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Zoo-Related Organizations Files.

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February 26, 1976 ⁴⁸

Tom Foose
Philadelphia Zoological Garden
34th Str. and Girard Ave.
Philadelphia, Penn. 19104

Dear Tom:

I am pleased that we had the opportunity to meet and discuss the application of your work with demographic models to the ISIS data base and to studbook data. I am looking forward to your visit with us in March. I have discussed the times we've talked about with Don and Brad, Nate and Dale. We suggest you plan on coming March 10th and stay one week, if we can get a contract approved in time. If not it would be the 17th or 24th. Don Bridgwater will be in touch regarding contract procedures and times.

I am particularly delighted that you feel it would be possible to develop the initial models and the computer programs for data analysis for Przewalski's horse and Arabian oryx studbook data prior to our meeting in Switzerland in May. As I indicated we would like to formulate a contract with you to accomplish these and several other tasks as we discussed them. The contract would be for \$1,500.00 with the understanding that your plane fare, room and board would be paid for by you under this upset limit. The projects to be completed under the terms of our discussion would be first, formulation of the models, computer programming of the models and their successful application to the Przewalski's horse and Arabian oryx data base. The models would evaluate on the basis of the data available the likely formation and composition of stable populations under one management concept and the consequences of a growing population with removal of animals for implantation in the wild. The latter should include an indication of the animals to be removed with considerations, of course, given to biological constraints required for the animals to survive in the wild. Alternatively it would, I presume, be possible to remove animals from the captive breeding population and rear them to an appropriate age with an initial formation of herds etc. It would also be of interest to estimate the kind and extend of introduction that should be accomplished over a period of how many years to reestablish a wild population, perhaps somewhat in the manner as has been done with the peregrine falcon population. I will determine what data will be available on the biology of these animals in the wild or where analogies might be drawn from some of the available zebra data. I will pass this on to you. The second task would be to accomplish essentially a Phase I analysis for the establishment and application of demographic analysis to the ISIS data base on a recurring basis. This would include a specification of any additional data elements needed and the types of arrangements of available data elements required to successfully

apply the demographic model. Consideration should also be given to the format of the output of the system so that it would be usable both for technical purposes and management purposes by the appropriate zoo people.

If you have further comments or suggestions to make concerning the above task, especially to allow more precise formulation, please do not hesitate to make them. I am delighted that you have developed and pursued this interest in demography as applied to captive populations for I think that it will make a tremendously important contribution in a sorely needed area where each individual institution has formulated its own ideas without having the benefit of computer projection using available models to estimate the consequences of the choices being made.

Best regards and looking forward to seeing you again.

Sincerely,

U.S. Seal

U.S. Seal

USS/kh

CONSERVATION - RESEARCH - EDUCATION - RECREATION
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UNDER THE MANAGEMENT OF THE
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Dr. U.S. Seal
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Dear Dr. Seal:

As I believe you know from Nate Flesness, with whom I have been communicating periodically for about a year now, I am very interested in and have been working on some demographic models for management of zoo populations. Somewhat belatedly perhaps, this letter is intended to indicate to you what I have been doing and hopefully to initiate more formally and completely the collaboration I believe I have tentatively begun with Nate.

Enclosed is a copy of a very preliminary paper on demographic models that I presented in December, 1975 to a meeting of ZEST (Zoo East Survival Trust, the embryonic consortium being gestated by Bronx, Philadelphia, and Washington). It was prepared in haste and perhaps overambitiously attempts to introduce laymen to some pertinent fundamentals of matrix algebra and to describe in general terms the models I am attempting to apply to management of zoo populations. Unfortunately, I'm afraid it does neither job very well. So let me try to restate a bit more directly, I hope, the kind of demographic methods and results that I think can be used to develop self-sustaining zoo populations.

Basically, I am attempting to apply models developed by Leslie. (See References on ZEST paper.) These models use three parameters:

n_{xt} = the number of females (see below) alive in each age group x to $x+1$ at time t , i.e. the age distribution of the population.

P_x = the probability that a female in age group x to $x+1$ at time t will be alive in the age group $x+1$ to $x+2$ at time $t+1$, i.e. this is the age-specific survival.

F_x = the number of female offspring (1) born to females age x to $x+1$ during the time interval t to $t+1$, and (2) surviving to time $t+1$, i.e. this is the age-specific fertility.

It is conventional and convenient to let the intervals of age (x) equal the intervals of time (t). Also animal demographers usually restrict their attention to the females, assuming males will take care of themselves.

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But in zoo situations, males must and can be treated equally as well; just substitute male for female in the above definitions and what follows and probably change offspring born to offspring conceived in the definition of F_x . (There is more on this matter in the ZEST paper.)

The values of these parameters can of course be compiled from studbooks and/or ISIS records. Studbooks provide what demographers would refer to as non-coeval cohort data. ISIS records will provide static data, i.e. survival and fertilities during a specific time period for each of the age classes entering that time interval.

In the ZEST paper, I distinguish between "potential" and "managed" F's and P's. (By potential F's, I am merely implying that there is no active attempt to prevent breeding; it does not imply that there are none of the myriad passive impediments to zoo breeding that zoo conditions can present.) The F's and P's compiled from studbooks and/or ISIS records represent a mixture of the potential and the managed. Moreover, even where animals are being allowed to breed more or less at liberty, it is probably important to distinguish between cases where young are removed, by necessity or just policy, to be raised by hand and those cases where animals are raised by their mothers. Being a "naturalist" I would prefer to consider only those cases where animals raise their own young for the potential values. But this may be unrealistic or subjective.

The F's and P's are probabilities, computed in practice as means. Elementary discussions usually treat the Leslie models as deterministic; but, of course they can be stochasticized.

With any set of F's and P's (potential and/or managed) and the n_{xt} 's (i.e., the age distribution at some time; the age distribution now is represented by the n_{x0} 's), the population size and age distribution in the next unit of time can be projected. To repeat, both deterministic and stochastic projections are possible. Mechanically, the projections are generated by forming the F's and P's into a "projection matrix" and postmultiplying this by the age distribution vector:

$$\begin{array}{c}
 \left[\begin{array}{cccccc}
 F_0 & F_1 & \dots & F_{m-1} & F_m & \\
 P_0 & 0 & & 0 & 0 & \\
 0 & P_1 & \dots & 0 & 0 & \\
 \dots & \dots & \dots & \dots & \dots & \\
 0 & 0 & \dots & P_{m-1} & 0 &
 \end{array} \right]
 \begin{array}{c}
 \left[\begin{array}{c}
 n_{00} \\
 n_{10} \\
 n_{20} \\
 \vdots \\
 n_{m0}
 \end{array} \right]
 =
 \begin{array}{c}
 \left[\begin{array}{c}
 n_{01} \\
 n_{11} \\
 n_{21} \\
 \vdots \\
 n_{m1}
 \end{array} \right]
 \end{array}
 \end{array}$$

$\underline{M} \qquad \underline{N}_0 \qquad \underline{N}_1$

If the F's and P's do not change, the population size and age distribution some r units of time from now is provided by:

$$\underline{N}_r = \underline{M}^r \underline{N}_0$$

If the F's and P's do change from time to time, future population states can be projected by a series of matrix multiplications:

$$\underline{N}_r = \underline{M}_r \underline{N}_{r-1} \cdots \underline{M}_2 \underline{M}_1 \underline{N}_0$$

If the F's and P's will or can be made to stay constant (as should be possible with managed F's and P's, especially if they are well below potential limits), the population will in most cases (See below) eventually tend to change in size at a constant rate and will attain a stable age distribution (i.e., a fixed distribution of the relative proportions in each age class). This ultimate, constant rate of change and the stable age distribution can be derived directly from the matrix \underline{M} of F's and P's.

With each such matrix \underline{M} , there will be associated a unique set of numbers, symbolized by λ 's and termed eigenvalues (also characteristic values, latent roots, etc.). The number of eigenvalues equals the order of the matrix \underline{M} (i.e., the number of rows or columns in the matrix). However, because of the nature of the entries (F's, P's and O's) in the projection matrices, only one of these eigenvalues will be real and positive. This is called the dominant eigenvalue, λ_1 , and is in fact the ultimate, constant rate of change described above. If $\lambda = 1$, the population will not change in size; if $\lambda > 1$, the population will ultimately increase; if $\lambda < 1$, the population will ultimately decrease to extinction.

With each eigenvalue, and only the dominant one will be of interest in this regard, there is associated a unique but infinite set of eigenvectors. Each eigenvector has the same number of entries as there are age classes distinguished in the population. Although there is theoretically an infinite number of such eigenvectors associated with any dominant eigenvalue of a projection matrix, the elements in any one of the eigenvectors are in the same proportions to one another as are the corresponding entries in any other eigenvector. For example, two eigenvectors in the set associated with some eigenvalue might be:

$$\begin{bmatrix} 10 \\ 5 \\ 2 \\ 1 \end{bmatrix} \quad \begin{bmatrix} 20 \\ 10 \\ 4 \\ 2 \end{bmatrix}$$

The eigenvectors indicate the relative proportions of numbers in each age class when the stable age distribution is reached.

The speed and smoothness with which a stable age distribution is attained depends on the values of the F's and P's as well as on the initial age distribution of the population. There are some values and combinations of F's and P's that when applied to certain initial age distributions will never eventuate in a stable age distribution. Other sets of F's, P's and n_{x0} 's will attain the stable condition only after severe fluctuations. Such problems can be detected by analyses of the relative values of the dominant eigenvalue versus the other eigenvalues, in relation to the initial age distribution. Fluctuations become severe and failure to attain stable age distributions becomes significant when the dominant eigenvalue is not sufficiently greater than the other values. In general, the larger the dominant eigenvalue, λ_1 , the faster and smoother will be the movement to the stable age distribution. It also usually helps if the initial age distribution is close to the stable age distribution.

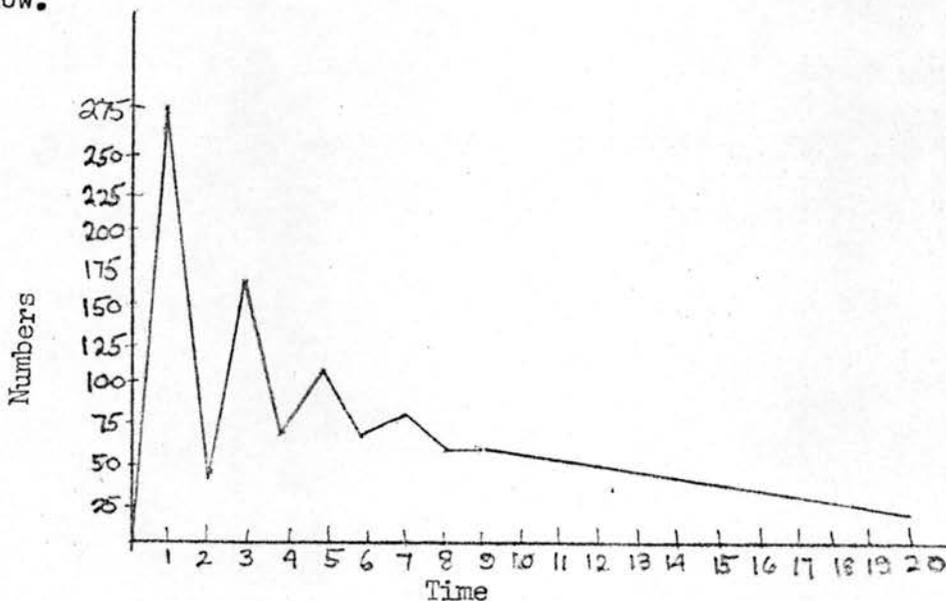
Consequently, if F's and P's stay relatively constant, it is possible not only to project the course of population numbers and age distribution but also to

- 1). determine if a stable age distribution is possible and if so what it will be.
- 2). determine what the ultimate, constant rate of change will be.
- 3). determine how long (how many time intervals) will be required to attain a stable age distribution.
- 4). predict the population size when the stable age distribution will be reached.
- 5). predict the fluctuations in population numbers and age distribution that will occur between now and the time the stable age distribution is attained.

The ability to generate such long-term predictions is of great value since short-term trends can be very deceptive. Consider an example presented by Poole (See References in ZEST paper.):

$$\text{Let } M = \begin{bmatrix} 0 & 6 & 18 & 18 \\ .10 & 0 & 0 & 0 \\ 0 & .09 & 0 & 0 \\ 0 & 0 & .05 & 0 \end{bmatrix} \quad \text{and let } N_0 = \begin{bmatrix} 0 \\ 0 \\ 20 \\ 0 \end{bmatrix}$$

Hence mortality is very high in the early age classes; the population begins with 20 individuals in the third age group. The dominant eigenvalue of the matrix is approximately 0.9, so the population is doomed to eventual extinction. However, beginning with N_0 , the population will change in total size as indicated by the graph below.



Even though the population is doomed to extinction, it increases to very high levels (over 275), persists for over 20 time intervals, and does not even decline below its initial size of 20 until 17 time intervals later.

This might be an appropriate point to comment on the note by Dick Thorington concerning definition of self-sustaining populations in a letter to John Perry dated Jan. 13, 1976. I just received a copy of this note yesterday through Wayne King so I have not had time to analyze it thoroughly. My initial reaction is that it is somewhat too simplistic and susceptible to miscalculations deriving from age

distribution problems such as the last example illustrates.

Beyond predicting how population size and age distribution will change from some initial state subject to some set of F's and P's, the Leslie models also demonstrate how to alter the F's and P's and/or the age distribution to produce and maintain some stable (if an increase or decrease is desired) or ultimately stationary population.

A stationary population is one in which the age distribution is stable and the population size is constant. The criteria for a matrix of F's and P's to characterize a stationary population is that the dominant eigenvalue, λ_1 , be equal to 1. A stationary population is in my opinion the ultimate manifestation of a "self-sustaining" population.

The ultimate projection matrix for a stationary population must have $\lambda_1 = 1$. But usually, there will be more than one set of F's and P's within the limits set by their potential or initial values for each species that will produce a matrix with $\lambda_1 = 1$. So there will be some latitude in selection of the stationary matrix to be ultimately applied as the management plan.

Conversion of an initial matrix into a stationary matrix will involve alteration of either or both of the F's and P's. In most cases, the conversion could probably be accomplished by manipulating the F's alone. This would have public relations and emotional appeal because it would not involve killing any animals. However, it is demographically sounder to depend on management of both F's and P's.

Among the reasons arguing for management of P's: 1) There will be genetic/phenotypic defectives and by always having a quota to remove in each age class (or at least those where defectives are most likely to become evident), such defectives can be removed without disrupting the age structure of the population. 2) The F's and P's are only probabilities. It may be expected that only 20% of some age class will expire in a certain interval of time. But, by chance, 30% might die. If the stationary management matrix is predicated on the 20% figure, the population would be seriously disrupted by the additional 10% mortality. However, if the managed P for that age class specified a 40% mortality or culling, then the additional 10% natural mortality would merely mean less culling would have to be done.

To reiterate, public relations and emotions will militate strongly for a minimum amount of lethal culling, at least in the immediate future, and it probably will be possible in most cases to develop and apply the models largely by manipulating the F's.

And it is very desirable for demographic reasons to manage the F's well below the potential values. When operational, the management models would specify the number of offspring that should be produced by animals of each age class in each interval of time. Presumably the individual from each age class to be bred would be selected from all those available by some set of genetic criteria and a biopolitical priority system. But a selected individual may fail to reproduce as expected. Another animal may have to be substituted. If the management model depends on all animals reproducing at the expected maximum (as Conway's theoretical model for Pere David's deer does), there can be problems.

This possible problem reveals another reason for imposing considerable culling as part of the management plan. By the time it is determined that an individual

selected for breeding is not going to reproduce as expected, it may be too late to mobilize the substitute in that time interval, again causing disruptions to the population. However, if culling is heavy in the first or several early age classes, an effective "excess" of young can be produced to insure against unexpected reproductive failures.

The major problem is how to get from the age distribution, population size, and schedule of F's and P's existing now (i.e., initially) to a stationary population of some desired size, i.e. K the carrying capacity of zoos (to be determined by some set of genetic, logistic, etc. criteria).

If the initial population is well below K and the initial F's and P's are such that the dominant eigenvalue is high and hence a stable age distribution and rapid rate of increase can be attained quickly, Leslie has presented a systematic model for converting the original population and its projection matrix into a stationary population and matrix at some K.

If the initial population is already large (near, at, or above K), but there is a good representation in all the age classes, the stationary population might be created in two ways. Within the limits of the initial or potential F's and P's, one or more stationary matrices (i.e., $\lambda_1 = 1$) could be constructed. Each such matrix will generate an associated stationary age distribution eigenvector. Then, it might be possible to create one or more of these stationary age distributions at some desired population size by immediate culling from the existing age distribution. Once such a stationary age distribution is created, application of the stationary matrix as the management model will maintain the population in the stationary condition.

As a second alternative, the stationary matrix could be applied directly as a management plan to the existing population and the conversion of the population to stationary status would then occur over several intervals of time. This might be the preferable alternative, especially if the stationary matrix is predicated mostly on contraception (management of F's) rather than killing (management of P's). (Of course as long as the management model is being applied to some subset of zoodom, such as U.S. zoos or if there is the possibility of returning animals to the wild, culling does not necessarily mean killing. However, frequently or ultimately, it probably will.)

As an example of converting an initial, nonstationary population to stationary status, consider the approximately stationary matrix ($\lambda_1 = .996$) of managed F's and P's from Conway's theoretical model for Pere David's deer. (See pages 22 and 23 of the ZEST paper.). The matrix and its associated stationary eigenvector are:

$$\begin{bmatrix} 0 & .38 & .38 & .38 & .38 \\ 1 & 0 & 0 & 0 & 0 \\ 0 & .80 & 0 & 0 & 0 \\ 0 & 0 & .75 & 0 & 0 \\ 0 & 0 & 0 & .33 & 0 \end{bmatrix} \begin{bmatrix} 5 \\ 5 \\ 4 \\ 3 \\ 1 \end{bmatrix}$$

Suppose the initial population is:
$$\begin{bmatrix} 26 \\ 14 \\ 10 \\ 4 \\ 7 \end{bmatrix}$$
 Total = 61

(This incidentally is the total numbers of both sexes in each age class in Conway's 1978 projection for Pere David's, but all animals are being considered females for purposes of this example.)

If a total population of 18 females can constitute the desired K in this case, then a stationary population could be attained immediately by culling to reduce the population to:

$$\begin{bmatrix} 5 \\ 5 \\ 4 \\ 3 \\ 1 \end{bmatrix}$$
 Total = 18

Note that another possible stationary population for this matrix would be:

$$\begin{bmatrix} 10 \\ 10 \\ 8 \\ 6 \\ 2 \end{bmatrix}$$
 Total = 36

However, this age distribution could not quite be created from the initial one above because there are not enough females (only 4) in the fourth age class.

Once the stationary age distribution of 18 females as presented above is created, the population size and age distribution can be kept constant by applying the stationary matrix as the management policy.

Alternatively, if a population of about 60 females could or would better constitute K, then the stationary matrix could be applied over successive intervals of time to the initial age distribution with the following results:

| | | | | | | | |
|----------|-----|-----|-----|-----|----------------------|---------------------------------------|---|
| 0 | .38 | .38 | .38 | .38 | 26 | 13 | 17 |
| 1 | 0 | 0 | 0 | 0 | 14 | 26 | 13 |
| 0 | .80 | 0 | 0 | 0 | 10 | 11 | 21 |
| 0 | .75 | 0 | 0 | 0 | 4 | 8 | 8 |
| 0 | 0 | 0 | .33 | 0 | 7 | 1 | 3 |
| <u>M</u> | | | | | <u>N₀</u> | <u>N₁ = MN₀</u> | <u>N₂ = M²N₀</u> |
| | | | | | Total = 61 | Total = 61 | Total = 59 |

| | | | |
|---|--|---|---|
| $\begin{bmatrix} 17 \\ 17 \\ 11 \\ 16 \\ 3 \end{bmatrix}$ $N_3 = M^3 N_0$ | $\begin{bmatrix} 18 \\ 17 \\ 14 \\ 8 \\ 5 \end{bmatrix}$ $N_4 = M^4 N_0$ | $\begin{bmatrix} 17 \\ 18 \\ 14 \\ 10 \\ 3 \end{bmatrix}$ $N_5 = M^5 N_0$ | $\begin{bmatrix} 17 \\ 17 \\ 14 \\ 10 \\ 4 \end{bmatrix}$ $N_6 = M^6 N_0$ |
| Total = 64 | Total = 62 | Total = 62 | Total = 62 |

By time interval 6, the age distribution has pretty well settled down to the stationary distribution. N_6 is proportional to:

| |
|------|
| 5.00 |
| 4.98 |
| 4.18 |
| 3.03 |
| 1.03 |

Total numbers stay fairly constant through the six time intervals.

Other situations of initial age distributions, population sizes, and sets of F's and P's may require some more playing around on the computer to determine the best course from initial to stationary conditions.

In any case, the models will produce bottom-line sets of recommendations about how many animals to retain or remove in each of the age classes and how many offspring should be produced by animals in each of the age classes to create or maintain some stable or stationary population.

The ability to project future population sizes and age distributions as well as to establish criteria for attaining and maintaining stable or stationary populations removes, I believe, any theoretical difficulty of defining a "self-sustaining population."

To recapitulate, a general algorithm for application of these demographic models is:

1. Determine the F's, P's and n_{x0} 's (i.e., the initial age distribution) for the population.
2. Project how the population will change from now until at least the next unit of time.

If the F's and P's remain constant

3. Project population changes further in time.
4. Compute the eigenvalues of the projection matrix; from the dominant eigenvalue, λ_1 , determine if population will ultimately increase, stay constant, or decrease to extinction.
5. Determine the stable age distribution if it exists and compare it with the present age distribution.
6. Determine how soon and at what population size the population would attain a stable age distribution.

7. Decide upon K .
8. Within limits of potential or initial values of the F 's and P 's, construct the one or more projection matrices whose dominant eigenvalue, λ_1 , is 1.
9. Determine the stationary age distribution eigenvectors associated with each of these matrices.
10. Devise how to get from the present or initial population size and age distribution to the stationary age distribution at K , in some desirable and possible way. (For example, we might want to minimize culling or to produce one of the stationary age distributions that for some reason is more attractive than other possible ones.)

I am still in the throes of trying to collect age-specific survival and fertility data for several species, and to compose a computer program for the models. Obviously, I am behind the schedule proposed in the ZEST paper. Part of the problem has been the difficulty in obtaining data (e.g. the Siberian tiger studbook) for the species I had originally selected for treatment on criteria other than having the data in hand (probably a mistake). —

However, most of the sluggishness in my progress is due to my other major commitment. Currently, I am conducting my Ph.D. research under Monte Lloyd out of the U. of Chicago. This research is attempting to compare how wild species of ruminants versus nonruminants extract various nutrients from hays varying in chemical composition (most importantly fiber content) to test some hypotheses relating to the ecological strategies and evolutionary histories of gastric versus cecal digester ungulates. Under separate cover I am sending you a copy of my N.S.F. proposal (now finally funded) for this research. Included will be my C.V.

By necessity I spend a lot of my time shovelling shit, grinding hay, etc. Winter is my busiest season because animals are inside and hence more manageable much of the time and there is not the complication of public feeding. As a consequence of this other research, my progress on the demographic model work has been slower than I would like, especially since in my opinion the problem of developing viable captive populations is more interesting and important than the necessarily rather academic research I'm doing for my degree. However, my professor sympathizes with my situation and appears willing to allow me to work as much as I want or need on the models. In any case, I hope to have all my nutritional data collected by December of this year at the latest.

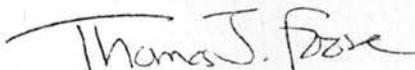
I would hope that I might be able to work with you, Nate, and others at ISIS in development of your overall management models for captive populations. As indicated in the ZEST paper, Nate and I have discussed the possibility of collaborating, dividing labor between us along genetic and demographic lines. To a large extent, I think the demographic and genetic components of an overall model can be developed independently and then applied sequentially. The demographic model will indicate the numbers and ages of animals to be retained or removed in the population and will specify the number of offspring to be produced by each age class. The genetic model will then identify the best of the several possible individuals in each class that should be selected for retention, removal, or reproduction.

If you are amenable to such collaboration, I would further be interested in the possibilities for post-doc or real job opportunities with ISIS sometime in the near future, i.e. in the fall or winter when I will be completing data collection for my nutritional research. Nate and I were discussing this prospect when I called him the other day and he may have mentioned it to you.

My long-term professional aspirations are to work with zoos, especially in the area of developing and implementing masterplans for preserving species in captivity. I do also enjoy everyday curatorial work, when it involves animals. Consequently, I might be particularly interested in some sort of joint position both working on the demographic models with ISIS and serving in a curatorial capacity at MZG. I know both Don Bridgewater and Brad House and have been intending to contact them about job possibilities in the near future.

I do expect to be at the AAAS meeting on zoos and conservation on Monday, Feb. 23. Perhaps we can discuss models, jobs, etc. further there.

Sincerely,

A handwritten signature in cursive script that reads "Thomas J. Foose". The signature is written in dark ink and is positioned above the typed name.

Thomas J. Foose

T.J. Foose
Philadelphia Zoo
Dec. 19, 1975

DEMOGRAPHIC MODELS FOR MANAGEMENT OF ZOO POPULATIONS

Introduction:

At the first meeting of ZEST in Philadelphia, August 15, 1975, I indicated my interest in and intention of attempting to develop models for management of captive populations of various species. A brief statement about the conceptual nature of such models was distributed at that time. (Foose, 1975) During the ZEST meeting, such models were discussed, in specific reference to several species, notably Siberian tigers (Panthera tigris altaica) and pigmy hippos (Choeropsis liberiensis). It was decided that I should proceed with development of some models, and when operational apply them to the particular problem of managing Siberian tigers in captivity in general and the ZEST zoos in particular.

This paper is a progress report on what I have been able and unable to do since the August meeting toward developing an operational version of my model.

Genetic and Demographic Nature of Complete Management Models:

Models for management of populations in captivity on a long-term basis will need to consist of both demographic and genetic components. The basic problem is to produce and/or perpetuate self-sustaining populations of some determined size. The size of the population to be maintained will have to be based on logistic, conservation, genetic, and demographic criteria, although in general the demographic models will be able to accommodate almost any size determined by the other criteria. As Perry and Kibbee (1975) discuss, the carrying capacity of zoos is painfully finite. Only so many animals of whatever species can be accommodated. The identity and numbers of each species maintained should be determined by the status of a species (relative to the status of other species) in the wild as well as by the ecological characteristics of the particular species (e.g. solitary versus social species).

Genetic considerations will probably argue for as large a population of any species as possible to maintain maximum genetic variability and heterozygosity. Genetic drift (loss of genes due to sampling errors) and inbreeding are both functions of population size and can become significant in populations of 100 or less.

Whatever the size of the population, it will consist of a number of individuals differing in age (i.e., the population has an age distribution or age structure), sex (i.e., the population has a sex ratio), and genotype (i.e., the population has a genetic composition). Some of these individuals can and may reproduce, but individuals will possess different reproductive patterns or potentials (i.e., fertilities or potencies) depending on age, sex, and genotype.

The demographic components of any management model must specify the numbers, ages, and in part sexes (sex ratio may be largely determined by genetic criteria) of the individuals to be maintained (or complementarily removed) from the population. It must also indicate the number of progeny that should be produced in any interval of time (for example, a year), and also indicate the number, ages and sexes of the individuals that are to be bred to produce these offspring.

The genetic components of a management model must specify which of the usually several animals of the same age or sex but different genotypes, are to be maintained, removed, or bred.

To an extent, the demographic and genetic components of a management model can operate independently. The demographic component provides general directions for management in terms of numbers, ages, and sexes. The genetic components refine the demographic criteria by specifying the actual individuals to be manipulated by management. So usually, the demographic and genetic components could be applied in sequence to a problem.

However, there are important areas of overlap and interaction between the demographic and genetic components. The age-specific survival and fertility

may vary significantly with genotype so that a realistic demographic model has to be sensitive to genetic differences among individuals. This conceptually and technically is not too difficult as will be discussed again later.

Other genetic criteria of a management model can have direct consequences on the demographic component. For example, when trying to reduce the genetic hazards of loss of heterozygosity or diminution of genetic variability through inbreeding or genetic drift, it is helpful to extend generation time as much as possible by postponing reproduction in individuals until older ages. The demographic component must reveal how much postponement is possible without dooming the population to extinction by menopause.

Moreover, as indicated earlier the problem of sex ratio is determined by both genetic and demographic criteria. Inbreeding and genetic drift both increase as population size decreases. However, the population size of relevance is not merely the body count of a species in the collection, but is rather the effective population size that is defined to depend on the number of males and females actually participating in reproduction as well as on the variance in family size (i.e., number of progeny) per individual. Flesness (1975) has presented a very informative graph of the relation among effective population size, sex ratio, and variance in family size.

As an example of the significance of these effects, consider the relation between effective population size and sex ratio (disregarding any variation in the size of families of individuals):

$$N_e = \frac{4N_m N_f}{N_m + N_f}$$

where

N_e = effective population size

N_m = number of males participating in reproduction.

N_f = number of females participating in reproduction.

Although the total census of Siberian tigers in the ZEST zoos is $5/10$ or a total of 15, only $2/3$ are breeding so the effective population size is 4.8 (i.e. a little less than five, the $.$ being a real decimal point and not a symbol to separate counts of males and females). For pigmy hippos, the total census in the ZEST zoos is $4/12$ or a total of 16, but only $3/6$ have been breeding so the effective population size is currently 4.5.

Naturally, behavioral criteria may also be relevant in determining sex ratios. Conway (1974) for example discovered that a social structure of at least $1/5$ has been requisite for effective reproduction of Przewalski horses (Equus przewalskii) in captivity. Still, genetically it is probably better to equalize sex ratios as nearly as possible. In this case, both the genetic and behavioral conditions for success could be satisfied by maintaining a number of males that could be rotated to herds of females.

In conclusion, with the realization of and communication about such areas of overlap, the demographic and genetic components of management models can be developed largely independently. Just such a division of labor has been arranged between myself and N. Flesness who is a graduate student working with Dr. U.S. Seal at I.S.I.S. and the U. of Minnesota. Consequently, my work and further comments in this paper will be largely limited to demographic components of management models. For an excellent discussion of the genetic components, refer to Flesness (1975).

As a final remark about the overall nature of management models, it should be realized the models themselves are not really species-specific but rather general and therefore applicable to any species for which the required data are available. Therefore, there is really no such beast as a Siberian tiger model in the work that I am doing. The models I am developing will be applicable to gorillas, pigmy hippos, Cuban crocodiles, or Andean flamingos as well as to Siberian tigers. However, the only data I have been attempting to compile so far is for Siberian tigers.

Progress in Development of a General Demographic Model:

Conceptually, my demographic model is more or less constructed. It is adapted from models developed by Lewis (1942), Leslie (1954, 1948); Darwin & Williams (1964), Lefkovich (1965), and Beddington (1973, 1975). Somewhat similar models have been developed in relation to sandhill (Grus canadensis) and whooping (Grus americana) cranes. (Miller & Botkin, 1974; Miller et.al., 1972, 1974)

Computationally, the model is not yet operational because manipulation of the model and the data is too cumbersome to do without the assistance of a computer. A computer program is absolutely essential to permit rapid and accurate application of the model to many or even to a single species. Conway (1974) has presented what is presumably a pencil and paper model for Pere David deer (Elaphurus davidianus). However, when there are many age classes with variable schedules of age-specific survival and fertility and where many species, individuals, or zoos are to be involved, computerized models will virtually essential.

Much of the delay in development of an operational version of my model is due to, what is for me, the difficult process of writing the mandatory computer program. I have made considerable progress with the program, assisted by the recent discovery of a program developed independently by J.R. Beddington (1973) for a very similar model in relation to optimal cropping of red deer (Cervus elaphus) in Scotland. Hopefully, my program will be ready for the computer in January. I will apply for at least limited access to the I.S.I.S. computer facilities. However, it would be helpful to have some computer facilities in Philadelphia and I am now exploring possibilities for obtaining some computer time there.

Description of the Demographic Model; Matrix Algebra Background:

Although my model is not yet operational and hence I do not have a bottom-line set of results to report, I think it is appropriate for me to describe briefly and,

I hope, simply the structure of the model and how it will operate.

The model employs the methods of matrix algebra. Matrix algebra provides a convenient system for compiling, storing, and manipulating large amounts of data. Moreover, some theoretical results of matrix algebra more or less solves the basic demographic problems of a management model. A good introduction to matrix algebra for biologists is provided by Searle (1966).

A matrix is simply a rectangular or square array of items, in our case numbers, arranged into rows and columns. The location of a number in the array has significance. For example, a matrix could be used to represent the number of Indian rhinos in prereproductive, reproductive and post-reproductive years at the three ZEST zoos.

| | Pre-reproductive | Reproductive | Post-reproductive |
|----------|------------------|--------------|-------------------|
| Bronx | 1/2 | 0/0 | 0/0 |
| National | 0/0 | 1/1 | 0/0 |
| Phila. | 0/0 | 1/1 | 0/0 |

In normal notation, the matrix appears as an array of numbers inside brackets:

$$\begin{bmatrix} 1/2 & 0/0 & 0/0 \\ 0/0 & 1/1 & 0/0 \\ 0/0 & 1/1 & 0/0 \end{bmatrix}$$

In sophisticated printings, it is conventional to denote a matrix by a letter, usually capitalized if the matrix has more than one row and column, in boldfaced type.

Since I don't have a boldfaced facility on my typewriter, I will use underlined letters to denote matrices.

$$\underline{R} = \begin{bmatrix} 1/2 & 0/0 & 0/0 \\ 0/0 & 1/1 & 0/0 \\ 0/0 & 1/1 & 0/0 \end{bmatrix}$$

In general terms, entries in a matrix are denoted by small case letters with two subscripts, e.g. $r_{i,j}$, where i indicates the row and j the column in which the entry is located. The rhino matrix above in general terms would be:

$$\underline{R} = \begin{bmatrix} r_{1,1} & r_{1,2} & r_{1,3} \\ r_{2,1} & r_{2,2} & r_{2,3} \\ r_{3,1} & r_{3,2} & r_{3,3} \end{bmatrix}$$

So, $r_{1,1} = 1/2$ in the original rhino matrix.

The rhino matrix has 3 rows and 3 columns and is called a 3 X 3 square matrix or a square matrix of order 3. In general, a matrix will have m rows and n columns and be termed an $m \times n$ matrix; in general, a square matrix will have n rows and n columns and be termed an $n \times n$ matrix or a square matrix of order n .

A matrix with only one column but any number of rows is called a column vector. Column vectors are usually denoted by small case letters. Column vectors are used to represent the age structure of a population. For example, the age structure of female registered Siberian tigers in the U.S. as of January 1, 1975 (Jones, 1975) can be represented by a column vector having 17 rows.

$$\underline{x}_t = \begin{bmatrix} x_{0t} \\ x_{1t} \\ x_{2t} \\ x_{3t} \\ x_{4t} \\ x_{5t} \\ x_{6t} \\ x_{7t} \\ x_{8t} \\ x_{9t} \\ x_{10t} \\ x_{11t} \\ x_{12t} \\ x_{13t} \\ x_{14t} \\ x_{15t} \\ x_{16t} \end{bmatrix} = \begin{bmatrix} 12 \\ 19 \\ 11 \\ 12 \\ 10 \\ 5 \\ 5 \\ 2 \\ 3 \\ 1 \\ 1 \\ 1 \\ 1 \\ 4 \\ 0 \\ 0 \\ 2 \end{bmatrix}$$

where n_{xt} denotes the number of females who are between the age of x and $x+1$ at some time t ; n_{0t} means the number of females between the ages of 0 and 1 at time t (in this case Jan. 1, 1975).

A 1×1 matrix, i.e. a single number or symbol (e.g. 5 or x), is called a scalar. All the matrices used in the model will be square, column vectors, or scalars.

The arithmetic operations of addition, subtraction, and multiplication can be performed with matrices. Two matrices can be added or subtracted only if they have the same number of rows and columns. For example, consider, a matrix representing the births of mammals, birds, and reptiles at three imaginary zoos for 1974 and 1975.

| | | | | | |
|----------|-------|-------|-------|-----------|------------|
| | Zoo X | Zoo Y | Zoo Z | | |
| Mammals | 25 | 76 | 33 | Year 1974 | = <u>A</u> |
| Birds | 30 | 45 | 10 | | |
| Reptiles | 15 | 16 | 17 | | |
| | Zoo X | Zoo Y | Zoo Z | | |
| Mammals | 35 | 84 | 37 | Year 1975 | = <u>B</u> |
| Birds | 25 | 50 | 15 | | |
| Reptiles | 11 | 13 | 29 | | |

Then the total for the two years can be determined by adding the matrices entry by entry:

$$\begin{array}{ccc}
 \left[\begin{array}{ccc} 25 & 76 & 33 \\ 30 & 45 & 10 \\ 15 & 16 & 17 \end{array} \right] & + & \left[\begin{array}{ccc} 35 & 84 & 37 \\ 25 & 50 & 15 \\ 11 & 13 & 29 \end{array} \right] & = & \left[\begin{array}{ccc} 25+35 & 76+84 & 33+37 \\ 30+25 & 45+50 & 10+15 \\ 15+11 & 16+13 & 17+29 \end{array} \right] \\
 \underline{A} & & \underline{B} & & \underline{C}
 \end{array}$$

$$= \begin{bmatrix} 60 & 160 & 70 \\ 55 & 95 & 25 \\ 26 & 29 & 46 \end{bmatrix} = \underline{C}$$

The difference between the two years could be found by subtracting one matrix from the other, again entry by entry.

Matrix multiplication is a bit more complicated. Easiest is the multiplication of an entire matrix by a scalar, e.g. $c =$ some constant number.

$$c \underline{A} = c \begin{bmatrix} a_{11} & a_{12} & a_{13} \\ a_{21} & a_{22} & a_{23} \\ a_{31} & a_{32} & a_{33} \end{bmatrix} = \begin{bmatrix} ca_{11} & ca_{12} & ca_{13} \\ ca_{21} & ca_{22} & ca_{23} \\ ca_{31} & ca_{32} & ca_{33} \end{bmatrix}$$

As a numerical example, suppose there was a matrix of the number of female tigers in pre-reproductive, reproductive, and post-reproductive stages at three imaginary zoos:

| | Pre-reproductive | Reproductive | Post-reproductive | |
|-------|---|--------------|-------------------|-----------------------------------|
| Zoo X | $\begin{bmatrix} 6 & & \\ & 4 & \\ & & 2 \end{bmatrix}$ | | | = $\underline{T}_{\text{before}}$ |
| Zoo Y | | | | |
| Zoo Z | | | | |

Then suppose a tiger plague descended on all three zoos and killed $\frac{1}{2}$ of all tigers in each age category in each zoo. In matrix terms:

$$\underline{T}_{\text{after}} = \frac{1}{2} \underline{T}_{\text{before}} = \frac{1}{2} \begin{bmatrix} 6 & 4 & 2 \\ 6 & 8 & 0 \\ 10 & 4 & 2 \end{bmatrix} = \begin{bmatrix} 3 & 2 & 1 \\ 3 & 4 & 0 \\ 5 & 2 & 1 \end{bmatrix}$$

The next easiest rule for multiplication is for postmultiplication of a square matrix by a column vector. For this operation to be possible the matrix must have the same number of columns as the column vector has rows. For example,

$$\underline{A} \times \underline{b} = \underline{C}$$

$$\begin{bmatrix} a_{11} & a_{12} & a_{13} \\ a_{21} & a_{22} & a_{23} \\ a_{31} & a_{32} & a_{33} \end{bmatrix} \begin{bmatrix} b_{11} \\ b_{21} \\ b_{31} \end{bmatrix} = \begin{bmatrix} a_{11}b_{11} + a_{12}b_{21} + a_{13}b_{31} \\ a_{21}b_{11} + a_{22}b_{21} + a_{23}b_{31} \\ a_{31}b_{11} + a_{32}b_{21} + a_{33}b_{31} \end{bmatrix}$$

$\underline{A} \qquad \underline{b} \qquad \underline{C}$

As a numerical example, consider the same matrix of tigers as before, but a different plague that affects the different age categories unequally, killing $\frac{1}{2}$ in the pre-reproductive years, none in the reproductive ages, and all of the animals in post-reproductive years. The effect of the plague on the total numbers in each zoo is:

$$\begin{bmatrix} 6 & 4 & 2 \\ 6 & 8 & 0 \\ 10 & 4 & 3 \end{bmatrix} \begin{bmatrix} \frac{1}{2} \\ 1 \\ 0 \end{bmatrix} = \begin{bmatrix} 3 + 4 + 0 \\ 3 + 8 + 0 \\ 5 + 4 + 0 \end{bmatrix} = \begin{bmatrix} 7 \\ 11 \\ 9 \end{bmatrix} \quad \text{versus} \quad \begin{bmatrix} 12 \\ 14 \\ 17 \end{bmatrix}$$

$\underline{T}_{\text{before}} \qquad \underline{S} \qquad = \qquad \underline{\text{Total}}_{\text{after}} \qquad \underline{\text{Total}}_{\text{before}}$

Here \underline{s} is a column vector of the percentage survival of the plague.

Two square matrices can be multiplied $\underline{A} \times \underline{B} = \underline{C}$, as long as they are of the same order (i.e. have the same number of rows and columns). The result is another matrix of the same order. The operation of actually determining the product is a little complicated but is analogous to the last rule for post-multiplying a square matrix by a column vector.

There is one last fundamental of matrix algebra that must be introduced before the actual demographic model can be described. This is the determinant. With every square matrix \underline{A} , there is associated a unique determinant denoted by $|\underline{A}|$. The determinant operation converts a square matrix into a polynomial of its elements. For example consider a 2 X 2 matrix containing an unknown x as

well as numbers:

$$\left| \underline{A} \right| = \begin{vmatrix} 4x & 9x \\ 3x & 7 \end{vmatrix}$$

The determinant of \underline{A} is

$$\left| \underline{A} \right| = \begin{vmatrix} 4x & 9x \\ 3x & 7 \end{vmatrix} = 28x - 27x^2$$

In general, the determinant of a square matrix of order n (i.e., having n rows and n columns) will be a polynomial whose highest power is n . For example, the determinant of a 5×5 matrix containing one unknown x will be a polynomial of the form:

$$c_5x^5 + c_4x^4 + c_3x^3 + c_2x^2 + c_1x + c_0$$

where the c 's represent numbers.

Determinants can then be part of algebraic equations. For example, for the matrix above

$$\left| \underline{A} \right| = 0 = 28x - 27x^2$$

Evaluation of determinants of matrices larger than 5×5 becomes virtually impossible without the aid of a computer.

The Demographic Model:

Basically, the demographic model uses data on age-specific survival (i.e., the probability that an animal of age x at some time t will survive to age $x+1$ at time $t+1$, where both ages and times are measured in the same units, e.g. months or years) and age-specific fertility (the average number of progeny expected from an animal from age x to age $x+1$) to project changes in population size and age distribution over time. More importantly, the model will direct how management should change the age-specific survival (by culling) and age-specific fertility (by permitting or preventing reproduction) so as to produce desired changes (increases, decreases or constancy) in population size and age distribution.

At any point in time, a population can be represented as a column vector whose entries are the numbers of animals in each of the several established age classes, e.g. the age distribution vector for female Siberian tigers in U.S. as of Jan. 1, 1975 presented earlier on the bottom of page 7. It is conventional and convenient for demographic models to treat females separately from males, either as if they were separate species or more often as if only the females were significant and the males could be ignored because there is always a surplus of them anyway in terms the numbers needed to impregnate all females. If treated separately but equally, the demographic model can be constructed for a single sex and then applied to males and females as if they were separate species. For example, if an even sex ratio is to be maintained, then one-half of the carrying capacity for the species can be allocated to each sex and the demographic model applied. Simple summation of results will then reintegrate the two sexes as a single species. It is a bit more complicated to treat both sexes in the same model. I am attempting the models both ways.

From the initial population state described by the column vector of age classes, future states of the population can be projected by using the two parameters of the demographic model:

P_x = age-specific survival = the probability that a female (or male) of age x at time t will survive to be age $x+1$ at time $t+1$. (Again x and t are measured in equal units.)

F_x = age-specific fertility = the average number of females (or males) that is expected to be produced from time t to time $t+1$ by a female (or male) of age x to age $x+1$. (Note for males, the age at insemination rather than the age at parturition is critical.)

Thus P_1 equals the probability that an animal will survive from age 1 until age 2 during an interval of time from $t=0$ to $t=1$; F_1 is the average number of progeny expected to be produced by any animal age 1 to age 2 during one period of time.

The P_x 's and F_x 's can be arranged into a matrix, conventionally denoted by the letter M.

$$\underline{M} = \begin{bmatrix} F_0 & F_1 & \dots & F_{m-1} & F_m \\ P_0 & 0 & \dots & 0 & 0 \\ 0 & P_1 & \dots & 0 & 0 \\ \dots & \dots & \dots & \dots & \dots \\ 0 & 0 & \dots & P_{m-1} & 0 \end{bmatrix}$$

The size and age distribution of the population at time $t=1$ (i.e., one unit of time from now) can be gotten by post multiplying the matrix M by the column vector representing the age distribution at time $t=0$ (now).

$$\underline{M} \times \underline{n}_t = \underline{n}_{t+1}$$

$$\begin{bmatrix} F_0 & F_1 & \dots & F_{m-1} & F_m \\ P_0 & 0 & \dots & 0 & 0 \\ 0 & P_1 & \dots & 0 & 0 \\ \dots & \dots & \dots & \dots & \dots \\ 0 & 0 & \dots & P_{m-1} & 0 \end{bmatrix} \begin{bmatrix} n_{00} \\ n_{10} \\ n_{20} \\ \vdots \\ n_{m0} \end{bmatrix} = \begin{bmatrix} F_0 n_{00} + \dots + F_m n_{00} \\ P_0 n_{00} \\ P_1 n_{10} \\ \vdots \\ P_{m-1} n_{m-1,0} \end{bmatrix}$$

$$= \begin{bmatrix} n_{01} \\ n_{11} \\ n_{21} \\ \vdots \\ n_{m1} \end{bmatrix}$$

Where, as before, n_{10} denotes the number of animals in the age class 1 to 2 at $t=0$. Products like $P_0 n_{00}$ represent the number of animals in the age group 0 to 1 at time 0 multiplied by the probability of surviving from 0 to 1 to produce the number that will be age 1 to 2 at time $t=1$.

The sum of products $F_0 n_{00} + \dots + F_m n_{m0}$ is the sum of the numbers in each age class multiplied by the average number of offspring animals of that age are expected to produce in an interval of time, so it equals the number of newborns at time $t=1$

As a numerical example, consider a population with five age classes with the following schedule of age-specific survival and fertility.

$P_0 = P_1 = P_2 = P_3 = \frac{1}{2}$ i.e., until the age of 4 one-half of all the animals die before they reach the next age; all remaining animals die between the age of 4 and 5.
 $P_4 = 0$

$F_0 = 0, F_1 = 0, F_2 = 4, F_3 = 3, F_4 = 0$ i.e., animals do not reproduce until they are between the ages of 2 and 3, then on the average an animal between the ages of 2 and 3 produces 4 young and an animal between the ages of 3 and 4 produce 3 young; animals older than 4 are sterile.

If the population at some time $t=0$ has the following age distribution,

$$n_0 = \begin{bmatrix} 10 \\ 10 \\ 10 \\ 10 \\ 10 \end{bmatrix}$$

after one unit of time has passed, i.e. at time $t=1$, the population will have changed to

$$\begin{bmatrix} 0 & 0 & 4 & 3 & 0 \\ \frac{1}{2} & 0 & 0 & 0 & 0 \\ 0 & \frac{1}{2} & 0 & 0 & 0 \\ 0 & 0 & \frac{1}{2} & 0 & 0 \\ 0 & 0 & 0 & \frac{1}{2} & 0 \end{bmatrix} = \begin{bmatrix} 10 \\ 10 \\ 10 \\ 10 \\ 10 \end{bmatrix} = \begin{bmatrix} (0)(10)+(0)(10)+(4)(10)+(3)(10)+(0)(10) \\ (\frac{1}{2})(10) \\ (\frac{1}{2})(10) \\ (\frac{1}{2})(10) \\ (\frac{1}{2})(10) \end{bmatrix} = \begin{bmatrix} 70 \\ 5 \\ 5 \\ 5 \\ 5 \end{bmatrix}$$

If the P_x 's and F_x 's do not change, the matrix M can continue to be used to project the changes in the population for future times.

$$n_1 = M n_0; n_2 = M n_1 = M^2 n_0; n_t = M^t n_0$$

If the values of the P_x 's and F_x 's change from one unit of time to the next, then a sequence of matrices can be used to project the population changes.

$$n_3 = M_3 M_2 M_1 n_0$$

The values of the P_x 's and F_x 's can be varied considerably within limits. Such variation constitutes management. At the upper limit, are the maxima or potential values of survival, attained in the zoo environment when no culling is occurring, and fertility, attained when the animals are permitted unrestricted opportunity to breed. Below these potential values, the P_x 's can be reduced by removing animals from certain age classes and the F_x 's can be reduced by preventing animals from breeding. These are the managed values of survival and fertility.

Effects of any such changes in the P_x 's and F_x 's produced by management (or changes of natural or unintended cause) can be rapidly and precisely investigated with the computer. Consequences both near and remote in time will be revealed.

However, the model will not only reveal the effects of management changes, but will indicate the changes management should impose on the P_x 's and F_x 's to attain or maintain desired sizes or age distributions of a population.

If the values of the P_x 's and F_x 's remain fairly constant over time (As they often do in an ameliorated environment and which they could be made to do for managed values comfortably below the potential values, Such low values will often pertain in zoos managing a population at carrying capacity.) the population will tend to a constant rate of change, designated by the symbol λ and termed the finite rate of change. (Almost all populations will do so unless they begin with a badly distorted age distribution, i.e. with all or mostly old animals beyond age of reproductivity.) This λ can be greater than 1, in which case the population is increasing; less than 1, in which case the population will be decreasing; or equal to 1, in which case, the population does not change size.

As the population tends to grow at this constant rate, it will also assume ~~a stable age distribution~~ a stable age distribution, which means that the population will indefinitely, until the P_x 's and F_x 's change (as they do in nature when populations grow crowded), maintain an age distribution in which the relative numbers in each age class stay the same. For example, the stable age distribution for a species with three age classes might have relative numbers 4, 2, and 1. The population might be doubling every unit of time, but the relative numbers in each age class will stay the same.

$$n_1 = \begin{bmatrix} 4 \\ 2 \\ 1 \end{bmatrix} \quad n_2 = \begin{bmatrix} 8 \\ 4 \\ 2 \end{bmatrix} \quad n_3 = \begin{bmatrix} 16 \\ 8 \\ 4 \end{bmatrix} \quad n_4 = \begin{bmatrix} 32 \\ 16 \\ 8 \end{bmatrix}$$

Poole (1974) and Pielou (1969) derive the stable age distribution theoretically and demonstrate it numerically.

In matrix terms, the stable age distribution can be represented as

$$\underline{M} \underline{n}_t = \lambda \underline{n}_t$$

where as before \underline{M} is the matrix of P_x 's and F_x 's; \underline{n}_t is the column vector of the age distribution at time t ; and λ is the finite rate of change.

Once, the P_x 's and F_x 's are known or created, the value of λ can be determined by solving the equation

$$|\underline{M} - \lambda \underline{I}| = 0$$

$|\dots|$ denotes the determinant operation as before.

The product $\lambda \underline{I}$ merely converts the scalar λ into a matrix so it can be subtracted from \underline{M}

This will produce a polynomial in λ where as before, the highest power of λ will equal the order of the matrix \underline{M} . If \underline{M} is 5 X 5, then the equation will be of the form $c_5 \lambda^5 + c_4 \lambda^4 + c_3 \lambda^3 + c_2 \lambda^2 + c_1 \lambda + c_0 = 0$

Solution of such equations requires assistance of a computer.

Having ascertained a value for λ (which is called an eigenvalue of the matrix \underline{M}), the stable age distribution can be determined by solving the equation

$$\underline{M} \underline{n}_t = \lambda \underline{n}_t$$

In terms of λ and the P_x 's the solution (for a population with $k+1$ age classes)

is

$$\underline{n}_{\text{stable}} = \begin{bmatrix} \lambda^k / (P_0 P_1 \dots P_{k-1}) \\ \lambda^{k-1} / P_1 P_2 \dots P_{k-1} \\ \lambda^{k-2} / P_2 P_3 \dots P_{k-1} \\ \vdots \\ \lambda / P_{k-1} \\ 1 \end{bmatrix}$$

The computer can be used to investigate what sort of rate of change, λ , and age distribution various schedules of P_x and F_x will produce and hence can indicate how to vary the P_x 's and F_x 's to produce a desired rate of change or ultimate age distribution.

There is a special case of the stable age distribution known as the stationary age distribution which occurs when the P_x 's and F_x 's are constant and such that $\lambda = 1$. A stationary population not only has a stable age distribution, but the population size remains constant.

Attainment and maintenance of a stationary population will probably be the ultimate management objective for any species being preserved in captivity. The computer can be used to investigate various combinations of values of the P_x 's and F_x 's (as always within the limits established by the potential values of these parameters) that would produce a $\lambda = 1$ and hence a stationary population.

In general, captive populations will either be below (probably the case with most endangered species right now) or at (e.g. Siberian tigers) the carrying capacity (K) of zoos. If the population is much below K , the population will probably

be encouraged to grow at the maximum λ possible for the species and consistent with the directions of the genetic models (e.g. Remember, for minimization of inbreeding and genetic drift, it is bad to allow any one animal to contribute too much to the next generation, if there are alternatives. Dacca, the tiger cited by Conway (1974) for her prolific production of offspring, is probably a genetic bane rather than boon to the captive tiger population.)

As the population grows in size, the P_x 's and F_x 's can be adjusted downward to eventually attain and maintain a stationary population at the carrying capacity for the species. For those populations that are already near or over perhaps the carrying capacity of zoos, the model will indicate how to control the P_x 's and F_x 's to maintain or reduce the population to a stationary condition.

More than one combination of various P_x 's and F_x 's, within the limits of the potential values, may produce a stationary population. Then there will be alternatives of age distributions and reproduction schedules from which zoos can select the most desirable. (e.g. For P.R. reasons, it might be desirable to have more babies of certain species even if this requires more culling later; for other species, it might be desirable to maintain animals as long as possible.)

Should there be natural or unintended changes in the potential values of the parameters such that they might descend below some currently established management values, the model will indicate how to vary other P_x 's and F_x 's to restore the desired condition.

The demographic model will direct how many animals of each age and sex should be maintained or removed and how many progeny should be produced by animals of which age to achieve some objective of population growth and/or maintenance. It does not indicate which subset of the animals of a certain age should be selected for retention, removal, or reproduction. This is what the genetic models like those proposed by Flesness (1975) will do.

However, the demographic model will be sensitive to genetically determined differences in P_x 's and F_x 's. The model can be refined to incorporate such genetic differences. For example, removal of three animals of genotype (operationally this will mean ancestry) A from age class x may affect P_x differently than removal of three animals of genotype B. The model will be capable of treating such genetically determined differences in demographic characteristics of individuals.

Note: I have received a great deal of criticism from Wayne King, Monte Lloyd, and others concerning this paragraph. King strongly objected to my use of the term genotype here. I admit it is a sloppy use of the term. As stated in the parenthetical clause above, what I intended to imply by the term genotype was merely a correlation between survival and fertility characteristics and the ancestry of individual animals. This I think is possible and necessary.

Application of the Model:

Application of the model requires that we have the data on the potential age-specific survival, the P_x 's, and age-specific fertility, the F_x 's. I have been trying to compile such data for Siberian tigers, but have been encountering problems.

To secure the potential age-specific survival data, we need to know either: 1. date of death of a large number of animals of known birth dates 2. or better, the percentage survival from one age to the next of a large number of animals of each age. Data of kind number 2 are better because the probability of survival may be changing from year to year as zoo conditions change. Studbooks have data of both kinds. The annual or semiannual I.S.I.S. reports will provide data of the second type.

Data on potential age-specific fertility is more difficult to obtain. What is needed is data on the numbers of offspring born to each of a large number of females (or males) of each age. Here data in the studbooks and I.S.I.S. reports is less reliable because these sources have no indication of what sort of management is occurring (i.e. whether animals are being permitted or prevented the opportunity to breed) or whether the young produced are being raised by mothers or humans. Both of these will significantly affect the F_x 's.

The potential P_x 's and F_x 's may, or probably often will, be affected by environmental and genetic factors. So depending on how and where the model is to be applied, the potential P_x 's and F_x 's can be computed for various sets of animals. In the case of the Siberian tigers, for example, different P_x and F_x schedules might be compiled for:

All tigers.

All Siberian tigers.

All U.S. Siberian tigers and those foreign
Siberian tigers in U.S. animals ancestry.

All U.S. Siberian tigers.

Only ZEST Siberian tigers.

As indicated before, once the potential P_x 's and F_x 's are determined, upper limits are established below which the parameters can be varied (P_x 's by culling; F_x 's by breeding or not) to produce the managed P_x 's and F_x 's.

As an example of potential and managed survival and fertility schedules, consider the data implied by Conway's (1974) data on Pere David's deer. (See Figure 1, presumptuously reproduced). Consider only the females. His model implies that usually no mortality occurs from age 1 to age 9 (i.e. follow what happens to the 5 females age 5 in 1974 until they reach age 9 in 1978, or the 3 females age 1 in 1974 until they reach age 5 in 1978). Actually no mortality is indicated until age 11, but the model implies reproduction effectively ends at age 9 and our model ignores animals in postreproductive age classes. Thus all the P_x 's (potential) are 1 in the unmanipulated (unculled) growing herd, 1974-1978.

In the theoretical model, the age classes are grouped into intervals of two years, 1-3 years, 3-5 years, 5-7 years, 7-9 years. Still the P_x 's would be 1 in the uncullled herd. these are the potential P_x 's.

In the managed herd, however, culling reduces the P_x 's as follows:

$$P_{1-3} = 1 \text{ or } 5/6$$

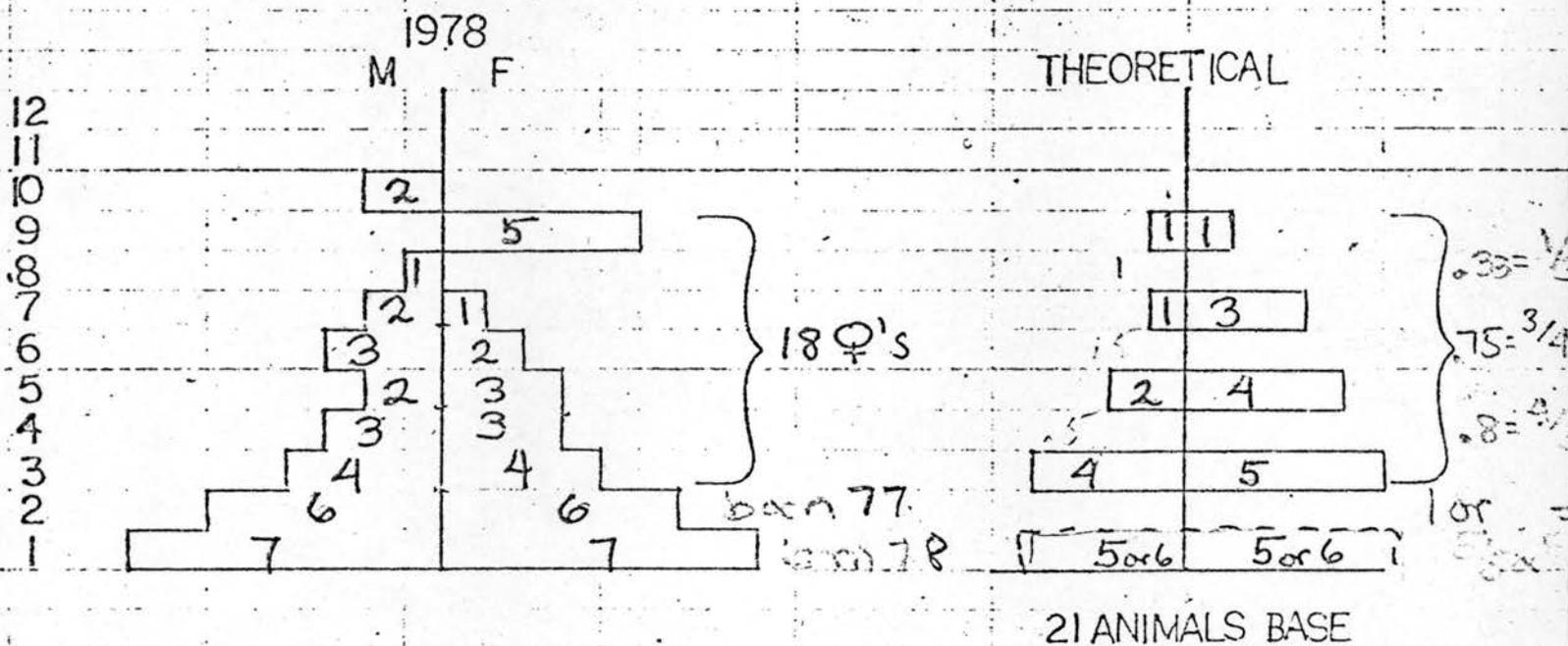
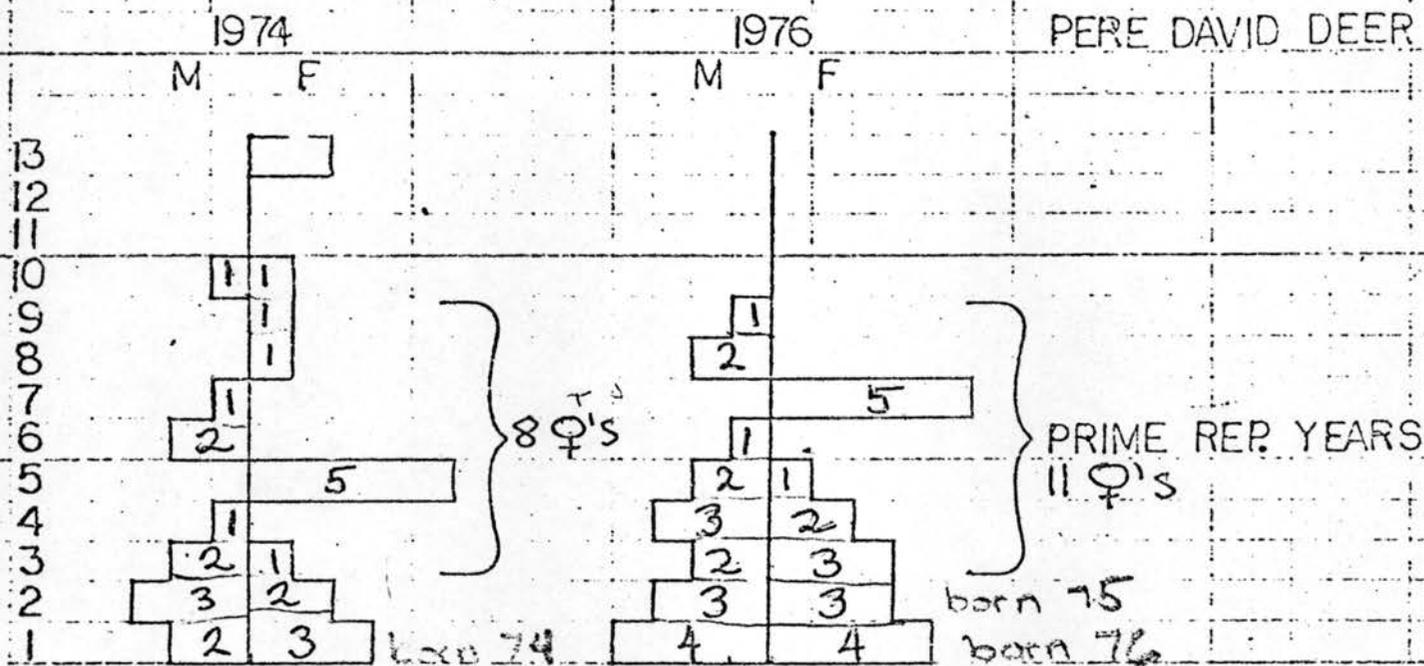
$$P_{3-5} = 4/5$$

$$P_{5-7} = 3/4$$

$$P_{7-9} = 1/3$$

NYZS, FIG. 1

PERE DAVID DEER



8 ♀'s produce 2.3 in 74

2 ♀'s produce 3.3 in 75

11 ♀'s produce 4.4 in 76

14 ♀'s produce 6.6 in 77

18 ♀'s produce 7.7 in 78

The F_x 's are a little more difficult to determine. However, for the years 1974-78 I averaged the number of female offspring produced by females in the prime reproductive years. If this value is distributed equally over all age classes, it provides a potential $F_{3-5} = F_{5-7} = F_{7-9} = F_{9-11} = 0.37$ female young/adult female. In the theoretical model, biannual production of 5 female fawns, necessary to generate and maintain the age distribution indicated, requires the F_x 's to be 0.38, i.e., virtually the same as the potential values.

In matrix form the managed values of the Conway model would be

$$\begin{bmatrix} 0 & .38 & .38 & .38 & .38 \\ 1 & 0 & 0 & 0 & 0 \\ 0 & .80 & 0 & 0 & 0 \\ 0 & 0 & .75 & 0 & 0 \\ 0 & 0 & 0 & .33 & 0 \end{bmatrix}$$

The dominant eigenvalue of this matrix is 0.996, i.e. almost 1.

The associated eigenvector is:

$$\begin{bmatrix} 5 \\ 5 \\ 4 \\ 3 \\ 1 \end{bmatrix}$$

Concerning compilation of data on survival and fertility of Siberian tigers, I have not yet obtained a copy of the complete and current studbook. I do have Marvin Jone's (1973) survey of registered Siberian tigers in North America through August of 1973. From this material, I have computed some preliminary values for age-specific survival, but much more drudgery is needed before my results are reportable. My computer program will facilitate compilation of the data.

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REFERENCES

- Beddington
1973 Exploitation of red deer (Cervus elaphus) in Scotland. Ph. D. thesis. University of Edinburgh
- Beddington
1975 Age structure, sex ratio, and population density in harvesting of natural animal populations. J. of Applied Ecology
- Comway, W.
1974 Animal mangement models and long-term captive propagation. Unpublished ms. of paper presented at AAZPA conference, Philadelphia
- Crow and Kimura
1970 An introduction to population genetics theory. Harper-and Row, New York
- Darwin, J.H. and Williams, R.M.
1964 The effect of time of hunting on the size of a rabbit population. N.Z.J. Sci. 7:341-52
- Flesness
1975 Gene pool conservation in zoos. Unpublished ms. of paper presented at AAZPA conference, Calgary, Canada
- Foose, T.J.
1975 Models for management of zoo populations. Unpublished ms., Philadelphia
- Jones, M.L.
1973 The siberian tiger (Panthera tigris altaica) in North America. AAZPA, Wheeling, W. Va.
- Jones, M.L.
1975 Status of studbook registered siberian tigers (Panthera tigris altaica) in the Americas. 31 March 1970 and 1 January 1975. Unpublished ms.
- Lefkovitch
1965 The study of population growth in organisms grouped by stages. Biometrics 21:1-18
- Leslie, P.H.
1945 On the use of matrices in certain population mathematics. Biometrika 33:183-212
- Leslie, P.H.
1948 Some further notes on the use of matrices in population mathematics. Biometrika 35:213-45
- Leslie, P.H.
1959 The properties of a certain lag type of population growth and the influence of an external random factor on a number of such populations. Physiological Zoology 32:151-159.

- Lewis
1942 On the generation and growth of a population. *Sankhya*
6:93-6
- Miller, R.S. and Botkin, D.B.
1974 Endangered species: models and predictions. *American Scientist* 62 (2):172-181
- Miller, R.S., Botkin, D.B. and Mendelsohn, R.
1974 The whooping crane (*Grus americana*) population of North America. *Biological Conservation* 6 (2):106-111
- Miller, R.S., Hochbaum, G.S. and Botkin, D.B.
1972 A simulation model for the management of sandhill cranes. Yale University: School of Forestry and Environmental Studies. Bulletin No. 80. Yale Univ., New Haven, Conn.
- Perry, J. and Kibbee, P.B.
1975 The capacity of American zoos. *Intern. Zoo Yearbook*
14:240-47
- Pielou, E.C.
1969 An introduction to mathematical ecology. John Wiley & Sons, New York
- Poole, R.W.
1974 An introduction to quantitative ecology. McGraw-Hill, New York
- Searle
1966 Matrix algebra for the biological sciences. John Wiley & Sons, New York

March 18, 1976

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Dear Tom:

Here is a copy of your contract. --
will see you on the 29th. Please
call if there are any questions
or to let us know plans, etc.

Received your CV ok.

Sincerely,

Donald D. Bridgwater
General Director

DDB vc