# 1 AlphaPart - R implementation of the method for

# 2 partitioning genetic trends

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### Abstract

**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 pig breeding examplestylized multi-tier breeding example, usually applied in poultry and pig breeding.

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 <a href="http://CRAN.R-project.org/package=AlphaPart">http://CRAN.R-project.org/package=AlphaPart</a>. We demonstrate the use of the package by examining the genetic gain in a <a href="pigstylized multi-tier">pigstylized multi-tier</a> breeding <a href="exampleprogramme">exampleprogramme</a>, in which the multiplier achieved higher breeding values than the nucleus for traits measured and selected in the multiplier. The partitioning analysis revealed that these higher values 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 achieved comparable or smaller genetic gain than the nucleus depending on the amount of gene flow.

**Conclusions:** AlphaPart implements a method for partitioning breeding values and genetic 42 trends and provides a useful tool for quantifying the sources of genetic gain in breeding

- 43 programmes. The use of AlphaPart will help breeders to better understand or improve their
- 44 breeding programmes.
- 45 **Keywords:** genetic trend, partition, Mendelian sampling term, R package, pigmulti-tier
- 46 breeding

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## Background

- 49 In this paper we present the AlphaPart R package that implements a method for partitioning
- 50 breeding values and genetic trends,. We and demonstrate the packageit with a pigstylized
- 51 <u>multi-tier</u> breeding example <u>usually applied in poultry and pig breeding</u>. Breeding
- 52 programmes improve populations for a set of traits by selecting and intermating genetically
- 53 superior individuals. Population improvement can be measured with a genetic trend calculated
- 54 from averaged year of birth estimated breeding values of selection candidates [1,2].

### 55 **Partitioning method**

- While sources of the overall genetic gain are generally known, their realised contributions are
- 57 hard to quantify in complex breeding programmes. García-Cortés et al. [3] proposed a method
- 58 for such analysis. For completeness of the manuscript we briefly summarize the method
- 59 below. First, the method partitions breeding values into parent average and Mendelian
- 60 sampling terms [4], and allocates the terms to analyst-defined "paths" (males, females, tested
- 61 sires, etc.). Next, it summarizes path specific terms to quantify path contributions to the
- 62 overall genetic trend.

The infinitesimal model assumes that the breeding values follow a normal distribution with mean zero and variance  $A\sigma_{a}^2$ , where A is the pedigree relationship matrix and  $\sigma_{a}^2$  is the genetic variance for the trait in the founder population. We can partition non-founders' breeding value a into parent average  $(0.5a_{sire} + 0.5a_{dam})$  and Mendelian sampling term (w) [4], which arises from independent segregation and recombination of parental chromosomes. For founders we have no parental information, hence we assign their breeding value completely to Mendelian sampling term.

We can decompose the variance of the breeding values to  $\mathbf{A}\sigma_a^2 = \mathbf{TDT'}\sigma_a^2$ , where  $\mathbf{T}$  is a triangular matrix relating individuals to their ancestors (it holds information on gene transmission), and  $\mathbf{D}\sigma_a^2$  includes the variance of the breeding values of the founders and variance of the Mendelian sampling terms of the non-founders. Following this, we can express additive genetic values  $\mathbf{a} = \mathbf{T}\mathbf{w}$ , where  $\mathbf{w}$  follows a normal distribution with mean zero and variance  $\mathbf{D}\sigma_a^2$ . Hence, we can further partition an individual's breeding value into the contribution of founders breeding values and non-founders' Mendelian sampling terms (including the individual itself) as

$$a_i = \sum_{j=1}^i T_{ij} w \quad [Woolliams et al., 1999].$$

We can then specify different groups generating the Mendelian sampling term and assign individuals to the groups (called "path" in the Implementation). If we summarise the group-specific contributions, we can partition the breeding values into  $\mathbf{a} = \mathbf{a}_1 + \mathbf{a}_2 + \ldots + \mathbf{a}_m$ , where 1 to m are different groups, and quantify group contributions to the overall genetic trend.

The partitioning method has been used in a number of cases. Gorjanc *et al.* [5] and Gorjanc *et al.* [6] estimated contributions of national breeding programmes to Brows-Swiss and Holstein country-specific and global genetic trends. Špehar *et al.* [7] estimated contributions of national selection and importation in Croatian Simmental cattle. Škorput *et al.* [8] 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 manual dedicated software—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 <u>pigstylized multi-tier</u> breeding example that quantifies nucleus-multiplier gene flow and the contribution of nucleus and multiplier selection on genetic gain in the two tiers.

## 95 Implementation

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

### AlphaPart

AlphaPart R **CRAN** is package available from repository an 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. The package includes an example dataset AlphaPart.ped, which includes a four-generation pedigree and information about 105 the generation, country, gender, and breeding values. Below we describe and demonstrate the 106 functions with the dataset.

107 We install and load the package with:

```
108
    > install.packages(pkg = "AlphaPart")
109
    > library(package = "AlphaPart")
```

The package includes an example dataset AlphaPart.ped. We show the first few lines below. , which 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). Below we describe and demonstrate the functions 114 with the dataset.

```
IId FId MId gen country gender bv1 bv2
A
             1 domestic F
                             100 88
В
             1 import M
                             105 110
C B A
             2 domestic F
                             104 100
```

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Here we describe and demonstrate the functions with the AlphaPart.ped dataset. We use 117 the AlphaPart () function to partition breeding values (bv1) in the AlphaPart.ped by 118 the country variable into domestic and import contributions:

```
119
     > data(AlphaPart.ped)
120
     > part <- AlphaPart(x = AlphaPart.ped,</pre>
121
                            colPath = "country",
122
                            colBV = "bv1")
```

The output part is an AlphaPart object, which 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 path levels (nP), names of path levels (lP), number of traits (nT), names of traits (lT), and putative warnings (warn). The trait element (shown below) bv1 is a table. It includes the input information, the breeding value for the trait (bv1), the parent average (bv1\_pa), the Mendelian sampling term (bv1\_w), and the contributions of each level of the path variable to the breeding value (bv1\_domestic, bv1\_import).

### 130 | > part\$bv1

	IId	FId	MId	gen	country	gender	<u>bv1</u>	bv1_pa	bv1_w	bv1_domestic	bv1_import
	<u>A</u>			<u>1</u>	domestic	<u>F</u>	100	<u>0</u>	<u>100</u>	<u>100</u>	<u>0</u>
	<u>B</u>			<u>1</u>	<u>import</u>	<u>M</u>	105	<u>0</u>	<u>105</u>	<u>0</u>	<u>105</u>
	<u>C</u>	<u>B</u>	<u>A</u>	<u>2</u>	<u>domestic</u>	<u>F</u>	104	102.5	<u>1.5</u>	<u>51.5</u>	<u>52.5</u>
1	T	<u>B</u>		<u>2</u>	import	<u>F</u>	102	<u>52.5</u>	49.5	<u>0</u>	102

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], wethe 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. 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, 8]. To speed-up calculations we use C++ and trait-vectorised partitioning. The function can

- also directly simultaneously partition and summarize path contributions by a grouping 141 142 variable "on-the-fly", which is a useful computational speed-up for huge pedigrees. Alternatively, we subsequently use summary () function to summarize the partitions. The 143 144 object of the AlphaPart() function is either output AlphaPart or 145 summaryAlphaPart class.
- We use the generic summary.AlphaPart() function to summarize an AlphaPart object by a grouping variable, say generation (gen):\_
- 148 | > sumPartByGen <- summary(part, by = "gen")
  - The output is an summaryAlphaPart object. It is a list with an info element and (as in AlphaPart object) and a bv1 element showed below, that we can display with print() function. The N columns shows the number of individuals in each generation. We used the default mean function to summarize the data, so Sum columns shown the mean of the breeding values of individuals in each generation. The columns domestic and import show the mean contribution of domestic selection and import.
- 155 > print(sumPartByGen)

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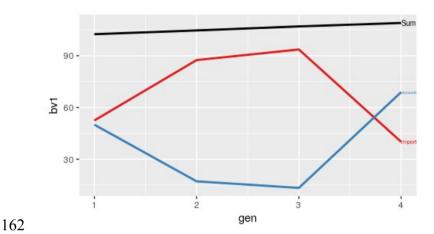
	gen	N	Sum	domestic	import
	<u>1</u>	<u>2</u>	102.5	<u>50</u>	<u>52.5</u>
	2	<u> </u>	104.6667	17.16667	<u>87.5</u>
	<u>3</u>	2	107	13.375	93.625
	<u>4</u>	1	109	68.875	40.125

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

function via the FUN argument. The summary () function can also summarize only a subset of the object via the subset argument.

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

161 > plot(sumPartByGen)



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

<u>Function</u>	Description
<pre>pedFixBirthYear()</pre>	Imputes missing of fixes erroneous years of birth.
pedSetBase()	Sets the base population by specifying founders and

	removing older pedigree records.
AlphaPartSubset()	keeps partitions for specified paths in the AlphaPart or
	summaryAlphaPart objects.
AlphaPartSum()	Sums the partitions of several paths in a
	summaryAlphaPart object.

### Stylized multi-tier breeding Pig breeding example

We applied the AlphaPart R package onto a simulated pigstylized multi-tier breeding example, usually applied in poultry and pig breeding. To We aimed to examine the nucleus-multiplier gene flow and the contribution of nucleus and multiplier selection on genetic gain in bothcach tiers. BPig breeders select in the nucleus and multiply this improvement in the multiplier to supply a large number of commercial animals. 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 stylised pigmulti-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 [9] to simulate a pigmulti-tier breeding programme for a single breed with 40 years 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 years of a burn-in and 20 years 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 year 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 based on the index of estimated breeding values for both traits. In the nucleus, we selected 25 males and 500 females each year and randomly crossed them to produce a new generation of 6,000 progeny (12 per cross). In the multiplier, we selected 750 females each year 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) or 2) the 25 best nucleus males and 100 best multiplier males (MaleFlow20 scenario).

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 [10] and used all available data from evaluation years. 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 years by the tier-gender variable and summary.AlphaPart() function to summarize the partitions by year to quantify the contribution of each tier-gender level to genetic trend in the nucleus and the multiplier.

```
20 111670 107396 106535 GN-M
                                                   <u>-0.17</u>
                                                           0.08 -0.04
             20 111671 107396 106535 GN-F
                                                   <u>-0.55</u>
                                                           0.05 -0.25
             20 111672 107396 106535 GN-M
                                                   -0.31
                                                           -0.17 -0.24
             20 111673 107396 106535 GN-F
                                                    0.70
                                                           -0.68
                                                                  0.01
211
212
     # Partition the standardized breeding value for trait 1, trait 2 and index
213
     Part1g <- AlphaPart(x = as.data.frame(PedEval1), sort = FALSE,</pre>
214
                            colId = "IId", colFid = "FId", colMid = "Mid",
215
         colPath = "TierGender",
216
          colBV = c("TbvT1 s", "TbvT2 s", "TbvI s"))
```

We repeated the simulation 10 times. 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 the year 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

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The results show partitions of true breeding values and genetic trends obtained with the AlphaPart for the two simulated pigstylized 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.

#### Partitioning the true breeding values and genetic trend of MaleFlow100 scenario

In MaleFlow100 scenario the multiplier achieved a higher final genetic gain than the nucleus for trait 1 due to selection of multiplier females. We show this in Figure 1 that presents the distribution of true breeding values and their partitions by trait and tier for two years of one replicate of MaleFlow100 scenario, and in Figure 2 that presents the genetic trends and their partitions summarised over 10 replicates. As expected, The partitioning expectedly showed that in the nucleus the genetic gain stemmed from selection of nucleus males and nucleus females. However, the contribution of male and female selection changed over the years. While in year 23 the contributions of male and female selection were more comparable, by year 40 male selection contributed more. The mean final genetic gain 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 genetic gain was higher than in the nucleus. In year 23 the multiplier had higher genetic gain than the nucleus for both traits, while in year 40 it had higher genetic gain only for trait 1. The higher genetic gain was partly due to larger contribution of nucleus males in multiplier than in nucleus (via gene flow) and partly due to non-zero contribution of multiplier female selection. The mean final genetic gain 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 final genetic gain and path partitions for trait 2 in the multiplier were comparable to the nucleus.

### Partitioning the true breeding values and genetic trend of MaleFlow20 scenario

In the MaleFlow20 scenario selection of multiplier males further increased the final genetic gain for trait 1 in the multiplier compared to the nucleus, but decreased the final genetic gain for trait 2. We show this in Figure 3 that presents the distribution of true breeding values and

their partitions by trait and tier for two year of one replicate of MaleFlow20 scenario, and Figure 4 that presents the genetic trends and their partitions summarised over 10 replicates. As in MaleFlow100 scenario, the nucleus genetic gain stemmed from selection of nucleus males and females. Progressing from year 23 to year 40, the contribution of nucleus males increased compared to nucleus females, but only for trait 1. The mean final genetic gain 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 consistent throughout the generations and was a result of selection of multiplier females and multiplier males, and reduced contribution of gene flow from the nucleus females (via reduced use of nucleus males). For trait 2, the multiplier performed progressively worse relative to the nucleus over the years. In year 40, 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 gene flow from the nucleus females and nucleus males. The mean final genetic gain 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.

## **Discussion**

In this paper we present AlphaPart, freely available R package that implements the method for partitioning breeding values and genetic trends. We demonstrate the package on a simulated pigstylized 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 pig breeding example.

#### **AlphaPart**

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AlphaPart is the first 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 the 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. Such users should take into account the accuracy of the estimated breeding values and their Mendelian sampling terms, which are driven by the biology of the trait and breeding programme structure. 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, 8].

### Stylized multi-tier Pig breeding breeding example

The <u>pig-multi-tier</u> 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 <u>pig-breeding programme</u>.

By partitioning the genetic trend in a simulated pigmulti-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 number 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. 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

323 reduced gene flow. This decrease was due to a smaller number of progeny per nucleus male 324 compared to the MaleFlow100 scenario. 325 On the contrary, trait 2 was not measured in the multiplier and had comparable or smaller 326 genetic trend in the multiplier than in the nucleus. For trait 2 the multiplier animals were 327 selected only on estimated parent average, which resulted in low accuracy selection. In the 328 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 329 330 the multiplier. In the MaleFlow20 scenario with a reduced nucleus-multiplier gene flow this 331 low accuracy selection resulted in the reduced genetic gain for trait 2.

### Conclusion

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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

338 Not applicable

### **Consent for publication**

340 Not applicable

### Availability of data and materials

342	Project name: AlphaPart				
343	Project home page: https://cran.r-project.org/package=AlphaPart				
344	Operating system(s): Windows, MacOS, Linux				
345	Programming language: R & C++				
346	License: GPL-2   GPL-3				
347	Any restrictions to use by non-academics: -				
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356	Acknowledgements				
357	Not applicable				
358	Author's information (optional)				
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## 361 Figures

362 Figure 1 Distribution of true breeding values and their partitions by trait, year, and tier in MaleFlow100 scenario. 363 364 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 365 366 and the multiplier, while trait 2 is measured only in the nucleus. Black vertical lines represent 367 the nucleus mean breeding value for a trait in a year. 368 369 Figure 2: Partitioning of genetic trend by tier-gender in MaleFlow100 scenario. 370 The scenario uses nucleus males in the multiplier. Trait 1 is measured in the nucleus and the 371 multiplier, while trait 2 is measured only in the nucleus. 372 373 Figure 3 Distribution of true breeding values and their partitions by trait, year, and tier 374 in MaleFlow20 scenario. 375 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 376 377 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. 378 379

- 380 Figure 4 Partitioning of the genetic trend by tier-gender in MaleFlow20 scenario.
- 381 The scenarios 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.