

The use of alternative breeding schemes to enhance genetic improvement in rainbow trout: II. Two-stage selection

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Abstract

The potential of selection in stages to increase genetic gain and profit in rainbow trout breeding was assessed. The theory of Cochran was utilized to predict genetic gains under alternative breeding schemes mimicking the actual Finnish breeding programme. The first stage of selection was based on the within-family deviations of body weight after the first growing season, and the second stage was based on a genetic index that included two body weight measurements at the fresh-water nucleus/central station, and body weight of sea ranched fish at harvest (the breeding objective). A fixed number of 200 family tanks were assumed in all schemes but initial family size and proportions of individuals selected at the two-stages were varied. The deterministic predictions showed that the two-stage selection schemes resulted in 7% and 14% higher genetic gains in the breeding objective compared to the one-stage schemes with equal number of fish reared from tagging to spawning. This result however depended on the population size. The results showed further that by switching from one-stage schemes to two-stage schemes, population size of a breeding programme can be considerably reduced without a decline in the rate of genetic gain. A linear profit function that included the most evident costs (tagging, rearing and management expenses) and returns from the programme showed that the maximum profit was achieved when selection was relatively strict in the first stage of selection. Due to high fertility and biological flexibility of fish, two-stage selection schemes can be easily applied; and this study confirms their benefits in reducing management costs and improving genetic gain in fish breeding.

Keywords: Two-stage selection; Breeding programmes; Fish; Profitability; Quantitative traits

1. Introduction

The aim of breeding programmes in aquaculture is to improve the productivity of farmed populations. Multi-

variate selection based upon the use of Best Linear Unbiased Predictors (BLUP) uses information on many traits jointly such that the breeding objective is predicted more accurately and therefore response is increased. Nevertheless, when the selection criteria incorporate many traits jointly, BLUP selection may be difficult in practice and economically costly, because all breeding candidates and their relatives need to be kept alive until measurements on all traits included in the index are available.

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One way to reduce production and management costs of a breeding programme is to practice selection in stages (Cochran, 1951; Mueller, 1984; Wade and James, 1996). The savings can be realized by culling at the first stage based on the least expensive traits that are correlated with a breeding objective. For example, selection can be carried out first on body size measured early in life, which correlates positively with body size at maturity (Martinez and Neira, 1998), reducing considerably the number of individuals needed to be reared up to reproduction. Due to the high reproductive capacity of many fish species, it may be possible to achieve relatively large selection intensities within families, compared to other farm animals, in which the family size is relatively low.

Experimental evidence has shown that when culling is practiced in the first stage, the response to selection does not differ significantly from the one obtained in a one-stage selection programme (Campo and Fuente, 1991). Xu and Muir (1992) found in the context of poultry breeding that in spite of a reduction in genetic improvement, such schemes increase the profitability of breeding programmes. Two-stage selection has not been incorporated or even discussed in studies aimed to optimize breeding designs in fish (Bentsen, 1990; Bentsen and Gjerde, 1994). In this paper, we examined the benefits of two-stage selection using the Finnish breeding programme for rainbow trout, *Oncorhynchus mykiss*, as a model. The outline of the rearing facilities and genetic parameters were attained from the actual breeding programme of rainbow trout (see Martinez et al., 2006).

The two objectives of the present study were: (1) to assess genetic gain in two-stage selection schemes with different initial population sizes at the first stage of selection, and to compare these results with a one-stage selection scheme that uses the same number of individuals reared from tagging onwards, and (2) to study the effect of the intensity of selection in the first and second stage on genetic progress and to find the optimal selection intensities based on returns and costs of the breeding programme.

2. Materials and methods

2.1. Assessing genetic gain in two-stage selection

2.1.1. The breeding programme

The breeding cycle of rainbow trout is described in detail in a companion paper (Martinez et al., 2006). In brief, the generation interval in the scheme is three years. At the fresh-water breeding station, body weight

is recorded after the first growing season when individuals are tagged (BW_I) and after the second (BW_{II}) and the third growing seasons (BW_{III}). After the measurement of BW_I , each family is split into groups to be reared either at the nucleus station or to be transported to a fish farm located at the sea. Body weight of the sea ranched fish is recorded after the second growing season at sea (considered as the breeding objective, BW_{IV}) just before the fish are slaughtered and marketed.

For the simulations, factorial random mating is used to produce the next generation of individuals. The mating ratio of 3:5 (males:females) was considered because it was shown previously that this mating system gives the highest response in one-stage selection programmes (Martinez et al., 2006). It was assumed that 200 family tanks were maintained in all alternative scenarios analyzed and therefore 34 males and 65 females were selected as replacements. Twenty randomly selected full-sibs from each family were assumed to be tested at the sea station, whereas the family size at the breeding station was varied to perform designs with different population sizes. The initial family sizes were equal and the same proportion was selected from each family at the first stage.

2.1.2. Selection in stages and prediction of genetic gain

Following the methods of Cochran (1951), genetic gain in the breeding objective (body weight after two growing seasons at sea) was calculated assuming that a multivariate normal distribution remains between selection criteria in the second stage and the breeding objective after selecting in the first stage (Cunningham, 1975; Cotteril and James, 1981; Xu et al., 1995; Wade and James, 1996). Although some departures from normality are expected after selecting in the first stage, this theory is expected to hold well under a range of alternative two-stage breeding programmes (Cunningham, 1975; Mueller, 1984; Ducrocq and Colleau, 1989). Monte-Carlo simulations also support this theoretical finding (data not shown) and was consistent with what has been observed in experimental populations (Campo and Fuente, 1991).

The genetic gain (in standard deviation units) in a two-stage selection programme can be approximated as (Cochran, 1951):

$$\Delta G_H = \frac{\rho_{I_1, H} Z_1 \Phi_2 + \rho_{I_2, H} Z_2 \Phi_1}{\alpha_{12}} \quad (1)$$

where $\rho_{I_1, H}$ and $\rho_{I_2, H}$ are the correlations of the within-family deviations (index I_1) and the index I_2 ,

respectively, with the breeding objective (H). These correlations are the same as those calculated in a non-selected population (Cochran, 1951; Cunningham, 1975) when normality approximately holds. z_1 and z_2 are the ordinates of the normal density function at k_1 and k_2 , the truncation points for the first and second stage, respectively. The product (α_{12}) is the proportion of bivariate normal distribution of survivors after two rounds of truncation selection and is the product of the proportions selected at each stage; Φ_1 and Φ_2 are the truncated areas of the normal curve after selecting on truncation points for the first and second stages. These areas were calculated using:

$$\Phi_1 = \Phi \left(\frac{k_1 - k_2 \rho_{1,2}}{\sqrt{1 - \rho_{1,2}^2}} \right) \quad (2)$$

$$\Phi_2 = \Phi \left(\frac{k_2 - k_1 \rho_{1,2}}{\sqrt{1 - \rho_{1,2}^2}} \right) \quad (3)$$

where $\rho_{1,2}$ is the correlation between the selection criteria used in the two-stages and Φ is the cumulative normal distribution function. The expected correlation between the indices used in the two-stages is equal to the ratio of the correlations of the first and the second selection criteria with the breeding objective, due to the fact that the same breeding objective is used in both stages (i.e. $\rho_{1,2} = \frac{\rho_{I_1,H}}{\rho_{I_2,H}}$; Cochran, 1951; Jain and Amble, 1962; Norrell et al., 1991). To obtain the expected rates of gain following selection in stages we need to derive the expected correlations between the criteria used in the two stages and the breeding objective (BW_{IV}); details are given below.

2.1.3. Selection criteria in the first stage

Selection at the first stage was applied when body weight is measured at the age of six months at the central breeding station (BW_I). The selection was based upon the within-family deviations in body size. Individuals were scored for body weight and those that surpassed a truncation point were selected, tagged, and reared until spawning. Indices consisting of pedigree information and records of relatives would have given higher genetic gains compared to within-family selection, but such indices were not included into the present study, since they are difficult to implement in practice, i.e., if tagging is needed in order to include information from relatives of breeding candidates.

The correlation between the first selection criteria (i.e. the within-family deviations for BW_I , henceforth index I_1) and the breeding objective is given by (see Appendix):

$$\rho_{I_1,H} = \frac{\frac{1}{2} \sigma_{(A_{BW_I}, A_{BW_{IV}})}}{\sqrt{(1-t) \sigma_{P_{BW_I}} \sigma_{P_{BW_{IV}}}}} \quad (4)$$

where $\sigma_{(A_{BW_I}, A_{BW_{IV}})}$ is the genetic covariance between BW_I and BW_{IV} , $\sigma_{P_{BW_I}}$ and $\sigma_{P_{BW_{IV}}}$ are the phenotypic standard deviations of BW_I and BW_{IV} , respectively and t is the full-sib family intra-class correlation for BW_I . Using this formula, the correlation between the first selection criteria and the objective in the breeding programme is 0.18 (after Kettunen et al., 1999).

2.1.4. Selection criteria in the second stage

The second stage of selection is applied at the age of three years just before spawning, and it is based on an index (I_2) that incorporates information on the traits BW_I , BW_{II} obtained from the candidates for selection and BW_{IV} from their relatives in the sea. The index in matrix notation is $I_2 = bE$ where E is the vector of the best linear unbiased predictors (BLUP) of breeding values obtained using a multi-trait model and b is the vector of the genetic regressions between the estimated breeding values and the breeding objective (Schneeberger et al., 1992; Martinez et al., 2006). The correlation of the index with the breeding objective is approximately equal 0.67, when information from all these traits and relatives is included jointly. It is important to note that this value depends little on the number of individuals measured for the traits expressed in the breeding station and accuracies were nearly equal when BW_{III} was included or not in the index (Martinez et al., 2006).

2.1.5. Genetic gain and variable initial population size

Two conditions were considered in assessing genetic gain of two-stage selection. In the first case, we assessed the rates of genetic gain in two-stage selection programmes with different initial population sizes for a fixed number of 200 full-sib families (i.e., by varying the family size and therefore the number of individuals measured for BW_I). This situation is appealing since there are no increases in tagging costs (which contributes to a major proportion of the total costs) when the number of individuals reared before measuring BW_I is constant. The main assumptions are that it is possible to keep population and family sizes relatively high before the first selection, and the cost of recording the body

weight at this stage is relatively low. The initial population sizes considered were 10,000, 15,000, 20,000, 25,000, 30,000 (full-sib family sizes of 50, 75, 100, 125, 150, respectively). The second condition was varying the proportion of individuals tagged so that after the first stage of selection the population size was either 5000 or 10,000 individuals; this had the added effect of varying selection intensity at the first stage. These schemes were compared to a one-stage selection scheme with either 5000 or 10,000 individuals reared from tagging to spawning. Replacements were selected using the same selection index (I_2) as for two-stage selection; the only difference being that selection was completely random with regards to BW_1 at tagging.

2.2. Selection intensity and profitability

Here we examined the impact of changing the selection intensity in the first and second stage on genetic gain and profitability using a fixed number of 200 full-sib families with family sizes of 50 and 150 individuals, giving rise to a total population size of 10,000 or 30,000 individuals at the breeding station. The proportions selected were varied from 0 to 1 in a matched pattern at both the first and second stages of selection. This type of analysis is of relevance to situations where in practice, it would not be possible to measure a large number of individuals from each of the full-sib families at the first stage, and therefore, it is necessary to keep the initial population size constant.

2.2.1. Profitability of two-stage selection programmes

For a given initial population size, it is expected that in two-stage selection programmes for a given fixed number of parents needed to produce the next generation, maximum gains will be obtained when there is no selection in the first stage. However, this practice may not be economically profitable. To compare benefits and costs of the different two-stage selection schemes, a simple approximation of a linear profit function was constructed. The profit function (P) was defined as the ratio between returns (R) and costs (C) of the breeding programme (Xu and Muir, 1992; Weller, 1994). They were defined as:

$$R = x_D T a \Delta G \quad (5)$$

$$C = C_1 N + \sum_{j=2}^4 C_j N \alpha_j + C_5 N \alpha_{12} \quad (6)$$

The returns are assumed to depend on x_D , the size of the full-sib family. T is the number of tanks available

(number of full-sib families), a is the economic value of a unit in the breeding objective (BW_{IV}) (assumed constant) and ΔG is the genetic change (in genetic standard deviations of the breeding objective). The price per kilogram of fish sold was 4 US dollars. The cost items were rearing and scoring before first stage of selection (C_1), tagging (C_2), costs of rearing (C_3) and measurement (C_4) before the second stage of selection, and costs of rearing, management and feeding after the second stage of selection (C_5). The costs per individual were appropriately weighted by the number of individuals available before the first selection (N), after the first selection ($N\alpha_1$) and after the second selection ($N\alpha_{12}$).

On an individual basis, the operations before the first stage accounted for some 9% of the total costs. These expenses were due to management in the hatchery, feeding and scoring the body at this stage. Between the first and the second stage the costs of tagging (44% of total), and management, feeding and scoring (14%). The costs of rearing after the second stage accounted for 33% of the total costs. These figures were obtained from the actual breeding programme (Otso Järvisalo, pers. comm.).

3. Results

3.1. Genetic gain from two-stage selection

Table 1 presents the effects of initial population size and constraining the number of individuals after the first stage selection to 5000 and 10,000. The magnitude of the genetic gain was investigated without changing the actual number of tagged fish reared after the first growing season until spawning. The gain was on average 10% greater (range from 7% to 14%) compared to the one-stage selection programme with the same number of individuals reared until spawning. For example, consider a two-stage selection programme started by raising 15,000 individuals (75 fingerlings per full-sib family before tagging) and 5000 of them (25 individuals per full-sib family) selected. The predicted genetic gain is equal to 1.70 (SD), which is approximately 10% greater than the one obtained in a one-stage selection programme with an initial population size of 5000 individuals (1.55 (SD)). As expected, the increase in genetic gain was smaller for a population size after first stage selection of 10,000.

On the other hand, we can assess the effect of selection intensity at the first stage by increasing the initial population size and by keeping constant the population size after tagging. When the population size after the

Table 1

Genetic gain for (ΔG_{two}) two-stage selection programmes and its ratio to one-stage selection (ΔG_{one}) (in standard deviation units), and the expected proportion selected at the first $E(\alpha_1)$, and second $E(\alpha_2)$ stages and overall $E(\alpha_{12})$ for varying initial population sizes and two post-stage-one population sizes

	Initial population size				
	10,000	15,000	20,000	25,000	30,000
Population size after first stage of selection=5000					
$E(\alpha_1)$	51.31%	33.43%	25.30%	21.27%	16.78%
$E(\alpha_2)$	2.92%	2.90%	2.85%	2.71%	2.95%
$E(\alpha_{12})$	1.50%	0.97%	0.72%	0.58%	0.49%
ΔG_{two}	1.65	1.70	1.74	1.77	1.77
$\Delta G_{\text{two}}/\Delta G_{\text{one}}$	107%	110%	112%	114%	114%
Population size after first stage of selection=10,000					
$E(\alpha_1)$	99.80%	67.56%	48.36%	39.32%	32.52%
$E(\alpha_2)$	1.44%	1.42%	1.49%	1.48%	1.48%
$E(\alpha_{12})$	1.50%	0.97%	0.72%	0.58%	0.49%
ΔG_{two}	1.72	1.79	1.82	1.85	1.87
$\Delta G_{\text{two}}/\Delta G_{\text{one}}$	100%	104%	106%	108%	109%

first stage is 5000 individuals increasing the initial population size from 10,000 to 30,000 resulted in the response increasing from 1.65 to 1.77, or a 7% increase. When the population size is increased after the first stage of selection to 10,000, the respective increase was about 9%.

3.2. Selection intensity and rate of genetic gain

The relationship between the proportion of individuals selected and genetic gain is presented in Fig. 1 for initial population sizes of 10,000 and 30,000 and a fixed number of individuals needed for producing replacements. As expected, when the intensity of selection decreases (proportion selected increases) at the first stage, selection response reaches values expected under one-stage selection. An interesting result is that the genetic gain did not decrease greatly when a relatively large proportion of the population was selected during the first stage. Note that when culling half of the population in the first stage, the loss in the rates of genetic improvement is less than 5%.

3.3. Profitability of two-stage selection programmes

Returns realized in the profit function were due to genetic changes in the breeding objective (BW_{IV}) and were lower than the costs of implementing the breeding programmes, i.e., profit values were smaller than unity; the income achieved was restricted to the fish in the breeding population. The genetic gain is presented in the same graph to illustrate the optimum selection pressure under the profitability criterion.

The maximum profitability was obtained when the amount of selection was relatively strict in the first stage, and this was quite independent of the population size. For example, considering the initial population size of 30,000 individuals, it appears that the maximum profit is achieved when the selection in both stages is less than 5%. The profit function for a population size of 10,000 reached its maximum when the proportion of selection in the first stage is around 7%.

It appears that the genetic improvement was below maximum at selection pressure giving maximum profit in the scenario considered. The responses were from 66% to 75% of the maximum attainable, when all the individuals are kept after the first stage of selection. This result is due to the fact that it is necessary to keep a greater number of individuals from the first stage onwards; therefore, the expenses are higher due to greater measurements and tagging costs.

4. Discussion

The main objective of the study was to compare selection response and profitability under two-stage selection programmes for growth in rainbow trout. The comparisons were realized utilizing within-family selection for body weight in the first stage and a genetic index incorporating all the information available in the second stage. The potential of two-stage selection in reducing management costs and improving genetic gain has not been widely realized among fish breeders while the present analyses suggest that under practical conditions, it is likely that this type of breeding schemes would yield profitable breeding programmes.

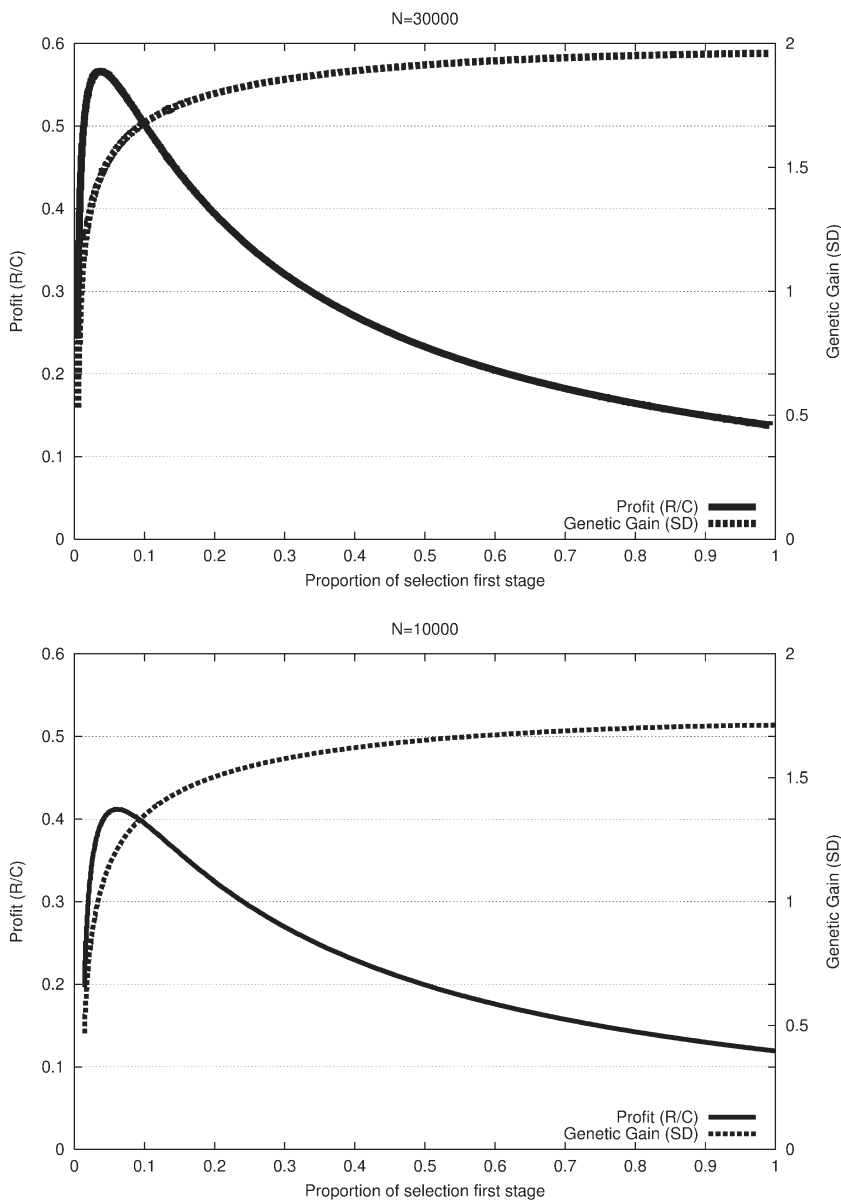


Fig. 1. Profitability of different two-stage selection programmes utilizing within-family selection in the first stage and index selection for the second stage (see text for details), given different sizes of breeding programmes (N =number of individuals scored when initiating the optimization). X axis is the proportion of individuals selected in the first stage, Y axes are the absolute profit and genetic gain (SD), in the primary and secondary, respectively.

The scenarios considered show that maximum profit is not necessarily coupled with maximum genetic improvement. Depending on the objective of the breeding programme, the outcome of the deterministic simulations presented here can be used for making decisions about traits to measure and proportions of individuals kept along the production cycle. However, when the breeding objective is more complex, the breeder would be interested in changes of individual traits, and

therefore, the optimality criteria would be different than the one considered in the present investigation.

Optimum designs were studied using the linear profit equation, which accounts for the most likely costs and returns from a single breeding programme. However, the scope of the breeding programme is likely to have a major impact when tailoring the profit equation. For example, it has been assumed that returns are only due to genetic change in the stock at the breeding station. It

is likely, however, that increases in the breeding objective from breeding programmes will have a major impact on commercial production derived from the breeding programme and costs in relative terms are likely to be of reduced importance. Under these circumstances, the returns need to consider the expected production of fish raised in the whole production system, instead of just the size of the breeding population used for selective breeding.

For example, in Finland, about 5 million of ova (around 20% of the total production) is obtained from the actual breeding programme, and so the total number of marketed fish would be around 3 million, after considering mortalities. This amount would be considered as the total population size benefited from the Finnish breeding programme in a steady state. Incorporating these values to Eq. (5), for a breeding programme with an initial population size of 10,000 individuals shows that as expected, profit is proportional to the increase in genetic gain and selecting more intensively in the first stage renders a less profitable production system (data not shown) since genetic gain decreases. This means that for national breeding programmes selection in stages is less efficient compared to programmes carried out in individual companies. Further research is needed, however, to study the gene flow from the nucleus to the commercial producers in such breeding programmes. Also of importance would be determination of the optimal strategy of schemes that comprise production systems on a national basis and multiple generations of selection, utilizing for example the methodology for obtaining profit functions proposed by Dekkers et al. (1995). The breeding station may, however, utilize the freed resources for other selection operations which benefit the commercial production yet another way.

Potentially the use of selection in two-stages can increase the rates of inbreeding and consequently decrease the rates of response in the long term when not all the information is used for selection decisions. For example, Mehrabani-Yeganeh et al. (1999) used computer simulation to obtain rates of response and inbreeding following multivariate BLUP selection. When information from the culled individuals was not carried forward for the second stage, the rates of inbreeding were significantly higher compared with schemes that use all available information obtained in the first stage. Considering the scheme proposed in the present paper, it is expected that the rates of inbreeding will not be higher than in the schemes that use all available information without selection in the first

stage (Martinez et al., 2006). This is because the selection in the first stage is based solely on the within-family deviations or the Mendelian sampling effects, which contribute little to the increases in the rate of inbreeding (Hill et al., 1996). Furthermore, since the criterion is uniform across families, there will be no variation in family size after selection at the first stage, as is the case for one-stage selection programmes where a fixed number of individuals are tagged per full-sib family.

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Appendix A. Derivation of the correlation between the within-family deviations and the breeding objective

If selection is practiced independently within each family, each can be regarded as a sub-population within which phenotypes $P1_{ij}$ and breeding values are distributed about the true family means ($X1i.$). For the example developed in this paper, the correlation between the within-family deviations for the trait 1 (BW_1) and the breeding value of BW_{IV} (i.e., the objective $A_{BW_{IV}}$) can be derived following the same principles used to derive the correlation between the index of within-family deviations for a trait and the breeding objective (H) (see Hill et al., 1996):

$$\rho_{I_1, H} = \frac{\text{Cov}(I_1, A_{BW_{IV}})}{\sqrt{\sigma_{I_1}^2 \sigma_{A_{BW_{IV}}}^2}} \quad (7)$$

where I_1 is the index value (the within-family deviations for BW_1 , equal to $P1_{ij} - X1i.$), $\sigma_{I_1}^2$ is the variance of this index (which is equal to $(1-t) \sigma_{P_1}^2$, where t is the full-sib intra-class correlation and $\sigma_{P_1}^2$ is the phenotypic standard deviation of BW_1), $\sigma_{A_{BW_{IV}}}^2$ is the variance of the breeding objective (the genetic variance of BW_{IV}). The theoretical covariance between the I_1 and $A_{BW_{IV}}$ is

derived assuming independence between the breeding values and residuals:

$$\begin{aligned} \text{Cov}(I_1, A_{\text{BW}_{\text{IV}}}) &= \text{Cov}(P_{1ij} - X_{1i}, A_{\text{BW}_{\text{IV}}}) \\ &= \sigma_{(A_{\text{BW}_I}, A_{\text{BW}_{\text{IV}}})} - \frac{1}{2} \sigma_{(A_{\text{BW}_I}, A_{\text{BW}_{\text{IV}}})} \\ &= \frac{1}{2} \sigma_{(A_{\text{BW}_I}, A_{\text{BW}_{\text{IV}}})} \end{aligned}$$

where A_{BW_I} is the breeding value of BW_I of an individual (see Hill et al., 1996 for details). In practice, the mean should be estimated from a sample in which case, the covariance should be multiplied by a factor of $1 - \frac{1}{n}$, where n is the number of individuals measured per family to compute the mean. The same holds for the variance of the within-family deviations. However, for most of the cases outlined in the study in which the number of individuals is relatively large for computing the mean (say, more than 25 individuals) this value is very near 1 and therefore Eq. (4) is expected to hold well under these circumstances.

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