# AlphaPart - R implementation of the method for partitioning genetic trends

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# Abstract

1. **Background:** In this paper we present the AlphaPart R package, an open-source software that implements a method for partitioning breeding values and genetic trends to identify sources of genetic gain. Breeding programmes improve populations for a set of traits, which can be measured with a genetic trend calculated from averaged year of birth estimated breeding values of selection candidates. While sources of the overall genetic gain are generally known, their realised contributions are hard to quantify in complex breeding programmes. The aim of this paper is to present the AlphaPart R package and demonstrate it with a simulated stylized multi‑tier breeding programme mimicking pig or poultry breeding programmes.
2. **Results:** The package includes the main partitioning function AlphaPart, that partitions the breeding values and genetic trends by analyst defined paths, and a set of functions for handling data and results. The package is freely available from CRAN repository at <http://CRAN.R-project.org/package=AlphaPart>. We demonstrate the use of the package by examining the sources of genetic gain in a stylized multi‑tier breeding programme. We partitioned the nucleus and multiplier genetic gain by tier‑gender path variable. For traits measured and selected in the multiplier, the multiplier selection generated additional genetic gain compared to closed nucleus. The increase depended on the accuracy and intensity of selection in the multiplier and the extent of gene flow from the nucleus. For traits measured only in the nucleus, the multiplier selection did not generate additional genetic gain.
3. **Conclusions:** AlphaPart implements the method for partitioning breeding values and genetic trends and provides a useful tool for quantifying the sources of genetic gain in breeding programmes. The use of AlphaPart will help breeders to improve genetic gain through a better understanding of the key selection points that are driving gains in each trait.

Keywords: genetic trend, partition, Mendelian sampling term, R package, multi‑tier breeding

# Background

In this paper we present the AlphaPart R package that implements a method for partitioning breeding values and genetic trends. We demonstrate the package with a stylized multi‑tier breeding example usually applied in pig and poultry breeding. Breeding programmes improve populations for a set of traits by selecting and mating genetically superior individuals. Population improvement can be measured with a genetic trend calculated by averaging estimated breeding values of selection candidates by year of birth [1,2].

While sources of the overall genetic gain are generally known, their realised contributions are hard to quantify in complex breeding programmes. García-Cortés *et al.* [3] proposed a method for such analysis. In summary, the method uses pedigree to first partition the breeding values into parent average and Mendelian sampling term: *ai = ½as +* *½ad + wi* [4], where *ai, as,* and *ad* are individual’s, sire’s, and dam’s breeding values, and *wi* is individual’s Mendelian sampling term. The method next allocates Mendelian sampling terms to different “paths”. For example, assume a small trio pedigree with two parents and a female progeny. Specifying gender as the path variable, we can write *ai = ½as +* *½ad + wi = (½ad + wi) + ½as  = ai,f + aim*, where the first term *ai,f* denotes the female partition and the second term *ai,m* denotes the male partition. Alternatively, assume that the sire is imported, then an interesting path specification is that of domestic versus imported, which in the example gives the same partitioning as for gender. The partitioning by origin allows for quantifying impact of import versus domestic selection. In general, we can write a vector of breeding values as a linear combination of Mendelian sampling terms of individuals and their ancestors **a** = **Tw**, where **T** is a triangular matrix of expected gene flow between ancestors and individuals [4,5]. The method of García-Cortés *et al.* [3] uses a path variable to partition the gene flow matrix into path specific gene flow matrices **T** = **T**1 + **T**2 + … + **T**p and with this partitions breeding values by paths **a** = (**T**1 + **T**2 + … + **T**p)**w** = **a**1 + **a**2 + … + **a**p. Summarising these partitions marginally or conditionally on other variables (such as year of birth) is a powerful way to analyse sources of genetic gain.

The partitioning method has been used in a number of cases. Gorjanc *et al.* [6] and Gorjanc *et al.* [7] estimated contributions of national breeding programmes to Brows-Swiss and Holstein country-specific and global genetic trends. Špehar *et al.* [8] estimated contributions of national selection and importation in Croatian Simmental cattle. Škorput *et al.* [9] estimated the contribution of national selection and importation in two pig breeds in Croatia, and extended the analysis with the quantification of uncertainty [2]. However, these studies used bespoke implementations of the partitioning method, for which no open-source software exists.

The aim of this paper is to: i) present the AlphaPart R package; and ii) demonstrate it with a simulated stylized multi‑tier breeding example that quantifies nucleus-multiplier gene flow and the contribution of nucleus and multiplier selection on genetic gain in the two tiers.

# Implementation

1. We first demonstrate the AlphaPart package and its functions on an example dataset. Next, we describe the simulation of a stylized multi‑tier breeding example to demonstrate the use of AlphaPart.

## AlphaPart

AlphaPart is an R package available from CRAN repository at <https://CRAN.R-project.org/package=AlphaPart>. It consists of the main function AlphaPart() for partitioning breeding values and auxiliary functions for manipulating data and summarizing, visualizing, and saving results. We install and load the package with:

> install.packages(pkg = “AlphaPart”)  
> library(package = "AlphaPart")

The package includes an example dataset AlphaPart.ped. The dataset includes a four‑generation pedigree (individual IId, father FId, and mother MId) and information about the generation (gen), country, gender, and breeding values for trait 1 (bv1) and trait 2 (bv2).

> head(AlphaPart.ped, n = 3)

|IId |FId |MId | gen|country |gender | bv1| bv2|

|:---|:---|:---|---:|:--------|:------|---:|---:|

|A | | | 1|domestic |F | 100| 88|

|B | | | 1|import |M | 105| 110|

|C |B |A | 2|domestic |F | 104| 100|

Here we describe and demonstrate the functions with the AlphaPart.ped dataset. We use the AlphaPart() function to partition breeding values for trait 1 (bv1) by the country variable into domestic and import contributions:

> data(AlphaPart.ped)  
> part <- AlphaPart(x = AlphaPart.ped,  
 colPath = “country”,  
 colBV = “bv1”)

The partitioning function AlphaPart() requires a data frame holding pedigree with animal/sire/dam or animal/sire/maternal-grandsire, a time-ordering variable such as year of birth, partition variable (path), and breeding values. Following the method described in García-Cortés *et al.* [3], the function recurses the pedigree from the oldest to the youngest individual, for each individual calculate parent average and Mendelian sampling terms for any number of traits and assign terms to paths (i.e. groups generating Mendelian sampling term). We partition multiple traits by specifying a vector of variables, say colBV = c(“bv1”, “bv2”). The multiple trait option can also serve to partition samples from a posterior distribution of breeding values to quantify uncertainty [2, 9]. To speed-up calculations we use C++ and trait-vectorised partitioning. The function can also simultaneously partition and summarize path contributions by a grouping variable, which is a useful computational speed-up for huge pedigrees. Alternatively, we subsequently use summary() function to summarize the partitions.

The output of the AlphaPart() function is an object of either AlphaPart or summaryAlphaPart class. The AlphaPart class is a list with an info element and an element for each of the partitioned traits. The info element is a list with information on the path variable (path), number of paths (nP), names of paths (lP), number of traits (nT), names of traits (lT), and putative warnings (warn). The trait element bv1 is a table (shown below). It includes the information from the original dataset as well parent average (bv1\_pa), Mendelian sampling term (bv1\_w), and breeding value partitions (bv1\_domestic and bv1\_import).

> head(part$bv1, n = 3)

|IId |FId |MId | gen|country |gender | bv2| bv1| bv1\_pa| bv1\_w| bv1\_domestic| bv1\_import|

|:---|:---|:---|---:|:--------|:------|---:|---:|------:|-----:|------------:|----------:|

|A | | | 1|domestic |F | 88| 100| 0.0| 100.0| 100.0| 0.0|

|B | | | 1|import |M | 110| 105| 0.0| 105.0| 0.0| 105.0|

|C |B |A | 2|domestic |F | 100| 104| 102.5| 1.5| 51.5| 52.5|

We use the generic summary.AlphaPart() function to summarize an AlphaPart object by a grouping variable, say generation (gen):

> sumPartByGen <- summary(part, by = “gen”)

The summary.AlphaPart() function summarizes breeding values and their path partitions by levels of a grouping variable. By default, we summarize with a mean, but the user can specify any R function via the FUN argument. The function can also summarize only a subset of the object via the subset argument.

The output of the summary.AlphaPart() function is an object of summaryAlphaPart class, which is a list with an info element and an element of summary for each of the partitioned traits. The summary contains the grouping variable levels (gen), number of individuals per level (N), and output of the summary function applied to the breeding values and its partitions (Sum, domestic, and import).

> print(sumPartByGen)

| gen| N| Sum| domestic| import|

|---:|--:|--------:|--------:|------:|

| 1| 2| 102.5000| 50.00000| 52.500|

| 2| 3| 104.6667| 17.16667| 87.500|

| 3| 2| 107.0000| 13.37500| 93.625|

| 4| 1| 109.0000| 68.87500| 40.125|

We use the generic plot.summaryAlphaPart function to plot summarized partitions:

> plot(sumPartByGen)

The output is an object of plotSummaryAlphaPart class. It is a list containing one plot for each partitioned trait. We show the output plot in Figure 1.

We also provide a number of utility functions that ease partitioning analysis. The pedFixBirthYear() function imputes missing or fix erroneous years of birth. The pedSetBase() function sets the base population by specifying founders and removing older pedigree records. The AlphaPartSubset() function keeps partitions for specified paths in the AlphaPart or summaryAlphaPart objects. The AlphaPartSum() function sums the partitions of several paths in a summaryAlphaPart object. The AlphaPartSubset() and AlphaPartSum() functions simplify the presentation of partitioning analysis.

## Stylized multi‑tier breeding example

We applied the AlphaPart R package on a simulated stylized multi‑tier breeding example, that mimics a pig breeding programme. We aimed to examine the directional gene flow between nucleus and multiplier and the contribution of nucleus and multiplier selection on genetic gain in each tier. Breeders select in the nucleus and multiply this improvement in the multiplier to supply a large number of breeding animals for commercial purposes. The multiplier generally has lower genetic mean than the nucleus due to time-lag. However, animals with very high breeding values are often observed in the multiplier for some traits and we aimed to use AlphaPart to explain the source of this observation. To this end we have first simulated a stylized multi‑tier breeding programme that exposes the drivers of real observations. We have next partitioned the genetic trend of true breeding values by a tier-gender variable to quantify sources of genetic gain in the nucleus and the multiplier.

We used the AlphaSimR package [10] to simulate the stylized multi‑tier breeding programme for a single breed with closed nucleus and directional flow of animals from the nucleus into the multiplier (Figure 2). We simulated 40 generations of selection on two uncorrelated traits. Trait 1 had heritability 0.25 and trait 2 had heritability 0.10. We measured both traits in the nucleus and only trait 1 in the multiplier. We selected on the index of the two traits with equal emphasis. We split the simulation into initial 20 generations of a burn‑in and 20 generations of evaluation.

In the burn-in we simulated only the nucleus and selected animals based on the index of phenotype values for both traits. We selected 25 males and 500 females each generation and randomly crossed them to produce a new generation of 6,000 progeny (12 per cross). At the end of the burn-in we generated 5,000 females to seed the multiplier.

In the evaluation we simulated both the nucleus and the multiplier and selected animals within each tier based on the index of estimated breeding values for both traits (Figure 2). In the nucleus, we selected 25 nucleus males and 500 nucleus females each generation and randomly crossed them to produce a new generation of 6,000 progeny (12 per cross). In the multiplier, we selected 750 multiplier females each generation and randomly crossed them to a set of males to produce a new generation of 9,000 progeny (12 per cross). To quantify the effect of selection in the multiplier on genetic gain we defined the set of males as either 1) the 25 best nucleus males (MaleFlow100 scenario – 100% of males are from the nucleus) or 2) the 25 best nucleus males and 100 best multiplier males (MaleFlow20 scenario – 20% of males are from the nucleus).

We estimated the breeding values for each trait independently before each nucleus or multiplier selection decision. We ran a pedigree‑based model implemented in blupf90 [11] and used all available data from evaluation generations. The model included the mean as a fixed effect and animal breeding values as a random effect modelled hierarchically with pedigree.

Finally, we partitioned the true breeding values and genetic trends with the AlphaPart as demonstrated above. We used AlphaPart() function to partition standardized true breeding values from the 20 evaluation generations by the tier‑gender variable and summary.AlphaPart() function to summarize the partitions by generations to quantify the contribution of each tier-gender level to genetic trend in the nucleus and the multiplier.

We repeated the simulation 10 times and measured the genetic trend separately in the nucleus and multiplier. We present standardized true breeding values and genetic trends, as well as their partitions with mean set to zero and genetic standard deviation set to one in generation 20. We chose to present true (instead of estimated) breeding values to assess the true sources of genetic gain. The simulation code for the datasets generated and/or analysed during the current study are available in the GitLab repository, <https://git.ecdf.ed.ac.uk/HighlanderLab_public/jobsteter_alphapart>.

# Results

The results show partitions of true breeding values and genetic trends in the nucleus and multiplier obtained with the AlphaPart for the two simulated stylized multi‑tier breeding scenarios. Partitioning showed that we can explain the situation with very high breeding values in the multiplier by the extent of nucleus-multiplier gene flow as well as accuracy and intensity of multiplier selection. For each scenario we first describe the distribution of true breeding values in the nucleus and multiplier in generation 40 of one replicate. Next we explain the sources of the observations by partitioning the nucleus and multiplier genetic trend and averaging the results across ten replicates. Additional files 1 and 2 show distributions of partitioned true breeding values for one replicate.

## MaleFlow100 scenario

### Distribution of breeding values

In MaleFlow100 scenario the multiplier had a higher genetic merit on average than the nucleus for trait 1 and trait 2. We show this in Figure 3 with the distribution of true breeding values in the nucleus and the multiplier by trait in generation 40 of one replicate. The multiplier had a higher genetic merit on average and hence produced animals with a higher breeding value than the nucleus for both traits, which reflected in a higher index value as well.

## *Partitioning the true breeding values and genetic trend*

The partitioning showed that the higher genetic gain in the multiplier compared to the nucleus for trait 1 was due to additional contribution from selection of multiplier females. We show this in Figure 4 with the genetic trends in the nucleus and multiplier by trait and their partitions summarised over 10 replicates. As expected, the nucleus genetic gain stemmed completely from selection of nucleus males and nucleus females. The selection of nucleus males contributed more to the genetic gain than the selection of nucleus females. The mean genetic gain in generation 40 in the nucleus for trait 1 was 9.75 and 8.34 for trait 2, with male selection contributing 5.65 for trait 1 and 4.92 for trait 2, and female selection contributing 4.10 for trait 1 and 3.42 for trait 2.

In the multiplier, the average genetic gain for trait 1 was higher than in the nucleus. This increase was driven by two sources. First, nucleus males made a larger contribution to the multiplier than to nucleus genetic gain, since they contributed directly by fathering the multiplier animals and indirectly through subsequent selection of their genes in future generations. Second, multiplier female selection made a non-zero contribution. The mean genetic gain in generation 40 in the multiplier for trait 1 was 10.00 with nucleus males contributing 5.75, nucleus females 4.09, and multiplier females 0.14. The mean genetic gain and path partitions in generation 40 for trait 2 in the multiplier were comparable to the nucleus. Additional files 1 shows distributions of partitioned true breeding values for one replicate.

## MaleFlow20 scenario

### Distribution of breeding values

In MaleFlow20 scenario the multiplier had a higher genetic merit than the nucleus for trait 1, but lower for trait 2. We show this in Figure 3 with the distribution of true breeding values and their partitions in nucleus and multiplier by trait in generation 40 of one replicate. We again observed animals with higher breeding values for trait 1 in the multiplier than in the nucleus, with an even larger difference than in MaleFlow100 scenario. We did not observe the same phenomena for trait 2.

### Partitioning the true breeding values and genetic trend

The partitioning revealed, that selection of multiplier males and females further increased the genetic gain for trait 1 in the multiplier compared to the nucleus, but decreased the genetic gain for trait 2. We show this in Figure 5 with the genetic trends in the nucleus and multiplier by trait and their partitions summarised over 10 replicates. As in MaleFlow100 scenario, the nucleus genetic gain stemmed from selection of nucleus males and females. The mean genetic gain in generation 40 for trait 1 was 10.09 and 8.39 for trait 2, with nucleus males contributing 5.69 for trait 1 and 5.17 for trait 2, and nucleus females contributing 4.40 for trait 1 and 3.22 for trait 2.

In the multiplier the genetic gain was again higher than in the nucleus, but only for trait 1. This higher genetic gain was a result of non‑zero contribution of multiplier female and male selection and reduced contribution of nucleus females. In MaleFlow20 we reduced the use of nucleus males in the multiplier, which reduced the contribution of nucleus females via reduced nucleus-multiplier gene flow. For trait 2, the genetic gain in the multiplier was lower than in the nucleus due to a small average negative contribution of multiplier females and multiplier males and reduced contribution of nucleus females and nucleus males via reduced gene flow. The mean genetic gain in generation 40 in the multiplier was 10.36 for trait 1 and 8.14 for trait 2, with nucleus males contributing 5.70 for trait 1 and 5.09 for trait 2, nucleus females contributing 4.21 for trait 1 and 3.13 for trait 2, multiplier males contributing 0.15 for trait 1 and -0.03 for trait 2, and multiplier females contributing 0.30 for trait 1 and -0.05 for trait 2. Additional file 2 shows distributions of partitioned true breeding values for one replicate.

# Discussion

In this paper we present AlphaPart, a freely available R package that implements the method for partitioning breeding values and genetic trends. We demonstrate the package on a simulated stylized multi‑tier breeding example with a higher genetic trend for some traits in the multiplier compared to the nucleus. Following this, we organized the discussion into two parts: i) advantages and disadvantages of the AlphaPart R package; ii) partitioning results of the breeding example.

## AlphaPart

AlphaPart is a free implementation of the method for partitioning breeding values and genetic trends. The method and the package are valuable for deciphering and quantifying the sources of genetic gain in breeding programmes. The package is easy to use, since it streamlines the partitioning analysis into a few lines of R code. AlphaPart presents a holistic tool to perform a partitioning analysis, from preparing the input data - such as manipulating the pedigree data - to handling of results and plotting. The partitioning step is fast, even for large pedigrees, since the main partitioning function is recursive and implemented in C++.

AlphaPart is aimed at researchers who are interested in quantifying the sources of genetic gain in their breeding programmes either to understand the dynamics of genetic gain, improve efficiency, asses the performance of different breeding actions, optimize investments etc. Users should take into account, that the accuracy of partitioning depends on the accuracy of the estimated breeding values and their Mendelian sampling terms, which are driven by the biology of the trait, breeding programme structure, and choice of the prediction model.

Our future work on AlphaPart will include extending the partitioning method in three areas. The first extension will utilise genomic information to inform which genome regions drive genetic change and what are sources of specific haplotypes or alleles. The second extension will use the partitioning method to analyse changes in genetic variance in addition to the genetic mean. The third extension will simplify handling of uncertainty of path contributions when working with samples from posterior distributions [2, 9].

## Stylized multi‑tier breeding example

The multi‑tier breeding example showed the investigative power of the partitioning method and the free AlphaPart implementation. Here we discuss the sources of genetic gain in the two tiers of a breeding programme.

By partitioning the genetic trend in a simulated multi‑tier breeding programme, we disentangled the observation of some multiplier animals having higher breeding values for some traits compared to the nucleus animals. While larger numbers of recombinations in the multiplier can potentially reveal more variation and occasional outlying animals, we expect lower breeding values in the multiplier due to time-lag between the nucleus and multiplier. The partitioning revealed that the gene flow from the nucleus into the multiplier was the main source of genetic gain in the multiplier, with the nucleus males contributing the most. This was expected due to nucleus-multiplier gene flow and higher intensity of selection in males.

However, the results also showed that selection in the multiplier can contribute genetic gain in addition to the gene flow from the nucleus. The multiplier outperformed the nucleus for trait 1, because with the 10,500 recorded multiplier animals there was substantial amount of information for accurate multiplier selection that generated additional genetic gain. We emphasise that this result is also down to a limited time-lag between the nucleus and multiplier as we used the nucleus males in nucleus and multiplier concurrently assuming artificial insemination. The partitioning of genetic trend for trait 1 showed that when we used only the nucleus males in the multiplier (MaleFlow100), the multiplier generated additional gain from two sources. First, compared to the nucleus, the contribution of the nucleus males increased because they contributed through the gene flow and through the selection of multiplier females. Second, the selection of multiplier females contributed as well. When we used both the nucleus males and the multiplier males in the multiplier (MaleFlow20), the multiplier generated further gain through a combination of the sources. First was the contribution of the selection of multiplier females and males. In contrast, the contribution of nucleus selection decreased due to the reduced gene flow. This decrease was due to a smaller number of progeny per nucleus male compared to the MaleFlow100 scenario. In both scenarios we observed a trend of decreasing contribution of multiplier selection over generations, though the average multiplier contribution was always above zero. Since we partitioned breeding values with generation 20 as a base generation, the parent average and Mendelian sampling terms for multiplier animals in the generation 20 were assigned to the multiplier path. Over the generations the nucleus and multiplier contributions converged since the used pedigree in next generations accounted for the origin of the nucleus males. This shows the importance of proper base population specification (including unknown parent groups) for meaningful partitioning. This long-term dynamic of contributions is related to the dynamic of “long-term genetic contributions” in the context of genetic gain and inbreeding [12, 13], but note that the “long-term genetic contributions” are trait agnostic (depend only on the pedigree). On a related note, with the implemented method in AlphaPart we can evaluate (long-term) genetic contributions by setting breeding values to the value one for all animals and partitioning the breeding values by analyst defined paths [6].

On the contrary, trait 2 was not measured in the multiplier and had comparable or smaller genetic trend in the multiplier than in the nucleus. For trait 2 the multiplier animals were selected only on estimated parent average, which resulted in low accuracy selection. In the MaleFlow100 scenario this low accuracy selection resulted in a null contribution of multiplier females to the genetic trend for trait 2 and comparable genetic trends between the nucleus and the multiplier. In the MaleFlow20 scenario with a reduced nucleus-multiplier gene flow this low accuracy selection resulted in the reduced genetic gain for trait 2.

# Conclusion

AlphaPart R package is a freely available software for partitioning breeding values and genetic trends. Use of AlphaPart will help breeders to better understand sources of genetic gain and improve their breeding programmes.

**Declarations**

## Ethics approval and consent to participate

Not applicable

## Consent for publication

Not applicable

## Availability of data and materials

Project name: AlphaPartProject home page: https://cran.r-project.org/package=AlphaPartOperating system(s): Windows, MacOS, LinuxProgramming language: R & C++License:**GPL-2 | GPL-3**Any restrictions to use by non-academics:**-**

## Competing interests

Not applicable

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## Authors’ contributions

Not applicable

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Not applicable

## Author’s information (optional)

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# Figures

Figure 1 The output of the plot.summaryAlphaPart() function.

The plot shows the overall genetic trend and its partition into the contributions of domestic selection and import by generation.

Figure 2 Design of the simulated stylized multi-tier breeding programmes.

We simulated two scenarios with a closed nucleus and a directional flow of animals from the nucleus into the multiplier. The scenarios differ in the percentage of multiplier males imported from the nucleus.

Figure 3 Distribution of true breeding values and their partitions by trait and tier in MaleFlow100 scenario.

We show scaled densities of partitions in generation 40 of one simulation replicate. MaleFlow100 uses only nucleus males in the multiplier. Trait 1 is measured in the nucleus and the multiplier, while trait 2 is measured only in the nucleus. Black vertical lines represent the nucleus mean breeding value for a trait.

* 1. Figure 4 Partitioning of genetic trend by tier-gender in MaleFlow100 scenario.

## The scenario uses nucleus males in the multiplier. Trait 1 is measured in the nucleus and the multiplier, while trait 2 is measured only in the nucleus.

Figure 5 Partitioning of the genetic trend by tier-gender in MaleFlow20 scenario.

The scenario uses nucleus and multiplier males in the multiplier. Trait 1 is measured in the nucleus and the multiplier, while trait 2 is measured only in the nucleus.

# Additional files

**Additional file 1 Figure S1** (file: Additional\_File\_1.docx)

Format: Figure in a .docx document

Title: Distribution of true breeding values and their partitions by trait, year, and tier in MaleFlow100 scenario.

Description: We show scaled densities of partitions in years 23 and 40 of one simulation replicate. MalerFlow100 uses only nucleus males in the multiplier. Trait 1 is measured in the nucleus and the multiplier, while trait 2 is measured only in the nucleus. Black vertical lines represent the nucleus mean breeding value for a trait in a year.

**Additional file 2 Figure S2** (file: Additional\_File\_2.docx)

Format: Figure in a .docx document

Title: Distribution of true breeding values and their partitions by trait, year, and tier in MaleFlow20 scenario.

Description: We show scaled densities of partitions in years 23 and 40 of one simulation replicate. MalerFlow20 uses nucleus and multiplier males in the multiplier. Trait 1 is measured in the nucleus and the multiplier, while trait 2 is measured only in the nucleus. Black vertical lines represent the nucleus mean breeding value for a trait in a year.