

Practical implementation of optimal management strategies in conservation programmes: a mate selection method

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Abstract

Practical implementation of optimal management strategies in conservation programmes: a mate selection method.— The maintenance of genetic diversity is, from a genetic point of view, a key objective of conservation programmes. The selection of individuals contributing offspring and the decision of the mating scheme are the steps on which managers can control genetic diversity, specially on "ex situ" programmes. Previous studies have shown that the optimal management strategy is to look for the parents' contributions that yield minimum group coancestry (overall probability of identity by descent in the population) and, then, to arrange mating couples following minimum pairwise coancestry. However, physiological constraints make it necessary to account for mating restrictions when deciding the contributions and, therefore, these should be implemented in a single step along with the mating plan. In the present paper, a single-step method is proposed to optimise the management of a conservation programme when restrictions on the mating scheme exist. The performance of the method is tested by computer simulation. The strategy turns out to be as efficient as the two-step method, regarding both the genetic diversity preserved and the fitness of the population.

Key words: Inbreeding, Genetic diversity, Genetic drift, Reproductive traits.

Resumen

Realización práctica de estrategias de manejo óptimo en programas de conservación: un método de selección de apareamiento.— El mantenimiento de la diversidad genética es, desde un punto de vista genético, un objetivo fundamental en programas de conservación. La selección de los individuos que dejarán descendientes y la decisión del esquema de apareamiento son los pasos en los que el conservador puede controlar la evolución de la diversidad, especialmente en programas "ex situ". Se ha demostrado que la estrategia óptima consiste en buscar las contribuciones de los reproductores que den el mínimo parentesco global (probabilidad de identidad por descendencia de la población) y, posteriormente, determinar las parejas utilizando el método de apareamientos de mínimo parentesco. Ciertas limitaciones fisiológicas y reproductivas pueden impedir que los apareamientos propuestos se lleven a cabo. Por esta razón, sugerimos la aplicación de un procedimiento que decida las contribuciones y el diseño de apareamientos en un solo paso. Mediante simulación con ordenador comparamos la eficiencia de dicho método frente al diseño óptimo en dos etapas. El procedimiento resultó ser tan eficiente como el método en dos pasos, tanto en el mantenimiento de variabilidad genética como en los niveles de eficacia biológica de la población.

Palabras clave: Endogamia, Diversidad genética, Tendencia genética, Rasgos reproductores.

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Introduction

From a genetic point of view, conservation programmes have two basic objectives: first, to reduce the increase in inbreeding and its collateral effects on fitness and other traits that can threaten the survival of the population; and second, to maintain the highest level of genetic variability in order for the population to be able to face future environmental changes, avoid adaptation to captive conditions (if referring to "ex situ" programmes) and assure a possible long-term response to selection for traits of interest (BALLOU & LACY, 1995; OLDENBROEK, 1999; BARKER, 2001).

Measures of genetic variability

To know to which extent a population is threatened from a genetic point of view, and to monitor the performance of a conservation programme, it must be possible to measure the amount of genetic variability present in a group of individuals. From an evolutionary perspective, a straightforward measure of variability is allelic diversity, i.e. the number of different alleles in a locus (or the average over loci) carried by the population. The increasing availability of highly polymorphic neutral molecular markers provides a powerful tool to trace allelic diversity.

Another proposed measure of genetic variability is the expected heterozygosity, usually called gene diversity (NEI, 1973). This represents the proportion of heterozygotes expected if the population were in Hardy–Weinberg equilibrium. Again, if we refer to several loci, gene diversity is the average over loci. Contrary to allelic diversity, gene diversity is not only influenced by the number of alleles present in the population, but also by their frequencies. High levels of heterozygosity also mean high levels of additive genetic variance and, thus, greater potential responses to selection (FALCONER & MACKAY, 1996). As in the case of allelic diversity, the only information available, in most cases, is that from the allelic frequencies in neutral molecular markers.

Another estimate of the amount of diversity preserved in a population can be found via the concept of number of founder genome equivalents. By definition (LACY, 1995), this is the number of founder individuals (individuals on top of the pedigree) required to explain the genetic variability observed in the present population, accounting for the genetic drift occurring during pedigree development. The number of founder genome equivalents is directly related to gene diversity and effective population size (LACY, 1995; CABALLERO & TORO, 2000).

Optimal management

The loss of alleles in a small population, like those under conservation, is mainly driven by genetic drift, i.e. the random fluctuation of allelic

frequencies due to finite population size (FALCONER & MACKAY, 1996). Therefore, any strategy directed to the minimisation of genetic drift will keep the largest number of alleles. Classical population genetics theory provides such methods, like the minimisation of variance in parents' contributions to the next generation (GOWE et al., 1959; WANG, 1997).

An indirect measure of genetic variability of the population is provided by the degree of relationship between individuals. It seems logical that a good strategy to maintain genetic diversity is to reduce kinship relationships in the population as much as possible, as less related individuals are more likely to carry different alleles. The common way of controlling relationships is through the coefficient of coancestry (kinship). As first defined by MALÉCOT (1948), the coefficient of co-ancestry (f_{ij}) between individuals i and j is the probability of identity by descent of two alleles taken at random, one from each individual, at any locus. Two alleles are identical by descent when they are copies of a unique allele of a common ancestor. If the pedigree of the population is known, coancestries between any pair of individuals can be calculated following very simple rules.

Analogously, using information from markers, we can define the molecular coancestry as the probability that two alleles taken at random at the marker locus, one from each individual, are identical in state (i.e., equal). Therefore, molecular coancestry measures the heterozygosity in a number of known loci. If a model where all alleles in the founder population are different at an infinite number of loci is assumed, molecular and pedigree coancestries are the same. Otherwise, two alleles of a marker can be identical in state but not by descent. The relationship between both types of coancestries is, in principle, simple and defined by

$$E(f_{Mi}) = p_i^2 + p_i(1 - p_i)f$$

where f_{Mi} is the molecular co-ancestry due to allele i , p_i is the frequency of this allele in the base population, and f is the genealogical coancestry. Different methods to estimate identity by descent from molecular information have been developed from this relationship (see LYNCH & RITLAND, 1999, for a review). Finally, if information from both molecular markers and pedigree are available, these can be used jointly to calculate the coancestry conditional on markers (TORO et al., 1999; WANG, 2000).

Several authors (BALLOU & LACY, 1995; MEUWISSEN, 1997; FERNÁNDEZ & TORO, 1999; CABALLERO & TORO, 2000) have demonstrated, theoretically and by computer simulation, that the most effective method to maintain genetic diversity is to find the contributions of parents so that global coancestry is minimised. Global coancestry is defined as the average pairwise coancestry among all possible combination of



individuals, including self-coancestries. Every coancestry must be weighted by the product of contributions of the two particular individuals. In this way, not only are individuals selected, but also the optimal number of offspring they should contribute. The optimality of this method comes from several facts (see CABALLERO & TORO, 2000). As gene diversity in the population is equal to $1 - f$, minimising global coancestry will maximise both expected heterozygosity and the number of founder genome equivalents. Furthermore, this strategy implies equalisation of contributions from all previous generations to the present one, thereby maximising the effective population size. An extension of this result to subdivided populations has been shown by CABALLERO & TORO (2001).

Mating scheme

Once the parents of the next generation and their contributions have been determined, the second decision a manager should take, is the way in which those parents should be mated to generate the offspring. Different strategies have been proposed to help in the achievement of conservation aims (WRIGHT, 1921; KIMURA & CROW, 1963; TORO et al., 1988; CABALLERO et al., 1996; SONESON & MEUWISSEN, 2000). Using computer simulations, FERNÁNDEZ & CABALLERO (2001) showed that, provided that contributions have been arranged to yield the minimum global coancestry, the mating scheme is less determinant, although the mating of pairs with minimum coancestry (TORO et al., 1988) has a slight superiority. This latter procedure consists of finding the combination of couples with the minimum average coancestry between the male and female involved in each mating.

Practical considerations

Theoretically, the solutions arising from the application of optimal strategies cover a large range of possibilities, from all offspring generated by a single couple to all individuals contributing equally. The same occurs with the mating scheme, where all combinations are possible. However, the practical implementation to particular conservation programmes may be restricted. The first restriction is the number of offspring an individual can contribute. If dealing with plants or animals such as fish, this may not be a constraint, but programmes on mammals or birds should take into account that a female can provide only one or a few offspring each reproductive season. Physiology also represents a restriction in the mating scheme as a female is generally fertilised by one male only. If performing a two-step conservation programme, it is likely that the optimal contributions will not be compatible with the physiological restrictions on the mating scheme. All these problems may be avoided if selection and mating are set up

simultaneously, in a single step, and take the restrictions into account.

BALLOU & LACY (1995) proposed a single-step method based on the minimisation of mean coancestry. This is an iterative procedure to find not only which parent will contribute an offspring but also the specific matings among them. As originally proposed, the method is quite efficient in the preservation of genetic diversity, but as it shows a tendency to mate close relatives, populations under this management procedure suffer a great decline in fitness, specially in the first generations, in relation to the high increase of inbreeding (FERNÁNDEZ & CABALLERO, 2001). Therefore, the implementation of this strategy would increase the probability of population extinction and should thus be discouraged. Further improvements (avoidance of close relatives' matings) suggested by BALLOU & LACY (1995) do not completely solve the problem, as some side-effects arise from the influence of mating design on the selection step (FERNÁNDEZ & CABALLERO, 2001).

In the animal breeding field, another method has been proposed to decide the parents and the mating scheme in a single step, the so called "mate selection" (ALLAIRE, 1980; TORO & PÉREZ-ENCISO, 1990; KLIEVE et al., 1994). In the present paper the use of mate selection in conservation programmes is proposed. Using this method, all reproductive and physiological restrictions are taken into account while the Ballou and Lacy method disadvantages are absent. Computer simulations were carried out to compare this strategy with the two-step design. Examples of restricted and unrestricted solutions are also presented to illustrate the performance of the method.

Methods

Mathematical models

Two-step procedure

The selection stage of the two-step procedure consists of minimising the global coancestry (from pedigree, from molecular markers or from both, depending on the availability). This process reduces (= "is reduced"?) to find the parental contributions that yield the minimum value of the following function

$$\sum_{i=1}^N \sum_{j=1}^N x_i x_j f_{ij} \quad (1)$$

where x_i is the number of offspring to be generated by individual i , f_{ij} is the coancestry coefficient between individuals i and j , and N is the number of individuals. Some constraints must be included to find reasonable solutions: (i) only positive and integer values of the variables are allowed

$$\begin{aligned} x_i &\geq 0 & i &= 1, \dots, N \\ x_i &\text{ integer} \end{aligned}$$

as no fractional or negative numbers of offspring are possible; (ii) the sum of contributions from parents must be twice the number of offspring to generate (N , if population size is constant), as each offspring needs two gametes from different parents

$$\sum_{i=1}^N x_i = 2N$$

(iii) half of the gametes must come from males and half from females

$$\sum_{i=1}^{N_m} x_i = N$$

assuming males are in the first N_m positions and females in the following N_f ($N = N_m + N_f$).

It is obvious that restrictions in the maximum number of offspring per individual are straightforwardly applied by giving an upper bound(?) to variable x . Moreover, different limits can be given to males and females, if the species' characteristics point in that direction

$$\begin{aligned} 0 \leq x_i \leq I_m & \quad i = 1, \Lambda, N_m \\ 0 \leq x_i \leq I_f & \quad i = N_m + 1, \Lambda, N \end{aligned}$$

where I_m and I_f are the maximum possible number of offspring generated by a male and a female, respectively.

Once the optimum contributions per individual are found, only those from males and females have to be adjusted in order to determine the exact mating scheme. A linear programming optimisation allows to find the assignation design of male and female contributions yielding the minimum coancestry matings (for details see, e.g., FERNÁNDEZ & CABALLERO, 2001). This mating arrangement, however, can be incompatible with the particular reproductive restrictions of the species or population (see examples below).

Mate selection procedure

To account for restrictions related to mating characteristics, selection and mating design must be arranged simultaneously. The present paper proposes a procedure based on the minimisation of the following combined function

$$\left\{ \sum_{i=1}^N \sum_{j=1}^N \left[\sum_{l=N_m+1}^N x_{ij} \left(\sum_{k=1}^{N_m} x_{kl} \right) (f_{ij}) \right] \right\} + \gamma \left\{ \sum_{i=1}^{N_m} \sum_{j=N_m+1}^N x_{ij} f_{ij} \right\} \quad (2)$$

where x_{ij} is the number of offspring to be generated by the couple between male i and female j , and γ is a weighting factor. The number of variables x is equal to the number of all possible couples between males and females, i.e., $N_m \times N_f$. The first term of the function represents the global coancestry (f) as in formula (1), while the second term is the average coancestry between the members of the actual mating pairs. If a value of $\gamma = 0$ is given, the solutions obtained are those with minimum global coancestry contributions, as in the selection stage of the two-step method, and random mating of parents afterwards. On the contrary,

if γ is very large, the solutions are those with random contributions from parents, with minimum coancestry matings afterwards. Because the objective is to apply minimum global coancestry contributions and, only when two solutions have the same f , apply coancestries between couples as a criterion, the optimum should be to use a very small value of γ . In this way, the minimum coancestry mating will be obtained but the individual contributions that yield the minimum global coancestry will be maintained.

As in the two-step procedure, some constraints must be added to find integer positive solutions and to fulfil the restrictions on the total number of offspring

$$\begin{aligned} x_{ij} &\geq 0 & i &= 1, \Lambda, N_m \\ x_{ij} &\text{integer} & j &= N_m + 1, \Lambda, N \\ \sum_{i=1}^{N_m} \sum_{j=N_m+1}^N x_{ij} &= N \end{aligned}$$

Additional! constraints can control the maximum number of offspring per male or female,

$$\begin{aligned} \sum_{j=N_m+1}^N x_{ij} &\leq I_m & i &= 1, \Lambda, N_m \\ \sum_{i=1}^{N_m} x_{ij} &\leq I_f & j &= N_m + 1, \Lambda, N \end{aligned}$$

the avoidance of full-sibs among the progeny,

$$x_{ij} \leq 1 \quad i = 1, \Lambda, N_m \quad j = N_m + 1, \Lambda, N$$

or the restriction of a single male mated to a particular female

$$\sum_{i=1}^{N_m} \gamma_{ij} = 1 \quad j = N_m + 1, \Lambda, N$$

where γ_{ij} is a dicotomic dummy variable with a value of one if the couple ij produces any offspring, and zero otherwise.

The problem is then reduced to the minimisation of a quadratic function with the corresponding restrictions. There are mathematical tools available that yield the exact solution, like the integer quadratic programming (McCORMICK, 1983), but they are difficult to implement in computer simulations. Some other approximated algorithms, like the genetic algorithms or the simulated annealing (PRESS et al., 1989), allow an easy and quite efficient implementation of optimisation processes into the simulations. In the present work optimisations were performed through the simulated annealing algorithm (further details on the implementation can be found in FERNÁNDEZ & TORO, 1999).

Computer simulations

Simulations were performed for a dioecious species, where fitness is controlled by a large number of loci (5800) acting multiplicatively through viability differences among individuals. Mildly or moderately

deleterious as well as lethal mutations arose every generation at rates and effects according to estimates in the literature (CROW & SIMMONS, 1983; CABALLERO & KEIGHTLEY, 1994; LYNCH et al., 1999). Neutral multiallelic loci were simulated in order to monitor changes in neutral genetic variation. Individuals in the initial sample were assumed to be unrelated, so they carried different alleles at all these neutral loci in order to calculate probabilities of identity by descent and measures of genetic diversity (gene diversity and allelic diversity). A more detailed description of the model and the parameters used can be found in FERNÁNDEZ & CABALLERO (2001).

Management procedures

From a large population with frequencies at mutation–selection–drift equilibrium, samples of 8, 24 or 48 individuals were randomly taken. Prior to the implementation of any conservation strategy the population underwent five unmanaged generations in order to generate a complex pedigree and differential coancestries between individuals. From that point (generation 0), two different schemes were performed for 15 generations and the mean population fitness and diversity measures were calculated each generation, and averaged over 100 replicates:

Two step

As described in FERNÁNDEZ & CABALLERO (2001), in this method the contribution of every available parent was decided minimising the global coancestry of the population (function [1]). Minimum coancestry matings were then arranged.

One step

Contributions and mating design were chosen minimising the joint function (2). Values for c were ranged from 0.0001 to 1. Two runs were performed restricting to one the number of matings in which a female could be involved, and not allowing more than one offspring per couple.

Global and pairwise coancestry were calculated from pedigree records. In both methods, descendants of each couple were evaluated for fitness, calculated as the product of the individual effects of the 5800 loci in each genotype. A random number from 0 to 1 was drawn for each offspring and compared to its viability. If this was lower than the random number, the descendant died and another offspring from the same couple was generated. Population size was constant over generations with equal numbers of males and females. Sex of offspring was assigned at random once all descendants had been obtained.

Results and Discussion

Table 1 shows the level of genetic diversity, measured as gene and allelic diversity, for the

Table 1. Gene diversity, allelic diversity (averaged over 200 neutral loci), mean population fitness (scaled to that in generation zero) and average inbreeding coefficient at generation 15. All values presented in percentage: N . Population size; γ . Weight given to mating criteria.

Tabla 1. Diversidad génica, diversidad alélica (promediadas para 200 loci neutros), eficacia biológica media de la población (relativa a la de la generación cero) y coeficiente de consanguinidad promedio en la generación 15. Todos los valores aparecen en porcentaje: N . Tamaño de la población; γ . Peso dado para criterios de apareamientos.

| | One-step | | | |
|-------------------|----------|------------|--------------|---------------|
| | Two-step | $\gamma=1$ | $\gamma=.01$ | $\gamma=.001$ |
| N = 8 | | | | |
| Gene diversity | 36.8 | 35.5 | 36.8 | 37.0 |
| Allelic diversity | 13.8 | 13.3 | 13.7 | 13.8 |
| Fitness | 72.0 | 69.5 | 72.6 | 71.2 |
| Inbreeding | 57.3 | 58.8 | 57.8 | 57.3 |
| N = 24 | | | | |
| Gene diversity | 72.6 | 71.7 | 72.5 | 72.7 |
| Allelic diversity | 12.3 | 11.8 | 12.2 | 12.3 |
| Fitness | 83.7 | 82.6 | 83.3 | 82.5 |
| Inbreeding | 23.0 | 25.2 | 24.0 | 23.9 |
| N = 48 | | | | |
| Gene diversity | 85.2 | 84.7 | 85.1 | 85.3 |
| Allelic diversity | 11.8 | 11.5 | 11.8 | 11.8 |
| Fitness | 86.5 | 85.8 | 86.6 | 86.3 |
| Inbreeding | 12.0 | 12.6 | 12.9 | 13.2 |

optimum two–step method and the single–step method using different values of γ .

The amount of genetic diversity preserved was quite similar for both methods, irrespective of the measure of diversity we used, although it was slightly lower for larger values of γ . This behaviour occurs because of the influence of mating criteria on the selection of parents if the weight given to pairwise coancestry is too high. As pointed out by FERNÁNDEZ & CABALLERO (2001), when performing a single–step method, being more strict in the level of coancestry between couples can lead to the use of fewer individuals or those with higher mean coancestry. In this case, the genetic diversity preserved in the population would be smaller and its fitness would suffer from a fall due to

inbreeding depression. Thus, in the same table, can be seen that mean population fitness is similar for both methods with $\gamma \leq 0.01$, but slightly lower for large γ , where the inbreeding level is somewhat higher. The above results suggest that the proposed method is as efficient as the optimal two-step strategy to manage populations under conservation, regarding both the amount of genetic diversity preserved and the fitness of the population.

When restrictions are included, the space of feasible solutions is reduced. But even in this constrained situation the one-step method looks for the solution with the lowest group coancestry and, afterwards, for the mating scheme yielding the lowest pairwise coancestry. Table 2 shows the optimal contributions (2A) and the optimal mating design (2B), for a particular group of individuals ($N = 8$), for the unrestricted situation and two restricted cases. The unrestricted situation has the same solution for the one-step and the two-step methods. In the first restricted case (one male, SM), females are allowed to mate to a single male. In the second (N°FS), there is a maximum of one offspring per couple, although individuals can be involved in different couples. This latter restriction implies that no full-sibs are to be found among the progeny. Some authors have suggested this strategy as a way to slow the increase of inbreeding in a population (WANG, 1997; SONESSON & MEUWISSEN, 2000).

In this particular population structure, if we implement minimisation of group coancestry alone to determine the optimal contributions (two-step method), the result is not compatible with any of the restrictions (table 2). Female number 7 should generate six offspring, but there is no male with such a high contribution (impossible to fulfil restriction one male, SM), and there are not six males either (some full-sibs will be created). With the one-step method, restrictions are taken into account when looking for the contributions and, there are therefore compatible mating schemes (table 2). The group coancestry and coancestry between couples of the unrestricted solution are 0.368 and 0.246, respectively. Group coancestry barely changes to 0.372 and 0.374 for one male (SM) and N°FS, respectively. The increase in pairwise coancestry is somehow larger (0.288 and 0.305), as expected, but differences are small.

The use of high values of γ (> 1) leads to worse results (higher inbreeding coefficients), as could be expected for the influence of mating coancestry in the selection of parents' contributions explained above. Eventually, the average fitness of the population in the very first generations can be slightly higher than that with low values of γ , because the avoidance of a high coancestry between the couples leads to the decrease of inbreeding depression in the offspring. But, over a longer period, both genetic diversity and fitness fall below the levels of the two-step method.

Table 2. A. Example of optimal contributions of each available individual when no restriction is imposed (UR), when each female can mate with a single male (SM), and when full-sibs are avoided in the offspring (N°FS); B. Optimum mating design (male-female), according to contributions obtained in A.

Tabla 2. A. Ejemplo de contribuciones óptimas de cada uno de los individuos disponibles cuando no se imponen restricciones (UR), cuando cada hembra puede aparearse con un sólo macho (SM) y cuando se evita la aparición de hermanos en la descendencia (N°FS); B. Esquema de apareamientos óptimo (macho-hembra), conforme a las contribuciones obtenidas en A.

| A. Parents | | | |
|---------------|-----|-----|------|
| | UR | SM | N°FS |
| Males | | | |
| 1 | 3 | 5 | 3 |
| 2 | 1 | 1 | 1 |
| 3 | 1 | 0 | 1 |
| 4 | 3 | 2 | 3 |
| Females | | | |
| 5 | 1 | 1 | 1 |
| 6 | 1 | 2 | 2 |
| 7 | 6 | 5 | 4 |
| 8 | 0 | 0 | 1 |
| B. Offsprings | | | |
| | UR | SM | N°FS |
| 1 | 1-7 | 1-7 | 1-6 |
| 2 | 1-7 | 1-7 | 1-7 |
| 3 | 1-7 | 1-7 | 1-8 |
| 4 | 2-7 | 1-7 | 2-7 |
| 5 | 3-7 | 1-7 | 3-7 |
| 6 | 4-5 | 2-5 | 4-5 |
| 7 | 4-6 | 4-6 | 4-6 |
| 8 | 4-7 | 4-6 | 4-7 |

Interestingly, using very small values of the weighting factor for the mating coancestry also produces poorer results (data not shown), contrary to what theory predicts. The reason is the use of an algorithm of random search to perform the optimisations. As the value of γ diminishes,

differences between solutions do so, and it is more difficult for the process to find the global optimum, specially for large populations. As previously pointed out, exact methods exist that can be implemented if only a round of optimisation is necessary, as in the management of a real population for conservation. In this case, therefore, the relative value of γ should be adjusted to the smallest number distinguished by the precision of the computer.

For the population sizes considered, there are no great differences in computing time between procedures, although it is larger for the mate selection method. In principle, this latter implies the optimisation of a function with $N_m \times N_f$ variables, while the two-step method needs two optimisation processes with N and $N \times N$ variables, respectively. However, the one-step method has a greater feasible space (more time required to find the optimum), and the mating step is just an assignation problem in the two-step method (McCORMICK, 1983). These factors make the two-step method less demanding.

Traditionally, the way to cope with the issue of physiological restrictions has been to use populations structured in families, with fixed numbers of selected males and females. Contributions of selected individuals would be equalised, so that it would be straightforward to find a mating design which fitted the restrictions. However, as several authors have pointed out (MEUWISSEN, 1997; GRUNDY et al., 1998; FERNÁNDEZ & TORO, 1999), allowing for differential contributions gives a better control of the increase of inbreeding and the loss of genetic information. The method presented in this paper, following this second strategy, is more flexible, has a larger feasible space of solutions and achieves better levels of genetic diversity.

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