

1 **Strategies for implementing genomic selection for feed efficiency in dairy**
2 **cattle breeding schemes**

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ABSTRACT

11 Alternative genomic selection and traditional BLUP breeding schemes were compared for
12 the genetic improvement of feed efficiency in simulated Norwegian Red dairy cattle populations.

13 The change in genetic gain over time and achievable selection accuracy were studied for milk yield
14 and residual feed intake, as a measure of feed efficiency. When including feed efficiency in

15 GBLUP schemes it was possible to achieve high selection accuracies for genomic selection, and
16 all GBLUP schemes gave better genetic gain for feed efficiency than ABLUP (Best Linear

17 Unbiased Prediction using pedigree relationship matrix). When using contracted test herds with
18 genotyped and feed efficiency recorded cows as a reference population, a reference population

19 size of 4,000 new heifers per year was needed in order to achieve considerable genetic
20 improvement of feed efficiency. With such a reference population it was possible to reach similar

21 selection accuracies of 0.75 for males than when using progeny testing. It was concluded that the
22 use of contracted test herds with additional recordings (e.g. feed efficiency) is a viable option,

23 possibly by international collaborations, for the genetic improvement of such difficult to record
24 traits.

25

26 **Key words:** genomic selection, feed efficiency, breeding scheme

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INTRODUCTION

29 Improving feed efficiency is economically important because feed costs comprise the
30 majority of the variable cost in the dairy industry. Hence, there are already some countries who
31 have included feed efficiency in their breeding goals (Pryce et al., 2014). Having access to accurate
32 and low-cost feed efficiency measurements is difficult hence; a lot of research efforts are devoted
33 to this problem (de Haas et al., 2012; Veerkamp et al., 2013). The main problem in including feed
34 efficiency in the breeding objective is to have access to phenotypic data from a large population
35 of animals, and that are daughters of progeny tested bulls. Since genomic selection can be based
36 on fewer phenotypes than traditional selection, genomic selection could be a useful tool to improve
37 feed efficiency.

38 Genomic selection uses dense markers covering the whole genome and it addresses most
39 of the genetic differences between the animals (Meuwissen et al., 2001). The total genetic value
40 of selection candidates is predicted based on the estimation of SNP effects, which are estimated
41 using reference individuals that have been genotyped and phenotyped. If the training set is large
42 enough and relevant to the selected population, genomic selection can result in an increase in the
43 accuracy compared to traditional selection (VanRaden et al., 2009). The number of individuals in
44 the training set and the marker density have the greatest impact on accuracy (Goddard, 2009; Hayes
45 and Goddard, 2008). Other factors are heritability (Daetwyler et al., 2008; Goddard, 2009),

46 effective population size (N_e), the effective number of segments (Goddard, 2009), relationship
47 between the evaluated animals and training data set (Habier et al., 2010; Wolc et al., 2011; Pszczola
48 et al., 2012) and variance of relationships within the reference population (Habier et al., 2010). For
49 the traits that have low heritabilities, a very large number of records will be required in the training
50 data set in order to achieve high accuracies of GEBV in unphenotyped animals (Hayes et al., 2009).
51 One possibility to overcome the limited size of the training set is to combine data across countries
52 as in the global Dry Matter Initiative (gDMI) (de Haas et al., 2012).

53 In this study, stochastic simulation was used to investigate how different breeding schemes
54 affect genetic gain without treating accuracy as a fixed value, but rather as an outcome of the
55 simulation. By using stochastic simulation, it is also possible to study complex and overlapping
56 generations and the changes in accuracy over time under different schemes (Lillehammer et al.,
57 2011a). We used residual feed intake (RFI) as a measure of feed efficiency. RFI is defined as the
58 difference between actual and predicted feed (or energy) intake based on the requirements of the
59 animal (Koch et al., 1963; Williams et al., 2011; Berry and Crowley, 2013). The benefits of GS
60 are greatest when selection is for difficult to measure traits, whose recording is either too expensive
61 or phenotypes are not easily accessible (Goddard, 2009). Both these arguments justify the use of
62 GS for improving feed efficiency (FE), because FE recording is too expensive to be carried out on
63 large numbers of cows and the feed efficiency of milk production cannot be recorded on bulls. In
64 this study, genomic selection strategies were developed for improving feed efficiency in
65 Norwegian Red dairy cattle. The objectives of this research were to compare strategies for
66 improving selection accuracy and genetic gain for FE by estimating SNP effects in experimental
67 herds with feed efficiency recordings or in large-scale field recordings of FE. Thus, we investigate

68 whether it is possible to use contracted test herds with additional recording for improving traits
69 that are difficult to measure such as feed efficiency.

70

71 **MATERIALS AND METHODS**

72 Historical populations were simulated in order to create realistic associations between
73 markers and genes and to create founder populations for the breeding schemes. In order to create
74 these associations and a mutation-drift balance the simulations consisted of 2,000 generations of
75 random mating following the Fisher-Wright population model (Fisher, 1930; Wright, 1931). The
76 founder population had an effective population size of 200 (100 males and 100 females) (Hillestad
77 et al., 2014). The simulated genome consisted of 30 pairs of chromosomes; each was 100 cM in
78 length. The expected number of mutations per meiosis per diploid chromosome was two.
79 Polymorphisms and recombinations were simulated following Sonesson and Meuwissen (2009).
80 From the created SNPs 3,000 were randomly selected as QTLs, and QTL effects were sampled
81 from a Normal distribution. Per chromosome 500 SNPs were randomly sampled to be used as
82 genetic markers in the breeding scheme, i.e. a total of 15,000 markers.

83 Seven different breeding schemes were investigated; basic, MY+FE population wide and
84 five test herd simulations. In the basic breeding scheme, only milk yield (MY) was included in the
85 breeding goal. Whereas, in MY+FE and test herd simulations milk yield and residual feed intake
86 (RFI) as a feed efficiency trait were included in the breeding goal and they were assumed to be
87 uncorrelated (since RFI as a measure of FE is not correlated to MY) and have equal economic
88 weights (in all the other breeding schemes except test herd 4,000 eco25 and test herd 4,000 eco50
89 schemes). In eco25 scheme, FE had $\frac{1}{4}$ of the economic weight of milk yield whereas in eco50
90 scheme FE had $\frac{1}{2}$ of the economic weight of milk yield. In test herd simulations, FE test herds

91 were set up (contracted), where RFI and MY were recorded. These test herds varied in total size
92 (500, 1,000 and 4,000) between the schemes. Basic and MY+FE schemes were investigated with
93 both genomic selection (Meuwissen et al., 2001) and with traditional BLUP selection (ABLUP;
94 Henderson, 1975). Test herd simulations were investigated only with genomic selection.

95 In basic schemes, all cows got records only for milk yield at age 3 (Table 1 and Figure 1).
96 Whereas, in MY+FE schemes all cows had records for both milk yield and RFI at age 3. In test
97 herd schemes, the test herd females had records for both RFI and milk yield at age 3, while other
98 cows had records for milk yield only. No repeated records were assumed for any of the traits,
99 which is conservative with respect to the amount of information that comes from recording a cow.
100 Females were available for selection at ages 2,3,4,5,6 years. All ages refer actually to the average
101 generation interval that results from their mating, i.e. the actual mating occurs 9 months earlier.
102 Males were selected to be parents at age 3 in GBLUP and at age 6 in ABLUP schemes. Males
103 were progeny tested for both milk yield and RFI in MY+FE schemes; progeny test results were
104 available at age 6 (Table 1, Figure 1). Whereas, in the basic and test herd schemes males were
105 progeny tested only for milk yield. The progeny test information was hence available when
106 selecting sires in the ABLUP-schemes, but not in the GBLUP-schemes, due to the shorter
107 generation interval. In GBLUP-schemes, progeny information was used to update the reference
108 population. One-third of the females were culled randomly every year starting when they were 3
109 years old. Females in the test herds and bull calves born from elite matings were assumed
110 genotyped in GBLUP schemes.

111 A base generation (generation 0) was created using the animals from the last generation of
112 the founder population and mating them randomly. All 4,000 animals in generation 0 were
113 assumed genotyped and progeny tested in all the schemes, which involved genomic selection and

114 those animals were used to estimate SNP effects for milk yield and RFI. The younger bulls were
 115 added to the simulated reference population when they got their progeny test records for
 116 production traits. The simulated breeding schemes closely resembled those of Lillehammer et al.
 117 (2011) where earlier progeny-tested bulls were genotyped and used to estimate SNP effects.

118 True breeding values (TBV) were calculated for all individuals as the sum of the QTL
 119 effects:

$$120 \quad TBV_i = \sum_{j=1}^{Numb.of\ QTL} x_{ij1}g_{j1} + x_{ij2}g_{j2}$$

121
 122 where x_{ijk} is the number of copies that individual i has at the j^{th} QTL position and k^{th} QTL
 123 allele, and g_{jk} is the effect of the k^{th} QTL at the j^{th} position which were sampled from the Normal
 124 distribution. The simulated traits, milk yield and residual feed intake, were assumed to have
 125 heritabilities of 0.3 and 0.15, respectively. Those heritabilities reflect the average heritability of
 126 milk production (Berry et al., 2003; Hoekstra et al., 1994) and the average heritability of feed
 127 efficiency traits (Berry and Crowley, 2013; Varga and Dechow, 2013).

128 The accuracy of the genomic breeding values was calculated, according to Sonesson and
 129 Meuwissen (2009), as the correlation between the estimated genomic breeding values and the true
 130 breeding values. Genomic breeding values were estimated by summing the marker effects:

$$131 \quad GEBV_i = \sum_{j=1}^n x_{ij}a_j,$$

132
 133 where a_j is the BLUP estimate of the j th SNP effect and n is the number of SNPs (15,000). To
 134 ensure that direct comparison between traditional and genomic EBVs was possible all EBVs were

135 scaled so that $b = 1$ where $b = Cov(TBV_i; [G]EBV_i) / Var([G]EBV_i)$. This is important for the
136 selection of females which is across GEBV and traditional EBV for some of the schemes.

137 Phenotypes were simulated by adding a normally distributed random error term to the true
138 breeding value:

$$P_i = TBV_i + \varepsilon_i,$$

140
141 where ε_i is an error term for animal i , which was normally distributed $(0, \sigma_e^2)$. In order to
142 express the results in genetic standard deviations (SD) and create phenotypic records with the
143 desired heritability the genetic variance (σ_g^2) was scaled to 1 for both of the traits and the residual
144 variance (σ_e^2) was adjusted following Sonesson and Meuwissen (2009).

145 The value of 1 genetic standard deviation of milk yield was arbitrary set to 100 monetary
146 units. When the economic value of RFI equaled that of milk yield, a genetic standard deviation of
147 RFI represented also 100 monetary units. In schemes with reduced economic values for RFI, eco50
148 and eco25 schemes, one genetic standard deviation of RFI represented 50 and 25, monetary units
149 respectively.

150 The BLUP method (Meuwissen et al., 2001) was used for the estimation of marker effects.
151 The statistical model used to estimate individual marker effects was:

$$y_i = \mu + \sum_{j=1}^n X_{ij}a_j + e_i,$$

152
153
154 where y_i is the record of individual i ; μ is the overall mean; X_{ij} is the marker genotype; a_j is the
155 random effect of the j th marker, with variance equal to the total genetic variance divided by the
156 number of markers; and e_i is a random residual.

157 Simulated population sizes were smaller than those of the real Norwegian Red
158 dairy cattle population in order to make stochastic simulation computationally possible. Population
159 sizes were rescaled as described by Lillehammer et al. (2011), so that selection steps for
160 conformation traits of bulls and bull dams were not considered in the simulation and selection
161 intensities for the included traits were maintained at realistic levels when population size was
162 reduced. The ABLUP schemes were designed to mimic the breeding structure of Norwegian Red
163 before implementation of genomic selection, while the GBLUP-schemes mimic the current
164 breeding structure of Norwegian Red after genomic selection was implemented.

165 For each scheme, 50 replicates were run and simulations were performed for 20 years.
166 Genetic gain and selection accuracy for males and females were reported as an average over years
167 10 to 20 of the simulations. In all the schemes, total genetic gain was calculated by summing up
168 the genetic gain (in monetary units) for milk yield and RFI. When results of the simulation study
169 are reported, omitting the first years of the simulation avoids the problem of the non-steady-state
170 population structure at the start of the scheme, where all animals are of the same age and that all
171 base generation animals are assumed to be genotyped and progeny tested, which affects early
172 simulation results.

173

174

RESULTS

175 Figure 2 shows the total genetic gain (in monetary units) for milk yield and residual feed
176 intake when RFI was included in the breeding scheme. The highest total genetic gain was found
177 when using the MY+FE GBLUP scheme, where bulls were progeny tested for both traits. ABLUP
178 schemes gave lower total genetic gain when compared to a similar GBLUP scheme. Increasing the
179 number of cows in the test herds caused an increase in genetic gain. Genotyping 500 or 1,000 cows

180 in test herds resulted lower genetic gain than using progeny test records to update the reference
181 population. Whereas, test herd size of 4,000 cows gave slightly lower genetic gain than MY+FE
182 GBLUP scheme. Using smaller economic values for feed efficiency in test herd 4,000 GBLUP eco
183 schemes decreased the total genetic gain.

184 As expected, the basic scheme gave the highest genetic gain for milk yield of the ABLUP
185 schemes (Table 2 and Figure 3), and GBLUP schemes gave higher genetic gain for milk yield than
186 similar ABLUP schemes. As expected, introducing a second trait in the breeding goal reduced
187 genetic gain for milk yield. Which is due to the fact that if selection pressure is devoted to more
188 traits the progress for each of the original traits reduces.

189 The highest genetic gain for residual feed intake was reached using the MY+FE GBLUP
190 scheme (Table 2 and Figure 4), where all cows had RFI records. Obtaining RFI records from test
191 herds of limited size gave less gain for RFI, but increasing the number of genotyped cows in the
192 test herd schemes increased the genetic gain for RFI. At a test herd size of 4,000 genotyped cows,
193 the genetic gain for RFI was very similar to obtaining records from all cows in the population. As
194 expected, test herd 4,000 GBLUP eco schemes gave lower genetic gain for RFI than other GBLUP
195 schemes where RFI was included, which is due to the smaller economic value for RFI in eco
196 schemes.

197 Selection accuracies for males ranged from 0.65 to 0.79 in GBLUP schemes and 0.94 to
198 0.96 in ABLUP schemes (Figure 5 and Table 3). Using lower economic values for RFI in the test
199 herd 4,000 GBLUP eco schemes slightly increased the selection accuracy for males (Figure 5).
200 Whereas, the selection accuracy for females was approximately 0.6 in all the other schemes except
201 the test herd schemes (Table 3). The test herd scenarios caused a decrease in the selection accuracy
202 for females because only a fraction of the females obtained RFI-records. However, increasing the

203 test herd size resulted an increase in the female selection accuracy. The highest selection accuracy
204 for females was reached using basic schemes, where the breeding goal included only MY.

205

206

DISCUSSION

207 This study compared different implementations of genomic selection and traditional BLUP
208 selection for the genetic improvement of feed efficiency, and investigated how the genetic gain
209 accumulates over time and which selection accuracies are achievable when increasing the number
210 of genotyped females in the reference population. We used residual feed intake as a feed efficiency
211 trait, since it is by definition the component of feed intake that is uncorrelated to milk yield.
212 Practical breeding schemes may select directly for MY and against feed intake, but also here only
213 the component that is uncorrelated to milk yield will be reduced, whereas the component of feed
214 intake that is associated with MY will increase together with the general increase in MY.

215 Table 3 showed that it is possible to achieve high selection accuracies for males when
216 including feed efficiency in GBLUP schemes. This can be done either by obtaining phenotypes
217 from all cows in the population and hence get progeny information for genotyped bulls that can be
218 used to update a reference population, or by updating the reference population through genotyping
219 of cows with records. The latter will be preferable if genotyping is cheap compared to phenotyping.
220 When using genomic selection to improve low heritability traits the number of records in the
221 reference population has to be sufficiently large in order to achieve high selection accuracies
222 (Hayes et al., 2009). Our study showed that 4,000 cows had to be phenotyped and genotyped every
223 year to achieve similar selection accuracy of genomic selection as if all cows were phenotyped,
224 but only bulls genotyped.

225 Females were always selected on ABLUP, except in test herd schemes, where the
226 genotyped test-herd females obtained genomic breeding values. The female selection accuracy
227 where hence first of all affected by whether the females had records for the trait under selection or
228 not, giving higher female selection accuracy for schemes where phenotypes for all traits under
229 selection were available for the entire cow population (Table 3). When test herds were used, the
230 females belonging to these herds will have more accurate breeding values than the cows outside
231 the test herds, due to their phenotypes and genotypes. The female selection accuracy will hence
232 depend on the fraction of the cows that are included in the test herds.

233 Genetic gain will depend on both male and female selection accuracy, although the male
234 selection accuracy has the highest impact because of the higher intensity of selection. Genetic gain
235 was therefore similar in Test herd 4k GBLUP as in MY+FE GBLUP, reflecting the similar
236 accuracy of the genomic breeding values in the two schemes. The small advantage of MY+FE
237 GBLUP, compared to Test herd 4k GBLUP may increase if a more intense selection of females is
238 used. However, if selection of females were also based on genomic selection, this difference could
239 disappear, as the fraction of the female population with RFI-phenotypes becomes less important.
240 The general level of the genetic gains agree with those found by Lillehammer et al., 2011.

241 We also investigated how reduced economic values for RFI affect the genetic gain and the
242 accuracy of selection by comparing the test herd 4,000 GBLUP at a half and a quarter of its original
243 economic value of RFI. As expected, test herd 4,000 GBLUP eco schemes gave higher genetic
244 gain for milk yield and lower genetic gain for RFI compared to other schemes. Lower economic
245 values for RFI increased the selection accuracy of both males and especially females, since much
246 more phenotypes were available for milk yield than for RFI in the test herd scheme. Total genetic
247 gain was reduced for the schemes with lower economic values for RFI. To build up test herds to

248 facilitate genomic selection for traits with low economic value, might hence not be economically
249 defendable, as the expected gain is sensitive to the weight put on these traits.

250 In these simulations, we assumed a large reference population at the start of the breeding
251 scheme, which might be optimistic. However, Figure 5 shows that genomic selection accuracies
252 during years 10-20 remain stable, implying that the gain of accuracy due to the genotyping of new
253 relevant reference animals is compensated for old reference animals becoming less relevant, i.e.
254 the start reference population is becoming less and less relevant during years 10-20. The results of
255 Table 3 and Figure 5 show that if progeny testing for feed efficiency is not feasible: genotyping
256 females in test herds that enter a reference population may compensate the lack of progeny testing.
257 However, this requires the genotyping and phenotyping of 4,000 test females annually, since
258 smaller test herd sizes resulted in markedly reduced genetic gains. Obtaining large amounts of
259 animals with multiple recordings is possible using for example collaboration between countries
260 (de Haas et al., 2012; Veerkamp et al., 2013) or milk MIR predicted feed efficiency records. In
261 2014 McParland et al. showed that mid-infrared (MIR) spectrometry of milk could be used to
262 predict residual feed intake (RFI) as a measure of feed efficiency in lactating dairy cows. Since,
263 individual animal milk samples are routinely taken as part of the dairy herd management, using
264 these samples to also predict feed intake and efficiency would be cost-effective and a relatively
265 undemanding approach to obtain large numbers of feed efficiency phenotypes.

266 In this study, we used RFI as a measure of feed efficiency. However, earlier studies showed
267 that weak unfavorable genetic correlations exist between RFI and fertility (Vallimont et al., 2013).
268 This is probably due to the mathematical similarity in the calculations of RFI and energy balance
269 and a failure to account correctly for body tissue mobilization which might lead to selection for a
270 trait that is similar to selecting for a negative energy balance (Pryce et al., 2014). Therefore, genetic

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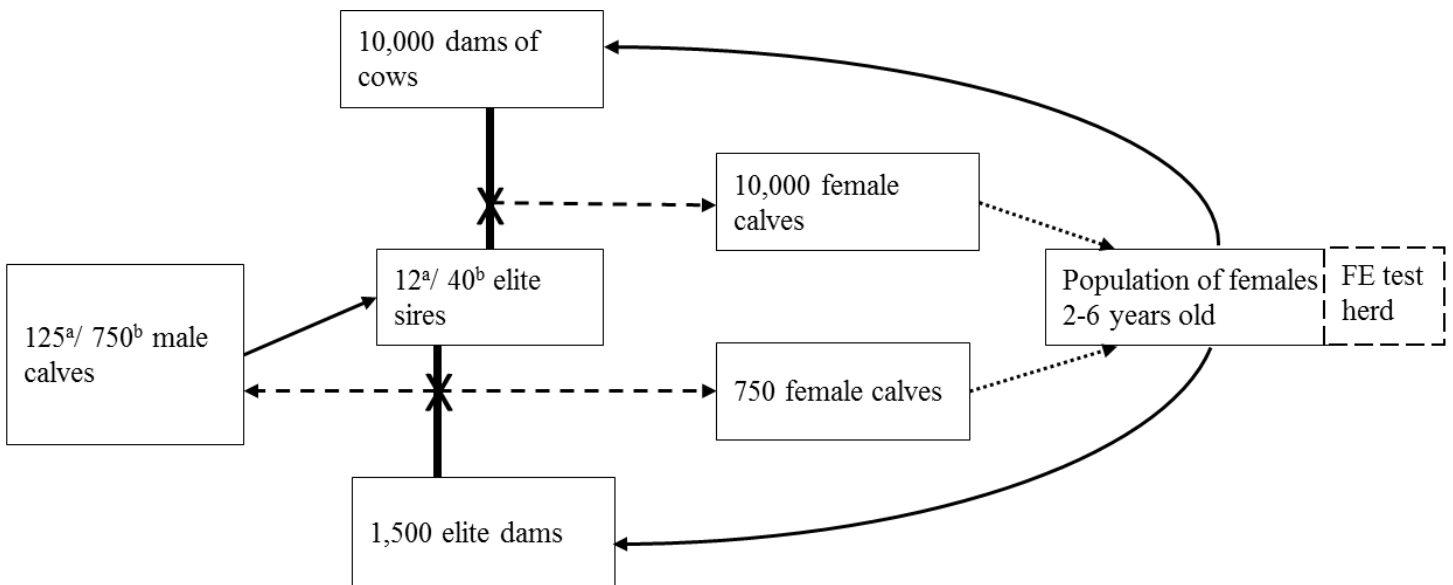
384 Table 1. Ages at which recording and selection take place.

	Age of dam	Age of sire	Milk record dam	RFI record dam	Progeny test sire
Basic ABLUP	2-6 yr	6 yr	3 yr	-	6 yr ^a
Basic GBLUP	2-6 yr	3 yr	3 yr	-	6 yr ^a
MY+FE ABLUP	2-6 yr	6 yr	3 yr	3 yr	6 yr ^b
MY+FE GBLUP	2-6 yr	3 yr	3 yr	3 yr	6 yr ^b
Test herd GBLUP	2-6 yr	3 yr	3 yr	3 yr ^a	6 yr ^b

385 Ages refer to the generation interval resulting from the mating of the parents (selected for the
 386 indicated record).

387 ^abreeding goal includes only milk yield

388 ^bbreeding goal includes both RFI and milk yield

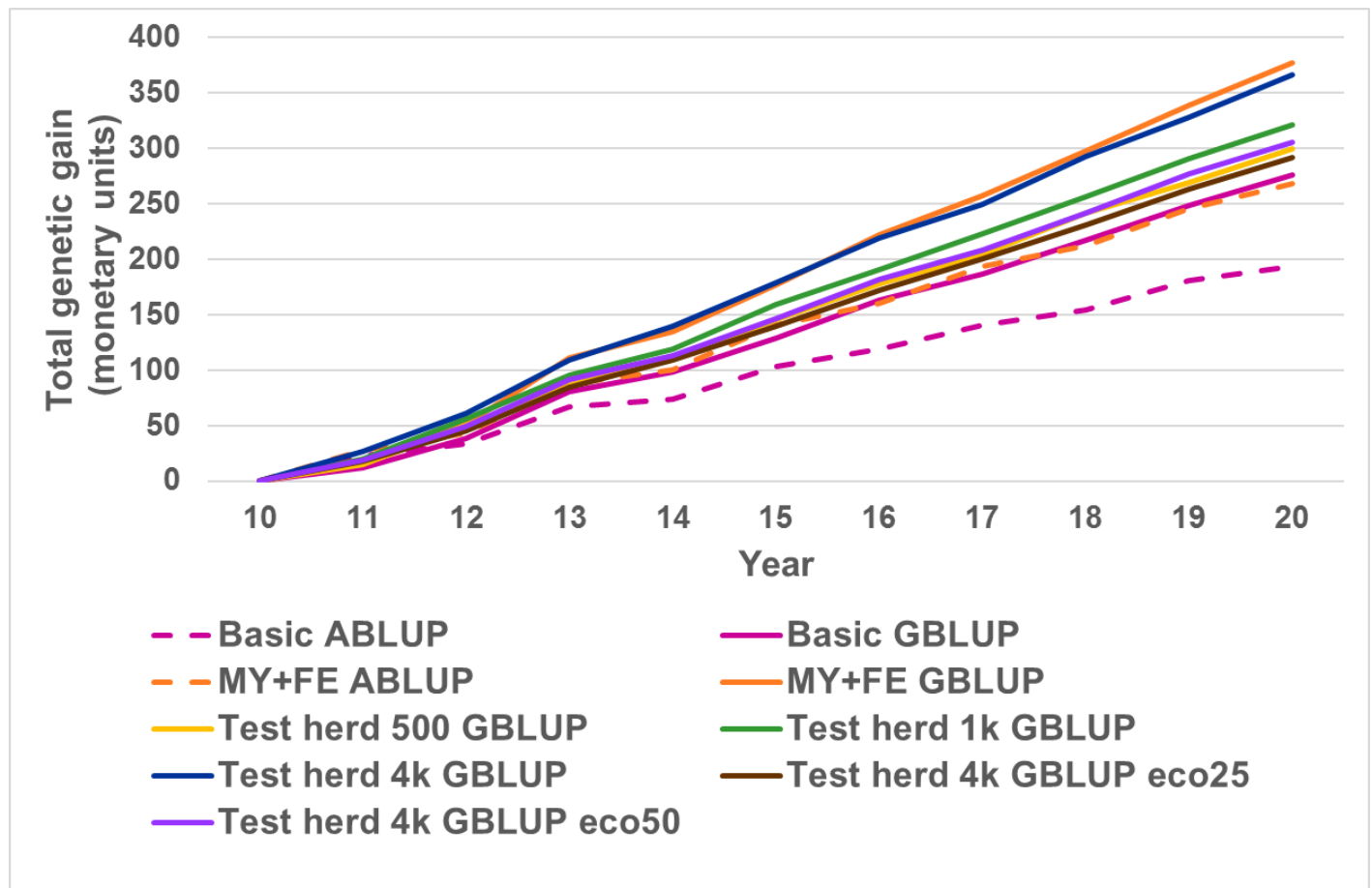


390 Figure 1. Overview of the breeding schemes. Solid lines with a cross represent matings and dashed
 391 arrows represent progeny produced by the matings. Dotted arrows represent that animals move
 392 from one category to another due to aging. Solid arrows represent selection of animals.

393 ^aIn ABLUP schemes 125 male calves were progeny tested and 12 elite sires were selected.

394 ^bIn GBLUP schemes 750 male calves were progeny tested and 40 elite sires were selected.

395



397 Figure 2. Total genetic gain measured as monetary units relative to year 10 onwards. In basic
 398 scheme, genetic gain is only for milk yield whereas in MY+FE and test herd schemes genetic gain
 399 is the total genetic gain when summing up the genetic gain for both residual feed intake and milk
 400 yield.

401

402 Table 2. Average genetic gain (ΔG) as monetary units with standard errors when $h^2 = 0.3$ for milk
 403 yield and $h^2 = 0.15$ for residual feed intake.

Breeding scheme ^a	Milk yield		Residual feed intake	
	ABLUP	GBLUP	ABLUP	GBLUP
	ΔG	ΔG	ΔG	ΔG
Basic	19.64 (0.2)	28.52 (0.2)	- ^b	- ^b
MY+FE	14.76 (0.2)	21.74 (0.3)	12.45 (0.2)	17.28 (0.3)
Test herd 500	-	18.37 (0.3)	-	12.49 (0.2)
Test herd 1,000	-	18.99 (0.3)	-	13.88 (0.3)
Test herd 4,000	-	20.06 (0.3)	-	17.18 (0.2)
Test herd 4,000 eco25	-	28.74 (0.06)	-	1.23 (0.06)
Test herd 4,000 eco50	-	26.08 (0.15)	-	5.21 (0.13)

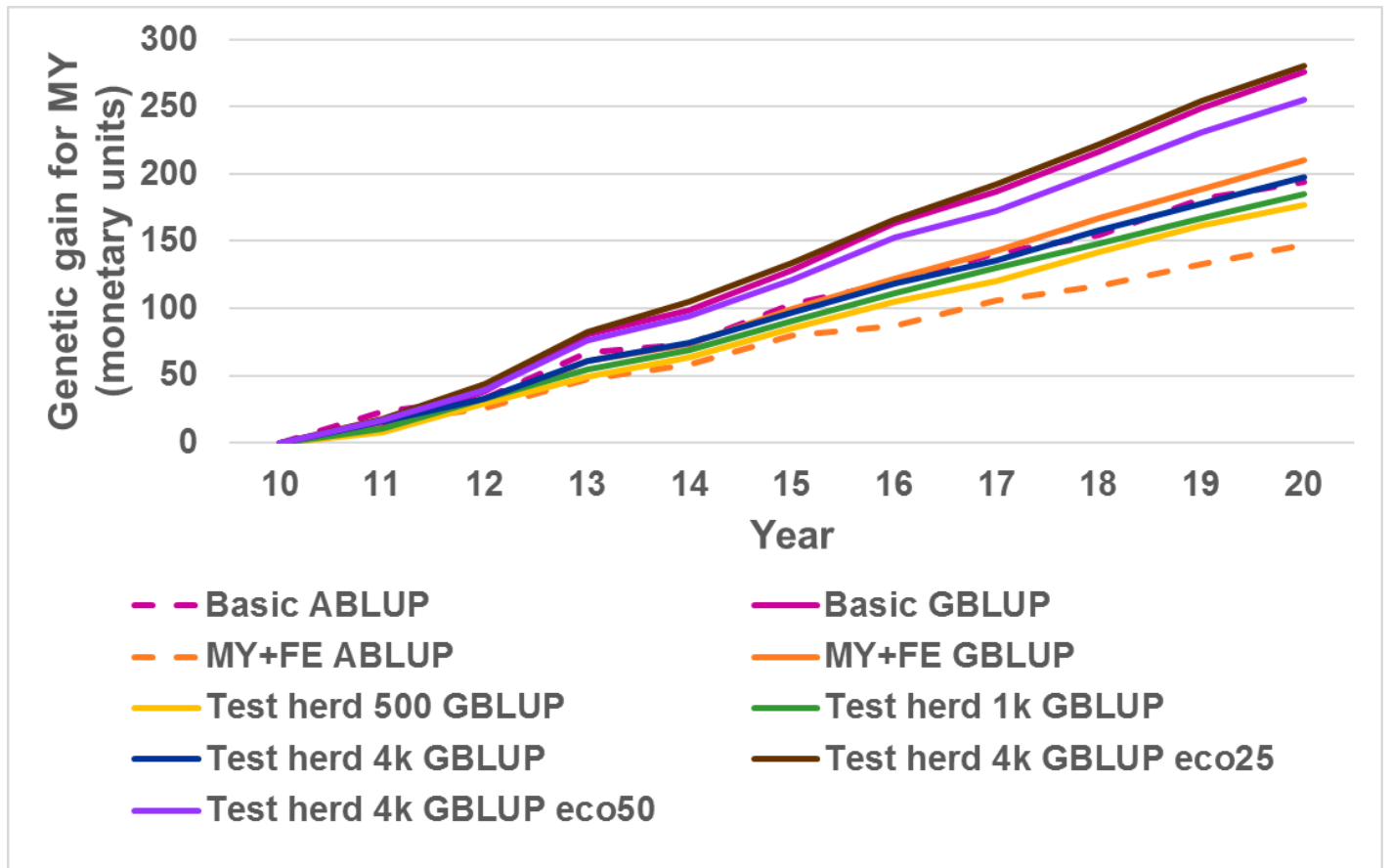
404 Average of genetic gain measured as genetic SD of years 10 to 20. The value of 1 genetic standard
 405 deviation of milk yield was arbitrary set to 100 monetary units. In eco50 and eco25 schemes, one
 406 genetic standard deviation of RFI represented 50 and 25, monetary units respectively.

407 ^aMY+FE and test herd schemes include both milk yield and residual feed intake in the breeding
 408 goal; basic scheme includes only milk yield.

409 ^bResidual feed intake is not included in the basic scheme.

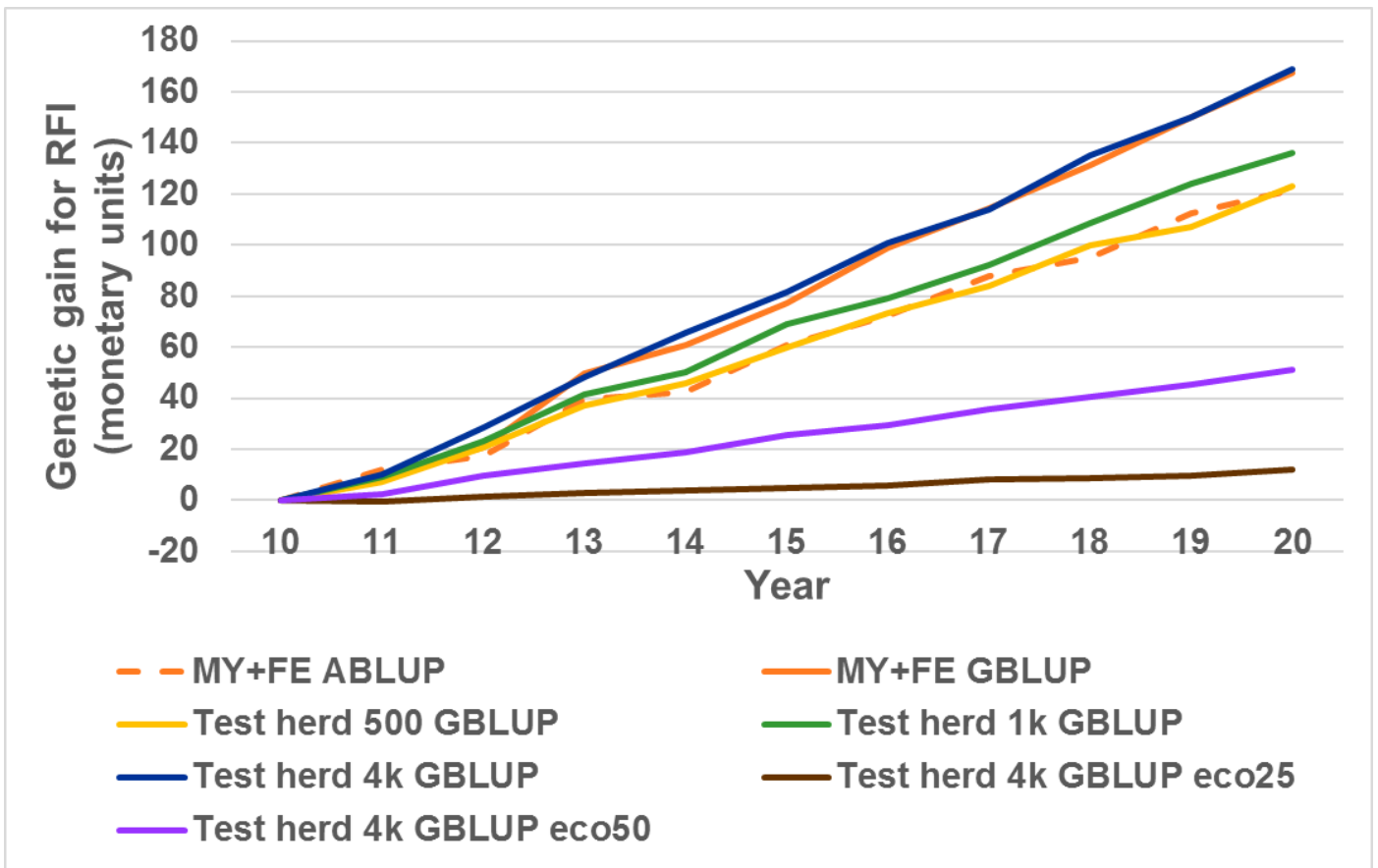
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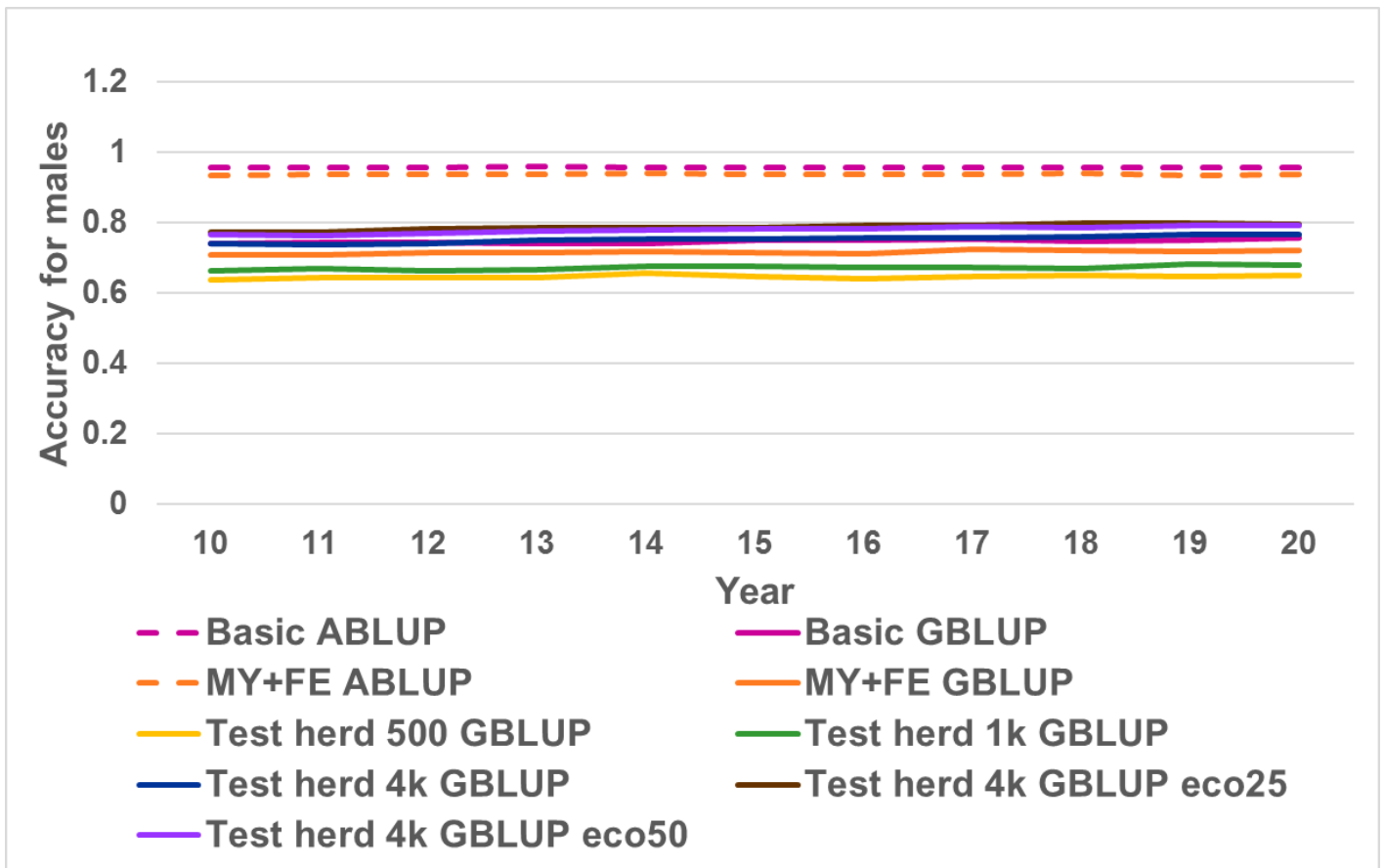


412 Figure 3. Genetic gain for milk yield measured as monetary units relative to year 10 onwards.

413



415 Figure 4. Genetic gain for residual feed intake measured as monetary units relative to year 10
 416 onwards.



418 Figure 5. Selection accuracy for males relative to year 10 onwards. MY+FE and test herd schemes
 419 include both milk yield and residual feed intake in the breeding goal; basic scheme includes only
 420 milk yield.

421

422 Table 3. Average selection accuracy of years 10 to 20 for males (M) and females (F) in the total
 423 breeding goal with standard errors when $h^2 = 0.3$ for milk yield and $h^2 = 0.15$ for residual feed
 424 intake.

Breeding	ABLUP	GBLUP	ABLUP	GBLUP
Scheme ^a	Accuracy M	Accuracy M	Accuracy F	Accuracy F
Basic	0.96 (0.0005)	0.75 (0.002)	0.61 (0.002)	0.62 (0.001)
MY+FE	0.94 (0.0007)	0.72 (0.002)	0.58 (0.001)	0.59 (0.001)
Test herd 500	-	0.65 (0.002)	-	0.21 (0.003)
Test herd 1,000	-	0.67 (0.002)	-	0.24 (0.003)
Test herd 4,000	-	0.75 (0.001)	-	0.42 (0.003)
Test herd 4,000 eco25	-	0.79 (0.001)	-	0.60 (0.002)
Test herd 4,000 eco50	-	0.78 (0.002)	-	0.53 (0.004)

425 ^aMY+FE and test herd schemes include both milk yield and residual feed intake; basic scheme
 426 includes only milk yield.

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