

Fixed Contributions Designs vs. Minimization of Global Coancestry to Control Inbreeding in Small Populations

J. Fernández,^{*,†,1} M. A. Toro^{*} and A. Caballero[†]

^{*}Departamento de Mejora Genética Animal, Instituto Nacional de Investigación y Tecnología Agraria y Alimentaria, 28040 Madrid, Spain and [†]Departamento de Bioquímica, Genética e Inmunología, Facultad de Ciencias, Universidade de Vigo, 36200 Vigo, Spain

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ABSTRACT

Populations with small census sizes are at risk because of the loss of genetic variability and the increase of inbreeding and its harmful consequences. For situations with different numbers of males and females, several hierarchical designs have been proposed to control inbreeding through the fixation of individuals' contributions. An alternative method, based on the minimization of global coancestry, has been proposed to determine contributions as to yield of the lowest levels of inbreeding in the population. We use computer simulations to assess the relative efficiency of the different methods. The results show that minimizing the global coancestry leads to equal or lower levels of inbreeding in the short and medium term, although one of the hierarchical designs provides lower asymptotic inbreeding rates and, thus, less net inbreeding in the long term. We also investigate the performance of the alternative methods against departures from the ideal conditions, such as inbred or differentially related base individuals and random failures in the expected contributions. The method of minimization of global coancestry turns out to be more flexible and robust under these realistic situations.

AN important aim of conservation programs is to maintain the highest possible genetic variation and the minimum inbreeding within the considered population (LACY 1994; BALLOU and LACY 1995; OLDENBROEK 1999; BARKER 2001). This also applies, to some extent, to breeding programs, as the increase of inbreeding usually implies undesirable effects of inbreeding depression on fitness, productive, or morphological traits, and the loss of genetic diversity could compromise a future response on the trait of interest or on new breeding objectives. The increase of inbreeding and the loss of genetic variability are consequences of the effective population size, N_e , so most efforts should be directed toward the increase of this parameter. This will lead to the minimization of the rate of inbreeding (ΔF), because of their inverse relationship. Classical population genetics theory recommends keeping equal numbers of males and females and constant census sizes over time in the population. In this situation, equalizing contributions, *i.e.*, forcing every individual to contribute one male and one female offspring, would maximize N_e , being nearly twice that of an ideal population (WRIGHT 1938; FALCONER and MACKAY 1996).

Due to management difficulties or economic costs, it is often impossible to fit the recommendation of a 1:1 sex ratio. Thus, animal populations are usually main-

tained with fewer males than females. When predicting the effective population size for such groups, variances of contributions of males and females and all possible covariances should be taken into account, along with the mating ratio (r), *i.e.*, the number of females per male (HILL 1979). In this context, some regular hierarchical designs have been proposed to control the rate of inbreeding. The first of these (GOWE *et al.* 1959) follows the principle of every male mated to r females and contributing one son and r daughters and every female leaving one daughter and a son with probability $1/r$. WANG (1997) improved the method (up to a 17% decrease in ΔF for low values of r) by imposing that the female contributing a son does not contribute a daughter and allowing another female from the same male family to contribute two daughters. Recently, SÁNCHEZ-RODRÍGUEZ *et al.* (2003) proposed managing contributions across generations, rather than controlling contributions for single generations. Briefly, the method uses Wang's scheme but the sex and number of offspring contributed by a female is dependent on the sex and number of offspring of her mother (see MATERIALS AND METHODS and SÁNCHEZ-RODRÍGUEZ *et al.* 2003 for further explanations). With this latter method, the reduction of the rate of inbreeding could be as large as 10% of that under Wang's scheme.

In conservation (BALLOU and LACY 1995; SONESSON and MEUWISSEN 2001) and animal breeding fields (see FERNÁNDEZ and TORO 1999 and references therein), it has been suggested that the best way to control the increase of inbreeding in a breeding or conservation program is to arrange contributions from one genera-

¹Corresponding author: Departamento de Mejora Genética Animal, Instituto Nacional de Investigación y Tecnología Agraria y Alimentaria, Ctra. Coruña Km 7,5, 28040 Madrid, Spain.
E-mail: jmj@inia.es

tion to the next to yield the minimum global coancestry of parents (including self-coancestries) weighted by those contributions. Global coancestry is calculated as

$$\bar{f} = \frac{1}{4}\bar{f}_{s,s} + \frac{1}{2}\bar{f}_{s,d} + \frac{1}{4}\bar{f}_{d,d},$$

where $\bar{f}_{s,s}$, $\bar{f}_{s,d}$, and $\bar{f}_{d,d}$ are the mean coancestry between males, between males and females, and between females, respectively. This is a flexible method that does not prefix the contributions of males or females and, as originally proposed, it does not assume any regular mating design.

All the above procedures refer to the number and sex of offspring to be obtained from every particular parent; *i.e.*, contributions are controlled but mating is assumed to be at random. However, managers may also control the mating scheme to further decrease inbreeding. In this context, different strategies have been suggested such as the “maximum avoidance of inbreeding” method, first proposed by WRIGHT (1921); the compensatory mating, *i.e.*, the mating between males with high average coancestry and females with low average coancestry (CABALLERO *et al.* 1996); or the minimum coancestry mating, *i.e.*, mating the individuals in a manner that yields the lower average pairwise coancestry between couples (TORO *et al.* 1988), among others. These mating methods, particularly the minimum coancestry mating, have been proven to be generally effective in reducing inbreeding in artificial selection schemes (CABALLERO *et al.* 1996; SONESSON and MEUWISSEN 2000) and conservation programs (FERNÁNDEZ and CABALLERO 2001; SONESSON and MEUWISSEN 2002).

The practical implementation of the methods is another issue of interest. Sometimes, a given strategy may be the most effective on theoretical grounds, but its implementation may be difficult, if not impossible, in a real program of living animals. On the one hand, physiological restrictions of the particular species we deal with, for example, the fact that females cannot be mated to more than one male, or economical or management considerations could condition the program. On the other hand, the different selection and mating schemes that have been proposed implicitly ignore stochastic factors that affect fecundity, viability, and sex ratio. In practice, however, some matings could fail or a lower number of males or females than desired could be obtained from a particular couple. Thus, the robustness of every method under these practical situations should be another key in the planning of a conservation or breeding program.

Finally, the selection and mating schemes proposed assume a lack of relatedness between individuals in the base population. However, all conserved populations have a previous history, in most cases involving extreme bottlenecks. The population may have undergone several generations of unmanaged conditions before the

program started, and the genealogical records have been kept or estimations of relatedness are available from molecular information. In these cases, the breeding methods should consider this prior information.

The purpose of this work is to compare, through computer simulations, the performance of hierarchical designs and minimization of global coancestry with respect to the inbreeding levels maintained in a small managed population. The robustness of every method against deviations from the ideal conditions and, therefore, its practical applicability are also investigated.

MATERIALS AND METHODS

Simulation procedure: Most simulations dealt with a population consisting of $s = 2-4$ males and $d = s \times r$ females, with $r = 3-6$. Other combinations were tested to investigate the behavior for large mating ratios ($r = 10$) or a larger number of males ($s = 8$). Fifty discrete generations were run in each case, and the population size and mating ratios were assumed to be constant over time.

Every generation the mean inbreeding coefficient of the population was calculated from pedigree relationships, weighted by the different numbers of males and females. The rate of inbreeding (ΔF) between two particular generations was calculated as $(F_t - F_{t-1}) / (1 - F_{t-1})$, where F_t is the mean inbreeding coefficient at generation t . The rate of coancestry (Δf) was also calculated in a similar way. The asymptotic value of these parameters was calculated as the average over generations 40–50. For most simulations, individuals in the base population (generation zero) were assumed to be unrelated and not inbred, although in some cases simulations started from differentially related base populations, as explained below. Every simulation was replicated 1000 (hierarchical designs) or 200 times (minimization of coancestry) and values were averaged over generations.

Management methods: Although the strategy of minimizing global coancestry does not assume any regular breeding system, to make a fair comparison among methods, we imposed a random mating scheme for all of them, where every male was mated to r females. Three different schemes were simulated.

W(scheme proposed by WANG 1997): Within each half-sib male family, one of the females was selected at random to contribute one son, another one to contribute two daughters, and the remainder contributed one daughter each.

*SBW(scheme proposed by SÁNCHEZ-RODRÍGUEZ *et al.* 2003):* Contributions of each individual were the same as in Wang’s scheme. Females were labeled in r classes: class 1 were females leaving one son; classes 2 to $r - 1$ were females leaving daughters to classes one level up; and class r were females leaving one daughter to class r and another daughter to class $r - 1$. Therefore, the condition of a female (*i.e.*, the class to which she belongs) is dependent on the condition of her mother, so that contributions are managed across generations. Figure 1 shows an illustration of this management design.

GC(the minimization of global coancestry): Contributions of each individual were decided so as to yield the minimum global coancestry of parents, weighted by these contributions. The objective function to minimize is

$$\frac{1}{4} \sum_{i=1}^s \sum_{j=1}^s \frac{x_i x_j f_{ij}}{s^2} + \frac{1}{2} \sum_{i=1}^s \sum_{j=s+1}^N \frac{x_i x_j f_{ij}}{sd} + \frac{1}{4} \sum_{i=s+1}^N \sum_{j=s+1}^N \frac{x_i x_j f_{ij}}{d^2},$$

where x_i is the variable to optimize that determines the number of offspring to obtain from parent i , f_{ij} is the coancestry between individuals i and j , and s and d are, respectively, the

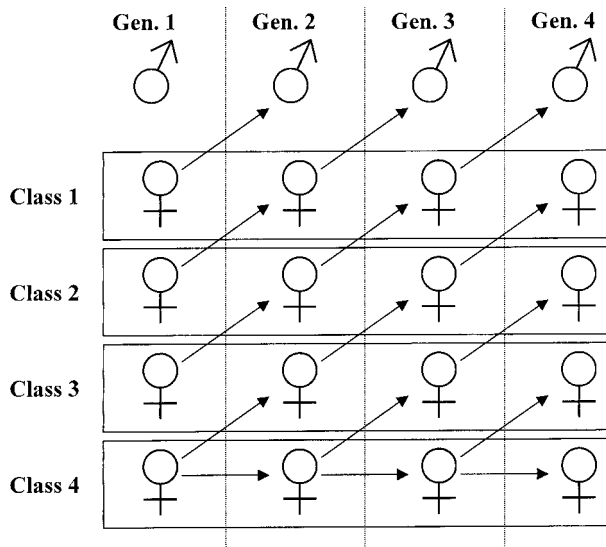


FIGURE 1.—Scheme of the method of management proposed by SÁNCHEZ-RODRÍGUEZ *et al.* (2003) for a situation with $r = 4$.

number of males and females in the population (adding up to N). As can be seen, this is a quadratic function and solutions have to be integers to have a biological meaning. Mathematical programming is difficult to implement in such problems, so we used the *simulated annealing* algorithm (PRESS *et al.* 1989) to find the optimum solutions. More explanations on the implementation of the algorithm to minimize global coancestry can be found, for example, in FERNÁNDEZ and TORO (1999).

Mating scheme: Some simulations were carried out allowing for a not-fixed design of matings; *i.e.*, females could mate to more than one male and males to more or less than r females. This strategy, although more difficult to implement in a real program when reproductive techniques are not available, should enlarge the feasible space of solutions and, *a priori*, provides a better control of inbreeding. For the Wang (W) and Sánchez-Rodríguez-Bijma-Woolliams (SBW) methods the contributions and the classification of females were kept invariant but females having two offspring (daughters) were mated to one or two different males at random (generating full-daughters or half-daughters, respectively). For the minimization of global coancestry (GC) method all possibilities were allowed, with females mated to one or several males.

The effect of implementing the minimum coancestry mating design was also tested for some population compositions. The implicit minimization process, performed through “simulated annealing” algorithms for all procedures, requires different approaches depending on the management strategy used to determine the number of offspring contributed. For the GC method the procedure implied including into the objective function to be minimized an extra term to account for the pairwise coancestry between couples. The weight given to this term was much smaller than that for the global coancestry, so that contributions were unaffected by the mating scheme (see FERNÁNDEZ *et al.* 2001 for details on the implementation of this mate selection strategy). In the case of hierarchical designs, and to assure the maintenance of the predefined scheme of contributions, we used the following strategy. The process started with every male mated randomly to r females. Alternative solutions were generated by exchanging the males mated to two females with the same type of contribution (one male, one female, or two female offspring) or exchanging the type of contribution between females mated to the same male (only in the case of the W strategy).

Practical implementation: To test the performance of the methods studied against departures from the predefined scheme, we carried out simulations where some random failures occurred. In some cases a maximum of one failure per generation was allowed, while in others, more than one failure could occur. In the first case, once the selection scheme was decided, the process assumed that, with a probability p (probability of failure), one randomly chosen offspring died (this implies that there was a failure every $1/p$ generations, on average). Thus, an “extra” individual should be obtained from another couple to complete the required total number of offspring. To draw a more realistic scenario, we defined the parameter c (probability of replacement) as the probability that another couple had more offspring than determined by its optimal contribution. Different combinations of p and c were tested. The way to replace the lost individual also depended on its sex and the considered strategy. Protocols were as follows:

W method:

- i. If a son was lost, we took another son, with a probability c , from one of the females (mated to the same male) who generates only one daughter; if none of these females had an extra son then it was generated from the female with two daughters.
- ii. If a daughter without sisters failed, we tried to get another from the remainder females with only one daughter (again with probability c of effectively replacing the lost offspring), then from the female with two daughters, and finally from the female contributing a son.
- iii. If failure occurred in a daughter from a female with two daughters, we looked for a replacement from females having one daughter and then from the female having a son. The general purpose of the replacement procedure was to limit the number of full-sibs, especially for the son of each family, in agreement with the spirit of Wang’s method. To avoid an eventual fall in the census size of the population, the replacement of lost individuals always took place, using, at least, the last option in every case.

SBW method: The replacement algorithm was identical to the one used in the W scheme. Daughters substituting random failures were assigned the class of the individual they were replacing, instead of the one corresponding to their mothers.

GC method: If a failure took place, a reoptimization was carried out but including some restrictions on the feasible solutions. The number of sons or daughters (depending on the sex of the lost individual) to get from the particular couple involved in the failure was limited to the present solution minus one. For example, if one of the sons to be contributed by a female with optimal contributions of three sons died, in the new optimization the maximum number of sons to get from that female should be two. The contributions from other couples were kept unbounded with probability c (*i.e.*, they could contribute as many extra individuals as desired) or were restricted to their present contribution otherwise (*i.e.*, they had produced exactly the number of offspring determined by the initial optimization).

A situation was also tested in which a random number of failures, Poisson distributed with mean $\lambda = 1-2$, occurred every generation. Diminishing of population census number was avoided by truncating the distribution (a maximum of three or four failures allowed, respectively, for $\lambda = 1$ and $\lambda = 2$) and by forcing every couple to have offspring to replace (*i.e.*, $c = 1$), unless it was itself involved in another failure. The process of replacement followed the same scheme as above, depending on the method performed.

The fact that many “base” populations in conservation pro-

TABLE 1
Asymptotic rate of coancestry (Δf)

<i>s</i>	<i>d</i>	W	SBW	GC	SBW (nf)	GC (nf)
2	6	0.0508	-4.8	-4.0	-3.1	-0.7
	8	0.0499	-5.7	-5.0	-2.9	-1.6
	10	0.0497	-6.0	-5.5	-2.3	-2.4
	12	0.0496	-6.0	-6.0	-1.7	-2.8
3	9	0.0324	-4.9	-4.2	-3.2	-2.0
	12	0.0321	-6.3	-5.5	-3.2	-3.5
	15	0.0320	-6.6	-5.9	-2.3	-4.1
	18	0.0320	-6.7	-6.3	-1.7	-4.4
4	12	0.0238	-4.9	-3.6	-3.2	-2.2
	16	0.0236	-6.2	-4.7	-3.1	-3.7
	20	0.0236	-6.8	-5.5	-2.4	-4.6
	24	0.0236	-6.9	-6.0	-7.0	-5.2
	40	0.0237	-7.6	-7.4	-0.6	-6.2
8	24	0.0116	-4.8	-2.7	-3.3	-2.7
	48	0.0115	-7.4	-6.0	-1.8	-6.1

SBW, Sánchez-Rodríguez *et al.* method; GC, minimization of global coancestry; nf, not-fixed mating design; *s*, number of males; *d*, number of females. Numbers in the column headed W are actual Δf values, while numbers in other columns are percentages relative to the Δf . Standard deviations for relative values are <0.2 .

grams are not made of unrelated individuals was investigated through simulations where five generations of no management were performed prior to the implementation of any of the studied strategies. In these generations, no control on either the mating scheme or the contributions of each individual was made, which were both randomly assigned. Thus, we obtained populations with differential coancestries and inbred individuals to test the behavior of the different methods.

RESULTS

As expected for a population with no permanent subdivision, in all situations ΔF and Δf reached the same value after a few generations (data not shown). Therefore, the relative performances of methods and the conclusions that arise from their comparisons are identical whatever the parameter used. Because Δf has smaller standard errors (as it is not influenced by mating), we present asymptotic values for this parameter in Table 1, although the subject of the article is the control of inbreeding levels and we refer to the rate of inbreeding henceforth. Numbers in the column headed W in Table 1 are actual Δf values, while the other numbers in the table are percentages relative to them. In general, SBW provides the lowest Δf (and ΔF) for most of the combinations, although differences from GC are small, and this latter method performs always better than the W strategy. Allowing a not-fixed mating design usually implies a lower inbreeding level in the short term (see Figure

2 below) but an increase in the asymptotic rate of inbreeding. This is a consequence of the greater deviation from Hardy-Weinberg proportions (α , calculated as $1 - [(1 - F)/(1 - f)]$) implied by the not-fixed designs. For example, for $s = 2$ and $r = 3$, $\alpha = -0.124$ and -0.125 for SBW and GC, respectively, in the fixed-mating case, whereas $\alpha = -0.131$ and -0.166 , respectively, in the not-fixed case. Nevertheless, the relative performance of methods does not change much, except for some combinations where the GC method outperforms the SBW method (Table 1).

It can be inferred from Table 1 that, in the long term, the SBW strategy would yield the lowest inbreeding levels in most situations. This is what actually occurs in most of our simulations at generation 50. But if we look at earlier generations the situation is different. Figure 2 shows the evolution of average inbreeding under the SBW and GC methods, as deviations from the levels reached under the W method.

In spite of the differences in the asymptotic ΔF , the values for SBW (thin solid line) and GC (thick line) methods are very similar, at least for the first 20 generations. In fact, lower levels of inbreeding are generated by the GC method at the short and medium term for some combinations of males and females. Therefore, the advantage of the SBW strategy does not appear until a large number of generations have elapsed, especially for populations with large r (see Figure 2, right side). This effect is more obvious for base populations with complex relationships, as can be seen in Figure 3, which shows average inbreeding for populations that had undergone five previous unmanaged generations.

A not-fixed mating design does not modify the values of inbreeding reached for populations under the W method. For SBW a little advantage can be detected in early generations but this produces higher levels of inbreeding later on (data not shown). As these hierarchical methods are designed for structured situations, they do not use properly the enlarged feasible space of solutions to reduce the increase of inbreeding. However, the GC method takes advantage of not-fixed designs and achieves much better results (lower inbreeding levels) in the short and medium term than those where every male mates r females strictly (broken line in Figures 2 and 3).

If a minimum coancestry mating design is used, all strategies improve the results obtained with the corresponding random mating methods, at least for the first 10 simulated generations (data not shown). Figure 4 shows the evolution of mean population inbreeding (again deviated from that obtained under the W management scheme) when minimum coancestry mating is implemented for different combinations of males and females.

When starting from noninbred, nonrelated individuals (Figure 4, left side), SBW produces the best results for small values of r , followed by the GC method, but

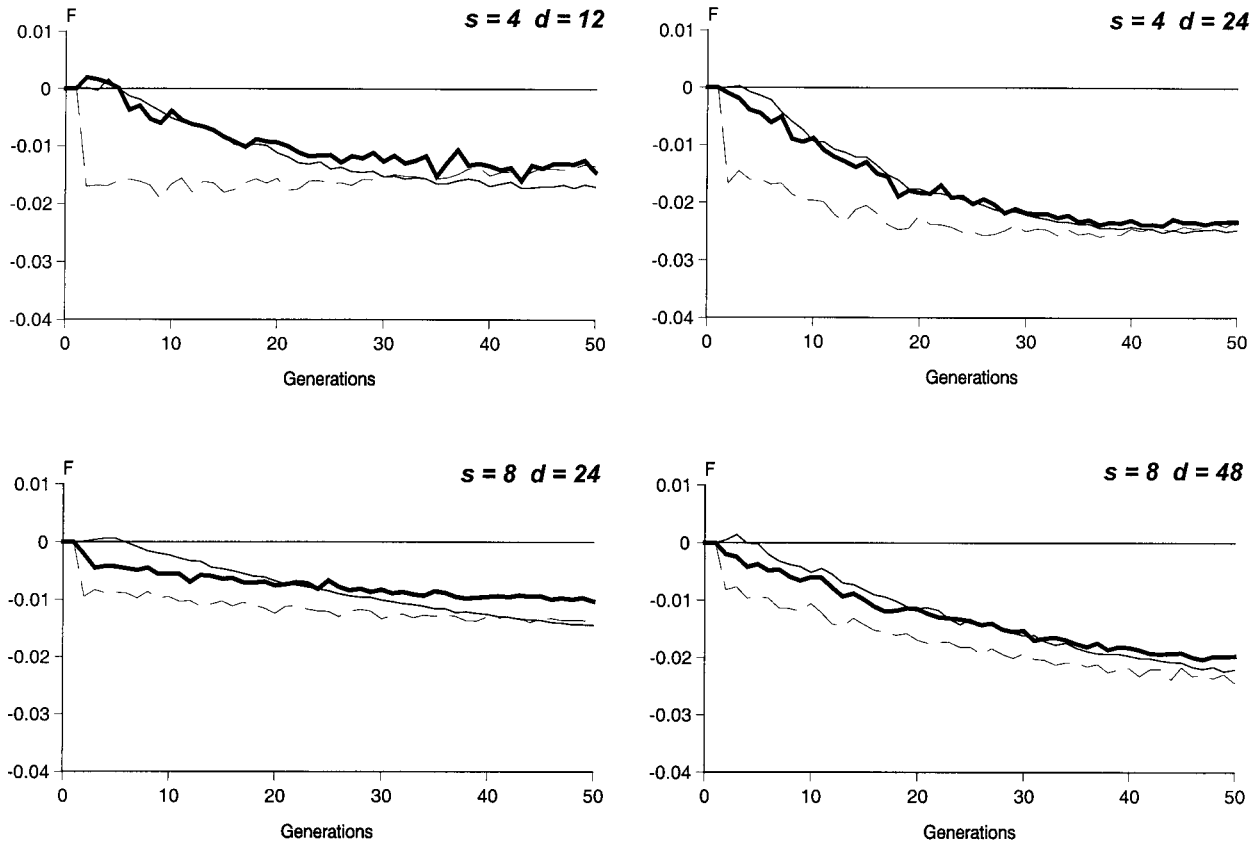


FIGURE 2.—Average population inbreeding against generation number under the Sánchez-Rodríguez *et al.* method (thin line), the minimization of coancestry method (thick line), and minimization of coancestry allowing for a not-fixed mating design (broken line). Values deviated from inbreeding of a population under Wang’s management method. Individuals are unrelated at generation 0.

the trend reverses for large r . The lower performance of GC for small r arises when deciding the contributions to create generation 1, where several solutions have the same global coancestry (because of equal relationships between all available parents), but not the same coancestry level in the offspring. Although inbreeding is well managed from this point, the early handicap makes GC inbreeding values slightly higher for the 10 generations

simulated. When base populations have differentially related individuals (Figure 4, right side), GC becomes more efficient in the control of inbreeding.

We tested the effect of random failures (offspring deaths) in the different procedures. As expected, the more severe the departure from the assumed scheme (*i.e.*, the higher the number of failures, the higher the probability of random “deaths,” and the lower the prob-

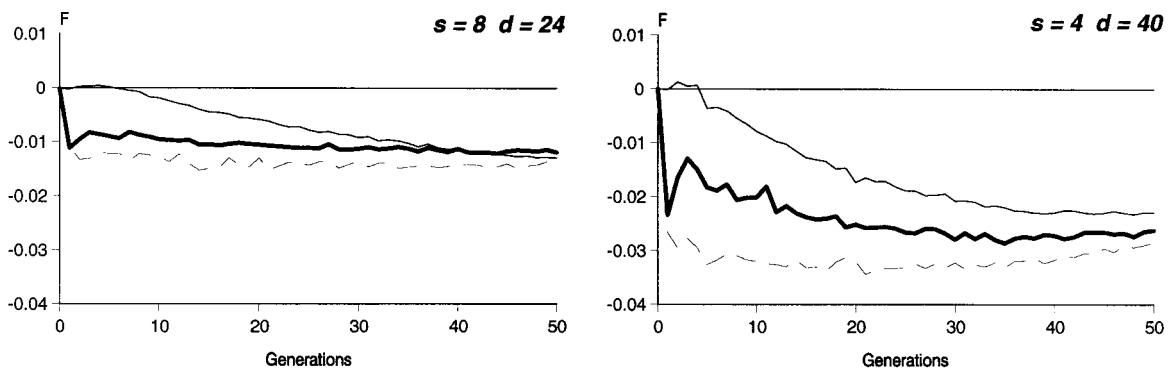


FIGURE 3.—Average population inbreeding against generation number when individuals at generation zero are inbred and differentially related (five previous unmanaged generations). Values deviated from inbreeding of a population under Wang’s management method. Meaning of lines is as in Figure 2.

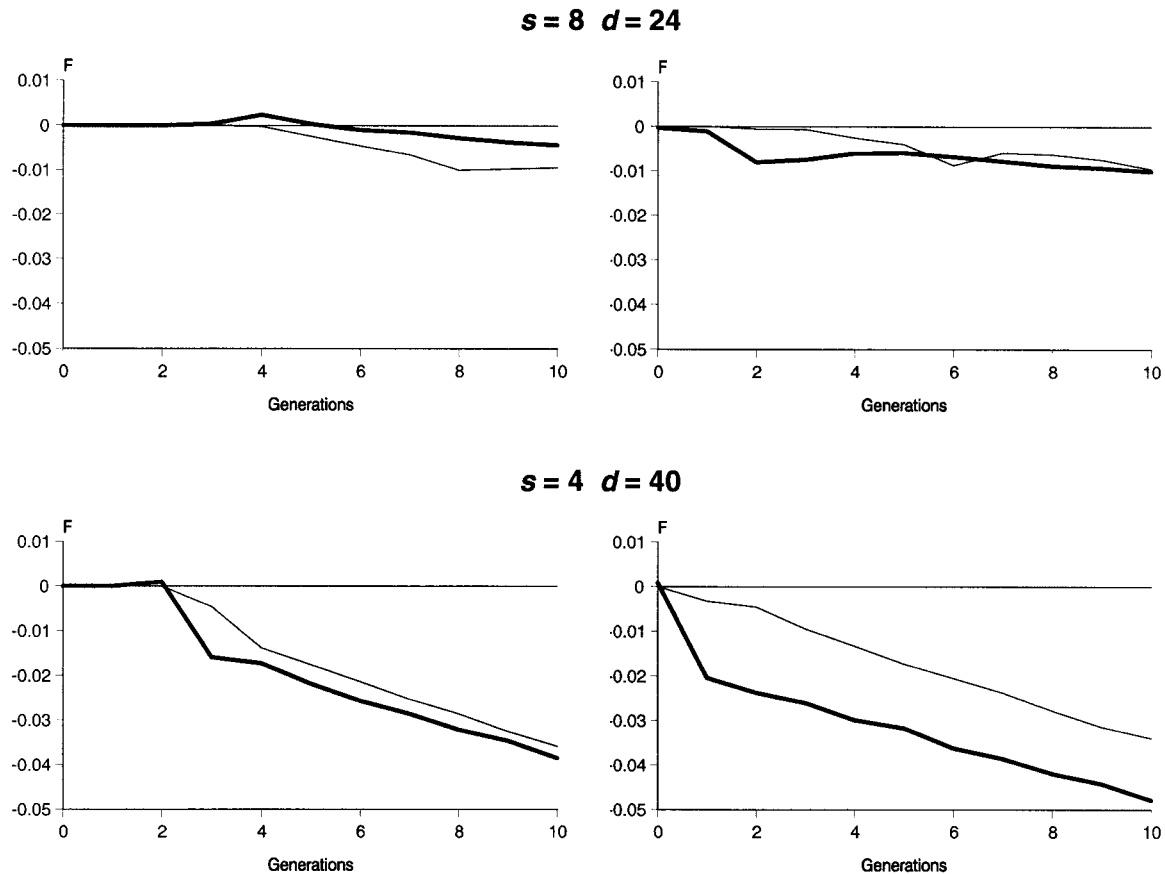


FIGURE 4.—Average population inbreeding against generation number under different management methods and minimum coancestry mating. Values deviated from inbreeding of a population under Wang's management method. Meaning of lines is as in Figure 2. Left, individuals at generation zero not related and noninbred. Right, differential relationships at generation zero (five unmanaged generations).

ability of replacement from other couples), the greater the effect on both the mean inbreeding coefficient and the rate of inbreeding (data not shown). This is general for all schemes and sex ratios, but the impact is lower for a large number of male families or large mating ratios. Table 2 shows the percentage of increase in average inbreeding coefficients at generations 20 and 50, relative to the situation with no failures, for some combinations of probabilities of random failures (p) and probabilities of replacement (c) from other couples.

It can be clearly seen that the SBW method suffers the greater distortion from original values when the requirements are not satisfied, followed by the W strategy, while the GC method is less affected by departures from the originally determined parents' contributions. This reduces differences in performance between the SBW and W methods, although SBW still yields lower inbreeding levels than W for all combinations of males and females. However, the relative performance of SBW and GC methods changes, the latter yielding lower inbreeding levels in more situations. Figure 5 shows this behavior for two particular combinations of numbers of males and females when an average of two random failures occur per generation. The results are presented

as deviations from Wang's method without failures, so they can be compared directly to the corresponding graphs in Figure 2.

DISCUSSION

The management of small populations in conservation or breeding programs should account for the increase of inbreeding and the loss of genetic diversity as a consequence of small effective population sizes. The increase in population homozygosity can be measured through the inbreeding coefficient, while the loss of diversity is related to the average coancestry coefficient. In regular breeding systems, the rates of increase of inbreeding and coancestry coefficients soon reach an asymptotic and equal value, except under a situation of complete subdivision. Classical population genetics theory shows the inversely proportional relation between effective population size and the asymptotic rate of inbreeding. Therefore, maximizing the effective population size or minimizing the asymptotic rate of inbreeding would provide, in principle, the lowest inbreeding levels in the long term, as they occur in the

TABLE 2
Mean inbreeding coefficient when random failures occur

		One failure						Poisson failures					
		$p = 0.3$			$p = 0.5$			$\lambda = 1$			$\lambda = 2$		
Generation		W	SBW	GC	W	SBW	GC	W	SBW	GC	W	SBW	GC
		$s = 4/d = 12$											
$c = 1$	20	0.5	1.1	0.0	1.0	2.1	0.1	2.3	3.8	0.5	5.0	7.5	2.4
	50	0.3	0.8	0.3	0.6	1.2	0.4	1.5	2.6	0.9	3.3	5.2	2.2
$c = 0.7$	20	0.8	1.2	0.2	1.5	2.3	0.3						
	50	0.5	0.8	0.3	0.9	1.4	0.5						
$c = 0.5$	20	1.0	1.3	0.9	1.8	2.4	0.2						
	50	0.6	0.9	0.4	1.1	1.4	0.5						
		$s = 8/d = 24$											
$c = 1$	20	0.4	0.4	0.4	0.6	0.9	0.5	1.1	2.2	0.4	2.4	4.1	0.9
	50	0.2	0.5	0.0	0.5	0.9	0.2	1.0	1.9	0.3	2.0	3.7	1.0
$c = 0.7$	20	0.6	0.5	0.2	0.9	1.1	0.5						
	50	0.4	0.6	0.1	0.7	0.9	0.3						
$c = 0.5$	20	0.7	0.5	0.3	1.0	1.1	0.2						
	50	0.5	0.6	0.0	0.8	1.0	0.3						

Numbers are percentage of increase with respect to the values obtained in the case without failures. W, Wang method; SBW, Sánchez-Rodríguez *et al.* method; GC, minimization of global coancestry; s , number of males; d , number of females; p , probability of failure; c , probability of replacement; λ , mean number of failures. Standard deviations range from 0.05 to 0.15.

simulations presented in this article. However, a successful program should also consider the short- and medium-term evolution of inbreeding, because the increase of inbreeding levels in the early generations could imply inbreeding depression on several traits, making the population unviable. It is well known that, if there were no problems of inbreeding depression, the way of keeping the lowest levels of inbreeding in the long term would be a complete sublining of the population (in the hope that different alleles are fixed in every line) and random

crossing of lines in the last generation (ROBERTSON 1964).

This work has addressed the relative performance, under different scenarios, of two different approaches to the problem of controlling the levels of inbreeding in a population of small census size. One of them involves hierarchical, regular designs that fix the individuals' contributions, while the other works by arranging the contributions from one generation to the next to get the minimum parents' global coancestry. Wang's method

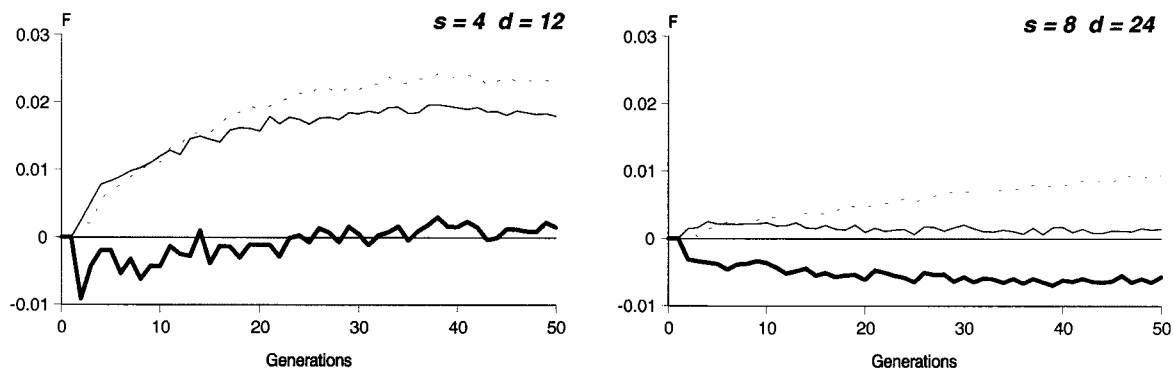


FIGURE 5.—Average population inbreeding against generation number under the Sánchez-Rodríguez *et al.* method (thin line), the minimization of coancestry method (thick line), and the Wang method (dotted line) when an average of two failures per generation occurs. Values deviated from inbreeding of a population under Wang's management method without failures.

showed the poorest behavior of the three compared methods, yielding higher asymptotic rates of inbreeding (Table 1) and higher population inbreeding levels in all generations (Figures 2–4). Moreover, as pointed out by SÁNCHEZ-RODRÍGUEZ *et al.* (2003), Wang's method, paradoxically, yields higher rates of inbreeding as the mating rate increases for a fixed number of males, even though the number of available individuals (females) in the population is actually larger. The two other considered methods (SBW and GC) behave differently according to the time horizon. SBW gives lower levels of inbreeding in the long term, as it gives lower asymptotic rates of inbreeding (Table 1). However, for shorter periods of time, inbreeding is equal or lower under the GC management strategy. The superiority of the SBW method does not appear before generation 20 and can be delayed further for some combinations of numbers of males and females. The different evolution of inbreeding levels under these methods can be explained by the different amount of deviation from Hardy-Weinberg proportions (α) generated by each of them. In all situations, values for this parameter are more negative under the GC method, but differences from values under SBW depend on the number of males and the mating ratio. For the same mating ratio, a larger number of males generate more differences between GC and SBW. For example, for $r = 3$ and $s = 2$, GC and SBW give $\alpha = -0.125$ and -0.124 , respectively, whereas for $s = 8$, $\alpha = -0.032$ and -0.026 , respectively. The effect of the mating ratio is smaller, but there is a tendency for differences between methods to decrease with increasing r 's. Thus, it can be seen in Figure 2 that performances of GC and SBW are more similar in the top (small number of males) than in the bottom, and in the right side (large mating ratios) relative to the left side.

The species usually involved in breeding or conservation programs have naturally long generation intervals, especially large mammals. Moreover, as genetic drift occurs when gametes are generated, one recommendation to delay the increase of inbreeding would be to enlarge the generation interval as much as possible. This means that a period of 20–50 generations, the time where SBW begins to be advantageous, is extremely long (>50 years). No conservation program is designed for such a long time, as market requirements, environmental or production conditions, and technical improvements are not predictable to such an extent.

As pointed out by CABALLERO and TORO (2000) for populations with equally related individuals, the GC and W methods are equivalent regarding just one generation. If more than one generation is considered the GC method performs better. This is because GC accounts for the decisions in previous generations (via the relationships between individuals), while the W method ignores information on the population's history. SBW manages contributions across all generations, and this is the reason for its good performance in the long-term

horizon, but ignores the possibility of individuals in the base population being related or inbred.

WANG (1997) also suggested the use of nonrandom mating schemes to improve his method. Actually, he derived equations for the inbreeding coefficient and the rate of inbreeding when imposing a mating system (called WS:NM in his article), where males are mated to a group of half-sib females, chosen at random but avoiding his own group. This method has two consequences: it reduces the value of the parameter α (and, thus, it generates lower inbreeding in the short term), but it also reduces the variance of contributions. Following WOOLLIAMS and BIJMA (2000), the net effect on the rate of inbreeding (ΔF) depends on the relative effect of those opposing forces. For cases of large r , the WS:NM method reduces the rate of inbreeding. In fact, as pointed out by SÁNCHEZ-RODRÍGUEZ *et al.* (2003), for very large r 's, the WS:NM method approaches the same ΔF as SBW with random mating. However, for not very large values of r (*e.g.*, for those cases presented in Table 1), this method gives larger rates of inbreeding than the SBW or GC methods.

Regarding mating designs, SÁNCHEZ-RODRÍGUEZ *et al.* (2003) suggested that mating relatives would further reduce the rate of inbreeding, due to an increased α . This practice implies partial sublining and, as noted above, this is the optimal way of reducing inbreeding in the long term from a theoretical point of view (ROBERTSON 1964; CABALLERO 1994). But this strategy generates high levels of inbreeding in the short term with the undesirable effects of inbreeding depression on fitness and other important traits.

The opposite idea would be to avoid, as much as possible, mating between all types of relatives. In this context, the minimum coancestry mating was proposed and proved as a useful way of arranging couples to minimize the increase of inbreeding in conservation or breeding populations (TORO *et al.* 1988; SONESSON and MEUWISSEN 2000, 2002; FERNÁNDEZ and CABALLERO 2001). WANG (1997) showed that, coupled with the W selection scheme, avoiding only sib matings (WS:NM) generated, as expected, lower levels of inbreeding in the long term than implementing minimum coancestry mating. But the superiority appeared only after >40 generations have elapsed (WANG 1997). This time horizon seems, again, too long in the planning of a realistic conservation program. In our simulations, minimum coancestry mating is shown to be very effective along with any of the selection schemes and more effective than other mating strategies in the short term.

There is no doubt about the utility of fixed contributions designs when ideal conditions hold, because they are easy to implement. The problem with hierarchical designs is that they are too rigid and are optimized for a particular situation. Thus, when departures from original assumptions occur, the efficiency of the methods declines, limiting its practical implementation. In

this article some of these situations have been pointed out. The first refers to the fact that individuals in the starting population can be either inbred or, at least, differently related. Regular methods do not account for this and they assign the same number of offspring to both individuals with high average coancestry and individuals loosely related to the rest of the population. When the “base” population is made of differentially related individuals the GC method shows a higher efficiency, as it is the only method that allows for integrating this information into the management criteria. Knowledge of pedigree coancestries in a population entering a conservation program is not usual, except for those species or breeds where studbooks have been well established before the management strategies were implemented. However, the increasing availability of molecular markers allows for an estimation of pedigree relations in the base populations, so that they can be accounted for in the selection and mating decisions. Molecular markers can also be a helpful tool for a whole conservation plan by complementing pedigree information (*e.g.*, TORO *et al.* 1999; WANG 2001).

Another consideration deals with the physiological characteristics of the common species in conservation or breeding programs, including not very high fecundity, prolificacy, or viability. We have shown that, even with slight distortions, the loss of performance for hierarchical designs is greater than that for minimization of coancestry, enlarging the differences between the GC and W methods and delaying the time after which SBW outperforms GC. Minimization of global coancestry is a flexible method that is able to explore a larger space of solutions looking for “second-best” decisions.

Differences between approaches also arise when reproductive techniques are available. Artificial insemination and multiple ovulation embryo transfer allow breaking the physiological limitations regarding the number of matings in which an individual, especially females, can be involved. Hierarchical methods imply little flexibility and, thus, little advantage can be taken from non-fixed mating designs. In contrast, GC does not prefix the number of mates of an individual and greatly improves the short-term performance (inbreeding levels) from free-mating designs. Therefore, the advantage of the GC method will hold for a longer period of time although the asymptotic rate of inbreeding will increase.

A final point to consider with respect to the different flexibility of the methods is that the number of individuals kept in a particular population is greatly dependent on economic resources and management restrictions. Therefore, census sizes may be fluctuating and/or an equal number of females may not be available to be mated to every male (noninteger mating ratios). Hierarchical designs do not provide solutions for such situations but the GC method can deal with them, as it does not implicitly assume a fixed total number of offspring or a predefined number of females mated to every male.

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