Genomic selection using indicator traits to reduce the environmental impact of milk production

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ABSTRACT

The aim of this simulation study was to test the hypothesis that phenotype information of specific indicator traits of environmental importance recorded on a small-scale can be implemented in breeding schemes with genomic selection to reduce the environmental impact of milk production. A stochastic simulation was undertaken to test alternative breeding strategies. The breeding goal consisted of milk production, a functional trait, and environmental impact (EI). The indicator traits (IT) for EI were categorized as large-, medium-, or small-scale, depending on how the traits were recorded. The large-scale traits were stayability and stature; the medium-scale traits were live weight and methane in the breath of the cow measured during milking; and the small-scale traits were residual feed intake and methane recorded in a respiration chamber. Simulated scenarios considered information for just one IT in addition to information for milk production and functional traits. The annual monetary genetic gain was highest in the large-scale scenario that included stayability as IT. The annual monetary gain in the scenarios with medium- or small-scale IT varied from €50.5 to 47.5. The genetic gain improvement in EI was, however, best in the scenarios where the genetic correlation between IT and EI was ≥ 0.30 and the accuracy of direct genomic value was ≥ 0.40 . The genetic gain in EI was 26 to 34% higher when indicator traits such as greenhouse gases in the breath of the cow and methane recorded in respiration chamber were used compared with a scenario where no indicator trait was included. It is possible to achieve increased genetic gain in EI by using a highly correlated indicator trait, but it requires that the established reference population for the indicator trait is large enough so that the accuracy of direct genomic values will be reasonably high.

Key words: methane mitigation, genomic selection, indicator trait, dairy cattle

INTRODUCTION

The environmental impact of dairy cattle is a well-recognized problem (Steinfeld et al., 2006). The dairy sector contributes to greenhouse gas (GHG) emissions through emissions of CO₂, N₂O, and CH₄, of which the enteric CH₄ emissions account for a major part of the total GHG emissions at a dairy farm (FAO, 2010). Different options for mitigation of enteric CH₄ emissions have been investigated by scientists worldwide (Beauchemin et al., 2009; Buddle et al., 2011; de Boer et al., 2011; Grainger and Beauchemin, 2011). Improved feeding and management can be efficient tools of mitigation in the short term (Beauchemin et al., 2009; Hegarty et al., 2010). Animal breeding is of potential relevance for the long-term mitigation, as genetic changes are permanent, cumulative, and routinely disseminated via AI from elite bulls.

It is known that improved efficiency of dairy cattle through breeding is capable of reducing enteric CH₄ emissions (Wall et al., 2010). Direct selection, however, is complicated, as measuring enteric CH₄ production requires special and costly equipment (Storm et al., 2012), and can only be undertaken in experimental settings in test stations or in a few selected herds. This means that the number of phenotype records available for the trait is limited, which makes it difficult to estimate accurate breeding values for bulls in a breeding scheme with progeny testing. Wall et al. (2010) proposed using indirect selection and correlated indicator traits to select for reduced environmental impact. However, if the recording of relevant indicator traits is costly, it can be done only on a small-scale. A solution could be using such indicator traits for environmental impact in breeding programs that implement genomic selection.

Genomic selection has been proposed as a helpful tool when recording and selecting for new and strenuous traits, as such selection small numbers of records are a less restrictive factor (Dekkers, 2010; Verbyla et

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al., 2010). The main idea is to create a reference population of genotyped animals with individual phenotypic records or with progeny information on the trait of interest (Hayes et al., 2009; Pszczola et al., 2012). Single nucleotide polymorphism effects are estimated in the reference population and then used to predict genomic enhanced breeding values (**GEV**) for all selection candidates (Dekkers, 2010). Schaeffer (2006) suggested using contractor herds to record more traits on fewer cows. However, because the accuracy of the **GEV** for traits with few phenotypic records might be low, it remains important to establish a representative reference population of acceptable size. Pryce et al. (2012) estimated the accuracy of genomic breeding values for residual feed intake (**RFI**) using 2,000 heifers from New Zealand and Australia and they found the accuracy to be 0.31 and 0.38 in those respective countries. Heritabilities estimated for **RFI** in their study varied from 0.22 to 0.38 depending on the data.

As yet, little attention has been given to the specific design of breeding programs for reducing environmental impact, and especially the choice of indicator traits and recording schemes. The aim of this simulation study was to test the hypothesis that phenotype information collected by recording specific indicator traits of environmental importance in specialized herds can be implemented in breeding schemes with genomic selection to reduce the environmental impact of milk production.

MATERIALS AND METHODS

Experimental Design

The breeding goal consisted of 3 traits: milk production (**MP**), functional trait (**FT**), and environmental impact (**EI**). Milk production and **FT** represented all traits in a current breeding goal of the Nordic Cattle Genetic Evaluation with economic values that were set at €83 and 82 per genetic standard deviation, respectively, following the study by Buch et al. (2012b). The economic values in the paper by Buch et al. (2012b) were calculated so that the correlation between the simulated breeding goal and **MP** was equal to the correlation between the Nordic total merit index and the milk production index. Environmental impact was a new trait in the breeding goal, defined as a trait including both the enteric CH_4 emissions and other enteric GHG emissions of dairy cows. The **EI** was given a negative economic value as we aimed to reduce the **EI**. The value was set to -€83 to give the same weight to **EI** as to the production trait **MP**.

In our experimental design, we assumed that phenotype records and genotypic information was available

for the breeding goal traits **MP** and **FT**, but not for **EI**. Instead, information for **EI** came from phenotype and genotype records of different indicator traits that were correlated with **EI**. The indicator traits were chosen after reviewing the literature. They were the traits most commonly linked, in the context of animal breeding, with reducing the **EI** of dairy cattle. The indicator traits were then divided into 3 categories based on the recording system and the number of phenotype records. These categories were large-, medium-, and small-scale traits. Large-scale indicator traits were recorded in all herds that participate in national milk recording. Medium-scale indicator traits were recorded in herds with an automatic milking system (**AMS**). Small-scale indicator traits were only recorded in a few contractor herds specialized in recording these traits.

The indicator traits recorded on a large scale exhibited low correlation with **EI**. Stayability after first lactation (**STAY**; 0 or 1) and stature measured in first lactation (**STAT**; cm) were used as representatives of this category. Indicator traits recorded on a medium scale have a moderate-to-high correlation with **EI**. Traits representing this category were live weight at first lactation (**LW**; kg) and CH_4 recorded in **AMS** from the breath of the cow (**BRH**; g/kg of milk). Indicator traits recorded on a small scale had a very high correlation with **EI**. Recording of these traits requires specific and expensive technical equipment; therefore, they can only be recorded in a few contractor herds. Residual feed intake (MJ/d) and CH_4 recorded in a respiration chamber (**METH**; g/kg of milk) were chosen to represent this category.

Description of the Scenarios

Six main scenarios were considered where 3 traits were included in the breeding goal (**MP**, **FT**, and **EI**) and 3 traits (**MP**, **FT**, and 1 **EI** indicator) were recorded. In addition, a scenario that included no specific indicator trait (**No IT**) indicated that no additional records for **EI** were used.

Owing to uncertainty about the genetic parameters for the traits **BRH** and **METH**, additional scenarios including these traits were tested. Subscripts U, N, and F stand for unfavorable, neutral, or favorable correlations between the actual indicator trait and **MP** and **FT** (the actual values for these correlations are given below). Subscripts 1 and 4 for **METH** represent 2 levels of assumed accuracies (0.1 and 0.4) in the direct genomic values (**DGV**). See Table 1 for definitions of all scenarios. For reference purposes, we considered a scenario (labeled **No EI**) mimicking the current Nordic breeding goal; however, **EI** was not included in the breeding goal and no indicator trait was recorded.

Table 1. Description of scenarios, indicator traits, scale of recording, and genetic correlations (r_g) between breeding goal traits and the indicator traits, heritabilities, number of bulls (N), and number of daughters per bull (N_d), as well as accuracies of direct genomic values (r_{IA}) used in scenarios¹

Scenario ²	Indicator trait	h^2	r_g of EI	r_g of MP	r_g of FT	N	N_d	r_{IA}
No indicator trait	No indicator trait	—	—	—	—	—	—	—
Large-scale milk recording herds								
STAY	Stayability	0.02	−0.30	0.20	0.20	4,000	150	0.67
STAT	Stature	0.40	0.10	0.35	0.10	4,000	150	0.72
Medium-scale automated milking system herds								
LW	Live weight	0.30	0.20	0.20	0.10	3,000	50	0.70
BRH _F	Breath of the cow	0.20	0.50	−0.10	−0.10	3,000	50	0.69
BRH _U	Breath of the cow	0.20	0.50	0.10	0.10	3,000	50	0.69
Small-scale contractor herds								
RFI	Residual feed intake	0.35	0.60	−0.45	0.20	—	—	0.46
METH _{N4}	Methane gas	0.25	0.80	−0.05	0.00	—	—	0.40
METH _{F4}	Methane gas	0.25	0.80	−0.20	−0.20	—	—	0.40
METH _{N1}	Methane gas	0.25	0.80	−0.05	0.00	—	—	0.10
METH _{F1}	Methane gas	0.25	0.80	−0.20	−0.20	—	—	0.10

¹MP = milk production; FT = functional traits; EI = environmental impact. The accuracy of direct genomic values (r_{IA}) is the correlation between the index (I) and true breeding value (A).

²Subscripts U, N, and F stand for unfavorable, neutral, or favorable correlations. Subscripts 1 and 4 for METH represent 2 levels of assumed accuracies (0.1 and 0.4).

Genetic Parameters

The genetic parameters for all 3 breeding goal traits were identical in all scenarios (Table 2). Heritabilities for MP and FT were the same as those used in the Nordic Cattle Genetic Evaluation. A moderately high heritability was given to EI. In the present study, EI was expressed as total enteric GHG emissions from the cow including the heifer period per lifetime milk production. Thus, reduced replacement rates and increased MP per cow were assumed to be beneficial for the environment. This is valid if the enteric GHG emissions related to the maintenance are the same regardless of milk production level. The genetic correlations for EI with MP and FT were based on the assumption that both productivity and functionality correlate favorably with EI (Garnsworthy, 2004; Wall et al., 2010; Bell et al., 2011).

Heritabilities and genetic and residual correlations used for STAY, STAT, LW, and RFI were drawn from a review of the literature in this field (Vollema and Groen, 1997; Bijma et al., 1998; Vollema et al., 2000,

Haile-Mariam et al., 2004; De Haas et al., 2007; Valimont et al., 2010; Williams et al., 2011; Table 1). Lassen (2011) estimated the heritability of BRH to be 0.33 (± 0.17). A more conservative heritability (0.20) than that presented by Lassen (2011) was used because of the large standard error. The heritability of METH was taken to be higher than that of BRH because the respiration chamber was assumed to be a more precise recording technique.

The genetic correlations between EI and indicator traits were set to values that depended on how strongly the indicator trait was connected to enteric emissions of CH₄. High lifetime milk production of a cow lowers the GHG emissions per kilogram of milk (Garnsworthy, 2004; Bell et al., 2011). In view of the positive effect of improved stayability on the environment, a genetic correlation of −0.30 was used between STAY and EI. In dairy cattle, smaller size and lower weight at the same level of production provide potential benefits for the environment, as the energy requirements for cow maintenance are higher in large and heavy cows. However, this very much depends on the cow's production, and,

Table 2. Genetic (above the diagonal) and residual (below the diagonal) correlations, heritabilities (on the diagonal) used for the breeding goal traits and correlations between true breeding values of MP and FT and their direct genomic values¹

Item	MP	FT	EI	MP _g	FT _g
MP	0.30	−0.30	−0.30	0.71	−0.21
FT	0.10	0.04	−0.20	−0.21	0.68
EI	0	0	0.20	−0.21	−0.14
MP _g	0	0	0	0.99	−0.15
FT _g	0	0	0	0	0.99

¹MP = milk production; FT = functional traits; EI = environmental impact; g = genomic trait.

therefore, low genetic correlations between STAT and EI and LW and EI were used. The genetic correlation between BRH and EI was set to 0.50. This might seem low, as BRH measures the enteric methane emission that is the main part of EI in the present study. However, we treated BRH and METH as different traits because BRH only measures the enteric GHG emissions from the breath of the cow during milking, and not the total enteric emissions that are recorded in respiration chambers. Residual feed intake is very often the focus of efforts to lower the enteric emissions by improving feed efficiency (Hegarty et al., 2007; Williams et al., 2011), and it was assumed to have a high genetic correlation to EI. The highest genetic correlation was assumed to be between METH and EI, as a respiration chamber is the most accurate way of measuring enteric GHG emissions from dairy cattle.

The genetic correlations between indicator traits such as BRH and METH and more traditional production and functional traits are still uncertain, so alternative sets of genetic correlations between these traits were tested. The correlations used for BRH and MP, and BRH and FT were both either -0.10 (favorable) or 0.1 (unfavorable; scenarios BRH_F and BRH_U). Neutral correlations used between METH and MP, and METH and FT were -0.05 and 0.00 (scenario $METH_N$), respectively. Favorable correlations between the same traits were -0.20 and -0.20 (scenario $METH_F$).

Phenotypes and True Breeding Values

True breeding values for all breeding goal and indicator traits were simulated for males and females. Phenotype records for MP and FT were simulated for first lactation cows. Daughter information (daughter deviations) was sampled for all young bulls on the basis of 150 daughters in the national milk recording scheme with records for MP, FT, and indicator traits recorded in all herds (STAT and STAY), and 50 daughters for medium-scale traits LW and BRH (Table 1). This progeny test information was available for bulls at 6 yr of age. The indicator traits RFI and METH were assumed to be recorded on dairy cows in a few contractor herds, and no daughter deviations from the national milk recording scheme were simulated for these traits.

Accuracy of Genomic Breeding Values

Direct genomic values were generated for all genotyped animals by modeling DGV as separate genomic traits (i.e., no actual chromosomes, genes, or markers were simulated). Each genomic trait had a heritability equal to 0.99 and a genetic correlation with the observed trait equal to the assumed accuracy of DGV. All other

genetic correlations among the real and genomic traits were derived following the path-coefficient approach described by Dekkers (2007) and Buch et al. (2012b). Accuracies of DGV were calculated using the method proposed by Goddard (2009) assuming that the reference population was sufficiently related to the selection candidates. The input parameters in these calculations were length of the genome in Morgans (30), historical effective population size (300), size of the reference population (N), number of offspring per animal in reference group (N_d), number of SNP in the chip (40,000), and heritability of the trait. The parameters N , N_d , and heritability varied among traits as shown in Table 1. The reference population for MP, FT, STAY, and STAT was larger than for LW and BRH, reflecting that the latter traits are not routinely recorded at present and a reference population needs to be established first.

The accuracy of DGV for RFI was set to 0.46. As an example, this accuracy could be achieved by having 300 sires with 10 daughters each in the reference population. The accuracies of DGV of METH scenarios were set to 2 levels: 0.40 and 0.10. The accuracies 0.40 and 0.10 could be gained by including 250 sires with 8 daughters each respective 10 sires with 8 daughters each in the reference population.

Breeding Scheme

The breeding scheme used in the simulations was selected as the best of the 4 designs tested by Buch et al. (2012b). The population consisted of 200 breeding herds representing the breeding nucleus part of the medium-sized dairy cattle population. Each herd had 100 cows, giving us 20,000 cows in total. Selection of females was performed within herd but across age groups, and cows were available for selection until they were 5-yr-old. Every selected female gave birth to 1 calf per year with a sex ratio of 0.5. Involuntary culling across the whole population was set to 15%.

Annually, 2,000 heifer calves and 2,000 bull calves were assumed to be genotyped. From the 2,000 genotyped bull calves, 200 young bulls were selected to be progeny tested. For each bull, 5,000 doses of semen were stored and bulls were subsequently culled. Test inseminations were assumed to have been performed in commercial herds only. Daughters used for progeny test in these commercial herds were not explicitly simulated, but information provided by them was summarized for the bulls (daughter deviations).

In all, 30 proven bulls were selected by truncation, but subject to rules to control levels of inbreeding, from among all available genotyped young bulls as well as genotyped and progeny tested bulls; this allowed young bulls with high GEBV to be used intensively.

Table 3. The annual genetic gain (ΔG) and the genetic response in milk production (ΔG_{MP}), functional traits (ΔG_{FT}), and environmental impact (ΔG_{EI})^{1,2,3}

Scenario	ΔG^4 (€)	ΔG_{MP}^5	ΔG_{FT}^5	ΔG_{EI}^5
No IT	46.6 (0.20)	0.251	0.161	-0.152
Large scale				
STAY	51.4 (0.24)	0.259	0.184	-0.180
STAT	49.4 (0.23)	0.260	0.180	-0.160
Medium scale				
LW	48.1 (0.24)	0.246	0.171	-0.166
BRH _F	50.5 (0.20)	0.238	0.171	-0.203
BRH _U	48.9 (0.22)	0.235	0.159	-0.198
Small scale				
RFI	49.6 (0.24)	0.252	0.164	-0.183
METH _{N4}	49.5 (0.22)	0.241	0.166	-0.192
METH _{F4}	49.8 (0.23)	0.242	0.171	-0.191
METH _{N1}	47.5 (0.22)	0.246	0.174	-0.156
METH _{F1}	47.7 (0.21)	0.247	0.173	-0.158

¹For abbreviations see Table 1.²The standard errors for the ΔG_{MP} , ΔG_{FT} , and ΔG_{EI} were 0.002.³All differences between scenarios in the annual monetary genetic gain larger than 0.6 and in genetic gains in breeding goal traits larger than 0.005 are significant at 5% level, according to Fischer's least significant difference test.⁴Standard errors for ΔG are in brackets.⁵Presented in genetic standard deviation units.

Proven bulls were used equally and randomly mated in all breeding herds, producing 667 offspring each. The age span of bulls accepted for breeding was set at 1 to 9 yr. The maximum number of offspring selected for genotyping per sire per year was set to 200 of each sex, and the total number of offspring over all years was set to 800. Each bull could sire a maximum of 20 young bulls per year and 40 young bulls in total; finally, each bull could sire a maximum of 6 proven bulls per year and 9 in total.

Data Analysis

The stochastic simulation program ADAM (Pedersen et al., 2009) was used to test the scenarios. The time period in each scenario was 25 yr. All scenarios were replicated 100 times. The results were averaged over years 11 to 25. Years 1 to 10 were excluded from the calculations to avoid noise caused by the establishment of equilibrium of age structure and the Bulmer effect. Fisher's least significant difference test was used to test whether the differences between scenarios were significant at 5% level.

RESULTS

When results from the scenarios using large-scale indicator traits were compared, it was found that the genetic gain in EI was higher in scenario STAY than in scenario STAT. Also, the genetic gain in FT was somewhat higher in scenario STAY. The difference in

genetic gain in MP between these 2 scenarios was very small. Scenario STAY consequently had higher annual monetary gain (Table 3).

Indicator traits LW and STAT represent the conformation of a dairy cow. Scenario LW was superior over scenario STAT in genetic gain in EI. The genetic gains in MP and FT were 6 and 5% higher in STAT compared with LW. Scenario STAT resulted in 3% higher annual monetary gain than scenario LW.

The traits STAY and STAT recorded in all herds and LW recorded in AMS herds are relatively easy to measure and could serve as indicator traits for EI without too much effort and expense. However, comparing these scenarios with scenario No IT shows that only scenario STAY resulted in substantial additional gain in EI; gains being 18% higher in scenario STAY than in scenario No IT. The same genetic gain was only 5 and 9% higher in scenarios STAT and LW than in scenario No IT. The genetic gain in MP and FT was also higher in STAY and STAT than in No IT. The annual monetary gain was €51.4 in scenario STAY, which was the highest annual monetary gain of all analyzed scenarios. This gain was 10% higher than the annual monetary gain in scenario No IT, whereas scenarios STAT and LW resulted in 6 and 3% additional gain, respectively, compared with No IT.

The medium-scale indicator trait BRH was more challenging to record than the indicator traits STAY, STAT, and LW, but as an indicator trait for EI it resulted in significantly higher genetic gain in EI. The genetic gains in EI in scenarios BRH_F and BRH_U were

−0.203 and −0.198, respectively, being about 20 to 27% higher than in scenarios STAT and LW and 10 to 13% higher than in STAY. The difference in annual monetary gain in scenarios with BRH_F and STAY was rather small. Using BRH_F and BRH_U as an indicator traits resulted in a 9 and 10% reduction in genetic gain in MP and an 8 and 16% reduction in genetic gain in FT, respectively, compared with scenario STAY.

The comparison of sets of favorable and unfavorable correlations between BRH and the breeding goal traits MP and FT showed that scenario BRH_F resulted in 3% higher annual monetary genetic gain compared with scenario BRH_U. Also, the genetic gain in FT was significantly larger when BRH was favorably correlated with MP and FT, whereas only a 1% difference in genetic gain in MP between these 2 scenarios was observed. The scenario BRH_F resulted in a slightly higher genetic gain in EI, this difference was insignificant, however. The differences between scenarios BRH_F and BRH_U confirm that information about genetic correlations between BRH and MP and FT is required when the consequences of the breeding program are predicted.

The genetic gain in EI in the scenario with the small-scale indicator trait RFI was 0.183 genetic standard deviation units and 20% higher than the genetic gain in EI in scenario No IT. When compared with BRH, the genetic gain in EI in scenario RFI was 8 to 11% lower, however, it resulted in significantly larger gain in MP compared with BRH_F and BRH_U. The differences in genetic gain in FT between these scenarios were small. When compared with METH_{F4} and METH_{N4} the scenario RFI also resulted in about 5% lower genetic gain in EI, whereas small differences in the annual monetary genetic gain were observed between these scenarios.

The METH scenarios with an accuracy of 0.10 resulted in the lowest annual monetary genetic gain of all scenarios with indicator trait. Neutral or favorable correlations to MP and FT had a small effect on the annual monetary genetic gain. Also, the genetic gains in EI were lowest in METH scenarios with low accuracy, whereas the genetic gains in EI in METH scenarios with an accuracy of 0.40 were among the best 4. The genetic gain in EI in scenarios METH_{N4} and METH_{F4} were 26% higher than in No IT. The genetic gain in MP was 4% lower in METH_{N4} and METH_{F4} than in No IT. These results show that it is important to have a rather high accuracy of DGV for traits such as METH to make significant genetic progress.

The scenarios BRH and METH use information about enteric CH₄ emissions from cows. The genetic gain in EI was larger in BRH scenarios, despite the higher correlation between EI and METH than between EI and BRH. The level of accuracy of DGV based on

the size of reference population is the main reason why BRH exceeds METH.

In the scenario No EI, where no economic weight was attached to EI and no indicator traits were recorded, a favorable genetic response in EI of −0.151 genetic standard deviation units was observed. The genetic response in MP and FT were 0.237 and 0.180 genetic standard deviation units, respectively.

The rate of inbreeding per generation was between 0.66% (±0.005) and 0.73% (±0.006) in all scenarios being lowest in METH and highest in LW. The generation interval was around 2.5 yr in all tested scenarios, varying from 2.53 (±0.003) years in scenario STAY to 2.67 (±0.002) years in scenario No IT.

DISCUSSION

This study tested the hypothesis that specific indicator traits recorded in a small number of contractor herds can be implemented in breeding schemes with genomic selection with a favorable outcome. The simulation showed, however, that the annual monetary genetic gain was highest in the scenario that included an indicator trait recorded on the large scale (STAY), despite the low heritability of this indicator trait and the modest correlation between EI and the indicator trait. Nevertheless, the genetic gain in EI was highest in scenarios that included an indicator trait that had high correlation to the breeding goal trait EI and high accuracy of direct genomic breeding values. The annual monetary gains were somewhat lower in these scenarios compared with the best large-scale scenario, but they were still significantly higher than the scenario that did not include any indicator trait for the environment. Therefore, genetic progress in EI is possible when specific indicator traits are used; however, it requires a reference population of an adequate size so that the accuracies of direct genomic breeding values are reasonably high. In this study, the indicator traits were related to EI, but the simulated results are valid for any trait that has a moderate heritability but is complicated to record; for example, coagulation properties of the milk or energy balance in cows.

The rate of inbreeding per generation was considerably lower than 1%, which is the maximum level of inbreeding per generation recommended by the Food and Agriculture Organization of the United Nations (Woolliams, 2007). The generation interval for bulls was around 2.5 yr, which is approximately 3 yr shorter than a progeny testing scheme. The opportunity this interval offers, to select accurately among young animals, is one of the main benefits of genomic selection (Pryce and Daetwyler, 2012). Short generation intervals

improve annual genetic gain through their interaction with the accuracy of genomic breeding values (Buch et al., 2012b).

The genetic gain in EI in scenario No EI, which had a breeding goal similar to that used in the Nordic countries, confirms that selection for increased production and improved functionality is good for the environment. This result is in agreement with studies that encourage improving the productivity, fertility, and health of the livestock to reduce EI (Wall et al., 2010; Bell et al., 2011).

Including EI in the breeding goal and recording a correlated indicator trait ensured that the genetic gain for EI was considerably higher than that in scenario No EI. However, no benefit was observed when EI was included in scenario No IT. This demonstrates that genetic progress would be faster if an indicator for EI is included among the selection criteria. The highest genetic responses were achieved when the accuracy of DGV of the indicator trait was at least 0.4 or when the indicator trait had a high correlation ($|r_g| \geq 0.3$) with EI. One of the positive findings was that a reduction in EI can be achieved with only a small decrease in genetic gain in milk production.

In this study, we simulated 2 scenarios with a large-scale indicator trait (STAY and STAT). Stayability after the first lactation was the only indicator trait in this study that had a low heritability. Still, STAY obtained a rate of annual monetary genetic gain that exceeded those of all other simulated scenarios. On the contrary, the indicator trait STAT had the highest heritability of all indicator traits used, the same number of phenotype records, and even slightly higher accuracy of DGV, but resulted in 4% lower annual monetary genetic gain than STAY. Also, the gain in EI in the scenario STAT was one of the lowest of all scenarios. This can be explained by the lower correlations between STAT and EI compared with the scenario STAY. In general, the combination of the correlation between IT and EI and the accuracy of the DGV determined the results. The heritability of the indicator trait had very little effect on the results in this study.

Two levels of accuracy were assumed for DGV of METH: 0.40 and 0.10. Calculations proposed by Goddard (2009) can be used to assess how large the reference population needs to be to achieve the required accuracies. For example, a reference population of 250 bulls with 8 daughters each would give an accuracy of 0.40 when the input parameters from the present study are used. The accuracy of 0.10 could be achieved with only 10 bulls with 8 daughters, but this level of accuracy was clearly not enough to achieve any additional genetic gain in the correlated breeding goal trait. Higher accuracies than 0.10 might be hard to reach

because of the costs and complexity of recording connected to METH. Studies have been published that see potential in reference populations, including genotyped cows, and also have phenotypic records for novel traits such as methane emission (Pryce and Daetwyler, 2012). Buch et al. (2012a) compared 2 reference populations consisting of either cows with phenotypic records or sires of these cows, and they found that the reference population consisting of cows resulted in highest accuracy of the DGV regardless of the heritability of the trait. Knowing the relationship between animals in the reference population is important and has an effect on the accuracy of DGV. A study by Pszczola et al. (2012) proposed using a reference population of closely related animals if the breeding values are predicted for selection candidates only, and a reference population of unrelated animals for predicting the breeding values for all animals in the population. Further research is needed to find the optimal design of the reference population for novel traits.

The idea of using contractor herds was first proposed by Schaeffer (2006) to decrease the costs of recording when new traits are included in a breeding scheme with genomic selection. Several breeding companies have experience in using nucleus herds in breeding programs; thus, it might be relatively easy for them to create a recording system for new traits based on contractor herds. The system where a novel trait is recorded in specific herds could be created of herds within a country, but it might be more beneficial to establish collaborations between countries. International collaboration could be a way to increase the number of phenotype records and the number of animals in the reference population (de Haas et al., 2011). It could also be an effective way to lower the costs of recording per country, as long as the relationship between the reference population and the selection candidates in all countries is sufficiently high.

Research into ways of finding and testing new technologies to collect more phenotype records with higher precision on enteric GHG emissions is being undertaken. Lassen et al. (2012) showed that Fourier transform infrared detection can be used to record gases in the breath of the cow, and that this information could potentially be used in the genetic evaluation of dairy cattle. As an indicator trait in the present study, BRH seemed very promising. The BRH with favorable correlations to all breeding goal traits resulted in an annual genetic gain that was highest of all indicator traits measured on a medium or a small scale. Whether the correlation between BRH and FT was favorable or not had almost no effect on the progress in EI, but it had a significant effect on the genetic change in FT. The genetic gain in FT decreased in scenario BRH_U (and also in RFI and METH_{N4}), but the trend was still favorable.

The accuracies of DGV for BRH were assumed to be rather high, because, owing to technological solutions that may make it possible to record BRH in ordinary AMS herds in the future, a much bigger reference population for this trait could be established than for any of the small-scale indicator traits. Meanwhile, STAY could be an easy alternative in spite of its very low heritability. Stayability after the first lactation requires no additional measurements and increases the genetic gain in EI by 18% compared with No IT. Nevertheless, a favorable genetic correlation (-0.30) between STAY and EI was used in the simulation based on the assumption that the enteric GHG emissions from the heifer period are more diluted if the cow has a long, productive life; if this correlation turns out to be lower, STAY may be less valuable as an indicator trait for EI. Reduced methane emissions can be related to lower feed intake (Beauchemin et al., 2009), which could influence cow longevity. Unfavorable consequences of increased loss of body reserves for reproduction and disease resistance have been reported in several studies (Bello et al., 2012).

The trait EI, included in our breeding goal, does not yet exist in any breeding goal in the world, but the EI caused by the dairy industry is attracting increasing public attention, and scientists and politicians are actively working on this issue. For example, the European Union is aiming to reduce net CH_4 emissions from dairy cows by 4% by 2015. This aim is expected to be fulfilled, partly owing to the decreasing number of cows (O'Mara, 2006). However, as the world's human population is growing rapidly, the need for food is growing as well. Therefore, it is important to breed for more efficient and productive cows. The dairy industry has an important role in providing people with high-quality food, but we also need to find a way to make milk production more sustainable. Genetic progress depends on the economic value of the goal traits, which, in turn, depends on costs and incomes. The costs of EI, such as climate change, are difficult to estimate. In this study, EI had the same economic value as MP. A realistic economic value for EI remains to be calculated, as no economic market value for EI exists yet. However, an economic market value for EI could be calculated through traits such as feed conversion efficiency, which have both an economic value and a high correlation with EI. Feed conversion efficiency is an economically interesting trait for dairy cattle breeders given rising feed costs (H. Stålhammar, Viking Genetic, Skara, Sweden, personal communication). A case can also be made for selecting to improve the energy efficiency of dairy cattle (Mäntysaari et al., 2012). Authors such as Wirsén et al. (2010) discuss GHG taxes on food of animal origin. It is not impossible that GHG taxes on

milk production could be implemented, or some form of climate label on dairy products. Either of these may influence consumers' willingness to pay for dairy products. Taxes, subsidies, and labeling would generate an economic market value for EI and stimulate interest in the addition of traits such as EI to the breeding goal.

The present study suggests that, by including the EI in the breeding goal and recording highly correlated indicator traits, it will be possible to achieve genetic gain that lowers the EI of milk production. The question remains whether this would make economic sense, however. As we know, the highly correlated indicator traits are exclusive and, therefore, costly to record. The next step would be to investigate the costs of the scenarios presented in this study.

CONCLUSIONS

Breeding goals, including production and functional traits, are beneficial for the environment. However, by including EI in the breeding goal and using phenotype records and genomic information of correlated indicator traits, the genetic gain in EI can be enhanced by 20 to 34%. The genetic gain in MP and FT decreased by 5 and 7% in a scenario using the methane in the breath of the cow as an indicator trait. The most valuable indicator traits for reducing EI are those with a high genetic correlation ($|r_g| \geq 0.3$) with EI that also have high accuracy of DGV. Therefore, it is important to establish a reference population that is large enough for estimation of adequate accuracies of the direct genomic breeding values. Low accuracy of DGV of an indicator trait recorded on a small scale resulted in no additional genetic gain in EI compared with a scenario with no indicator trait, despite a high correlation between the breeding goal trait and the indicator trait.

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