must have prevailed for several decades prior to census, (c) the group must be in a viable state at the time of observation and of size at least 50 and preferably closer to 100 or more, (d) the census must be complete, and (e) one must be willing to accept the occasional severely distorted population, or out-lier, in the usual statistical sense.

It is obvious that recently disturbed populations should not be used to estimate general prevailing demographic rates, and that an incomplete census or a census for which many peoples' ages are doubtful must be dealt with carefully. We have shown that stochastic processes *by themselves* do not constitute a prohibitive disturbing force. This finding is somewhat corroborated by the general similarity of censuses from widespread anthropological populations (e.g. see Acsádi & Nemeskéri, 1970; Salzano, 1972; Weiss, 1973). This is true of some subpopulation census data as well: age distributions appear very similar to each other; this has been observed, for example, among Yanomama and in Micronesian data (personally examined by K.M.W.).

It seems well-established from our results that stochastic processes of life and death do not provide any substantial problem to the analysis of skeletal demographic data, if deposition has accumulated over a few generations. The overwhelmingly more

important problems with such data involve the proper exhumation of juveniles, correct aging of skeletons, and the representativeness of the cemetery. Often, with care, these can be overcome (e.g. see Ubelaker, 1974).

Many different sets of age-specific birth and death rates can produce the same age distribution. However, if growth has been zero, or at least constant, for several decades, one can reconstruct death rates from a census. If we can further assume (or determine) a pattern of relative age-specific fertilities (Talwar, 1970; Weiss, 1973), then we can estimate the actual fertility rates as well, and can compute most demographic measures which are of interest to us.

Although we can reconstruct the details of the equilibrium population, we cannot infer the density-dependent process by which it is brought about. This is because we reconstruct only the values of $P(i, *)$ and $F(i, *)$, but the density factors are combined inseparably within these rates. Reasonable assumptions on the pattern of feedback might be made in some ethnological cases, however.

This model has instantaneous density feedback. Real populations will experience some lag time in response, although this must be limited, since if it were too great the feedback system would not be adaptive. Lag times are unlikely to affect the results we have found in any important way, but should increase the magnitude of the variance in all measures. Our experimental work with this model has been extensive, and we have had difficulty even contriving deviant cases. Our results depend only to the extent of fine detail on the particular type of density feedback used, which may affect the age distribution at equilibrium greatly, but has little effect on stability or stochastic resilience,

We cannot deal here with the question of the existence of biological equilibria in the first place. If the time period is long enough for largescale disturbances to be smoothed out, and short enough not be be affected by major ecological changes (such as climate, food sources, etc.), then it seems clear that a population will be constrained to a great extent in terms of size and age distribution. The similarity of anthropological populations in this regard is strong support for this statement. We have sought to estimate prevailing equilibrium rates. From the standpoint of many questions about human populations, it is the approximating of these general prevailing rates which is important. Their fine detail, and specific aspects of their fluctuations, are useful questions in their own right, but we are here interested in the average rates rather than in the variances. If anthropological data do not supply adequate information on average underlying equilibrium conditions, then surely we have no hope of analyzing the fluctuations about these averages. We have found that the data may be sufficiently reliable for the equilibrium vital rates to be inferred.

Appendix

We let the census at time t, grouped into m age classes of equal length, be represented by the vector $N(t)$ with elements $n(i, t)$, the census count for the ith age class. The probability that an individual in age class i at time t survives to age class $i + 1$ at time $t + 1$ is $P(i, t)$, and similarly, the chance that individual produces an offspring of the same sex is $F(i, t)$.

If we represent the transition of the population from $N(t)$ to $N(t + 1)$ in the standard matrix way (e.g. see Keyfitz, 1968), then with $M(t)$ the density-dependent transition

matrix, we have

$$N(t + 1) = \mathbf{M}(t)N(t) \tag{A1}$$

or

$$N(t+1) = \begin{bmatrix} P(0,t)F(1,t) & P(0,t)F(2,t) & \cdots & P(0,t)F(m,t) \\ P(1,t) & 0 & & 0 \\ & & \cdot & \\ & & \cdot & \\ 0 & P(2,t) & \cdot & \\ \cdot & \cdot & \cdot & \\ \cdot & 0 & \cdot & \cdot \\ \cdot & \cdot & \cdot & \cdot \\ 0 & \cdot & \cdot & \cdot \\ & \cdot & \cdot & \cdot \\ & 0 & P(m-1,t) & 0 \end{bmatrix} N(t). \tag{A2}$$

$P(i, t)$ and $F(i, t)$ are the functions of $N(t)$ given in equations (1) of the text. Since $\mathbf{M}(t)$ varies with $N(t)$, it is *not* generally true that $N(t + k) = M(t)^k N(0)$, as is fundamental to the approach to equilibrium of the *fixed-rate* model. In that model, the fixed matrix $\mathbf{M}$ has dominant eigen value λ, and eventually the population approaches an age-distribution equilibrium and a growth rate of λ. Hence, eventually $N(t) = \lambda^t N(0)$, taking as the zero point, a time when the age distribution has converged close to its equilibrium.

At any time t, our model has dominant eigen value $\lambda(t)$, which converges to a stationary value of $\lambda(*) = 1$. Using (*) to represent the fact that the system is no longer changing we can say that

$$N(*) = \mathbf{M}^* N(*), \tag{A3}$$

and then the equilibrium age-specific vital rates, $P(i, *)$ and $F(i, *)$, are fixed. The details of this model, including a discussion of its stability, are given in Smouse & Weiss (1975). We have slightly modified the indices of convergences here since we know $N(*)$.

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