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RESEARCH ARTICLES

Analysis of Founder Representation in Pedigrees: Founder Equivalents and Founder Genome Equivalents

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The concepts of "founder equivalent" and "founder genome equivalent" are introduced to facilitate analysis of the founding stocks of captive or other populations for which pedigrees are available. The founder equivalents of a population are the number of equally contributing founders that would be expected to produce the same genetic diversity as in the population under study. Unequal genetic contributions by founders decrease the founder equivalents, portend greater inbreeding in future generations than would be necessary, and reflect a greater loss of the genetic diversity initially present in the founders. The number of founder genome equivalents of a population is 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. The number of founder genome equivalents is approximately that number of wild-caught animals that would be needed to obtain the same amount of genetic diversity as is in the descendant captive population. Founder equivalents and founder genome equivalents allow comparison of the genetic merits of adding new wild-caught stock vs. further equalizing founder representations in a captive population.

Key words: allelic diversity, genetic diversity, genetic management, pedigree analysis

INTRODUCTION

Small captive populations lose genetic diversity because of random genetic drift. Even in the absence of selection, alleles present in one generation may by chance become more or less frequent, or even "extinct," in subsequent generations. Because genetic drift can eliminate alleles, but only mutation or immigration can restore lost variants, randomly fluctuating allele frequencies result in a decay of genetic diversity. This loss of variation is reflected in both a loss of heterozygosity in the population [see Lacy, 1987, for a discussion of the fate of heterozygosity in small populations subject to drift] and a loss of allelic variants [for treatments of the loss of alleles, see Allendorf, 1986; Fuerst and Maruyama, 1986]. Lower heterozygosity

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often results in lower average fitness of individuals (inbreeding depression), whereas a lack of allelic variants prevents long-term adaptive response to selection [Falconer, 1981; Selander, 1983; Allendorf and Leary, 1986].

The rate of genetic drift is critically dependent on population size. Greater random fluctuations in allele frequencies (and therefore greater average loss of heterozygosity and of allelic variants) occur when the population "sampled" each generation is smaller. The loss of heterozygosity and the loss of alleles are related (heterozygosity depends on the presence of alternate alleles). However, the presence of very rare alleles contributes little to overall population heterozygosity, and rare alleles are lost from small populations much more rapidly than is heterozygosity [Allendorf, 1986; Fuerst and Maruyama, 1986]. The expected loss of heterozygosity in one generation of random reproduction in a population of diploid, sexually reproducing organisms is given by

$$H_t = H_{t-1} \times (1 - 1/(2N))$$

in which H_t is the heterozygosity at generation t, and N the number of breeding individuals [Crow and Kimura, 1970]. The probability that a genetic variant will be lost in any one generation of random mating is

$$\Pr[\text{loss}] = (1 - p)^{2N}$$

in which p is the frequency of the allele in the parental generation.

Probably no population reproduces at random: selection leads to disparities among individuals in the probability of reproduction, and mate choice, habitat choice, and limited dispersal lead to incomplete mixing of the breeding population and nonrandom pairings. Formulae have been developed for calculating the genetically "effective population size" (N_e), that size of a randomly mating population that would lose heterozygosity at the rate expected in a nonideal population under study [Wright, 1969; Crow and Kimura, 1970].

The sampling of genetic alleles during transmission from one generation to the next can be split into two components: reproductive success by individuals and the random determination of which of the two alleles at each genetic locus in a reproductive individual will be present in a haploid gamete that contributes to a progeny. Variation among individuals in reproductive success is, in part, under the control of a population manager, who can pair potential mates and perhaps cull offspring to minimize the variation in family size [Foose, 1977; Flesness, 1977; Foose et al., 1986]. The determination of which allele is included in each successful gamete is not generally controllable.

Because of the potentially deleterious or even disastrous consequences of loss of genetic diversity in small captive populations [Ralls et al., 1979; Ralls and Ballou, 1983], retrospective and prospective pedigree analysis is often recommended to allow breeding plans to be designed so as to minimize the variation in family size, maximize the genetically effective population size relative to the census population size, and thereby minimize genetic drift [MacCluer et al., 1986; Thompson, 1986]. Techniques for calculating the rate of inbreeding (expected loss of heterozygosity per individual resulting from common ancestry of parents of an inbred individual) are widely available [Wright, 1969; Crow and Kimura, 1970; Jacquard, 1974; Falconer, 1981;

Ballou, 1983]. The analysis of the loss of alleles in a pedigree has only recently received attention, and some methodologies require considerable or even prohibitive computer memory [Thompson, 1986] or computer time [MacCluer et al., 1986] for even moderate-size pedigrees.

Pedigree analysis, whether for heterozygosity loss (inbreeding) or loss of allelic variation, must begin with the "founder" population, individuals of unknown and presumed independent ancestries from which the pedigree population descends. All determinations of genetic loss are relative to the genetic variability in the founding population. The analysis of allelic loss is then a determination of the probability that alleles present in the founding population still reside within the descendant population. Thompson [1986] derived analytical solutions for the probability that an allele present in a founder exists in the living animals and for the expected number of copies of each founder allele in a population. MacCluer et al. [1986] used computer simulation of the Mendelian transmission of founder alleles through a pedigree to determine the probability of loss and the expected number of descendant copies of founder alleles. In both cases, the results can be used to identify founders whose genetic contributions are poorly represented in the pedigree (high probability of allele loss and low frequency of occurrence). By setting breeding plans to increase the number of descendants of poorly represented founders, population managers can minimize the expected loss of genetic variants from the population [Foose et al., 1986]. Equalized founder representations usually also will result ultimately in less inbreeding in a population, although inbreeding may not be minimized during generations in which past imbalances in founder contributions are being rectified.

The average genetic contribution of each founder to the descendant generations can be determined readily from the "additive-matrix" analysis of genetic relatedness between each pair of individuals in a population [see Ballou, 1983, for a description of the methodology]. The expected proportion of the genes within an individual that have descended from the genes of a founder is equal to the coefficient of genetic relatedness between the descendant and the founder. Therefore, the summation of the relatednesses between a founder and all living descendants will be equal to the expected number of copies of each of that founder's alleles in the living population. The expected number of copies of a founder's alleles in a population can also be determined by computer simulation of the stochastic transmission of alleles through the known pedigree ["gene drop" simulations: MacCluer et al., 1986]. Although inequalities in the genetic representations of founders can be calculated from the additive matrix of genetic relationships or from a gene drop simulation, no method has been available for summarizing the genetic impact of such inequalities. Here I provide two metrics which allow comparison of different arrays of founder representations and calculation of the equivalently sized, genetically ideal population for any population with a completely known pedigree.

METHODS

A founder is defined as an animal with no known genetic relationship to any other animal in the pedigree except for its own descendants: wild-caught animals, animals introduced to the pedigreed population from other captive sources for which no information on parentage is available, and other animals with unknown parents. If one parent is known (for example, when a wild-caught female produces an offspring

sired in the wild), the unknown parent is considered a founder of the captive population, even though that founder was perhaps never itself in the captive population. Founder analyses generally overestimate the genetic diversity contained within a population (for the same reason, so do inbreeding analyses) because animals with unknown parents (whether wild-caught or simply without records of captive history) are assumed to be unrelated. The genetic analyses cannot do otherwise. Wild-caught animals that have no living descendants in captivity are not considered founders, although they would become founders upon production of offspring.

To maximize the retention of genetic variability within a closed population, an animal manager would breed a large and equal number of descendants from each founder. Large numbers of descendants minimize the subsequent random loss of genetic variants that had been present in the founding population. Equal founder representations in the descendant generations assure that the genetic variants that had been present in each founder are not excluded from the descendant population while other founder alleles are present in many copies. A descendant population with unequal representation of founders will contain less genetic variability (both less heterozygosity and fewer allelic variants per locus) than will a population with the same number of founders, but in which the founders have made equal contributions to future generations.

To measure the overall founder representation in a managed population, accounting for the loss of genetic variability from unequal founder contributions, I define the number of "founder equivalents" (symbolized f_e) of a population as that number of founders that would produce a population with the same diversity of founder alleles as in the pedigree population if all founders had contributed equally to each descendant generation (while the number of descendants remained the same). Directly analogous to the concept of "effective number of alleles" at a genetic locus [Wright, 1969; Crow and Kimura, 1970] and conceptually although not mathematically related to the "effective population size" [Wright, 1969], the number of founder equivalents of a population is

$$f_e = 1 / \Sigma (p_i^2)$$

in which p_i is the proportion of the genes of the living, descendant population contributed by founder i. (See Appendix A for an example of the calculations.) Living founders are not summed into (their own) founder representations. If all founders contribute equally to the descendant population, the founder equivalent number is equal to the actual number of founders. Unequal contributions result in fewer founder equivalents. For example, if one founder contributes half of the genes to descendant generations and two other founders each contribute one-fourth, f_e is 2.67. If one founder contributes half of the descendants' genes, f_e rapidly approaches 4 as the number of founders jointly contributing the other half becomes large.

Even if all founders contribute equally to a population, genetic variability will be lost by genetic drift. Whenever the genes of a founder are channeled through one or relatively few living descendants (a genetic "bottleneck"), there is a nonzero probability that any given allele from that founder will not be passed on to any of those descendants. In the extreme, if a single descendant of a founder is an ancestor to all living descendants of that founder (e.g., when a founder has only one offspring

and that offspring produces a number of descendants), then at most, only one of the two alleles at each genetic locus of the founder could have remained in the population. For simple pedigrees, the fraction of a founder's alleles that have been retained in the descendant population can be calculated from probability theory (see Appendix A) [Thomas and Thompson, 1984; Thompson, 1986]. For extensive pedigrees, the fraction of each founder's alleles retained can be determined by computer simulation [MacCluer et al., 1986].

To equate the diversity of founder alleles in a managed population to the genetic diversity that would be present if all founders had contributed equally *and* no alleles had been lost by drift during bottlenecks, I define "founder genome equivalent" (symbolized f_g) similarly to "founder equivalent," but with devaluation of the contribution of each founder by the proportion of its genome that likely has been lost by random drift:

$$f_g = 1 / \Sigma (p_i^2/r_i)$$

in which r_i is the expected proportion of founder i's alleles that have been retained within the descendant population, and p_i is the proportion of the genes in the descendant population contributed by founder i. (See Appendix A for an example of the calculation of founder allele retention, r_i, and the founder genome equivalent, f_g.) If a constant fraction r of each founder's genes have been retained, then $f_g = r \times f_e$. The founder genome equivalent corrects not only for unequal founder contributions (as does the founder equivalent number), but also for those fractions of founder genomes irretrievably lost from the pedigree during bottlenecks. Thus, it is the more accurate description of the amount of founder variation present in the descendant population, but unfortunately, it can be only calculated for very simple pedigrees or approximated from computer simulation results.

The term "effective number of founders" has been used by this author and other zoo biologists for the concepts "founder equivalent" and "founder genome equivalent" or simply to designate the number of founders (as opposed to wild-caught animals that may or may not have contributed to the descendant population). Because the effective number of founders has never been defined in the literature and has taken on many related but not identical meanings, I have refrained from defining it at this time to be any one of these concepts. I encourage zoo biologists to use the terms "founder equivalent" and "founder genome equivalent" only as they have been defined above or to define precisely new terminology for alternative concepts and measures that are used.

The number of founder genome equivalents is related to the expected loss of genetic diversity resulting from genetic drift. In a randomly mating population, the average inbreeding coefficient is approximated by $1/(2 \times f_g)$, the probability that any two alleles in an individual are identical because they both descended from the same founder allele. (This will give a modest underestimate of the average inbreeding coefficient because f_g is a function of a product of expected, or mean, founder allele frequencies, whereas the mean inbreeding coefficient is a mean of a function of a product of founder allele frequencies—a mean of products is greater than the product of the means.) Although the average inbreeding coefficient estimated from f_g will rarely be of practical use (the actual inbreeding coefficients can be readily determined

TABLE 1. Effects of founder contributions on founder and founder genome equivalents*

Numbers of offspring from two founder pairs	f_e	f_g	r_1	r_2	H
2,2	4.00	3.00	.750	.750	.812
3,3	4.00	3.50	.875	.875	.833
4,4	4.00	3.75	.938	.938	.844
8,8	4.00	3.98	.996	.996	.860
2,4	3.60	3.21	.750	.938	.819
4,8	3.60	3.54	.938	.996	.840
8,16	3.60	3.60	.996	1.00	.851

*Founder equivalents (f_e), founder genome equivalents (f_g), proportion of alleles from founder pair 1 (r_1) and founder pair 2 (r_2) retained in the descendant population, and mean proportion of founder gene diversity (H, "expected heterozygosity") remaining in the descendant generation for seven sets of first-generation descendants of two pairs of founders ($f = 4$); f_g and r_i were calculated from probability theory (for a founder with x first-generation descendants, $r_i = 1 - .5^x$), whereas H was determined from 10,000 computer simulations.

from the additive matrix needed to calculate the founder representations), the relation does demonstrate that populations with the same number of founder genome equivalents will be expected to lose genetic variability at similar rates. Thus, the founder genome equivalent does provide a genetically meaningful metric for comparing populations with very different arrays of founder representations.

ILLUSTRATIVE EXAMPLES

The relationships between founder contributions, founder equivalents, founder genome equivalents, and loss of genetic variability can best be understood by examination of some simple pedigrees. Consider a captive population started with two breeding pairs of founders. If each pair produced an infinite number of progeny, none of the founder alleles would be lost by drift, the number of founders (f), founder equivalents (f_e), and founder genome equivalents (f_g) would all be 4.0, and the average inbreeding coefficient in the next generation with random mating would be 0.125 ($= 1/[2 \times f]$). Table 1 shows how these metrics change if offspring are limited and the founders produce unequal numbers of descendants.

As can be seen in Table 1, founder equivalents are affected by inequalities in the proportional contributions of founders, but not by the total numbers of progeny. Founder genome equivalents are diminished both by unequal founder contributions and by limited opportunity for founder alleles to be passed on to future generations. The number of founder genome equivalents is always less than the number of founder equivalents, approaching it as the number of offspring increases (and therefore the founder allele retentions increase). The gene diversity (H, heterozygosity expected if the population were randomly mating, in Hardy-Weinberg-Castle equilibrium) of each descendant population is approximated, but slightly underestimated, by $1 - 1/(2 \times f_g)$.

RESULTS

To demonstrate the use and usefulness of the concepts founder equivalent and founder genome equivalent, founder representations in international studbooks from two captive populations, okapis and Goeldi's monkeys, were analyzed. Founder contributions to the living populations were determined by the additive matrix

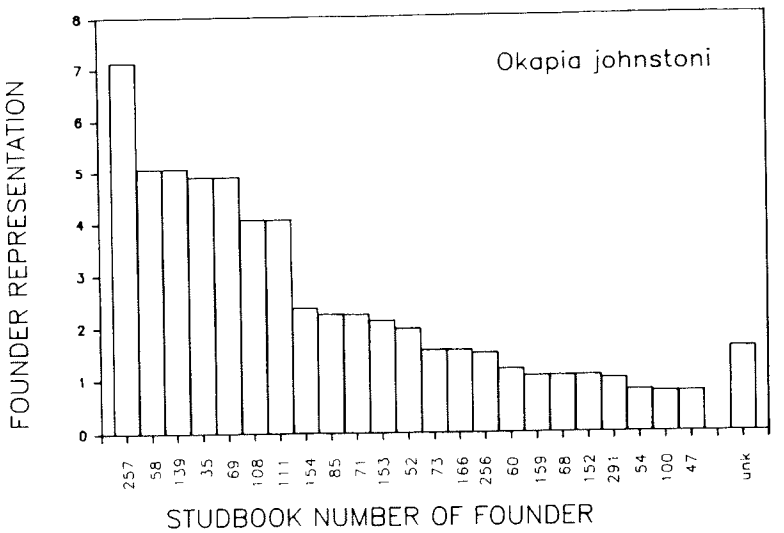

Fig. 1. Founder representations (expected numbers of copies of founder genes) in the okapi population in North American and European zoos. At the far right is the contribution of the unknown sire of studbook 209.

method, founder allele retentions were determined by 10,000 computer simulations, and the founder equivalents and founder genome equivalents were calculated as described above and in Appendix A.

North American and European Captive Okapi

The pedigree of the captive population of okapi (*Okapia johnstoni*) was obtained from the 1987 Studbook of the Okapi [Van Puijenbroeck, 1987]. The analysis was restricted to the captive population in European and North American zoos, because pedigree information for animals in captivity in Zaire is often lacking. Currently, there are 60 captive-born (nonfounder) okapis in European and North American zoos. Of 75 wild-caught okapis contributing to the captive populations in Europe and North America (70 brought to zoos in Europe or North America, five producing progeny while captive in Zaire, which were subsequently brought to northern hemisphere zoos), 30 have reproduced in captivity and 23 have living descendants. The sire of one captive-born ancestor of the captive herd is unknown; therefore, that unknown sire must be considered a "founder" in genetic calculations. The percentage representation of these 24 founders in the European–North American herd varies from 1.25% to 11.88% (Fig. 1). The number of founder equivalents calculated from the founder contributions in the pedigree is 16.05. If the genetic contributions of the one unknown "founder" are omitted from the analysis, there would be 15.39 founder equivalents. An equalization of the contributions from the 23 founders (although it is probably not now possible to achieve this fully) and incorporation of genes from one wild-caught animal that has yet to reproduce in captivity would be as useful as the introduction of nine new wild-caught stock, or more, assuming that newly captured animals may not breed according to optimal plans.

Analysis of founder allele retention in 10,000 gene drop computer simulations

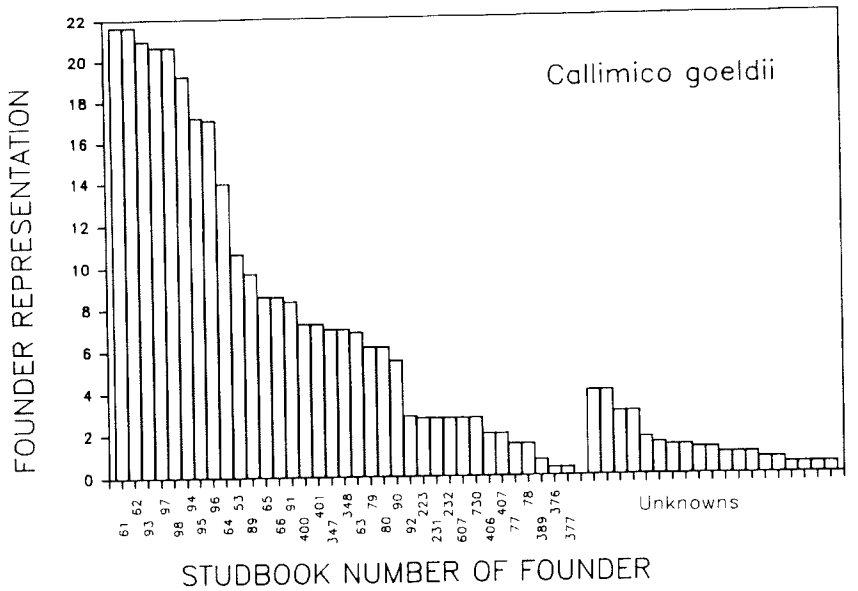

Fig. 2. Founder representations (expected numbers of copies of founder genes) in the captive population of Goeldi's monkeys. At the right are contributions of 19 animals with unknown parents.

yielded 12.13 founder genome equivalents and a mean of 94.57% of gene diversity (expected heterozygosity) of the founding population remaining in the living descendants. Omitting the genetic contributions of the one unknown "founder," there are 11.76 founder genome equivalents. The okapi founder genome equivalents are substantially lower than the founder equivalents because many of the okapi founders produced few offspring (eight of 23 founders had just one offspring that is alive or produced living descendants). Thus, many founder alleles have likely been lost from the living population. (A mean of 59% of founder alleles were retained in the computer simulations.)

Goeldi's Monkey

The pedigree of the captive population of Goeldi's monkey (*Callimico goeldii*) was obtained from the 1988 International Callimico Studbook [Warneke, 1988]. Currently, there are 326 captive-born (nonfounder) Goeldi's monkeys in captivity and also 18 living captive-born animals with unknown parents. Of 80 wild-caught Goeldi's monkeys brought to zoos, 44 have reproduced in captivity, and 35 have living descendants. Nineteen Goeldi's monkeys with living descendants in captivity have unknown parents and must be treated as "founders" if the entire captive population is to be analyzed. The percent representation of the 54 founders ranges from 0.12% to 6.64% (Fig. 2). The captive population has 24.79 founder equivalents. Ignoring the genetic contributions of the 19 "founders" with unknown parents (or, equivalently, assuming that the distribution of wild-caught founder genes in those 19 animals is the same as in the captive-born animals of known ancestry), the population is calculated to have 20.97 founder equivalents. The 19 "founders" of unknown parentage contribute relatively little to the founder equivalents because they have few living descendants. An equalization of founder representations among the 35 wild-

caught founders and the one living wild-caught animal (a potential founder) which has not yet contributed living offspring would be as useful as the introduction of more than 15 newly wild-caught stock.

Analysis of founder allele retention in 10,000 gene drop computer simulations yielded 23.79 founder genome equivalents in the captive *Callimico* population and a mean of 97.40% of gene diversity of the founding population remaining in the living descendants. Omitting the genetic contributions of the 19 unknown "founders," there are 20.15 founder genome equivalents. Most *Callimico* founders had several offspring and many later-generation descendants; therefore, the founder genome equivalents are similar to the founder equivalents. Relatively few founder alleles have been lost from the living population (mean proportion of founder alleles retained in the computer simulations was 78%).

DISCUSSION

To achieve adequate genetic representation of the wild population, approximately 20 founders are often recommended for establishing a captive stock [Foose, 1983; Foose et al., 1986]. Twenty founders, if randomly sampled from the wild, would contain 97.5% of the genetic variability (as measured by genetic variance, heterozygosity, or gene diversity) present in the wild populations. Caveats about avoiding initially inbred and/or related founders are often given [e.g., Foose, 1983; Senner, 1980], and the value of equalizing the genetic contributions of founders to the descendant captive population is stressed [Foose, 1983; Foose et al., 1986]. Yet methods for evaluation of the effect of unequal founder representation and irreversible loss of founder alleles on the numbers of founders needed have not been presented before. Calculation of the number of founder equivalents of a captive population provides a means of determining how many "ideal," equally represented founders would correspond genetically to the unequally represented founders of a population. The founder genome equivalent further discounts the founder number to account for the founder alleles already lost from a population. The recommendation of 20 founders for a genetically diverse captive population should be revised to a recommendation of 20 founder equivalents or, more conservatively, founder genome equivalents. A population with 20 founder genome equivalents would contain about 97.5% of the genetic variation present in the wild population from which the founders were taken, thus assuring that sufficient founder variability was present at the outset of a captive management program to allow a long-term propagation goal of retaining 90% of genetic variation.

For both okapis and Goeldi's monkeys, less than half of the wild-caught animals brought to European and North American zoos have reproduced in captivity to become genetic founders of the captive populations. The founder equivalent numbers (f_e about 15 and 21, respectively) are about 60–65% of the actual number of founders, although the founder genome equivalents are somewhat less (about 12) for okapis. Although large numbers of wild-caught Goeldi's monkeys have contributed little or nothing to the living captive populations, the captive population descends from apparently adequate founder stock. Many Goeldi's monkeys now exist in captive breeding colonies; therefore, the population is expected to retain a substantial percentage of the genetic variability of wild populations. Although the initial okapi founders may have been adequate in number, the unequal and often minimal contri-

bution to future generations has led to founder equivalents and founder genome equivalents that may be too low to sustain a long-term captive propagation program. Moreover, poor breeding success and a continued small captive population may lead to considerable further depletion of the founder equivalents, founder genome equivalents, and genetic variability within relatively few generations.

A reduction in founder equivalents relative to the actual number of founders is a consequence of the overrepresentation of some founders and the minimal genetic contributions of other founders. These inequalities will impede attempts to minimize inbreeding in the captive populations, because noninbred pairings become difficult when much of a captive stock is related, sharing a common founder in the ancestry. More equal representation from founders and from as yet nonreproductive, wild-caught, potential founders could alleviate or forestall impending genetic problems.

CONCLUSIONS

A metric, the founder equivalent, is offered as a means of equating the distribution of founder representations in a captive population to a genetically equivalent number of equally represented founders.

A related measure, the founder genome equivalent, further discounts from founder calculations the founder alleles that have likely been lost from the population; it describes the genetic base of a captive population as a genetically equivalent number of equally represented founders if no alleles have been lost by genetic drift.

It is recommended that 20 founder genome equivalents be obtained to assure adequate genetic variability to initiate a long-term captive propagation effort.

Adequate founder equivalents can often be obtained by increasing the genetic contributions of poorly represented founders and previously nonreproductive potential founders already in captivity, rather than by introducing additional wild-caught animals.

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APPENDIX A. CALCULATION OF FOUNDER CONTRIBUTIONS, FOUNDER EQUIVALENTS, AND FOUNDER GENOME EQUIVALENTS

Table 2 shows the additive matrix of genetic relationships for the simple pedigree in Figure 3. The additive matrix is formed by first listing all individuals along the top and down the side of a square matrix and placing 1s along the diagonal. Parents are noted above each individual. All offspring must follow their parents in the matrix. One row at a time, the genetic relatedness of each row individual to each column individual is calculated as .5 times the relatedness of the row individual to the

TABLE 2. Additive matrix of genetic relatednesses among individuals shown in the pedigree in Figure 3

			A × B	A × B		D × E	D × E
	A	**B**	**C**	**D**	**E**	**F**	**G**
A	1	0	.5	.5	0	.25	.25
B	0	1	.5	.5	0	.25	.25
C	.5	.5	1	.5	0	.25	.25
D	.5	.5	.5	1	0	.5	.5
E	0	0	0	0	1	.5	.5
F	.25	.25	.25	.5	.5	1	.5
G	.25	.25	.25	.5	.5	.5	1

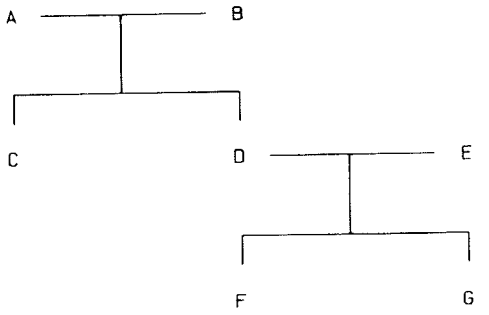

Fig. 3. Hypothetical pedigree of three founders and four descendants. The founders (**A,B,E**) have unknown parentages and are assumed to have independent ancestries.

TABLE 3. Founder contributions to the descendant generations of the pedigree shown in Figure 3

	Founders		
	A	**B**	**E**
C	.5	.5	0
D	.5	.5	0
F	.25	.25	.5
G	.25	.25	.5
Founder contributions:	1.50	1.50	1.00
Proportional founder contributions (p_i):	.375	.375	.25

sire of the column individual + .5 times the relatedness of the row individual to the dam of the column individual. To the 1 on the diagonal is added that individual's inbreeding coefficient, .5 times the relatedness between the sire and the dam. (All inbreeding coefficients in this pedigree are zero.) The values in the row are then copied into the corresponding (transposed) column. For example, the relatedness between C and F is .5 × C–D relatedness + .5 × C–E relatedness, because D and E are the parents of F. See Ballou [1986] for a more detailed description of the additive matrix methodology.

The founder contributions to each living descendant, given in Table 3, are simply the genetic relatednesses between the founders and the descendants (from Table 2). Each founder's contribution to the living, descendant population is then the sum of that founder's column in Table 3. The proportional contributions (p_i) are obtained by dividing each founder's contribution by the number of living descendants.

For a complex pedigree, the fraction of a founder's alleles that are expected to have been retained in the descendant population (r_i) would be determined by a gene drop computer simulation; in this simple pedigree, r_i values can be determined directly. For each allele in founders A and B, there is a probability of 0.5 that the allele was transmitted to C, a probability of 0.5 that the allele was transmitted to D, and a 0.25 probability that the allele was transmitted to neither C nor D and therefore was lost from the descendant population. Similarly, for each allele in founder E, there is a 0.25 probability that the allele was transmitted to neither F nor G and was

therefore lost from the descendant population. For each founder (A, B, and E), therefore, the fraction of alleles retained in the descendants (r_i) is 0.75.

For these three founders, the founder equivalents and founder genome equivalents are

$$f_e = 1 / \Sigma (p_i^2) = 1 / (.375^2 + .375^2 + .25^2) = 2.91$$

and

$$f_g = 1 / \Sigma (p_i^2/r_i) = 1 / (.375^2/.75 + .375^2/.75 + .25^2/.75) = 2.18.$$