https://doi.org/10.17221/149/2022-CJAS

General resilience in dairy cows: A review

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Citation: Kašná E., Zavadilová L., Vařeka J., Kyselová J. (2022): General resilience in dairy cows: A review. Czech J. Anim. Sci., 67: 475–482.

Abstract: Dairy farming is deeply affected by climate change, especially by rising temperatures and heat waves, poorer availability of quality food and water, and the spread of new diseases and pests outside their original ecological niche. Their impact can be mitigated not only by changes in technologies, management and treatment, but also by breeding and selection of more resilient cows. General resilience encompasses the animal's capacity to cope with environmental, social and disease challenges. It is described as the capacity of the animal to be minimally affected by a disturbance or to rapidly return to the physiological, behavioural, cognitive, health, affective and production states that pertained before exposure to a disturbance. As disturbances can be of different natures, general resilience is a composite trait consisting of different resilience types according to the nature of the disturbance. Resilience can be quantified through time series data that capture fluctuations in the daily performance. Recent studies have worked with deviations in the daily milk yield and daily live weight from optimal performance or have focused on the assessment of the daily activity in terms of the daily step count. To observe the duration and magnitude of the response to perturbance, two indicators were suggested: the autocorrelation (r_{auto}) and the natural logarithm of deviations (LnVar). Based on the daily milk yield deviations, both indicators have shown sufficient genetic variabilities with the estimated heritability ~0.1 for r_{auto} and ~0.2 for LnVar. Low values of both indicators were genetically related to better udder health, better hoof health, better longevity, better fertility, higher body condition score, less ketosis but also lower milk yield level. The selection for improved resilience could benefit from the use of genomic information as several genes and biological pathways associated with disease resilience and resilience to heat stress have already been identified. The presented results suggest that the integration of resilience into the cattle breeding programmes would improve the capacity of the dairy industry to cope with global climate change.

Keywords: dairy cattle; animal breeding; adaptability; health; sustainability

Dairy farming is facing the increasingly significant impacts of climate change. For Central Europe, summers are expected to be hotter and drier. According to the Czech Environmental Information Agency (CENIA 2021), the average annual temperature in the Czech Republic is increasing at a rate of 0.35 °C per decade. The annual number of tropical days with temperatures above 30 °C has more than doubled over the last 30 years to an average of 12 tropical days per year. The occurrence of heat waves has been without any trend with the highest number of days occurring in 2018 (42 days) and 2015 (41 days). Climate change influences dairy farming both by directly affecting the performance and well-being of the cows and indirectly via the quality and quantity of fodder

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Supported by the Ministry of Agriculture of the Czech Republic (Project NAZV QK22020280 and institutional support MZE-RO0718).

production (FAO and GDP 2018). Another aspect is the higher infection pressure due to the distribution of specific pathogens further to the north as a response to the global temperature shifts (Samy and Peterson 2016). The associated economic impact might be neutral if some form of adaptation is integrated, with mitigation and adaptation strategies covering available tools from management, nutrition, and health treatment to plant and animal breeding (Gauly et al. 2013). Animal breeding and genetic selection of more resilient animals could play an essential role in improving the capacity of dairy cows to cope with the impact of environmental challenges. Resilient animals are healthy, fertile, easy-to-manage, with better longevity and consistent production (Elgersma et al. 2018), which is a prerequisite for the stability and sustainability of the dairy industry. The data generated by precision livestock farming technologies provide new analytical tools to generate dynamic resilience indicators (Scheffer et al. 2018). This study aimed to describe the state of the art in resilience evaluation and select appropriate general resilience phenotypes for use in dairy cattle breeding programmes.

Definition of resilience

The term resilience has been used in many disciplines (e.g., material science, psychology, ecology) for the capacity to deal with perturbations (Scheffer et al. 2018). In animal science, resilience was introduced as the productivity of an animal in the face of infection or parasite challenge, i.e., disease resilience (Albers et al. 1987; Bisset and Morris 1996). Hermesch and Dominik (2014) further extended this concept to environmental resilience which characterises the ability of an animal to recover from any type of environmental challenge and to return to an optimal level of productivity and profitability. Recently, Colditz and Hine (2016) suggested a broader definition of general resilience encompassing the animal's capacity to cope with environmental, social and disease challenges. General resilience is then described as the capacity of the animal to be minimally affected by a disturbance or to rapidly return to the physiological, behavioural, cognitive, health, affective and production states that pertained before exposure to a disturbance. As disturbances can be of different natures, general resilience is a composite trait consisting of different resilience types according to the nature of the disturbance (Elgersma et al. 2018).

Resilience results from the interactions of animals with their environment. As such, it is associated with some other discussed concepts, for example, tolerance and resistance (Konig and May 2019; Knap and Doeschl-Wilson 2020), genotype by environment interaction (Mulder 2016) and others (see list in Berghof et al. 2019). Over the past two decades, cattle breeding research has been concerned with the biological robustness of dairy cows (Klopcic et al. 2009). Strandberg et al. (2013) saw robustness as the ability to function well in the environment cows live in, being resilient to the changes in the microenvironment that they encounter during their life, and also the ability to function well over a wide range of (macro) environments, for example, climates or production systems of herds. Resilience, tolerance, and resistance are the components of the overall robustness, referring to adaptability to a broad range of environmental conditions (Konig and May 2019). Colditz and Hine (2016) mentioned the temporal boundary between robustness and resilience: while robustness relates to perturbations persisting over longer time frames, and adaptation/acclimatisation is driven by the homeorhetic physiological responses, resilience is associated with short-term episodic fluctuations in environmental conditions, that animals cope through acute physiological stress responses coupled with innate and learnt behaviours.

Indicators of resilience

The prerequisite of successful genetic improvement involves the precise description and measurement of the desired phenotype or its indicator trait. Indicator traits should capture the biological essence of the phenotype; they should be easily measurable at a low cost and strongly genetically correlated with the phenotype. From a practical point of view, resilient animals cope well with their conditions; they reproduce easily, produce consistently, and react well to different types of challenges. Colditz and Hine (2016) suggested that the general resilience phenotype might be identified by measuring the rate of recovery to baseline and normality of performance following the disturbance. They

https://doi.org/10.17221/149/2022-CJAS

suggested the following variables that could be useful for defining resilient phenotypes:

- core body temperature (normality of the circadian pattern, dynamic range),
- heart rate and heart rate variability,
- normality of the circadian ethogram and expression of the behavioural complexity,
- feed intake,
- growth rate or principal production variable of the species,
- immune responsiveness,
- normality of the demeanour,
- speed of acquisition of the predictive behaviours that are cognate with positive environmental cues (feeding, entry to the milking parlour),
- normality of the vocalisation.

However, according to Berghof et al. (2019), a deviation between the observed production means and the estimated potential might not fully cover the definition of resilience, as resilient animals might have a severe drop in production. Still, they can also rapidly return to the state that pertained before exposure to a disturbance compared to less resilient ones. Thus, resilience should be measured based on deviations of the expected production and observed production (residuals) over a period. The capacity of animals to resist or recover from the perturbation is captured in longitudinal measurements of the performance before, during and after the perturbation period (Llonch et al. 2020). The measurement of this volume of data was enabled by the development and use of precision livestock farming technologies. These time-series data of response variables are routinely available from real-time monitoring of dairy cows via wearable electronics, automatic milking systems (AMS), automatic feeding systems, etc.

Adriaens et al. (2020) investigated whether the lifetime resilience and productive life span of dairy cows could be predicted using sensor-derived proxies of the first-parity milk meter and activity sensor data. They ranked cows within their herds based on their lifetime resilience, which was scored for each cow based on her number of lactations, her 305-day milk yield, her age at first calving, her calving intervals, and the days in milk at the moment of culling, accounting for her entire life. Based on that ranking, cows were classified as having low, moderate or high resilience. In the next step, 45 sensor features were defined from the time series data, including measurements in the variability, lactation curve shape, milk yield perturbations, activity spikes and activity dynamics. These features calculated on the first-lactation date were used for the lifetime resilience prediction using a stepwise linear regression model. In their study, the high-ranked cows represent animals recalving many times, having the optimal age at first calving, having a short calving interval (good reproductive performance), and producing proportionally more milk compared with their herd mates. However, a common model structure across all the farms was not found, which showed the variability in the culling and management strategies.

Most of the studies aimed at deriving resilience indicators in animal husbandry followed the study of Scheffer et al. (2015), who described a family of methods for quantifying ecological resilience based on observations. The first group of methods used the phenomenon of critical slowing down, which implies a slower recovery upon small perturbations when a system approaches a tipping point. The second group characterised the resilience of alternative states in probabilistic terms based on a large number of observations (long time series). Later Scheffer et al. (2018) focused on quantifying dynamic indicators of resilience usable for monitoring the risk of systemic failure and managing the health of humans and their livestock.

Elgersma et al. (2018) used daily milk yield records from AMS. They defined three traits related to fluctuations in the milk yield: the number of drops in the milk yield during lactation based on (1) a rolling average or (2) a regression, and (3) a natural logarithm of the variance in the milk yield of an individual cow per lactation. They found that all the defined traits were heritable (heritability ranged between 0.06 and 0.10) and genetically correlated with fertility, health and longevity traits. The study showed that the variability in performance contains information related to the health and longevity, and could facilitate the breeding of resilient and easy-to-manage cows.

Berghof et al. (2019) elaborated on resilience indicators under animal production conditions and recommended to use:

1. Variance of the deviations (RawVar) or its natural logarithm (LnVar) indicates the impact of the disturbances. Then a lower variance is connected with animals not influenced by the disturbances and a higher variance with animals influenced by the disturbance. This indicator cannot disen-

https://doi.org/10.17221/149/2022-CJAS

tangle the contribution of the severity and endurance of the perturbation.

2. (Lag-one) autocorrelation of deviations (r_{auto}) indicates the length of the impact of the disturbances. Autocorrelations around 0 are connected with animals not influenced by the disturbances, or fast recovery from disturbances. An autocorrelation toward +1 is connected with animals influenced by disturbances and with a slow recovery. An autocorrelation toward –1 is connected with a fast and over-compensating response to a disturbance. The autocorrelation of deviations captures the duration of the perturbation, i.e., rate of recovery.
3. Skewness of deviations (Skew) indicates the direction of the deviations. A skewness around 0 is connected with animals not influenced by disturbances. Positive skewness mainly indicates a positive deviation due to the positive responses to the improvement of the environment; negative skewness indicates negative deviations due to disturbances. The skewness of deviations captures the severity of the indications.
4. Slope of the reaction norm (RN) indicates resilience toward a macro-environmental disturbance such as a disease outbreak or heat wave. The slope of a reaction norm is estimated based on an individual's production given the disturbance level. A slope of 0 is connected with animals not influenced by the disturbance, and a slope below 0 for animals influenced by the disturbance with steeper, negative slopes for animals that are influenced more. The slope of the reaction norm captures the severity of the macro-environmental perturbations. Mulder (2016) used RN models for heat stress evaluation and he showed that RN models are better able to deal with the continuity of the environment and to express resilience as a phenotypic response of animal performance to changing environment. Knap and Doeschl-Wilson (2020) assessed disease resilience as the reaction norm of animals' performance on the environmental pathogen load.

Poppe et al. (2020) explored the deviations in the daily milk yield levels from the optimal lactation curves. The lactation curves were fitted by different methods (non-parametric, model-based, and quantile polynomial regression method). They calculated three resilience indicators as the LnVar, r_{auto}, and Skew of the daily milk yield deviations from these curves. Poppe et al. (2020) found satisfying the heritability for LnVar (h^2~0.2) and r_{auto} (h^2~0.1). The same authors reported that low values of LnVar were genetically related to better udder health with genetic correlations from –0.26 to –0.32, better hoof health (–0.10 to –0.14), better longevity (–0.13 to –0.29), better fertility (–0.12 to –0.40), a higher body condition score (–0.32 to –0.41), less ketosis (–0.21 to –0.48) and also a lower milk yield level (0.20 to 0.79). A lower r_{auto} was also genetically related to better health, fertility and longevity, a higher dry matter intake and body condition score, but the genetic correlations were weaker (–0.20 to 0.20). The Skew was not considered to be a good indicator of resilience due to the low genetic variation and weak and unexpected genetic correlations (–0.25 to 0.17) with the LnVar, health, longevity, fertility and metabolic traits.

Another approach was presented by Ben Abdelkrim et al. (2021), who supposed that drawing a general conclusion on such a complex trait as resilience based on one response variable is insufficient. Therefore, they simultaneously evaluated the body weight and milk yield dynamics over lactation. They used the smoothing method to estimate the unperturbed performance based on actual observations and their short-term (STV) and long-term (LTV) variations. The perturbations were defined as (1) the area between the STV curve and the LTV curve, which was considered as the estimated performance loss during the whole period of perturbation, (2) the duration of perturbation, (3) the duration of the collapse and recovery phases, (4) the maximum value of the difference between the LTV and STV recorded during the deviation and (5) the minimum value of the performance recorded during the deviation. Comparing the effect of the perturbation on two different aspects of an animal's performance and measuring the degree of synchronisation between responses allowed them to characterise the average response-recovery dynamics, and the individual variation in the traits, and to compare animal strategies when facing different types of perturbation.

Kok et al. (2021) assessed whether the LnVar and r_{auto} of the deviations in the daily milk yield in the first month and the 305-day lactation were related to the occurrence of clinical mastitis. In early lactation, they found a greater LnVar and lower

https://doi.org/10.17221/149/2022-CJAS

r_{auto} in cows with early mastitis than for cows with no or late mastitis. In the whole lactation period, LnVar was greater and r_{auto} smaller for cows with early or late mastitis than for cows with no mastitis. The different dynamics of the r_{auto} compared to the expectations were explained by missing records during the treatment of mastitis, which could have removed the large and similar deviations in the milk yield. However, the LnVar was a sufficiently robust indicator of perturbance, despite the missing records. Their study also showed a greater LnVar in multiparous cows compared to primiparous cows, which was related to (1) greater fluctuations in multiparous cows due to the higher milk yield levels or to (2) higher occurrence of other diseases (ketosis, claw disorders) in multiparous cows.

In their later study, Poppe et al. (2022) focused on the daily activity data that are expected to be more directly affected by the disturbances than the daily milk yield. They evaluated the daily step count, from which they derived two types of indicators: (1) indicators based on the mean step count level at different stages of lactation, and (2) indicators based on fluctuations in the step count level. They found that most of the activity-based indicators had only weak or negligible genetic correlations with the health traits, longevity, fertility and body condition score. However, both the r_{auto_step} and the number of step count drops had moderate genetic correlations with the hoof health, fertility and body condition score, which means that cows with a genetically low autocorrelation or a small number of step count drops often had a genetic predisposition to good hoof health and fertility, and a high body condition score.

Genomic selection on better resilience

Genetic improvement of dairy cattle is based on selection index theory, where the well-balanced breeding objective expressed by precisely defined traits is crucial. The expected aim is a cumulative and permanent improvement of an animal performance, which leads to the enhanced profitability of the animal production. The economic weights that express the economic importance of the individual traits are estimated using bioeconomic models considering the current state of the production system. Berghof et al. (2019) calculated the economic value of resilience indicators using the assumption that the lack of resilience is linked with higher production losses, costs of health treatments, veterinary costs and labour costs of the farmer for observing less resilient animals. When health-related traits were already present in the selection index, the effect of including the resilience indicator was smaller. However, the overall selection response to the breeding goal increased, which resulted in less labour-demanding and easier-to-manage livestock. Also, according to Krupova et al. (2020), the economic consequences of improved animal adaptability are comprehensive and mostly indirect through improved animal performance, which is reflected in better production, reproduction, survivability and lower additional capital and operating costs needed for management interventions. Knap and Doeschl-Wilson (2020) dealt with the economic value of disease resilience traits which was assessed as the value of the amount of production that is recaptured by a unit improvement in resilience. This improvement can result from increased tolerance, better resistance, or a combination of both component traits.

Traditional selective breeding in dairy cattle has a slow rate of genetic gain due to the long generation intervals. Acceleration could be achieved through genomic selection. Genomic selection uses genome-wide DNA markers [thousands of single nucleotide polymorphism (SNP) markers, distributed across the genome] to capture the effects of many mutations that influence the variability of complex traits. The implementation of genomic selection in the past decade has substantially contributed to the acceleration of genetic progress by increasing the reliability of breeding values of young animals, reducing the generation interval, and evaluating a larger number of the selection candidates in comparison to conventional progeny testing (Wiggans et al. 2017).

Another way to better understand resilience is to identify the genes underlying the trait. We assume that SNP markers might be linked to genes affecting the selected traits. There have been several genome-wide association studies focused on the identification of genes and biological pathways associated with resilience, though they are mainly concerned with disease resilience (Knap and Doeschl-Wilson 2020) and resilience to heat stress (Silpa et al. 2021). While disease resilience studies deal primarily with other livestock species (small ruminants, pigs, salmon), thermal tolerance is a hot topic in dairy cattle as it is evident that genetics plays a crucial role in the resistance of cows to heat stress (Bezdicek et al. 2021).

Cheruiyot et al. (2021) studied the genetic basis of heat tolerance in Australian Holsteins. Using reaction norm models, they calculated the heat tolerance phenotypes as the rate of decline (slope) in milk, fat, and protein yield due to heat stress. They revealed multiple novel loci for heat tolerance in dairy cows, including 61 potential functional variants at sites highly conserved across 100 vertebrate species. The specific candidate variants and genes were related to the neuronal system (*ITPR1* associated with environmental adaptation in the domestic yak; *ITPR2* associated with heat stress in Holstein or sweating in humans and mice; *GRIA4* linked to thermoregulation in Siberian cattle) and neuroactive ligand-receptor interaction functions for heat tolerance (*NPFR2* plays a crucial role, in regulating diet-inducing thermogenesis and bone homeostasis in mice; *CALCR* – calcitonin receptors regulate daily body temperature rhythm in mammals and insects and are essential for maintaining homeostasis; *GHR* – an expression of growth hormone receptor gene is down-regulated during heat stress in livestock).

Another field that is focused on exploring the link between gene expression and phenotype is functional genomics, which may help to describe pathways associated with adaptation during perturbance. The functional genomic approaches may focus on the DNA level (genomic and microarray technologies), RNA level (transcriptomic studies), protein level (proteomics), and metabolite level (metabolomics), as described by Silpa et al. (2021). In terms of the results obtained so far, Liu et al. (2020) investigated the heat tolerance associated with genes and molecular mechanisms in Chinese Holstein using a high-throughput sequencing approach and bioinformatics analysis. The phenotypes were described as the change in the respiratory rate, rectal temperature and milk yield with an increase in the temperature-humidity index. They identified 200 significantly differentially expressed genes in heat tolerant versus non-heat tolerant cows. Of those genes, 14 were involved in the protein-protein interaction network. Several hub genes (*OAS2, MX2, IFIT5* and *TGFB2*) were significantly enriched in the immune effector process. Another study on Chinese Holstein cattle was performed by Fang et al. (2021). They examined the regulation of 55 candidate genes under cold or heat stress and revealed that *HIF1A* after cold stress and the *EIF2A*, *HSPA1A*, *HSP90AA1* and *HSF1* after heat stress had consistent trend changes at the cellular transcription and translation levels. The heat-shock protein families participate in numerous regulatory pathways related to cellular thermal stress response and possess key cytoprotective effects, which made those genes the key genes associated with the thermal stress response.

Such studies open new possibilities to assess the genetic potential of animals to optimally produce under stressful environmental conditions and provide new information to be used for more effective selection and animal breeding.

Conclusion

General resilience is the ability of animals to cope with changing environmental conditions. The prerequisite for its genetic improvement is the measurement of its expression in the population. Recent studies have shown that resilience can be quantified through the data generated by precision livestock farming technologies. Time series data capture the impact of stressors and subsequent recoveries through fluctuations in the daily performance such as the daily milk yield, daily live weight or daily activity in terms of the step count. The variance of the deviations, which reflects the degree of the perturbation, and autocorrelation of the deviations, which reflects the duration of the perturbation, appear to be promising indicators. Both of these indicators are favourably genetically correlated with the dairy cow longevity, fertility, health, dry matter intake and body condition scores. Defining suitable resilience indicators is an essential prerequisite for identifying the genes underlying the trait and implementing an effective genomic selection of resilient animals. Improving general resilience has the potential to contribute significantly to the stability and sustainability of dairy farming.

Conflict of interest:

The authors declare no conflict of interest.

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Received: September 21, 2022
Accepted: December 6, 2022