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Current challenges for trait economic values in animal breeding

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Abstract: Modern selection approaches are expected to bring about the cumulative and permanent improvement of animal performance and profitability of animal production. Breeding values of traits along with trait economic values (EVs) are utilised for economic selection purposes with many species all over the world. Currently, some challenges related to trait EVs in animal breeding should be considered. First, the selection response based on the higher accuracy of genomic selection may be reduced due to improper weighting of the trait breeding values of selection candidates. A comprehensive approach applied in bioeconomic models allows suitable trait EV calculations. Further challenges comprise the new breeding objectives associated with climate change, environmental mitigation and animal adaptability. The estimation of EVs for traits influencing greenhouse gas (GHG) emissions has been mostly based on including the value of CO_2 emission equivalent in the trait EVs, on calculating EVs for feed efficiency traits and on methane yield as a direct trait of GHG emission. Genetic improvement of production, functional, feed efficiency and methane traits through the application of multi-trait selection indices was found to be crucial for mitigation of emissions and farm profitability. Defining the non-market values of traits connected with climate protection could be a useful solution for including these traits in an economic breeding objective. While GHG emissions mostly change the costs per unit of production, animal adaptability in its complexity influences animal performance. Clear definitions of disease, fertility, mortality and other breeding objective traits allow the proper calculation of trait EVs, and an accurate estimation of trait genetic parameters could lead to sufficient economic selection response. This complex approach could be beneficial for more effective utilisation of inputs and overall economic and environmental sustainability of animal production.

Keywords: breeding objectives; selection index; bioeconomic model; climate change; emission mitigation; heat tolerance

Introduction

Modern selection approaches are expected to bring about a cumulative and permanent improvement of animal performance and subsequently the enhanced profitability of animal production. Estimated genetic and genomic breeding values of traits along with trait economic importance (trait economic weights; EVs) are used for economic selection purposes with many species all over the world. The basic definition of an economic breeding objective (aggregate genotype) and its importance in selection processes were established by Hazel (1943). In his theory, the trait EV is defined as a change in the profit of a specific animal production system derived from increasing the trait mean by one unit while keeping the means of all other traits in the aggregate genotype unchanged.

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The methodological framework for deriving the trait economic weights to solve the current challenges in the construction of selection indices was presented by Amer et al. (2018). Recently, trait EVs were published in many papers dealing with dairy and beef cattle (Krupova et al. 2018; 2020a), goats (Fuerst-Waltl et al. 2018), pigs (Krupa et al. 2020), rabbits (Krupova et al. 2020b), poultry (Chaowu et al. 2016), fish (Besson et al. 2020) and other livestock species. To define the trait EVs and provide their proper application in a breeding process, several aspects were considered in the literature (e.g., Wall et al. 2010; Wolfova and Wolf 2013; Chaowu et al. 2016; Hietala and Juga 2017; Ali et al. 2018; Besson et al. 2020). Various methodologies for the calculation, trait definitions, analyses of trait EV sensitivity to national legislation (subsidies, production quotas, climate changes) and to production and economic conditions as well as the environmental, social and health consequences of economic selection have been studied. Currently, there are some challenges associated with the estimation of EVs for breeding objectives and selection traits, mainly considering the proper calculation of EVs (Hirooka 2019), climate change and environmental mitigation (Cassandro 2020).

The main aim of the present study was to perform an overview of actual trends and challenges related to trait EVs applied in animal breeding.

Economic values of breeding objective traits

PROPER TRAIT EVs

In the genomic selection area, the proper derivation of trait EVs is more important than it was previously due to the higher accuracy of genomic selection (Hirooka 2019). The author noted that the comprehensive approach applied in bioeconomic models allows suitable trait EV calculation. Variability in animal performances, in production, management and marketing strategies or in economic input data can be considered in such models. Bioeconomic models have already been effectively applied in many studies (some of them are listed above). The number of traits for which the EVs were calculated by these models varied greatly depending on the evaluated population and its breeding objective. For instance, in sheep breeding, specific bioeconomic models were targeted to lamb and wool traits of meat breeds (Wang and Dickerson 1991), whereas more general models evaluating dairy, meat, functional, carcass, and wool traits were developed for dual-purpose sheep breeds (e.g., Wolfova et al. 2009).

General principles (mostly based on normative approaches) applied in bioeconomic model construction allow successful application for various livestock species. The model developed for cattle was adopted for goats (Fuerst-Waltl et al. 2018). Similarly, comprehensive models for trait EV calculation in different production systems of cattle, sheep, pigs and rabbits and related computer programs (Wolfova et al. 2009; Krupova et al. 2018; Krupa et al. 2020; Krupova et al. 2020a,b) have been gradually developed and upgraded as part of the software package ECOWEIGHT. Likewise, in bioeconomic models for chickens developed to calculate trait EVs, comparable principles were applied for broilers and for quality production systems (Chaowu et al. 2016), and the authors suggested extending this model for other poultry types, such as turkeys and ducks.

CLIMATE CHANGES AND ENVIRONMENTAL MITIGATION

Further selection challenges have been concerned with new objectives associated with climate change, environmental mitigation and animal adaptability (Cassandro 2020). Artificial intelligence, genome editing, and comprehensive and effective approaches are recommended by the author as strategic tools that livestock breeders will face to reach healthy and effective production in the near future. In addition to dietary and management interventions, breeding and selection are commonly recommended to gain from long-term and cumulative changes in animal performance. It can be stated that after decades of breeding for improved "classical" production, reproduction, carcass and health traits, the door has been open for more complex breeding to improve so-called "climate traits". In this context, the selection of animals for objectives linked to climate change (e.g., to global warming) would reduce the environmental footprint of animal production and improve animal adaptability to the retroactive impact of climate change on animal performance. Along with comprehensive genetic and genomic evaluation (reviewed by Chesnais et al. 2016; Pryce et al. 2018

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and applied by Nguyen et al. 2017), the economic importance of such climate traits in the breeding process should be known. Similarly, as carried out in selection for improving "classical" traits, objective and subjective approaches have been applied in the literature to estimate the impact of animal resistance to climate change and animal climate trait levels on the economic efficiency of animal production.

Feed efficiency. Greenhouse gas (GHG) emissions play an important role when evaluating climate change and the environmental footprint of animal production. Ideally, direct environmentally related traits (such as greenhouse gas emissions and nitrogen excretion) should be included in national breeding objectives with their own EVs (Berry 2013). However, methods for practical collection of information about methane emissions and feed intake on an animal basis that are needed for direct selection are not clear (Fennessy et al. 2019) and may be difficult in practice (Wall et al. 2010). Moreover, focusing the breeding objectives solely on reducing animal environmental footprints is not recommended (Berry 2013). Methane emissions could mostly be measured as total production per whole production system or per animal (as gross emissions) and per unit of the trait of interest [as emissions intensity; Amer et al. (2018)]. Reduction of environmental load per unit of production is suggested as a relevant solution. Expressing the emissions from livestock as a function of the appropriate trait level, the environmental value of that trait can be calculated and used to construct environmental selection indices (Wall et al. 2010). Generally, under the current conditions, direct improvement (e.g., reduction) of the environmental footprint through GHG emissions as a direct selection criterion is not economically, and thus practically, applicable. Additional costs are not overweighed by economic benefits. Genomic methods should probably provide sufficient solutions for direct selection of such traits in the future. These aspects are discussed in detail in the following text.

Animal selection considering environmental mitigation has mostly focused on an indirect reduction of emissions per unit of animal products by effective improvement of production and functional traits (Wall et al. 2010). The next possibility has been accomplished by improving animal feed efficiency traits (Bell et al. 2013). In some studies (Bell et al. 2016; Fennessy et al. 2019; Richardson et al. 2020), methane yield as a direct trait for selection on GHG mitigation was applied. Therefore, the estimation of weighting coefficients for breeding objective and selection index traits influencing GHG emissions has been mostly based on:

1. Inclusion of the value of CO_2 emission equivalent in trait EVs;
2. calculation of EVs for feed efficiency traits;
3. calculation of EVs for methane yield.

To calculate cattle trait EVs under the assessment of the carbon emissions from cattle production systems, the shadow price of carbon (SPC) has been involved in production costs (Aby et al. 2013), or carbon credits offsetting GHG emissions have been applied as income (Bell et al. 2013). In both approaches, the indirect economic consequence of the given carbon price is considered as the SPC providing the rising monetary value for GHG emissions through time (Wall et al. 2010). Carbon credits (which represent the provision coming from the public sector to compensate the carbon price) relevant for the year 2012 were applied to calculate EVs of eight traits in the Australian dairy production system (Bell et al. 2013). Accounting for such incomes, the marginal EVs for some of the evaluated traits (live weight, cow survival, DMI and calving interval) slightly increased (by 8% on average), remained the same (such as milk volume and SCC) or were slightly reduced (fat yield by 8%); thus, their relative participation in the total net income changed minimally (±2% points on average). A small variation in marginal trait EVs for Holstein and Jersey breeds just reflected different levels of production and fitness traits of these breeds (Bell et al. 2013).

Aby et al. (2013) accounted for the SPC relevant for the years 2020 and 2030 in the EV calculation for 14 production and functional traits of beef cattle using a bioeconomic model. The overall effect of SPC on the trait relative EVs was negligible, suggesting that trait EVs are robust towards the inclusion or absence of GHG emission costs in the calculation. Similar results, i.e., a slight increase in the marginal and thus relative EVs (because the trait genetic standard deviations remained the same) of production traits and a decrease in those of functional traits were obtained after adding SPC for 2015 in pigs (Ali et al. 2018). However, these authors expected that the impact of mitigation costs on trait EVs could increase due

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to increased SPC in the future. Most likely, the comprehensive revaluation of trait EVs under a new relevant price of carbon and under further changed circumstances of animal production systems will be needed. This revaluation has also been regularly done for the EVs of "classical" traits after certain periods. Some uncertainty about parameter values used for trait EV calculation in different production systems remains a limiting factor in both types of GHG emission evaluations. In addition to the relevant production and economic conditions of livestock production systems, feed quality may be important for the trait EVs incorporating the SPC. Aby et al. (2013) showed that relative EVs of functional traits (productive lifetime of cows, age at first calving and calving interval) were slightly reduced when decreasing roughage quality, which could become more relevant under climate change in the future.

Genetic improvement of production and functional traits was found to be the key point for reducing GHG emissions and for farm profit in the above-mentioned papers and in papers reviewed by Wall et al. (2010). The reduction of GHG emissions due to animal selection would lower the environmental footprint of these traits (Berry 2013). Functional traits (e.g., productive lifetime and survival in general) have been commonly considered to be responsible for the effective utilization of inputs for the elimination of wastage and measurable environment mitigation (Wall et al. 2010). In pig breeding, it was found that GHG emissions were more intensively reduced by genetic improvement of production than by reproduction traits (Ali et al. 2018). Similarly, in dairy cattle breeding, a reduction in emissions could be achieved more easily by improving production traits than by improving fitness traits because of the low heritability of the latter traits (Bell et al. 2013). Higher genetic variation and significantly higher contribution of production traits to economic selection gain were the main reasons for these findings. For the Irish dairy cattle sector, it was estimated that the genetic trends in production and functional traits in the last decade favourably reduced the emission intensity by approximately 5% (Amer et al. 2018). Further reduction of emission intensity by 15% is expected in this study due to acceleration of genetic trends in the next 15 years. When considering the current genetic trends in the New Zealand national breeding objective traits (Zhang et al. 2019), the annual emission intensity is reduced by 0.43% per milk protein equivalent and per cow with a direct positive effect on production efficiency. To reach the national methane reduction targets in the next 20 years, some new criteria for reduced methane production should be considered in selection (Zhang et al. 2019). Similarly, in the Australian dairy sector, the reduction of carbon emissions by 10% and 6% was calculated after 10 years and for the next 10 years of selection, respectively. The emission reduction over the last decade was based on the fact that higher emissions per cow (by ~55 kg carbon equivalent) have been fully outweighed by reduced numbers of cows (by 140 000 cows) in the dairy sector. Generally, such trends in reducing the environmental impact are recommended to improve both the economic efficiency and public acceptability of livestock farming.

An enhancement of feed efficiency, through an improvement of feed conversion or DMI (as a proxy trait) or through decreasing animal residual feed intake (RFI), is generally beneficial for the reduction of GHG emissions. In addition to climate protection, this improvement has brought measurable economic gains. High feed efficiency represents savings of feed per unit of product. The relative economic importance (relative EVs) of feed efficiency traits varied among species and production systems and depended on the number of traits simultaneously evaluated. In dairy cattle systems, RFI participated by 6% to 13% in the total economic importance of the complex of 12 to 20 traits (Bell et al. 2016; Hietala and Juga 2017; Krupova et al. 2018). When DMI, as a proxy trait of feed efficiency, was used in the selection index of the Australian dairy population (covering the complex of 10 traits), the contribution of this trait to the total trait economic importance was approximately 24% and 25%. The first value was obtained after omitting, the second after including the incomes from carbon credits (Bell et al. 2013). In the extensive beef cattle production systems based on pasture (a system with low feed prices), the relative EVs of heifer and cow RFI were low [4% both; Krupova et al. (2020a)]. Contrary to chicken breeding, where feed is generally the main source of farm expenses, the contribution of RFI to the total economic value of seven traits was approximately 35% (Chaowu et al. 2016). For the feed conversion ratio in a pig enterprise, a similar contribution to the total economic importance (over 30%) of five evaluated traits was calculated (Ali et al.

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2018). When a complex of 19 traits in dam and sire pig breeds was taken into account (Krupa et al. 2020), this contribution ranged from 16% to 24%. Calculating relative EVs for two fish traits, the feed conversion ratio participated in the economic importance of both traits with 76% (Besson et al. 2020). In an example commercial rabbit production system, the feed conversion ratio would contribute approximately 15% to the total economic importance of 12 traits (Krupova et al. 2020b). Generally, systematic revaluation of trait EVs will be desirable because the EV of traits connected with emission mitigation will probably increase in the future, favouring animals with more environmentally efficient production.

Improving feed efficiency and decreasing methane emissions will be one of the most important selection objectives to mitigate the environmental impact of ruminants (and general livestock) all over the world (Pryce et al. 2018). The Australian dairy cattle breeding program has already taken into account the carbon credits and calculated the EVs of feed efficiency traits, as was already mentioned when citing the study of Bell et al. (2013) above. For the Canadian dairy industry, the EV of a trait called "feed performance" was estimated that combined the effect of improved feed efficiency (DMI) on feed costs with carbon price relevant for the year 2022 (Richardson et al. 2020). The EV of the final feed performance trait was then 0.89 CAD per cow lifetime considering that 1 kg of feed used more effectively by a cow on the first parity represents a decrease of 3.23 kg of DM and a reduction of 0.055 kg of methane per whole lifetime of a cow. The reduced DMI precipitated with 0.82 CAD and the reduced methane emission with 0.07 CAD to the total feed performance EV. In the study of Fennessy et al. (2019), the EV of the current beef cattle traits was adjusted to account for the carbon costs in Australian conditions. Current selection for production and functional traits could reduce methane emissions with an economic response of AUD 0.38 per cow mated per year. In this study, the EV for the trait methane yield (excreted from different animal categories) was also calculated. It expressed, in monetary units, the value of kg change of methane excretion per tonne of DM per cow. It would be alternatively included in the selection indices and breeding objectives of the local beef population. EV of enteric methane yield was calculated for the UK dairy conditions (Bell et al. 2016) considering that one kg of enteric methane per lactation leads to extra feed required for energy lost as methane (for herd replacements and lactations) along with the change in energy lost due to the heat increment from fermentation. The authors expected that selection for this trait would have the potential to improve profit and reduce emissions per cow. Direct breeding on methane would lead to a more intensive reduction in methane than indirect reduction based on improvement in production and fitness traits. However, the difficulty of measuring such phenotypes and improvements in correlated traits (e.g., feed efficiency and survival) may be more cost-effective in reducing emissions.

Additional costs associated with feed intake and methane measurements are the main inhibitors in regular monitoring of such climate traits. Furthermore, selection for improvement of traits that mitigate GHG emissions could reduce genetic gain in other traits included in breeding objectives. To solve this problem, the following considerations are taken into account:

1. Elimination of data collection on each animal in the population using genomic information, which opens possibilities for practical selection;
2. using composite multi-trait selection indices simultaneously, including feed efficiency, methane yield, production and functional traits.

Using these approaches, desired selection gain in feed efficiency traits and methane yield along with maintaining favourable genetic (and thus economic) progress in other breeding objective traits can be reached (Bell et al. 2013; Gonzalez-Recio et al. 2014; Bell et al. 2016; Hietala and Juga 2017; Krupova et al. 2018; Pryce et al. 2018). In Australian dairy herds, the desirable increase in net income and reduced production of emissions per unit of milk solids were achieved by selection based on the complex production and functional traits along with the trait DMI (Bell et al. 2013). A slight reduction in selection response for production traits achieved in this study (as an indirect consequence of decreased DMI) was compensated by lower feed costs that finally resulted in improved profitability. Later, the genomic information for RFI was incorporated into this index to add valuable information for improving the feed efficiency in the selected population (Pryce et al. 2018). The breed-

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ing value of body weight estimated from type traits combined with the genomic component of RFI was taken into consideration. As a result, the same level of milk yield could be obtained from cows predicted to eat 65 kg of DM less per year (Pryce et al. 2018).

Hietala and Juga (2017) pointed out that if the correlations of RFI with other traits of interest are not known, genetic gain in RFI can be relatively small. Including RFI in the current breeding objective and in the comprehensive selection index with 17 traits for the Czech Holstein population and using genetic parameters for RFI from the literature, a positive change (+6%) in the overall economic selection response could be achieved (Krupova et al. 2018). Similarly, an expansion of the selection index for the Australian dairy population, including cow and heifer RFIs (Gonzalez-Recio et al. 2014), improved the overall economic selection response by 3%. The relatively small increase in the total economic response after inclusion of RFI in the index in comparison with the economic response reached by selection on the original index was caused by a positive correlation between milk yield (with high positive EV) and cow weight (with negative EV connected with higher maintenance feed costs for heavier cows). Similar results were obtained by Krupova et al. (2018) after including cow and heifer RFIs in the breeding objective for the Czech Holstein population because a negative EV of mature weight and positive EV of milk production traits were also estimated. In both studies, adding the RFI in the index decreases DMI by 1.76 and 1.46 kg/cow and year, respectively, and thus indirectly reduces emissions from production.

Suckler cow herds generally produce higher emissions per kg of beef meat than dairy herds. To reduce the GHG emissions per unit of beef meat and to improve dairy farm profitability through reduced feed costs, beef meat production from dairy herds was recommended as a valuable solution under the economic conditions of Finland (Hietala and Juga 2017). Adding growth and carcass traits into the breeding objective for dairy cattle and preventing cow live weight increase (through negative EV) had a positive impact on breeding program profitability in this study. To reduce the GHG emissions in extensive beef cattle production systems without direct selection for feed efficiency traits [as is currently done, e.g., in the Czech Angus breed, Krupova et al. (2020a)], the improvement of production and functional traits using a comprehensive selection index could be aspirational. Currently, four live weight traits and easy calving only are considered in the selection of Czech Angus, although calf survival rate and cow productive lifetime have been found to be economically important traits [both covering 19% of the total economic importance of 17 evaluated traits; Krupova et al. (2020a)]. Assuming that such functional traits have a positive impact on the effective utilization of inputs and on environmental mitigation (mentioned above in the text citing Wall et al. 2010), a comprehensive selection would be economically and environmentally favourable. Genotyping of animals, recently ongoing in beef cattle populations (which is also the case for the mentioned herds), could provide important information appreciated for the reliability of the current breeding objective traits and of new feed efficiency traits.

Selection indices presently used in animal breeding usually join economic to non-economic aspects of breeding. The weight coefficients of some traits in breeding objectives and selection indices compound the trait economic value and the trait non-market value. Defining the non-market values of traits connected with climate protection (that has no objective economic market value) could be a useful solution for including these traits in an economic breeding objective. Various approaches have been developed to apply environmental considerations in the breeding process [reviewed in detail by Wall et al. (2010)]. In some of them, the non-market values were added to trait EVs to take into account losses in genetic gain for production traits in favour of desired genetic gain for other traits of interest. Another option has been to consider preferences; the public, breeders and consumers have given the traits in breeding objectives. The trait non-market values, defined in this way, can substitute the relevant economic data directly associated with such traits. The idea has been to capture consumer or farmer preferences that cannot be quantified by standard economic evaluation (Pryce et al. 2018).

Animal adaptability. The next selection challenge involves understanding animal adaptability to climate changes through the detection of genomic regions responsible for this adaptability (Cassandro 2020). In the context of the previous text, the actual genetic progress in production and climate traits has led to more environmentally friendly animals that unfortunately have reduced adaptability to changes in environmental condi-

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tions (Misztal 2017). Resilience and robustness are commonly considered general animal attributes, and heat tolerance practically represents animal adaptability to environmental conditions. While GHG emissions mostly change the costs per unit of production (through the shadow price of carbon and carbon credits), the adaptability influences animal production performance in its complexity. Heat stress induces economic losses owing to a deterioration of production, reproduction, survivability and additional capital and operating costs needed for management interventions (e.g., cooling). Generally, the economic consequences of improved animal adaptability are comprehensive and mostly indirect through improved animal performance.

Misztal (2017), in his review study, found that it is useful to combine performance testing data (milk yield, fertility, morbidity, mortality, parity, etc.) with weather measurements [temperature (T) and humidity (H)] in a joined index THI to improve animal environment adaptability. Management improvement, the collection of additional trait measurements (e.g., mortality rates) and commercial data are needed for adequate selection strategies under climate change (Misztal 2017). Moreover, many potential biomarkers, such as enzymes, serum metabolites, hormone levels and body fluids, have been found to be sensitive to THI values and to animal heat stress (Konig and May 2019). These authors reviewed them in detail, e.g., as biomarkers related to physiology (body temperature, respiration rate, pulse), disease incidence (milk SCS), metabolic diseases (creatine, acetoacetate, β-hydroxybutyrate known as BHB), plasma metabolite levels (urea, insulin, glucose), fractions of milk proteins, plasma heat shock protein, composition of rumen microbiome and specific semen traits and body fluids.

Many of the above-mentioned biomarkers have been defined as novel traits for improving robustness to diseases. Nevertheless, the optimal breeding strategy is unclear, and simultaneous utilization of all phenotypic data through the index methodology and appropriate weighting of traits should be developed (Konig and May 2019). The first genomic selection for improving heat tolerance was established in Australia in 2017 (Nguyen et al. 2017). The direct genomic values for declines in milk, fat and protein yield per unit increase of THI were multiplied by appropriate marginal EV of the given milk traits.

The final value expresses, in monetary terms, the decline in the national selection index per unit increase of THI. However, the authors further indicated that heat tolerance should be included in the multi-trait selection index, and genetic variation of heat stress on functional traits should be known to breed for more robust cows. Moreover, Pryce et al. (2018) pointed out that environmental regional differences may affect the economic value of selecting for heat tolerance. Therefore, greater importance of animal adaptability traits is expected in warmer climates, where the environmental heat load is higher. In these regions, the sires predicted to have daughters that are more heat tolerant should be served.

It can be anticipated that the clear definitions of diseases, fertility, mortality and other breeding objective traits, the proper calculation of their economic importance (trait EVs) and the accurate estimation of trait genetic parameters could lead to sufficient economic selection response. Misztal (2017) stated that on the precondition that selection for heat tolerance will lead to preservation of dairy farms in several regions, the complex approach used in breeding programs could be beneficial for more effective utilization of inputs and overall economic and environmental sustainability of animal production. Potential losses in selection responses for some current breeding objective traits should be fully compensated by the correlated response for the newly established traits.

Conclusion

Trait economic values are the key parameters for economically oriented breeding programs. The introduction of trait genomic breeding value estimation in livestock, leading to increased trait breeding value reliabilities, has increased the requirements for a precise calculation of economic values for a whole complex of production and functional traits. The comprehensive approaches incorporated into bioeconomic models of livestock production systems promise objective and precise trait economic evaluation. Animal adaptability to climate change, environmental mitigation and customer preferences represents future challenges in animal breeding. Direct selection for "climate" traits is not always possible and practically applicable. Selection gain in these traits could be achieved by increasing the

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efficient use of feed, e.g., by decreasing animal RFI and methane yield. The growing public interest in environmental protection and in slowing down climate change will lead to a higher pressure to incorporate climate traits directly into breeding objectives and selection indices. New indicators (traits, biomarkers) associated with climate traits are genetically related to each other and to currently evaluated traits.

Precise definition of traits included in breeding objectives and selection indices and proper estimation of trait economic values are needed to attain the desired genetic gain and environmental mitigation.

Conflict of interest

The authors declare no conflict of interest.

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