Methods of Selection Using the Quantitative Genetics in Aquaculture-A Short Review

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Abstract

Efficient breeding programs can contribute significantly to the development of fish farming by reducing production costs, improving the resistance of farmed organisms to disease, improving food use and product quality. Unfortunately, less than 20% of the world's inland fish production comes from genetically improved stocks. In breeding programs for these fish (and also from other origins or species), three strategies can be applied: selection, crosses and hybridizations, and chromosome manipulation. Selection was poorly applied in inland fishes, being restricted mainly in trout, carp and tilapia. The most common selection goals in fish breeding programs include growth rate, feed conversion, disease resistance and survival, quality and meat yields. Three selection methods have already been applied to this animal group: individual selection, selection between and within families and the combined selection. The first one was the most practiced, but usually entails a rapid increase in inbreeding rates. The second method, used for low heritability traits or those that require animal sacrifice for measurement, may result in increased inbreeding when the selection is made between families or be less efficient when animals are selected in all families. The combined selection associates the individual information of the animal and its relatives. It is expected that the dissemination and use of these tools in fish farming will increase considerably in the coming years given the history of their low (even traditional) uses and that gains in productivity will improve the efficiency of the use of natural resources (water and land) needed for which may contribute to the growing need for animal protein for human consumption.

Keywords: Selection methods; Breeding programs; Aquaculture; Individual selection; Family selection introduction

Introduction

Aquaculture is predicted to play a major and ever increasing role in meeting human needs for animal source food. In terrestrial animal and plant species genetic improvement programmes have made a substantial contribution to agricultural productivity and viability. As a result of decades of selective breeding and domestication in these terrestrial species, thousands of genetically distinct breeds, strains and varieties now exist worldwide and are collectively termed genetic resources [1].

Theoretically, the principles of quantitative genetics and the studies of the variance components are the same which applied in the aquatic organisms, however the progress genetic obtained until now it is so superficial in comparison with terrestrial animals and plants. Although poorly exploited, fish have advantageous characteristics for breeding programs compared to terrestrial domestic animals, such as the high fertility and external fertilization, which guarantees flexibility in the definition of mating with the formation of full-sibs and half-sibling groups. As disadvantages, this animal group presents young forms much small, such as larvae and small fingerling, preventing early identification, with an increase in the cost of the program due to the need to grow whole-sibling families in separate structures, to a size sufficient for marking. This could provoke the emergence of the family effect among them (non-genetic, non-additive and maternal effects) and the rate of inbreeding would be easily increased by high prolificity of the animals.

According to Mair [2], less than 20% (or even less than 10%, according to Gjedrem [3] of world aquaculture production originates from genetically improved stocks. The existence of few genetic improvement programs in the sector is due to three main reasons [4]: (1) little information about the reproductive cycles of several cultivated species; (2) regular capture of wild specimens for breeding, which compromises the domestication of the species; (3) researchers, extensionists and fish farmers

with little knowledge about quantitative genetics, theories and breeding programs.

Efficient breeding programs will be crucial to the development of fish farming, not only to achieve the necessary global demand, but also to reduce production costs, improve the resistance of farmed organisms to disease, improve food use and product quality [5]. Aquatic animals allow the implementation of several approaches to genetic improvement. These include the hybridizations and cross-breeding, chromosome manipulation, sex control, transgenesis and selective breeding.

But of all existing genetic approaches, only selective breeding offers the opportunity of continued genetic gain, that the gain made can be permanent, that it is the only approach in which the gain can be transmitted from generation and that gains in a nucleus can be multiplied and expressed in thousands or millions of individuals in the production sector. The term selective breeding (or artificial selection) describes the various methods by which humans derive organisms with genetically based desirable traits through the use of chosen parents to make controlled crossed. The aim of selection is to identify and select as parents for the next generation the individuals whose progeny, as a group, have the highest possible additive genetic merit for the trait or traits in question. This is almost equivalent to selecting as parents those whose own additive genetic merit is highest. The basic effect of selection is to change the gene frequencies, and the effects that can be observed are changes of the population mean.

According to Chavanne et al [6], one way to describe a selective breeding program is to document its breeding scheme. In the simplest and often least costly designs, such as individual selection, pedigree information is not required and the number of selected traits is therefore limited. In contrast, so-called family-based design require the family origin of the breeding candidates to be traced, which makes them more flexible regarding the number and the type of traits that can be selected. The advancement of molecular markers and their application in traditional breeding has led to the emergence of novel breeding approaches such as marker-assisted selection (MAS) and, more recently, genomic selection. The latter method in particular represents a great opportunity to improve selection routines and methodologies, although the technical sustainability of its implementation needs to be carefully assessed.

Breeding goals, the number and type of selected traits, are another essential feature of a breeding program. The traits of interest can be recorded directly on candidate breeders, as in the case of growth, morphology and some reproduction-related traits or on their sibs when the traits measurement requires a fish to be killed, assessment of disease resistance of processing yield. When a number of traits are targeted simultaneously, they are combined into an index in multi-generation and multi-trait selection, with each trait weighted according to its economic value.

In aquaculture, the traits of economic importance in aquaculture are generally quantitative, governed by a large number of genes. This is particularly evident with genes with additive effects. The effect of changing the frequencies of the favorable alleles at these genes can be observed as a change of population mean for the trait under selection. Eknath et al. [7] and Gjedrem [8] point out that the objectives of selection of breeding programs for aquaculture organisms can be changed with certain ease, including or withdrawing candidate characteristics, redirecting the program to new horizons quickly. According to the authors, this is possible due to the great additive genetic variability of the characteristics of interest in the aquaculture populations, the reproductive precocity of several species and their prolificacy. These aspects accelerate the annual genetic gain of a particular trait, since the high prolificacy is related to the increase of the degree of selection intensity, the precocity, the short generation interval and the additive genetic variability, the heritability.

In general terms, two traits are particularly important in aquaculture: the time required to reach commercial weight and the volume of food the animal will consume to reach that size. However, none of them are subject to direct evaluation, since the first former is replaced by weight or length at a fixed age and the second by weight gain per unit of time until that age. In this perspective, we can make the evaluation of these traits more easily, because the description quantification of this data, in both traits, having high correlation with each other.

Considering the complexity and the importance of the applied to these techniques on the production of fish, we review the main selection methods that have been developed for genetic improvement in aquaculture, and made a short discuss about their virtues and shortcomings. Illustrate that fundamental principles of genetic management are common in the implementation of both selective breeding and should be emphasized in capacity development efforts. We highlight the methods were most application in aquaculture in wide world, as individual or mass selection, family selection within cohort, within family and combined selection are given. The efficiency of each method can be predicted by calculating the expected genetic response for a given set of parameters, which will partly dependent on how accurately the breeding values of individual animals will be evaluated.

According to Gjedrem and Baranski [9], the choice of selection method for a given situation (species, production environment, scale) will depend on a range of importance factors, which including:

• Target traits for which genetic improvement is desired

• Feasibility of recording the trait on live animals

• Magnitude of heritability for the traits in question

• Reproduction capacity of the species.

Individual or mass selection

The terms individual selection and mass selection are often used interchangeably, and they refer to selection solely based on the individual's phenotype. This is a well-known and widely used method of selection in animal breeding, and for several aquaculture species. Can be used on characteristics that can be

measured in the candidate animal itself, as weight gain, being most efficient in characteristics of high heritability.

Individual selection is usually the simplest method to operate and in many circumstances, it yields the most rapid response. It is does not require individual identification or the maintenance of pedigree records, hence, it may be considered the least costly method. In principle, it can produce rapid improvement if the heritability of the trait(s) under selection is high. For growth rate and morphological traits (easily assessed, expressed in both sexes), It can be suitable. By contrast, individual selection is not suitable for situations in which the estimation of breeding values requires slaughter of the animals (carcass and flesh quality traits) of challenge of some sort (selection for salinity tolerance for disease resistance) [1].

When applying individual selection, it is necessary that the evaluated animals are under equal environmental conditions; therefore, it is very important that the environmental conditions have been controlled. In this case, the influence of external conditions should be minimal and kept the same for all individuals that are to be compared at any stage of the life cycle. In this manner, the probability of correct ranking of the individuals based on thus genetic merit is maximized. Differences between individuals or groups of individuals for environmental factors like water temperature and salinity, different tanks, ponds or cages, density, light condition, and type of food and feeding regimes, may reduce the accuracy of the selection substantially, and in that way, can also reduce the possibility for genetic improvement.

In species with total spawning, it is not difficult to establish at the same time the same conditions for all candidate animals, since all hatching occur in a small-time interval. In species with split spawning, in which breeding herds reproduce asynchronously, it is important to form contemporary groups and select within them. To obtain as equal environmental conditions as possible all individuals to be compared should be hatched at the same day or within a few days' period and thereafter reared under identical environmental conditions. Therefore, it is important to form groups of animals with similar ages, grown in the same production systems, with similar control of water quality, storage density, handling and feeding.

However, mass selection may be unsuitable if there is large uncontrolled systematic environmental variation (for example age differences). Additionally, there is no control of inbreeding with mass selection, and this has caused problems in a number of fish breeding programs [10-16].

The lack of pedigree information often leads to a rapid increase in rates of inbreeding, especially in species where reproduction occurs naturally in a growing environment, such as tilapia. Normally in these situations, few dominant males reproduced with existing females. In tilapias, there is the possibility of contouring this problem with the practice of collecting eggs in the mouths of females, kept in hapas with males. In this way, it is easier to separate animals of both sexes that have already reproduced and contributed genetically to the progeny to be selected.

Family selection

Family selection refers to a selection method in which family groups are ranked according to the mean performance of each family and whole families are saved or discarded [17]. The difficulty of the individual marking of the animals (which is still a fact in crustaceans) led to the recurrent use of these methods in fish farming, with the constant impediment of the emergence of the family effect.

The efficiency of family selection rests on the fact that the environmental deviations of the individuals tend to cancel each other out in the mean value of the family. Accordingly, the phenotypic mean of the family comes close to being a measure of its genotypic mean. The advantage of family selection over other types of selection is greater when environmental deviations constitute a large part of the phenotypic variance. This method has been widely used in fish farming for the selection of low heritability characteristics, in this situation; the use of family mean gives an increased accuracy when estimating breeding value.

Another great advantage in used family selection, it based on the programs where need improvement traits that cannot be currently measure on live individuals, like product quality traits, in this case, the use of family information is essential, recording these traits on sibs makes it possible to estimate breeding values with high accuracy. The improvement of traits like carcass quality and disease resistance only can be included in the breeding objective when applying family selection. Family selection is also far more effective than individual selection for threshold traits such as age at sexual maturity, particularly at low frequencies or incidence of the trait [4].

On the other hand, environmental variation common to members of a family impairs the efficiency of family selection. If this component is large it will tend to swamp the genetic differences between families and family selection will be correspondingly ineffective. Another important factor affecting the efficiency of family selection is the number of individuals in the families; the family size. The larger the family, the closer is the correspondence between mean phenotypic value and the mean genotypic value. The high reproductive capacity in aquatic animals makes family selection important for these species.

The other point is the difficult to keep the rate of inbreeding low and the intensity of selection high, the number of family groups bred and measured should not be smaller than 50-100. In the period prior to tagging, the family groups have to be kept separately. This makes family selection costly in terms of space. If breeding space is limited in this period, the intensity of selection that can be achieved under family selection may be quite small.

According to Gjedrem and Baranski [9], to apply family selection, it is necessary to know the parentage of each individual and hence important to maintain good pedigree records. This usually necessitates individual tagging of animals. Since it is not possible to physically tag the animals at hatching, each full-sib family must therefore be reared in separate units from egg stage through to the onset of feeding until they reach sufficient size to be physically tagged. During this period, each

family will have a common environment that is different from other families. This common environmental effect will to some extent reduce the accuracy of the use of the family average as a prediction of genetic merit. Therefore, this period should be made as short as possible. This stresses the importance of providing all families with as equal environmental conditions as possible during the testing period in order to minimize the common environmental effects. And the mating could be performed between individuals from the different group on a rotational basis to avoid inbreeding.

Within-family selection

This is the opposite of the previous method. The selection is based on the deviation of each animal from the average of your family. There is the choice of animals of all families, then the method requires identification of the families. This may be achieved by maintaining them in separate tank, cages, hapas or any other means of containment, without necessarily tagging the fish. The full-sib groups reared in unreplicated hapas or any other form of containment fall into this category. Under such circumstances selection between families would be misleading from a genetic viewpoint because of the confounding between genetic merit and common environmental effects. If replacements are chosen so that every family contributes the same number of individual to the next generation (chose one female and one male from each family) the effective population size is twice the actual [18].

The criterion of selection is the deviation of each individual from the mean of the family to which it belongs. This type of selection is the reverse of family selection; the family means being given zero weight in the selection decision. The chief condition under which this method has an advantage over the others is when there is a large component of environmental variance common to members of a family. Selection within families would eliminate this large non-genetic component from the variation operated on by selection [19]. So, the within-family selection is especially advantageous when there is a large component of environmental variance common to members of the same family.

However, not all the additive genetic variance is available for selection, but only a fraction equal to the coefficient of relationship, but only a fraction equal to the coefficient of relationship among the family relatives in question will be available (0.50 and 0.25 for full-sibs and half-sibs, respectively). The lower within-family heritability can be compensated for by the high within-family selection intensity that can be applied without increasing the rate of inbreeding. The selection intensity within families will be limited only by the number of individuals tested per family. The number of families involved in the programme will determine the lower limit of inbreeding, which can easily be controlled by applying a rotational mating system such as that earlier suggested for selection within cohorts [1]. An important practical advantage of selection within families, especially in laboratory experiments, is that it economizes breeding space, unlike family selection. The method reduces the need for tagging large numbers of individuals. They estimate that the implementation of a selection method that entailed the

individual identification of large numbers of fish and a period of communal rearing would be more expensive and difficult to implement. Within family selection has low efficiency compared to most other selection methods [20,21].

Combined selection

The term, combined selection in a broad sense, meaning selection that is based on individual information as well as on information coming from relatives, combine in an optimal way all available sources of information that can add to our knowledge about the breeding value of an animal, as well information recorded on the animal itself, information about full-sibs and/or half-sibs and progenies as well as pedigree information. In this case, all of the additive genetic variance is available for selection and the use of information from relatives increases the accuracy of the estimation of breeding values.

It represents the general solution for obtaining the maximum rate of genetic gain, and the other simpler methods are special cases of this method. Combined selection is therefore in principle always the best method. [4]. Furthermore, relatives' records can be used to estimate breeding values for traits that require slaughter of the animals (carcass and flesh quality traits) or that entail a risky challenge (disease resistance, tolerance to some environmental component). This is not possible with the other methods (mass selection or within-family selection) [1].

A selection index can be very useful in combining such information, but the approach has limitations that have been overcome with Best Linear Unbiased Prediction (BLUP). Those procedures rely on mixed model methodology for the estimation of individuals' genetic merit. In the case of aquaculture, all systematic effects (batch, sex, production environment, age variation) associated with traits of interest can be accounted for in the model fitted to the data.

One particular advantage of BLUP procedures is that genetic gain can be estimated from the mean of the estimated breeding values in each year or generation of selection provided there are genetic links. A drawback of BLUP selection is that if truncation selection on estimated breeding values is practiced, it also results in higher levels of inbreeding than individual selection, especially for lowly heritable traits. This is because BLUP uses family information leading to co-selection for relatives. Hence, a mating strategy should be used that results in genetic gain while controlling the rate of inbreeding [22].

However, the costs to apply this methodology are higher due to the need to mark the evaluated animals with the cultivation of families in separate structures up to a minimum weight for identification. Cultivation of the families separately up to part of the evaluation period may lead to the emergence of a family effect, causing confounding of existing genetic effects and reducing the accuracy of predictions of genetic values.

The genetic improvement programs in aquaculture

Most animal breeding programs have focused on cumulative short-term genetic changes of production traits, because breeding optimization has to a very large extent been based on

market economic values. Sustainable genetic improvement by animal breeding is a long-term and complex process. Farmed fish is at an early stage of domestication and selection, but rapid selection responses for growth rate are already documented for several species. Precautions should be taken to avoid the same unwanted side effects, such as increased frequencies of diseases (e.g. mastitis in dairy cattle) and leg problems, which we have often seen in breeding programs for agricultural livestock. Careful monitoring of possible correlated responses is needed. More basic knowledge of, e.g. animal welfare and behavioural needs of fish may also be required, as we know very little about its perception of pain and satisfaction, and what it prefers.

Starting a selective breeding program should then focus on expected benefits of, e.g. faster growing fish with higher survival rates and the costs, by improving the aquaculture species in question. Because of the great fecundity of most aquaculture species, a single, well-organized breeding nucleus may supply a huge market with continuously upgraded seed by delivering selected brood stock to a number of multiplier farmers after each generation of selection. Consequently, the running costs of the breeding programs will be more or less constant and independent of the volume of the target industry. The benefit/cost ratio will then often depend more on the volume of the target industry than on the price of the end product, both from the consumers' point of view and from a private business point of view. The total impact of an aquaculture breeding program on food supply and resource efficiency for the society will usually be greater for a large volume species [23].

Genetically improvement strains are essential to aquaculture development. The application of proven quantitative genetic theory should continue for relevant species. There is an ample proof of the success such programmes can have. Greater emphasis is required in the areas of dissemination of the improved stock to farmers to ensure impact at the production level. However, consideration must be given to the potential impacts of fish escapees and the conservation of wild fish genetic resources. So, genetic management is necessary for both genetic improvement and conservation of genetic variation in cultured fish populations and should be emphasized in future capacity development initiatives

From an economic viewpoint, investment appraisal studies indicate very favorable benefit-to-cost ratios for genetic improvement programmes in *Nile tilápia* [24] and common carp [25]. This was show to be so even for situation in which there was genotype by environmental interaction [25] and a single program had to service more than one environment. It is reasonable to think that these results can be generalized to other, similar, aquatic animal species.

Limitations and constraints during the implementation of genetic improvement programmes in fish often occur, particularly in developing countries. Issues are commonly related to financial resources, and to a paucity of human capacity in this field. Other constraints include technical issues related to individual identification of fish but these can be overcome with relatively small investment.

Before initiating a selective breeding programme, a farmer must ask the following question: Is a selective breeding programme appropriate or necessary? The adoption of a selective breeding programme should be restricted to farmers who are capable of keeping and maintaining records, who are good managers, who adopt and maintain new technologies and who are willing to incorporate some long-term planning into their management programmes.

In order to control fertilization, hatching and first feeding, it is essential that the entire reproduction cycle for a species is controlled in captivity. Furthermore, an inexpensive marking or tagging system is advantageous and a necessity for a breeding program based on testing and selection within and between families. In order to select the best individuals for breeding, we need records of the traits in the breeding objective or traits correlated to the breeding goal. The records should be obtained for many animals at a reasonable cost during a limited time interval. Knowledge and methodology to optimize selection by predicting and using breeding values is also essential [26].

The programmes starting with a population with ample genetic variation is a trademark of successful fish genetic improvement programmes. Although this in itself is not a sufficient condition for success, it is indeed a necessary condition. The failure of some attempts to achieve genetic improvement with aquatic animals may have been due more to weakness in the base population than to be selection method utilized. Irrespective of the method of choice, continued genetic improvement will hinge upon the adequate balance between high selection intensity and the maintenance of low inbreeding rate.

Before the selection is made, it is preponderant that the beginning of an improvement program originates from a base population with great additive genetic variability. In this way, it is important that the nucleus is formed by lots from several genetic sources, such as several sites or collection points of a particular river. Examples are the Norwegian Atlantic salmon program, which originated from 41 wild genetic sources [27,28] and the GIFT program for Nile tilapia originated from the diallele crossing of 8 strains of the species [29].

The success of an aquaculture breeding program critically depends on the way which the base population of breeders is constructed. In particular, all the genetic variability that can be used for selection on the traits initially included in the breeding objective is that found in the original breeders. Also, the decisions taken when creating the base population will have consequences on the genetic progress for any other additional trait that may be part of future breeding goals, whatever production or fitness related traits [30].

Strains originating from the base population may be selected to serve crops in different environments, since there may be genotype-environment interaction, as evaluated by Bentsen et al. [31] for the characteristic weight at Nile tilapia farms cultivated in tanks-net and nurseries. However, until then, little or no interaction was found in rainbow trout, Atlantic salmon and catfish, suggesting that it is not necessary to select several lineages for this species. However, there is always a need for

previous studies to confirm the lack of genotype-environment interaction, mainly due to the great variation between and within existing production systems in fish farming.

The decision on the type of selection to be adopted will depend on the program's long-term objectives, available resources, the nature of the goal and the value of heritability. Ideal program designs maximize the likelihood of correct ordering of organisms as to the true genetic value for the target in question. However, perfect programs are rarely possible, restricted by the limitation of individual identification and the physical separation of families to communal storage Mair [2].

The major goal to most selective breeding programmes that are going to be used to improve quantitative phenotypes is to improve growth rate, and this will also increase yield. There are two basic approaches to improving yields. One is to use a breeding programme to improve the fish that are being cultured. The other is to improve the improvements in management are often inexpensive. For that, they must to conduct an assessment to determine its usefulness, needs to quantify his goals and know how the phenotype(s) will be measured, to determine the type of selective breeding programme he will use, needs to know how the results will be evaluated and must plan an annual evaluation and reassessment of the programme.

The overall aim of all selection schemes is to maximize the probability of correctly ranking all potential breeders with regard to their breeding value. An animal's breeding value can be defined as the average performance of an infinite number of its progeny or from a practical points of view its ability to produce good or bad progeny.

Selection that combines the individual information of the animal and its relatives. More efficient method, but more expensive. From this method, it is possible to predict the genetic values of the animals by BLUP (Best Linear Unbiased Predictions). Method adopted for the Norwegian National Program for Genetic Improvement of Atlantic salmon and the GIFT program for Nile tilapia. With the information of pedigree, it becomes possible the direct selection of characteristics of meat quality and survival to diseases.

One of the major difficulties of these programs in fish breeding is the mark used for the identification of animals. Most available and accessible such as numbered ribbons that span the musculature or nylon strands with small numbered labels that are also affixed in the same way, have high loss rates. Thus, more animals must be identified to compensate for information losses, increasing program costs. The emergence of identification tags improved pitfalls considerably (almost 0%), but it is the most expensive option on the market.

For each selection methods than can be chosen, always have the side of the advantages and disadvantages. That choice will be influence for a given particular breeding scenario. However, for most methods, there is a theoretical maximum value of the correlation between the true and estimated breeding values, given different heritability for the traits in question.

Final considerations

Genetically improved strains are essential to aquaculture development and have been shown by Nguyen and Ponzoni [32] to be among the most important factors resulting in increased production, lower costs, increased consumption and, in some cases, improved overall nutritional status of certain sectors of the human population. The application of quantitative genetic theory to the improvement of farmed aquaculture species is still at an early stage, and its use should be expanded to develop important aquaculture species to further increase the productivity and quality of aquaculture products.

Selection was still poorly applied in fish, being restricted mainly in salmonids, carp and tilapia. This was mainly due to the lack of efficient methods of individual marking (until recently) and, consequently, controlled mating and pedigree information to improve the accuracy of the estimates. The maintenance of the additive genetic variability in the core population of the program should be guaranteed, but there is a reduction of the same that should be avoided, inbreeding. This is normally harmful promoting the reduction of performance of organisms to zootechnical characteristics, inbred depression. In aquaculture, with the increase of endogamy, the worsening of several zootechnical characteristics, such as the reduction of reproductive performance and larval survival, as well as the increase in deformities of the same, have been confirmed. In the literature, values of 0.9% to >20% of performance reduction of inbred lines are found for each 10% increase in the coefficient of inbreeding of the original control population.

As we have pointed out, less than 20% of the fish production in the world comes from genetically improved stocks. This indicates that there is a great need for investment (public or private investment, training of personnel) to fill this gap. Considering the good results obtained in the few breeding programs implemented for some fish species (*Nilotica tilapia*, carp), it is expected that the dissemination and use of genetic improvement tools in fish farming will increase considerably in the coming years given the history (Even of traditional uses) and that gains in productivity improve the efficiency of the use of natural resources (water and land) needed for cultivation, which may contribute to the growing need for animal protein for human consumption.

The successful achievements of new genetic programmes depend not only on systematic steps involved in the design and conduct of experimental field work but also on the establishment of a base population with ample genetic variability to ensure a long-term response to selection. Choice of selection methods depends on species, objectives and the available resources of aquaculture enterprises. Ideally, a fully pedigreed population should be maintained to enable the applications and utilizations of advanced statistical methods, such as best linear unbiased prediction (BLUP), for genetic evaluation and selection. Within- and between-family selection, based on an individual's genetic merits and its relationship with other animals in the pedigree, shows several advantages over other methods [32].

Falconer and Mackay [18] compared the effect of individual, family and within-family selection with the efficiency of combined family and within-family selection. The correlation between phenotypic values of family members is known as the intraclass correlation (t) and is estimated as:

t=r.h2+c2

where r is the correlation between family members, h2 is heritability of the trait in question and c2 is the proportion of the total variance accounted for by common environmental effects.

When the intraclass correlation (t) varies from around 0.25 to around 0.75, individual selection is more efficient than both family and within-family selection. This is because individual selection exploits the entire scope of genetic variation present, while family and within-family selection only utilizes part of the genetic variation.

When the intraclass correlation is low, family selection is more efficient than individual selection. Within-family selection compares favourably to both family and individual selection when the intraclass correlation is very high. Individual selection is approximately as efficient as combined selection when t=0.50 and for such and interclass correlation, family selection and within-family selection are equally efficient.

When the intraclass correlation is high due to members of a family being more alike phenotypically rather than genetically (t>r=0.50), within family selection is more efficient than both individual and family selection. However, this is a very rare scenario and the primary advantage of within-family selection is the reduction of common environmental effects between families [19].

A comparison of expected selection responses from individual, family, within and combined family and within-family selection demonstrated the superiority of the combined selection strategy [20], a finding supported by theoretical responses show in **Figure 1**.
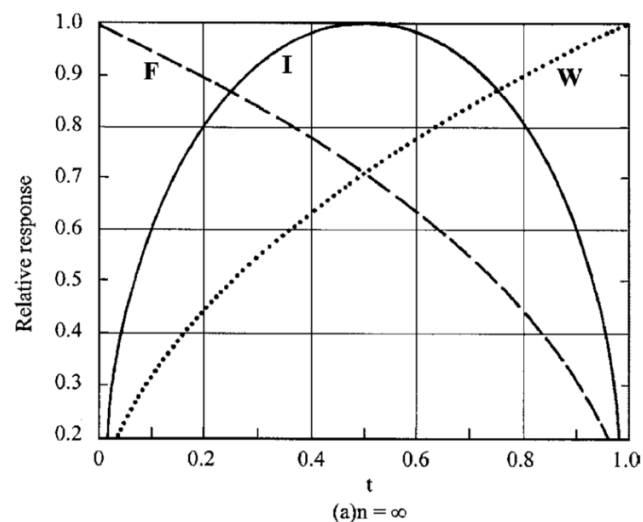

Figure 1 Relative merits of the different methods of selection, responses relative to that for combined selection plotted against the phenotypic intraclass correlation, t. F=family selection; I=individual selection; W=within-family selection, reproduced form Falconer and Mackay [18].

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