THE ESTIMATION OF THE BREEDING EFFECTIVE POPULATION SIZE OF CAPTIVE POPULATIONS: THE GORILLA IN NORTH AMERICAN ZOOS

Paul A. Fuerst
Department of Genetics
The Ohio State University
Columbus, Ohio

INTRODUCTION

When considering the genetic conservation of endangered species, one theoretical concept adapted from population genetics which has increasingly appeared is that of effective population size. This concept of "effective population size" is important for long range planning of species management, but can take on an almost mystical interpretation, far beyond the actual practical insights which it provides for the zoo biologist. In this paper I hope to to clarify certain aspects of this theoretical measure which may confuse the nonexpert, and to consider some approaches to estimating and using the effective size which have often been mentioned in passing in the conservation literature, but which have received little explicit consideration. Finally, I will illustrate the methods using data gathered by the Gorilla SSP group on breeding individuals in North American zoos.

EFFECTIVE POPULATION SIZE

To determine to probable rate of loss of genetic variation from a population, the population geneticist has developed the concept of effective population size. It is important for the zoo biologist to keep in mind that this is a theoretical concept, a "fudge factor" to be used in equations. Specifically, it represents the size (in number of breeding individuals) of an "ideal" natural population of randomly mating organisms which will lose genetic variation at a rate equivalent to the rate which is occuring in some "real" population which we are monitoring. Usually, the measure of genetic variability which we are following is the "heterozygosity" in the population. This is directly related to the inbreeding level of the population, since heterozygosity is defined as the probability that two genes taken at random from the population will not be identical in type (i.e. they will not be homozygous because they were not inherited from a common ancestor). It has been known since the 1930's that heterozygosity will be lost from the population at a rate of about 1/2N per generation, where N is the value of the effective population size. Thus, we can use the N value to guide us in the management of species. For instance, the Front Royal meeting on genetic conservation suggested that species managers should aim for population sizes which will retain 90% of the heterozygosity after 200 years.

In practice, the estimation of the fudge factor is not necessarily straight forward. This is because several common biological factors act to confound our estimate. Most easily dealt with is the general fact that (especially in captive breeding populations) the number of individuals in the two sexes contributing to reproduction is not usually equal. Breeding males are most often provided with multiple potential mates, while some, or even many males may not be provided with the opportunity to reproduce. If sexual contribution is unequal, the effective population size will be affected. As an example, over the last 15 years there have been 134 potentially reproducing male gorillas and 147 potentially reproducing female gorillas. (I am defining potential reproduction for this example as reaching age eight for either sex. Behavioral studies suggest that this may not be completely appropriate, but I wish to use the data here simply to illustrate methodology. A more detailed report on gorillas, taking into account additional complications, is being prepared for future publication). The raw sex ratio among potential reporductives is 1:1.09. In this same 15 year period, the actuals number of each sex which were recorded as contributing to captive reproduction was 52 males and 72 females, a sex ration of 1:1.38. How has this change in contribution by sex altered the effective population size?

We can approach this first estimation problem using a well known relationship developed during the 1930's by Sewall Wright. To correct for sex bias we use the formula:

$$N' = \frac{4MF}{M + F}, \qquad \text{(formula 1)}$$

where M refers to the number of breeding males, F refers to the number of breeding females, and N' is the resulting effective number. Applying this formula to our data on the gorilla, we see that N' is calculated to be 120.8 (i.e. 4 x 52 x 72 / 124), comapred to a beeding number of 124 individuals. Thus, despite a fairly substantial difference in the sex ratio of breeding individuals, the resulting effective population size is 97% of the size it would be were male and female reproductives equalized.

(I want to emphasize that the numbers given here are illustrative only, although drawn from the gorilla SSP data. Since the number of individuals contributing to reproduction today is much smaller than those which have contributed over a fifteen year period, the corresponding percentage effect of unequal sex ratios will be larger. A more extensive demographic analysis than that presented here is called for. Nevertheless, the conclusion that unequal sex ratios do not contribute greatly to a depression in the effective population size will, I believe, still remain correct.)

A second factor which will act to reduce the effective size of the population (compared to the actual number of individuals) is the demographic constitution of the real population. Generations overlap, and a direct count of individuals who may not have completed reproduction will not correctly reflect the effective population size. I have not included a demographic analysis of the gorilla data for this paper (such an anaysis of reproductive rates has been done by members of the gorilla SSP, however). One factor which is apparent in the data, and which will contribute to the long term estimate of effective population size is the trend in age of reproduction of individuals over the past decade. There has been a slight trend to increasing age of reproduction for both males and females. This is illustrated by Figure 1. Two factors contribute to this pattern. First, many of the same reproductive individuals are represented in different years, as they age, while few young individuals are entering the breeding pool. This is clearly a negative factor for the gorilla population. Secondly, some of the increase results from first reproduction of previously non-reproducing older individuals, due to movement of specimens to other zoos, and to advances in knowledge of reproductive biology of great apes. This is clearly a positive factor. The longterm effects of these two patterns remain to be determined. Hopefully, the positve effects of knowledge in reproductive biology will also result in more young individuals contributing to the population.

A third factor affecting the effective population size has been often mentioned, but rarely determined. This is the effect of variation in offspring number among individuals of the same sex. In human population genetics this is sometimes referred to as the "headman effect" and is known to cause significant reductions in the effective population size. The theoretical methods available to calculate this change involve approximations, and have been given in Cavlli-Sforza and Bodmer (1971). The correction factor for use in determining effective population size is given by:

$$\frac{1}{1 + \frac{V(k)}{k^2} - \frac{1}{k}}, \qquad \text{(formula 2)}$$

where k is the average number of offspring per reproductive individual (non-reproductive individuals are excluded), and V(k) is the variance in offspring number.

We can use the data from the gorilla SSP to calculate the mean and variance of offspring number for reproductive individuals over the last fifteen years. (Note that, again, this results in the data being used as an illustration, since we would like to calculate the current effective population size and not all these individuals are currently reproductives). The calculated average and variance of offspring production are as follows. For males: average = 2.86 offspring/reproductive male; variance = 5.65. For females: average = 2.19 offspring/reproductive female; variance = 2.19. Note that the variance and mean for females are essentially equal, while the variance is much greater than the mean for males. Theoretical assumptions in population genetics usually begin with the "ideal" population, which would have a mean and variance equal, as for female gorillas in captivity. As the variance increases, the effective population size decreases; conversely, with decreasing variance in offspring number, the effective size will increase. In fact, if we can reduce the variance to zero, we can make the effective size double the size of the actual population. The effect of the increased variance in males will be to decrease to size of the effective population size. To illustrate the type of variation in offsping production which we are observing, the distribution of offsping number among different reproducing male gorillas is shown in Figure 2. In contrast, the distribution among females, which is shown in Figure 3, is similar but causes little alteration in the effective population size of females.

To return to the gorilla data, we can determine that the correction factors calculated from formula (2) for males and females will be 0.747 and 0.999, respectively. We can then apply these correction factors to the number of breeding males and females in the population and then use formula (1) to obtain a final corrected effective population size. This is determined to be approximately 100.8, a 17% reduction in effective population size. In my opinion, this is a relatively minor reduction in the population size.

To illustrate this point, Table 1 shows the rate of loss of heterozygosity (compared to the present level) for populations which have an effective population size equal to the actual size of the present population, the size utilizing Formula (1) and the size utilizing Formula (2), when the SSP data for gorillas reproducing over the last 15 years is analyzed. The time span is taken to be twenty generations, assuming a ten year generation period as a very preliminary starting point. This would provide us with an estimate of the total loss over 200 years, the time period suggested by the Front Royal Conference as being the target management period. It can be seen that even over 20 generations there will be only a 2% difference in the amount of genetic variability which is expected to be retained in the population.

DISCUSSION

I feel that the small size of the correction to the effective population size causes one to question the utility of excluding (or reducing) the contribution of males who already are "well represented" in the offspring gene pool. It is often argued that we must act vigorously to equalize offspring contribution to maximize effective population size. Since the males most likely to be excluded are known successful breeders, their usefullness in contributing to the population as breeders would appear to override the small negative effect of increased loss of genetic variability (i.e. increased rate of population inbreeding). Only if the effective population size were very small, and male reproductive contributions even more variable than seen for gorillas, would the increased difficulties of equalizing male contributions seem to be worthwhile. For populations such as gorillas or some of the large cats in which founder population size is fairly large, it would appear to me to be more profitable to work for maintaining the population size, rather than making an extraordinary effort to equalize offspring number by reducing the contribution of any "supermales." Table 1 indicates that even with the unmanaged variation in offspring numbers, the difference in rate of loss of genetic heterozygosity will be trivial (especially compared to other potential factors which will be operating).

The methods which are presented here form a first step in the estimation of effective population size. Additional calculations may be necessary to take into account the demographic structure of the population. For most purposes, however, the additional complications of the demographic analyses may not result in substantially greater insight into the factors reducing genetic variability, and simple approximations of the methods given here should be useful for most management applications.

ACKNOWLEDGEMENTS

This work is partially supported by a grant from the National Science Foundation.

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TABLE 1

PERCENT OF INITIAL HETEROZYGOSITY RETAINED IN THE POPULATION
(rate of loss calculated as 1/2N per generation)

GENERATION	RAW DATA (N=124)	SIMPLE CORRECTION (N=120.8)	CORRECTION FOR FERTILITY VARIATION (N=100.8)
5	98.0%	97.95%	97.54%
10	96.04%	95.94%	95.15%
15	94.12%	93.97%	92.81%
20	92.23%	92.04%	90.53%

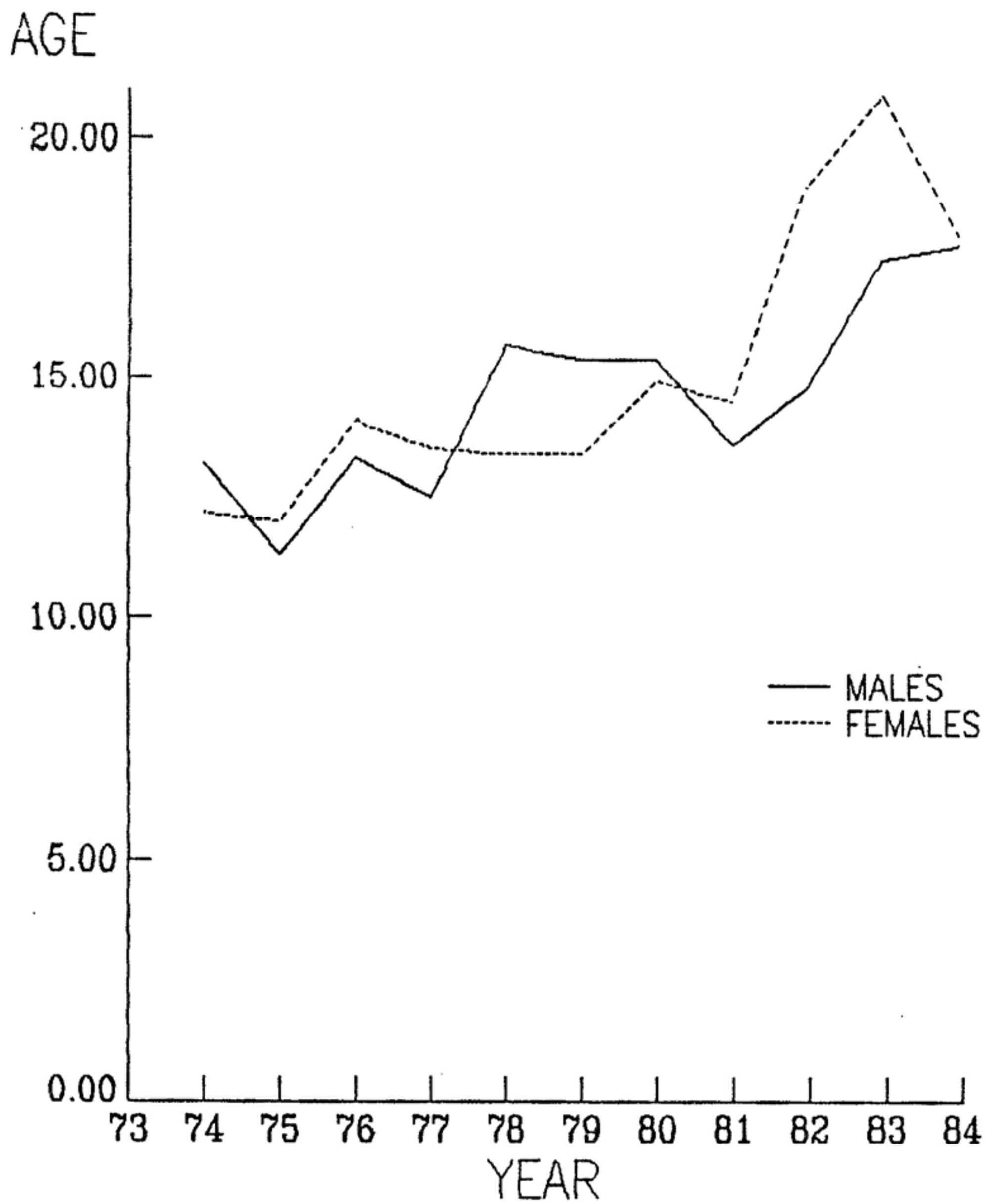

FIGURE 1

AVERAGE AGE OF REPRODUCTION
PARENTS OF GORILLA OFFSPRING BORN IN EACH YEAR

FIGURE 2

VARIATION IN PROGENY PRODUCTION - MALES

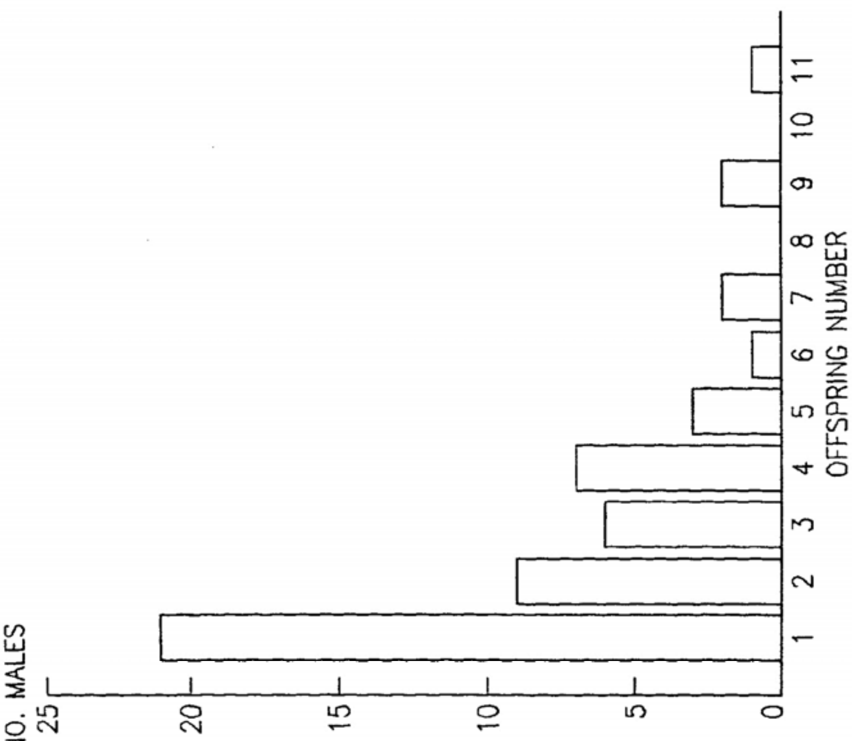

FIGURE 3

VARIATION IN PROGENY PRODUCTION- FEMALES