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LAB EXPERIMENTS ON OPTIMUM CONTRIBUTION SELECTION

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INTRODUCTION

In recent years considerable work has been carried out on the design of strategies to maintain genetic diversity in selection and conservation programmes. One of the strategies is to act on the number of selected individuals and their contributions to the next generation (see Fernández and Toro, 1999 and references therein). The idea of modifying the contribution of the selected individuals to the evaluated individuals of the next generation was first proposed by Toro and Nieto (1984) under the name of *weighted selection*. With unequal contributions a larger numbers of individuals may be selected, but with each selected individual making a contribution to the next generation that is proportional to its breeding value in such a way that the selection differential is maintained but the expected inbreeding is minimised. Similar ideas were proposed in the context of cloning of trees (Lindgren, 1990).

A limitation of the weighted selection, as originally proposed, is that it does not take into account the fact that, after the first generation, the selected animals become genetically related. Wray and Goddard (1994) and Brisbane and Gibson (1995) in the context of animal breeding and Ballou and Lacy (1995) in the context of conservation programmes proposed to take account of coancestry among selected individuals weighted by their contribution to the population to be evaluated in the next generation. This strategy could be called *restricted coancestry weighted selection* (Fernández and Toro, 1999). There are several ways of implementing the *restricted coancestry weighted selection,* but mate selection strategies are attractive because they combine many of the aims of the other methods into a single procedure, performing a joint control of the mating allocation and the selection pressure to achieve each generation. These strategies are also flexible because, depending on the involved restrictions, it is possible to optimise the mating design, either hierarchical or factorial, with a variable number of males, females or offspring per mating.

The potential utility of all these methods has been shown by computer simulation assuming oversimplified genetic models for the studied characters, with additive and homogeneous gene effects, and simple mechanisms of inbreeding depression. The final tests should be based on experiments carried out on real populations. In what follows, we make a short review of experiments manipulating the genetic contributions in selection or conservation plans.

RESULTS AND DISCUSSION

Early *Drosophila* experiment (Nieto *et al*., 1986). A typical selection scheme (Method A) was compared with a similar scheme but imposing unequal contributions (Method B). In

Method A, three males and three females were selected out of 15 males and 15 females scored. Mating was completely positive assortative and each pair contributed an equal number of progeny (five males and five females) to the next generation. In Method B, five males and five females were selected and mated in a positive assortative manner. However the progeny contributions of the pairs were unequal (w_1=6♂, 6♀; w_2=4♂, 4♀; w_3=3♂, 2♀; w_4=1♂, 2♀; w_5=1♂, 1♀). The expected selection intensities were almost identical for the two methods (i=1.31 for method A and i=1.29 for method B), but the expected population sizes were N_e=7.78 for method A and N_e= 8.97 for method B). The selection objective was to decrease the number of bristles on the left sternopleural plate and there were twelve 13-generations replicates of each method. The results of the experiment are summarised in table 1.

Table 1. Experiments on optimum contribution theory

Drosophila experiment (1986)	Method A	Method B
Realised heritability	0.17 (0.04)	0.24 (0.02)
Cumulative selection differential	12.85	12.34
Mating without offspring (%)	18.52 (2.16)	13.83 (1.41)
Replicates lost	4	0
Mouse experiment (1997)		
Realised heritability	0.31 (0.08)	0.29 (0.06)
Cumulative selection differential	34.4	34.0
Intrauterine mortality at generation 16 (%)	19.2	12.27
Birth mortality at generation 16 (%)	9.05	4.85
Drosophila experiment (1999)		
Realised heritability	0.32	0.37
Cumulative selection differential	70.04	77.48

In the first 5 generations the Method B showed higher selection response, although by the end of the experiment both lines had reached the same selection limit, probably because few loci are responsible of the trait. However, the effective population size was 19% greater with Method B and as a consequence, the variance of response was lower and there was significantly lower fitness deterioration with less mating without offspring and no a replicate lost.

***Mouse* experiment (Moreno, 1997).** Selection was applied only to the male sex for growth measured as the increase in body weight from 21 to 42 days. In Method A, 8 males were selected out of 32 males. They were randomly mated with 16 females. Each male contributed four males and each female one female to the next generation. In Method B, twelve males were selected but their male progeny contribution was unequal and dependent on their phenotypic value (w_1=6; w_2=w_3=4; w_4=w_5=w_6=3; w_7=w_8=w_9=2; w_{10}=w_{11}=w_{12}=1. The expected selection intensities on males were equal for the two methods (i=1.235) but however the expected populations sizes were N_e=19.8 for method A and N_e=31.5 for method B. There were 17 generations of selection and three replicates for each method.

The selection responses were very similar for both methods, but the effective population size was Ne=18.1 for Method A and Ne=27.5 for Method B (table 1). Accordingly, the line selected with Method B showed a much lower deterioration in fitness measures.

***Drosophila* experiment on conservation genetics (Montgomery *et al.*, 1997)**. A base population (generation 0) of four males and four females was constructed in such a way that the four females and three of the males were derived from two founders that had suffered two generations of full-sib mating. The other male was derived from eight founders (great-grandparents). In Method A, each male and each female contributed one male and one female to generation 1. In Method B, the unrelated male was mated to the four females and contributed all the offspring (one male and one female per dam). After this point, there were four generations that were maintained in the same way with both methods. The number of replicates was 40.

The Method B retained significantly more allelic diversity based on six microsatellites and seven allozyme loci (table 2). Reproductive fitness under both benign and competitive conditions did not differ significantly.

Table 2. Molecular measures of gene diversity (SE) with two conservation methods

	Method A		Method B	
	Microsatellites	Allozymes	Microsatellites	Allozymes
Mean heterozygosity	0.27 (0.02)	0.17 (0.01)	0.30 (0.02)	0.19 (0.01)
% of polymorphic loci	63.9 (3.9)	41.5 (2.5)	67.2 (3.5)	44.7 (3.1)
Allelic diversity	1.82 (0.06)	1.44 (0.03)	1.95 (0.07)	1.48 (0.03)

***Drosophila* experiment on mate selection (Sánchez *et al.*, 1999).** In Method A, 8 males and 64 females were selected out of 256 males and 256 females evaluated using BLUP methodology. Each selected male was randomly mated with 8 selected females. Each female contributed an equal number of progeny (four males and four females) to the next generation. In Method B we searched between among all possible matings of evaluated individuals (256 x 256) the set of 64 matings that maximised the expected selection response in the next generation under the following restrictions: a) a female could be mated with only one male; b) a male could be mated with a variable number of females (between 0 and 12); c) the rate of inbreeding should not exceed the value of 3% per generation. The experiment had three replicates of six generations for each method, and the selection objective was to increase pupa length. The average results of accumulated selection response R and inbreeding (F) are also summarised in table 1.

The line selected with method B showed an increase in cumulated phenotypic selection differential of 10.7% and at the same time a reduction in the mean inbreeding coefficient and variance of 20% and 60%, respectively. The increased selection pressure brought an increase of 31% in the selected trait selection response, and this was possible without compromising the genetic variability. Both pedigree analysis and long-term variability expectations based on genetic contributions showed no relevant differences between methods, despite the higher performance attained by method B.

CONCLUSIONS

Since the idea of managing genetic contributions of the selected individuals to the evaluated individuals of the next generation was proposed under the name of weighted selection (Toro and Nieto, 1984) there has been important theoretical developments (see Woolliams and Bijma, 2000, for the latest development of the genetic contribution theory) and many computer simulations (Toro *et al*., 1988 ; Toro *et al.,* 1991 ; Meuwissen, 1997 ; Grundy *et al*., 1998) have shown the advantages of the strategies to simultaneously optimise genetic gain and inbreeding, either by reducing the rates of inbreeding while keeping genetic gains at the same level, or by increasing selection response under a restriction on inbreeding.

We have shown that there is clear experimental evidence using lab animals for the existence of advantages in the use of procedures to optimise the mating pattern and the array of genetic contributions in selection or conservation plans. We have shown also that these advantages are important enough to be appreciated even in populations of small size. It will be desirable to implement these strategies in practical breeding programmes. Some practical approaches have been given for trees (Anderson *et al*., 1999 ; Fernández and Toro, 2001), and dairy cattle (Weigel, 2001).

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