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TECHNICAL REPORT

Clarification of Genetic Terms and Their Use in the Management of Captive Populations

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Some of the concepts, terms, and methods used in the genetic management of captive populations have not been defined precisely in the scientific literature and consequently have been misunderstood and misused. The definitions and interrelationships among gene diversity, effective population size, founder genome equivalents, inbreeding, allelic diversity, mean kinship, and kinship value are presented here. It is important to understand what populations and generations are used as the baselines against which losses of genetic variation are measured. Gene diversity and founder genome equivalents are defined relative to a source population from which founders of the captive population were randomly sampled. Inbreeding and allelic diversity are assessed relative to the founders. The potential gene diversity that would result from an equalization of frequencies of founder alleles retained in the population can never be achieved because, among other limitations, the random process of gene transmission will prevent equalization of allele frequencies even if animals are bred optimally. The gene diversity achievable with the population can be determined by iterative production of hypothetical offspring from the pairs with lowest mean kinship. The long-term objective for offspring production from each animal is also thereby generated. Mean kinships should be recalculated with each real or hypothetical birth and death, because offspring objectives based on current mean kinships might correlate poorly with the optimal long-term offspring objectives.

Key words: captive propagation, founder genome equivalent, gene diversity, gene value, inbreeding, kinship value, mean kinship

INTRODUCTION

The methods of pedigree analysis used to help guide the genetic management of captive populations have been evolving rapidly. While various papers have described

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some of the methodologies used [e.g., Ballou, 1983, 1991; Ballou and Foose, in press; Ballou and Lacy, 1995; Boyce, 1983; DeBoer, 1988; Foose and Ballou, 1988; Lacy, 1988, 1989, 1993, 1994; Lacy et al., 1995; MacCluer et al., 1986; Thomas, 1990; Willis and Wiese, 1993], there remain aspects of pedigree analysis that have been increasingly used by American Zoo and Aquarium Association (AZA) Species Survival Plans© (SSPs) but which have not been described adequately in the professional literature. For example, due to the lack of formal published definitions and descriptions of some terms and concepts, there has been confusion regarding the use of the genetic metrics calculated by the GENES computer program [Lacy, 1993]. The purpose of this note is to clarify the definitions of some terms and to discuss appropriate uses of some genetic metrics that have been applied to SSP management.

TERMINOLOGY AND CONCEPTS

Gene Diversity

Gene diversity (GD), also termed *expected heterozygosity*, is a common and useful measure of genetic variation within a population [Wright, 1969; Nei, 1973; Willis and Wiese, 1993]. GD is the variance in allele frequencies at a genetic locus and is equal to the heterozygosity expected in a population with random union of gametes (i.e., in Hardy-Weinberg equilibrium). For a single genetic locus, GD is defined as

$$GD = 1 - \sum(p_i^2) \tag{1}$$

in which p_i is the frequency of allele i and the summation is over all alleles at that locus. GD reflects both the number of alleles and the evenness of their frequencies. GD can be applied to describe variation at a single locus, as above, or it can be averaged over loci to provide a genome-wide metric of genetic variation. In the absence of new variation introduced to a population by mutation or immigration, in the absence of natural selection, and in a randomly mating population of constant size, GD decays due to genetic drift according to

$$GD_t = GD_0 \times [1 - 1/(2N)]^t \tag{2}$$

in which the subscripts denote generations and N is the number of individuals in each generation. The decay of GD due to genetic drift is a result of the sampling of the gene pool that occurs when each generation is produced from the previous generation.

The rate of decay of GD is independent of initial level of gene diversity and of the allele frequencies at the loci. Therefore, it is often useful to represent the genetic variation of a population by the proportional gene diversity, relative to some baseline generation. The proportional gene diversity (GD_t/GD_0) is a widely used metric in the management of captive breeding programs, although frequently it is called "gene diversity," with the unstated implication that it is proportional to a baseline population. For example, Willis and Wiese [1993] assumed $GD_0 = 1$, so that absolute and proportional gene diversity were the same and were symbolized interchangeably as GD in their equations. Usually, GD_0 of the baseline population is not known. To obtain GD_0 for a single locus would require random sampling of individuals from that

baseline population; to obtain GD_0 averaged across the genome would require random sampling of genetic loci as well.

Although GD_0 is not needed to determine GD_t/GD_0, it is essential that the baseline used in each analysis be explicitly understood. For example, the GENES program calculates GD of a captive population relative to GD_0 of the possibly hypothetical population from which the founders were randomly sampled. This is not the same as the GD of the founders themselves, because the founders are a (usually small) sample of a larger population (for example, in the wild). The founders will therefore contain only a subset of the GD of the population from which they were sampled. The baseline GD_0 is also not necessarily the same as GD of the entire wild population, because often the founders of a captive stock were sampled nonrandomly from a subset of the range of the taxon. Thus, GD_0 of the true source population might be less than GD of the entire wild population. The sampling of founders from the wild is analogous to the production of an offspring generation, and the GD of the founders is therefore reduced relative to the population from which they were sampled according to equation 2, with N being the number of founders and $t = 1$, and with the assumption that the founders were a random sample of the source population [Lacy, 1988, 1994; Willis and Wiese, 1993].

The loss of gene diversity as founders are sampled from a source population, and then as subsequent generations are "sampled" from the founders, is most easily understood when the founders are obtained at the same time and descendant generations are discrete. Equation 2, for example, is only applicable if the living individuals are all the same number of generations (t) removed from the source population. If founders contributed to the captive population at various times, or lineages descended from different founders have otherwise passed through different numbers of generations, then it is still possible and useful to calculate the amount of gene diversity in the living population relative to the founders by using mean kinship or gene drop methods (described below).

Effective Population Size

The above discussion assumed that the genes transmitted to each generation are a random sample of the genes of the previous generation. If individuals do not breed randomly, then the rate of loss of GD might be slower or (much more commonly) faster than predicted from equation 2. The genetically *effective population size* (N_e) has multiple related meanings [Crow and Kimura, 1970; Crow and Denniston, 1988], but the form most commonly used in the design of captive breeding programs is the *variance effective size*. The variance N_e is defined as the size of an idealized population, with random union of gametes each generation, which would have the same intergenerational variance in allele frequencies as does the studied population. Thus, the variance effective population size is the number N that must be used in equation 2 to yield the observed rate of loss of GD. Because captive breeding programs are often directed toward minimizing the loss of GD, the variance effective size is appropriate. (For example, it is the one that should be used in the CAPACITY computer program [Ballou, 1992] for estimating the required population size to achieve a desired low rate of loss of GD.) The effective population size is reduced relative to the census population if there is greater variance among individuals in reproduction than expected by chance, as would happen if some individuals were particularly successful breeders, or if there are not equal numbers of male and female

breeders [Crow and Kimura, 1970; Lande and Barrowclough, 1987]. Moreover, most species have overlapping generations, so that a portion of the existing population consists of the present generation breeders, a portion consists of the future breeders of the next generation, and a portion may consist of postreproductive individuals from the previous generation. Only the present-generation breeders contribute to the effective population size (of their generation).

The reduction in the effective size relative to the census size of a captive or wild population can be substantial. Estimates of N_e/N based on the expected genetic effect of the demographic structure of the population (sex ratio, variance in reproduction, overlapping generations) seem typically to fall in the range of 0.10–0.50 for the managed captive populations of SSPs. More direct calculations based on the measured rate of loss of genetic diversity have indicated N_e/N to be in the range of only 0.004–0.051 for unmanaged laboratory populations of *Drosophila* flies [Briscoe et al., 1992].

Founder Genome Equivalents

The concept of *founder genome equivalent* (FGE) was introduced by Lacy [1989] as "that number of equally contributing founders with no random loss of founder alleles in descendants that would be expected to produce the same genetic diversity as in the population under study." FGE provides another metric of the amount of genetic variation in a captive population, expressed in units of randomly sampled founders. Like GD_t/GD_0, FGE is relative to a baseline, in that it is the number of founders drawn at random from a defined source population which would contain the observed amount of gene diversity. Two populations with the same FGE may have very different gene diversities, if the source populations differed in genetic variation. I originally [Lacy, 1989] defined FGE by the equation

$$FGE \equiv 1/\sum(p_i^2/r_i) \tag{3}$$

in which p_i is the proportion of genes in the descendant population that are contributed by founder i and r_i is the proportion of founder i's alleles that have been retained within the descendants. In that paper, I pointed out that FGE, defined in this way, provides a means of approximating the loss of GD, in that

$$GD_t/GD_0 \approx 1 - 1/(2FGE). \tag{4}$$

This approximation is quite accurate for large pedigrees but can deviate by about 1–5% for pedigrees of fewer than about 10 individuals. However, the pedigree analysis method of mean kinship, developed subsequently, provides a method of calculating exactly the proportional loss of GD expected in a pedigree [Ballou, 1991; Lacy, 1994; Ballou and Lacy, 1995]. Therefore, it is more useful to use this precise method to quantify losses of GD and to determine and define FGE by

$$FGE \equiv 0.5 \,/\, [1 - (GD_t/GD_0)] \tag{5}$$

so that the relationship between GD and FGE in equation 4 holds exactly. With this

modified definition of FGE, more precisely representing the original concept, equation 3 is now only approximate.

It is important to exclude founders themselves from tallies of genetic variation within a captive population [Lacy, 1989, 1994] in order to ensure that the genetic metrics reflect the progress of the captive propagation program and not simply the number of (possibly nonbreeding) animals collected from the wild. For example, the GENES program calculates metrics summarizing the genetic variation present in a captive population based only on the genetic variation present within the captive-born descendants of the founders. Thus, adding a new wild-caught animal to a captive population does not change the GD, the FGE, or the number of founders. That animal remains a "potential founder" until it contributes genes (in the form of offspring) to the captive-born population. When it breeds in captivity, the number of founders increases by one, and GD and FGE will also increase.

FGE and N_e share some similarities as methods of quantifying the loss of genetic variation from a population. FGE represents the *cumulative* loss of GD since the baseline generation as the number of founders that would contain that amount of gene diversity (equation 5). The variance N_e represents the *per generation rate* of loss of GD as the number of randomly breeding animals that would lose GD at the observed rate (equation 2). If N_e is moderately large (on the order of ten or more), then equation 2 becomes approximately

$$GD_t/GD_0 \approx 1 - t/(2N_e) \tag{6}$$

so that, combining with equation 4,

$$FGE \approx N_e/t. \tag{7}$$

For example, if a randomly breeding population of 20 founders produces 20 offspring, which in turn produce 20 grand-offspring ($N_e = N = 20$ each generation), then the percent of GD retained would be (by equation 2) $GD_t/GD_0 = 97.5\%, 95.1\%, 92.7\%$, and 90.4% in the founders, first, second, and third generation descendants, and FGE = 20, 10.1, 6.8, and 5.2, respectively (by equation 5).

Inbreeding

Inbreeding is the mating between animals that are related by descent from a common ancestor, subsequent to a defined baseline generation. The baseline generation for inbreeding calculations is normally taken as the founders of the population, which are defined arbitrarily to be noninbred and unrelated to each other. If more distant ancestors are known (for example, kinships among animals from the wild can be determined by molecular genetic methods [Geyer et al., 1993]), then an earlier baseline can be defined and inbreeding coefficients might be greater. Thus, whether an animal is inbred is dependent upon the baseline chosen, but earlier baselines can only increase the quantified level of inbreeding, by revealing additional shared ancestors in the pedigree. The first descendant generation of sexually reproducing, nonhermaphroditic species can contain animals that are interrelated but cannot contain inbred animals, because (by definition) their founder parents were unrelated. Thus, the second generation descendants are the first animals that can be considered

to be inbred. The inbreeding coefficient (or coefficient of consanguinity), F, in a pedigree is commonly taken to be the probability that the two alleles at homologous loci in the individual are identical by descent from a common ancestor of the parents [Wright, 1922, 1969; Jacquard, 1975]. Inbreeding reduces average heterozygosity, therefore, by a proportion F. (Because random genetic drift also reduces heterozygosity, the rate of loss of GD—"expected heterozygosity"—due to drift is at times quantified by an "inbreeding" coefficient, with $F = 1 - GD_t/GD_0$, even though there may have been no inbreeding in the sense of matings between relatives [Templeton and Read, 1994]).

Gene diversity is the heterozygosity expected if breeding is at random, so it might seem problematic that GD in the founders is less than GD_0, and GD decreases with each generation, but it is not until the second generation of captive-born animals that there can be any inbreeding or individuals homozygous with two copies of an allele descended from a founder. This conflict is resolved, however, because the baseline generation used in inbreeding calculations is the founders while the baseline for GD calculations is the (wild) parental population of the founders. Moreover, the "random breeding" assumed in equating GD with heterozygosity includes the possibility that an animal will mate with itself. Hermaphroditic animals can be inbred in the first generation, if one founder was both their sire and dam. In nonhermaphroditic animals, the requirement of bisexual reproduction causes irregular accumulation of inbreeding in early generations of random breeding, while GD declines regularly according to equation 2.

Inbreeding is relative in another sense: inbreeding is a scalar quantity, not a categorical quality. It makes little sense to consider (as is often done) animals with inbreeding coefficients of, say, $F = 0.0156$ (from second-cousin matings), $F = 0.0625$ (from first-cousin matings), and $F = 0.25$ (from full-sib matings) to be a distinct class of "inbred" animals to be contrasted with "noninbred" animals ($F = 0.00$). Animals with $F = 0.0625$ would, with respect to heterozygosity and various measures of fitness, be much more similar to animals with $F = 0.00$ than to animals with $F = 0.25$. The concern with low levels of inbreeding in managed pedigrees should not be with immediate loss of fitness (which would be undetectably small, especially in a captive environment) but with the cumulative aspect of inbreeding. Unless reversed by later outcrossing to less related animals, an incremental increase of, say, 0.03 per generation would cause an unobservable incremental loss of genetic variation and fitness which could, within about four generations, lead to a damaging cumulative loss of fitness in the population. Breeding programs designed to sustain a healthy population without further import of new founders for 100 or more years should keep incremental increases in inbreeding and losses of gene diversity to minimal levels.

Allelic Diversity

The loss of allelic variants due to genetic drift is much more difficult to predict, because the rate of loss is dependent upon the initial allele frequencies [Fuerst and Maruyama, 1986; Lacy, 1994]. Rarer alleles are more likely not to be transmitted to any offspring in the next generation than are more common alleles. To model the loss of alleles, a common practice in "gene drop" simulations is to assume that each founder carries two unique alleles at each genetic locus [MacCluer et al., 1986]. This is the limiting case, with each allele initially present in just one copy, and it will lead

to the most rapid loss of allelic diversity. Thus, gene drop analyses assume a baseline of the founder generation and assess the probability that an allele unique to a founder would be lost in subsequent generations. If an earlier generation were chosen as the baseline or, equivalently, the founder generation were assumed not to contain all unique alleles, then the rate of loss of allelic diversity would be less. This dependency on initial conditions can make interpretation of metrics of allelic diversity difficult.

The assumption of all unique founder alleles in a gene drop simulation facilitates calculation of several other metrics of genetic variation. First, the frequency, over many iterations of the simulation, of an individual being homozygous at the modeled locus will be equal to that animal's inbreeding coefficient, as both are measures of the probability of homozygosity by descent since the baseline, founder generation. (Homozygosity due to identical alleles descending from unrelated ancestors is excluded by the assumption that all founder alleles are unique.) Second, GD calculated from the allele frequencies of the founders ($GD = 1 - \sum[1/(2N)]^2 = 1 - [1/(2N)]$, in which N is the number of founders) gives a standard measure of the "founder effect," or loss of GD in the founders relative to the source population from which they came [Willis and Wiese, 1993; Lacy, 1994]. The GD of the source population must be considered to be 1.0 (i.e., it consisted of an infinite number of heterozygous and genetically unique individuals), in order for the founders to all have been (by assumption) heterozygous. Under the assumption that the source (wild) population had $GD_0 = 1$, GD_t/GD_0 will equal GD_t, leading to common confusion regarding the distinction between absolute and relative GD.

Mean Kinship and Kinship Value

Mean kinship (MK), the average coefficient of kinship of an animal to each living, nonfounder animal in a pedigree (including itself, if it is not a founder), can be a useful metric for summarizing the genetic value of an animal to a breeding program [Ballou, 1991; Lacy, 1994; Ballou and Lacy, 1995]. The overall mean kinship of a population (the mean MK) equals $1 - GD_t/GD_0$; both are the probability that two alleles sampled at random from homologous loci in the population will be homozygous by descent from a common ancestor. Breeding the animals with lowest MK will necessarily maximize GD in the next generation, as it ensures that the founder alleles with lowest frequency are preferentially propagated. Simulations have shown that a program of breeding animals based on choosing those with lowest MK is a better strategy for maximizing long-term preservation of gene diversity and allelic diversity, and avoiding future inbreeding, than is minimizing immediate inbreeding, equalizing founder contributions, or breeding animals most likely to contain unique alleles [Ballou and Lacy, 1995].

A complication with the use of MK to select breeders is that each offspring added to a pedigree (or dead animal removed from a pedigree) changes the matrix of kinships and changes the MK of every animal in the population. Thus, for selecting breeders, MKs should be used and recalculated iteratively, with the kinship matrix [Ballou, 1983] updated by the addition of a hypothetical offspring each time a mating is selected.

Not all individuals in a population are equally likely to survive and produce future offspring. Therefore, the most probable future distibution of allele frequencies in a population might be skewed relative to the present distibution. In the extreme case, alleles unique to postreproductive or otherwise sterile animals are certain to be

lost. Animals in the prime of their reproductive life spans have high probabilities of contributing many more copies of their genes to the population. Therefore, better genetic management might be achieved by considering the shifts in the gene pool of the population that will likely occur due to the age structure of the population. Top priority for breeding should be given to those animals who have the least commonality of genes with the probable next generation.

A modification of mean kinship, *kinship value* (KV), has been proposed to adjust breeding priorities for the reproductive potential of each animal in the present generation [Ballou and Lacy, 1995]. The KV of an animal is the weighted mean kinship of the animal to each living nonfounder, with the weights being the reproductive value of each kin entered into the calculation. Reproductive value is age-specific and is defined as the expected future lifetime reproduction [Fisher, 1930]. Reproductive values are determined from analysis of age-specific fecundity and mortality rates. It is important to note that KV is not the MK multiplied by an animal's own reproductive value but rather is a mean weighted by the reproductive values of all kin to that animal. Thus, the kinships of postreproductive kin do not contribute to an animal's KV, and an animal with mostly aged kin would likely be a priority breeder. An animal with many kin of young breeding age would have its KV elevated relative to its MK and would therefore not likely be a priority breeder.

Just as the GD (= 1 − mean MK) of a population predicts the heterozygosity of the next generation (relative to the baseline generation) expected if breeding is at random, (1 − mean KV) predicts the heterozygosity of the next generation if all animals produce the number of future offspring expected based on the population fecundity and mortality rates. One minus the mean KV of a population has therefore been termed the *gene value* of the population in the GENES program, in reference to it being a modification of gene diversity to account for reproductive values.

MANAGEMENT ISSUES

How Potential Are Potential Founders, FGEs, and GD?

The gene drop analysis performed by the GENES program provides summary statistics not only on the living captive-born population as it exists when the analysis was run but also on the potential population that could be derived from the existing captive population if there were perfect genetic management in the future. These metrics of the potential population can be useful in providing an indication of the scope for genetic improvement through wise genetic management, in the absence of any further import of newly wild-caught animals. This scope for genetic improvement provides a target for the future, an indication of the need or lack thereof for new wild-caught animals to achieve genetic objectives, and an upper ceiling to future genetic variation in the absence of further imports. It is important, therefore, to consider how closely and under what circumstances the potential can be reached.

Potential founders are already in the captive collection, and the probability of their ever contributing progeny should be assessed by consideration of their age, health, behaviors, responses to past breeding opportunities, and the biology and history of captive propagation for the species. For each potential founder that is lost, the potential FGE is decreased by 1. The resulting decrease in potential GD depends

on the number of founders (and can be determined from equation 4), as each additional founder contributes proportionately less to the acquisition and preservation of GD [Lacy, 1994].

The potential FGE and GD that is actually achievable will be reduced further for several reasons. The full potential is reached when all founder and potential founder alleles still existing in the captive population are brought to equal frequencies through genetic management. (For a given set of alleles, GD is maximized if all allele frequencies are equal—Eq. 1.) As is well known, however, even if managers plan the optimal breeding program, rarely if ever do all animals that are paired produce exactly the number of offspring that are desired from them. Not only might some not breed or not produce the numbers of progeny that are desired, but unequal numbers of males and females in the population will diminish the effectiveness of the breeding program in preserving GD. Moreover, even if all animals do produce exactly the desired number of offspring, we still cannot control which of the two homologous at each locus are transmitted to each offspring. Thus, the mechanisms of Mendelian genetics include a random sampling process that invariably adds variation to the allele frequencies in future generations. For example, even if contributions are kept equal among founders, the frequencies of the two alleles contributed by each founder will deviate randomly. Therefore, it should be recognized that the potential values given by analyses as in the GENES program can never, even in theory, be achieved.

It is possible to determine how close to the potential FGE and GD it may be possible to reach, if managers plan the perfect breeding program and animals all reproduce as desired, but allelic transmission is still random and animals are constrained to breed only with the opposite sex. GENES provides the option of testing the genetic effects of producing future offspring from any desired mating. By iterating this process to produce hundreds or thousands of offspring, always selecting the most genetically valuable pair (those with the lowest MK) as parents, the theoretically achievable FGE and GD can be generated. (Many fewer matings are usually adequate to approximate the effect of optimal genetic management and, for most species, would be more realistic. The very large number of matings simply provides numerical precision to the calculations.)

Table 1 shows for two SSPs, okapi (*Okapia johnstoni*) and Goeldi's monkey (*Callimico goeldii*), the metrics summarizing the genetic variation in the existing SSP population as of late 1994, the potential if all founder alleles still retained within the population were brought to equal frequency, and the theoretically achievable levels of genetic variation as determined by the production of 1,000 optimal offspring. Potential values of genetic variation were obtained from a gene drop simulation with 100,000 iterations. Matings to produce optimal offspring were constrained to be between a male and female, but no restrictions were placed on the numbers of progeny that could be produced from any pair. The okapi population has received recent imports of three new founders that are not yet well represented, so founder allele frequencies are presently quite unequal. Through good genetic management it might be possible to reach levels of GD and FGE that are close to their potentials. Goeldi's monkey have a large, complex pedigree, with no living founders, and presently more equal representation of founder alleles. Only about one-third of their potential increase in GD and FGE could be recovered even with optimal genetic management.

TABLE 1. Number of founders (N_f), founder genome equivalents (FGE), and percent of original gene diversity (%GD) in SSP populations of okapi and Goeldi's monkey at present, the potential if all founder alleles still retained in the populations were to be brought to equal frequencies, and achievable after 1,000 hypothetical offspring are added to the population

	Okapia johnstoni[a]			*Callimico goeldii*		
	Present	Potential	Achieved after 1,000 matings	Present	Potential	Achieved after 1,000 matings
N_f	25	25	25	22	22	22
FGE	6.0	11.4	10.4	10.0	16.0	11.7
%GD	91.7	95.6	95.2	95.0	96.9	95.7

[a]Metrics calculated after omitting genes descended from an unknown, nonfounder ancestor.

Lifetime Offspring Objectives for Breeders

Planning of breeding programs often involves determination of the number of offspring to be desired from each breeder in the population. Such offspring objectives can be valuable aids in determining how to assign males to females as pairs for breeding, whether it is worth moving an animal to a new social group or institution for future breeding, and how to space breeding attempts over time. Various methods have been employed by SSPs in the past to try to determine desired lifetime offspring objectives. Most attempts can be described as guesses about how far down a list of MKs (or some other prioritizing metric) we might desire fewer (or no) progeny.

MKs (or KVs, if one wishes to adjust for expected future reproduction by kin) can be used to assign offspring objectives to each animal but not in the manner that has typically been employed. Because MKs are dynamic, changing with each birth or death in the population, it is not adequate to use a static list of MK to set lifetime offspring objectives. For example, a large cohort of siblings may all have high MK (because they have many kin) and therefore be assigned low or no breeding priority. However, after some of that cohort die, or nonkin produce many offspring, the MK of each of the remaining siblings in the cohort will decrease and their priority for future breeding will rise. Similarly, two siblings of an otherwise unrepresented founder pair may both have low MK and be given high priority for breeding. As soon as one produces progeny, however, the MK of both will increase (although the MK of the breeding sib will increase more), and the future priority for breeding either sibling will decline.

Unfortunately, because of the complexities of kinship relationships in many pedigrees, it is not appropriate to use a static MK list to determine relative offspring objectives for optimal future breeding. Optimal long-term breeding programs (those that always select breeders with the lowest continuously updated MK) may produce more offspring from some animals of higher current MK than from other animals with greater present breeding priority. Table 2 shows the current MK and the optimal number of progeny for okapis, with the assumptions that 10, 100, or 1,000 progeny are desired. Although MK gives an approximate ranking of the number of offspring to be desired from each okapi, the rank order of present-day MK does not match the order of offspring objectives. Moreover, the first 10 optimal offspring do not give a good indication of the longer range offspring objectives, nor does use in the first 100 matings predict accurately the frequency of use over the first 1,000 matings. Animals

TABLE 2. Present mean kinships, frequency of use in 10, 100, or 1,000 matings, and first mating used for *Okapia johnstoni* in the SSP

				Matings out of			First					Matings out of			First
♂♂[a]	Sire[b]	Dam[b]	MK[c]	10	100	1,000	use	♀♀[a]	Sire[b]	Dam[b]	MK[c]	10	100	1,000	use
389	358	372	.017	5	26	200	1	348	WILD	WILD	.011	4	26	202	1
391	WILD	381	.017	4	26	200	2	315	WILD	WILD	.017	4	24	201	2
299	219	273	.035	1	14	108	9	292	257	248	.022	2	19	152	4
283	219	249	.057	0	10	106	30	390	247	315	.051	0	0	0	
933	331	315	.064	0	0	0		908	247	315	.051	0	0	0	
931	391	397	.064	0	0	0		929	389	351	.057	0	0	0	
392	259	348	.065	0	0	0		253	198	160	.061	0	16	144	24
414	259	348	.065	0	0	0		317	247	275	.076	0	6	67	43
369	283	317	.072	0	0	0		906	283	368	.082	0	0	0	
247	58	139	.073	0	11	112	27	336	214	253	.084	0	0	22	133
338	283	275	.082	0	2	70	72	932	283	396	.084	0	0	0	
325	214	253	.082	0	1	21	73	351	214	253	.085	0	0	21	162
408	331	351	.098	0	0	0		383	331	253	.086	0	0	0	
331	259	216	.099	0	5	73	48	368	247	313	.094	0	0	0	
416	338	386	.103	0	0	0		417	310	313	.095	0	0	6	270
411	338	333	.103	0	0	0		272	214	196	.096	0	5	110	66
377	338	333	.103	0	0	0		313	259	216	.098	0	4	69	56
936	338	342	.105	0	0	0		396	310	313	.098	0	0	6	371
412	259	272	.107	0	0	0		397	331	336	.100	0	0	0	
934	259	272	.107	0	0	0		907	325	378	.101	0	0	0	
259	172	153	.107	0	5	110	62	935	338	386	.103	0	0	0	
								398	338	342	.105	0	0	0	
								378	338	342	.108	0	0	0	
								333	259	272	.113	0	0	0	
								386	259	272	.113	0	0	0	
								342	259	272	.117	0	0	0	

[a]Studbook numbers greater than 900 are temporary numbers for recent births.
[b]Dead parents underlined.
[c]MK calculated after omitting portions (up to 12.5%) of the genome descended from an unknown ancestor.

chosen more often as breeders are not always chosen for the first time sooner than animals with lower long-term offspring objectives.

Much of the discordance between present MK rankings and long-term offspring objectives derived by iterative use of MK results from the low utilization as breeders animals who have living parents. Among the okapi, none of the animals with both parents still in the population were chosen in the next 1,000 matings. This is a common but not inevitable consequence of choosing matings based on iterative MKs. A male okapi (studbook #259) with the highest present MK but neither parent living was chosen for 11% of the future matings, while some of his sons (studbook 392 and 414), with much lower present MKs, were never chosen. This phenomenon, of animals with living parents rarely being chosen for breeding, results from progeny containing no genes not present in their parents (but containing only a subset of those genes). When the parents die, the reduced MKs of the progeny immediately give them higher priority for breeding. A secondary consequence is that generation time will be extended, as animals are kept as breeders until they die or become physiologically postreproductive. Although the projected numbers of matings for priority

breeders in Table 2 are unrealistic for okapi, little additional genetic variation is lost if, after a moderate number of matings, parents are replaced by their offspring as breeders.

Although generating hypothetical matings provides a method for estimating long-term offspring objectives, it would be counterproductive to use such offspring objectives, rather than the dynamic ranked list of MK, to select breeders in the short term. Animals that are presently low on the MK ranking but who are assigned large proportions of future offspring (e.g., okapi #259) will become optimal future breeders only if and when animals with present priority for breeding have produced a number of offspring. Optimal retention of gene diversity is achieved by always selecting breeders with the lowest MK while constantly updating the MK calculations to adjust for new progeny, deaths, or animals otherwise removed from the potential breeding population.

CONCLUSIONS

While training in the management of populations and increased use in SSPs has over the past decade produced considerable understanding and familiarity with genetic concepts among zoo animal managers, some of the details of genetic metrics and techniques in use have been unavailable, overlooked, or misused. Many SSPs and other breeding programs set goals of maintaining prescribed levels of original gene diversity, so it is important to understand and specify the baseline population that defines the goals to which we aspire. The precise meaning of metrics of genetic variation must be clear if we are to use quantitative methods to plan breeding programs and to assess progress. Iterative procedures can be used to project the genetic improvement possible through pedigree management and can provide long-term breeding objectives for animals in the population. Intuitive guesses about the priority and timing of breeding of animals for optimizing genetic variation can yield poor results.

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