Personality and production: Nervous cows produce less milk

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INTERPRETIVE SUMMARY
Title: Personality and milk production in dairy cows.
First Author: Hedlund
Summary: We investigated the relationship between variation in animal personality and production traits in dairy cows. Behaviors were scored during milking, in response to novel object and social separation. We demonstrate that cows that step more during milking, or that respond stronger to social separation have lower milk production. These results are of interest to researchers in animal personality, animal production and welfare, and may have implications for improvement of milk production and welfare of dairy cows.

Running title: PERSONALITY AND MILK PRODUCTION IN DAIRY COWS

Title: Personality and production: Nervous cows produce less milk

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ABSTRACT

The objective of this study was to investigate relationships between animal personality (i.e. consistency in behavioral responses, also called temperament) and milk production in dairy cows. There has recently been a growing research interest in animal personality, which in production animals can have important impact on welfare and production potential. Despite this, the relationship between personality and milk production in dairy cows remains unclear. Here we investigate links between behavioral responses during milking and in personality tests (responses to novel object and social isolation) with milk production in two breeds of dairy cattle, Swedish red and white cattle (SRB) and Holstein. The milk production parameters investigated were ECM (Energy Corrected Milk in kg) for the cows’ first lactation, and ECM for their current lactation. Overall, cows that stepped more during milking, or spent more time facing the herd during social isolation produced less milk in their first lactation. Cows that vocalized more during isolation had a lower current milk production. Variation in other behavioral responses showed limited relationships with milk production. Taken together, our results support a relationship between behavioral responses and milk production, where cows showing signs of nervousness produce less milk. However, observed relationships are dependent on the milk measure utilized, behavior and breed investigated, supporting that the relationship between behavior and production traits is not straightforward.

Keywords: *Bos taurus*, dairy cattle, neophobia, temperament, vocalization
INTRODUCTION

There is significant variation in how individuals behave and respond to their environment, which for production animals can have important welfare and production implications. A rapidly growing research field with focus on individual variation in behavior is ‘animal personality’. Animal personality is defined as individual differences in behavior that are consistent over time and or over contexts (a.k.a. temperament, coping styles, Koolhaas et al., 1999; Dall et al., 2004; Réale et al., 2007; Carere and Maestripieri, 2013). Variation in animal personality has been demonstrated to be related to traits relevant for production, such as variation in growth (e.g. Müller and von Keyserlingk, 2005) and susceptibility to diseases (e.g. Hulbert et al., 2011). Estimates of personality and investigation of links with production traits are therefore of relevance to animal production, due to the potential for improvements in health and productivity (Boissy, 1995; Boissy et al., 2005; Adamczyk et al., 2013). Nevertheless, despite current interest and potential implications, the origin and consequences of personality variation are still poorly understood (Dall et al., 2004; Wolf et al., 2007; Dingemanse and Wolf, 2010; Carere and Maestripieri, 2013).

Classical personality gradients used to describe individual variation in behavioral responses are boldness, exploration, activity, aggressiveness, and sociability (Réale et al., 2007). When using the term temperament, variables including also emotionality are sometimes used, such as fearfulness, anxiety or nervousness (Boissy, 1995; Réale et al., 2007). Stress is the body’s reaction to a challenge that triggers a response by the sympathetic nervous system (e.g. flight-fight responses). Fear describes stress responses to direct threats, while anxiety and nervousness describe responses to potential danger (Forkman et al., 2007; Öhman, 2010). For dairy cows, several responses to potential threats are commonly recorded, such as responses to unfamiliar humans (e.g., Gibbons et al., 2009), or novelty (also called neophobia, Kilgour et al., 2006; Forkman et al., 2007). In addition, because cows are strictly social animals, social isolation elicits behavior related to fear and nervousness, such as vigilance and vocalization (Müller and Schrader, 2005). Also behavior during handling, and particular during milking, such as kicking and stepping (measured as weight changes from one foot to another, e.g. Rousing et al., 2004), are often recorded and used to describe fearfulness or nervousness. Cows that step more during milking have been described as more nervous (Wenzel et al., 2003; Rousing et al 2004; Dodzi and Muchenje, 2011 and references therein), further confirmed by that increased stepping is positively correlated with hearth rate and milk cortisol.
Kicking during milking on the other hand has been used to describe cows that are less fearful or nervous (Rousing et al., 2004, and references therein). Although these behavioral responses often are claimed to describe variation in personality, whether they show consistency within individuals over time or context is actually rarely explored. Behavioral responses that have been described to be consistent within individuals, thus describing variation in personality, include responses to humans (Gibbons et al., 2009), to novel environments (Le Neindre, 1989), to novel objects (Kilgour et al., 2006), and responses to social isolation (e.g., Müller and Schrader, 2005). Consistency in stepping and kicking behavior during milking is to our knowledge not yet demonstrated, despite its common use as a behavioral test in cattle (e.g. Rousing et al., 2004).

While variation in the personality traits activity and boldness have been found to correlate positively with production in terms of growth rate in beef cattle (Biro and Stamp, 2008), the relationship between fecundity-related traits, like milk production, and personality is less clear. This is because the relationship seem to differ dependent on both the traits compared, and also between studies investigating the same behavioral responses. For example, fear of humans has been observed to be negatively associated with milk yield (Uetake et al., 2004), positively correlated with milk flow rates (Sutherland and Dowling, 2014), to correlate only weakly with milk yield (Breuer et al., 2000; Hemsworth et al., 2000), or that the relationship between fear of humans and milk yield is lacking (Purcell et al., 1988; Rousing et al., 2004). Similarly inconsistent, a negative relationships was observed between behavior during milking and milk yield (Breuer et al., 2000; Sutherland and Dowling, 2014), a positive link between milk yield and stepping (Willis, 1983; Uetake et al., 2004), and no relationship observed between behavior during milking and milk yield (van Reenen et al., 2002). Thus, it is still not clear how behavioral responses describing variation in personality traits relates to milk production.

In addition to that the overall relationship between personality and milk production is unclear, the framework for exploring links between personality and fecundity related traits is currently poorly developed. The framework used to explain variation in growth rate and personality is based on that individuals differentially allocate resources between current and future investments (Dall et al., 2004; Stamps, 2007; Wolf et al., 2007; Dingemanse and Wolf, 2010). A framework based on trade-offs is ‘resource allocation theory’ which presents the idea that individuals investing more in a particular trait will invest less in another, because total amount
of resources are limited (Beilharz et al., 1993). When individuals are selected for higher production, less resources are thus available for other processes (Rauw et al., 1998; Oltenacu and Broom, 2010). As a consequence of investment in production traits, we thus predicts production and personality to be overall negatively related, predicting docile individuals to produce more. Within the same framework, also stronger stress responses should link with reduced production (Rushen et al., 1999; 2001; Breuer et al., 2000; Forkman et al., 2007).

We here investigate association between behavioral indicators of personality and milk yield in dairy cows. We score behavioral variation during milking (stepping and kicking), during exposure to novel object (neophobia) and social isolation (vigilance and vocalization). Based on resource allocation theory, we expect a negative relationship between the behavioral responses we here record and milk production, in other words that individuals performing more of a behavior will produce less milk.

MATERIAL AND METHODS

Animals, Housing and Management Routines

The study was carried out at Vreta Farm School in Linköping (Sweden) on a population of Swedish red and white cattle (SRB) and Holstein cows kept for milk production and education of farming student. Animals were kept indoors in a loose housing systems designed for 28 animals, with two automatic feeders and four automatic water cups. The cows were fed roughage ad libitum and an individual amount of concentrated cow feed (‘Unik72’ and ‘Vida’ from Lantmänn, Sweden) based on lactation status. Cows were milked in a milking parlor every day between 07:30 - 09:00, 14:30 - 16:00, and 21:30 - 23:00 local time. The cows varied in their stage of pregnancy (days since last successful insemination), age (in days), and current lactation (1st to 7th lactation). In total, data from 56 cows were obtained (nSRB = 27; nHolstein = 29). Number of cows differs somewhat between observations due to practical reasons in farming and production (e.g. due to cows giving birth).

Behavioral Observations

Three sets of observations were conducted at 8 wk intervals in September 2012, December 2012 and February 2013. Each set of observations included observations of all behaviors
described below. To investigate behavioral consistency over time, each individual was observed in two of these sets of observations. The first set of observations of an individual is termed ‘Observation 1’ (regardless of whether it was conducted in September or December), and the second is called ‘Observation 2’ (regardless of whether it was conducted in December or February). ‘Observation 2’ is therefore the most recent observation of the cows’ behavior.

To score variation in stepping and kicking behavior during milking, cows were observed during midday milking (14:30 - 16:00) on 2 d per set of observations. We recorded stepping and kicking as rates (frequencies over seconds) from when the first teat cup was attached until the last teat cup was removed (referred to as ‘Stepping rate’ and ‘Kicking rate’ respectively). Stepping was recorded by counting every individual’s weight shifting from one hind foot to the other, with the foot lifted less than 10 cm off the ground. Kicking was recorded as every individual’s lift of the hind foot 10 cm or more off the ground. Behaviors were not recorded during udder preparation and after-treatment, or if the milking machine became detached.

To investigate variation in neophobia, behavioral responses during exposure to a novel object were observed. A new object was used for each observation set to avoid habituation (according to e.g. Kilgour et al., 2006). The objects used were a blue Pilates ball (Ø 60 cm), a pink umbrella (Ø 1 m), and a blue and white plastic bag (60 x 60 x 25 cm). These objects were estimated to cause similar and comparable behavioral reactions within individuals based on results from previous studies (Forkman et al., 2007). The arena used for this test was a section of the cows’ normal pathway to the milking parlor temporarily blocked with gates. The test was carried out in a familiar environment in order to avoid testing behavioral reactions to a new environment (Réale et al., 2007). One cow at the time was herded from her home pen to the testing arena. When in the arena, the cow was presented with the novel object in front of her to make sure she observed it immediately. Behaviors were video recorded for 3 min after the novel object was presented to a cow. Latency (in seconds) to interact with the novel object (sniffing, licking, or butting, referred to as ‘Latency to approach the novel object’), frequency (number of occurrences) and time (in seconds) of interactions with the object (referred to as ‘Frequency of interaction with novel object’, and ‘Duration of interaction with novel object’, respectively), as well as time (in seconds) standing with any part of the body within one body length distance from the novel object (referred to as ‘Duration standing within 2 meters from the object’), was recorded. During isolation for the novel object test, we also recorded responses typically recorded during social isolation. We
recorded vocalization rate (number of occurrences divided by seconds observed, referred to as ‘Vocalization rate’) and proportion of time standing in upright position and being vigilant with head turned in the direction towards the herd (seconds facing the herd divided by seconds observed, referred to as ‘Time facing the herd’), were recorded.

Behavioral observations were conducted by Louise Hedlund. The study was carried out according to ethical requirements in Sweden, and approval by Linköping Ethical committee (ethical permit number 123-10).

Milk Production Data

The automatic daily registered production data were imported from the Individual RAM (NorFor) database. Milk quality is scored by a test-milking every month. To investigate the relationship between behavior and milk production, we used the amount of produced milk in kilo ECM (‘Energy Corrected Milk’, a commonly used measurement of milk production describing the energy content of the milk). As a measure of milk production early in life, and also a milk measure comparable among cows of otherwise slightly different ages, we used ECM from the five first test-milkings during individual cow’s first lactation (‘First lactation ECM’). To obtain a measure of current milk production, we used the mean of the test-milking performed one month before, the current month, and one month after the last observation (i.e. Observation 2) was carried out (‘Current ECM’).

Statistical Analyses

Age and lactation status correlated strongly (R_s = 0.82, p < 0.0001, n = 54). Thus, only one of the variables were used for further analyses, age. Age did not differ between breeds (H = 1.83, p = 0.18). Age did not affect behavioral responses recorded (R_s ≤ 0.19, p ≥ 0.16), but for time facing the herd (R_s = 0.39, p = 0.004). Therefore, only when analyzing variation in time facing the herd was age added as a covariate (see below).

For stepping and kicking, values used for statistical analyses are individuals’ mean rate of performed behavior per set of observation. Because mastitis may affect behavior during milking (Chapinal et al., 2013), we recorded mastitis status of the observed cows. Eighteen of the focal cows were recorded to have mastitis, however mastitis status did not affect behavior during milking (stepping rate, H = 1.21, p = 0.27; kicking rate, H = 1.62, p = 0.20).
A Principle Component Analyses (PCA) was used to investigate the relationship among behaviors recorded when cows were isolated and exposed to a novel object. For this analyses, these behavioral variables were entered for separate PCAs for breed and observation occasion; Latency to approach the novel object, Duration of interaction with novel object, Frequency of interaction with novel object, Duration standing within 2 meters from the object, Vocalization rate, Time spent facing the herd. Variables describing variation in neophobia all loaded in the first component (PC1), while time facing the herd and vocalization rate primarily loaded in the second component (PC2, Table 1a). Time facing the herd and vocalization rate loaded differently for first and second observations. For further analyses we therefore analyzed variables describing neophobia, time facing the herd and vocalization rate separately. To reduce the responses describing variation in neophobia to one component (referred to as ‘Neophobia’), we conducted a new PCA including only these variables; Latency to approach the novel object, Duration of interaction with novel object, Frequency of interaction with novel object, Duration standing within 2 meters from the object (for ‘Observation 1’ and ‘Observation 2’, for each breed separately, Table 1b). This aggregated component was used for further analyses.

(*Table 1a and 1b can be presented for example here*)

Correlations among variables were investigated with Spearman rank-order correlations. To investigate consistencies of behavioral responses over time, correlations between the recorded behavioral responses from Observation 1 and Observation 2 were carried out. The relationship among the different behavioral responses, and behavior and milk measures, were carried out by comparing the most recent variables we recorded (i.e. variables obtained from Observation 2). To include variation in age in the analyses of time spent facing the herd, a Generalized Linear Model (GLZ) was used with the most recent behavioral response as response variable, age (in days) and the previously recorded behavioral response as covariates. For analyses of variation in time spent facing the herd and the two milk traits investigated, a GLZ was used including the most recent behavioral variable as response variable, age, early ECM and current ECM as covariates. These models were fitted with a Poisson distribution and Log link function, corrected for overdispersion.

Differences between groups (i.e. breed, mastitis status) were investigated by the use of Kruskal-Wallis Anovas. For the variable vocalization rate, one Holstein cow had a rate around
tenfold as high as the mean rate of the other cows (vocalization rate of outlier: 0.21, mean vocalization rate not including the outlier: 0.02). This variable was therefore analyzed both with and without this outlier. The analyses produced qualitatively similar outputs (see Figure 1e, for results with and without the outlier for the analyses of vocalization rate and milk yield), and the analyses including the outlier are presented.

Analyses were performed in Statistica 12.

**RESULTS**

**Behavioral Responses**

There were limited differences between the breeds in their behavioral responses (stepping rate: \( H = 1.69, \ p = 0.19, n_{SRB} = 26, n_{Holstein} = 28 \), mean ± SE, SRB: 0.046 ± 0.005, Holstein: 0.037 ± 0.004; kicking rate: \( H = 3.27, \ p = 0.07, n_{SRB} = 26, n_{Holstein} = 28 \), mean ± SE, SRB: 0.005 ± 0.001, Holstein: 0.011 ± 0.003; neophobia: \( H = 0.0, \ p = 1.0, n_{SRB} = 24, n_{Holstein} = 28 \), SRB: 0.0 ± 0.29, Holstein: 0.068 ± 0.29; time facing the herd: \( H = 1.27, \ p = 0.26, n_{SRB} = 23, n_{Holstein} = 28 \), SRB: 0.25 ± 0.031, Holstein: 0.20 ± 0.02; vocalization rate: \( H = 0.02, \ p = 0.88, n_{SRB} = 24, n_{Holstein} = 28 \), SRB: 0.02 ± 0.005, Holstein: 0.017 ± 0.005). Because breed sometimes had some effect on response variables obtained, we present both separate and combined results for the two breeds, throughout.

Overall, responses obtained at least eight weeks previously explained variation in current observations of cows’ behavior, although how much differed between behavior and breeds (Table 2). Correlations within behavior over time were stronger for Holsteins (Table 2), and stronger for stepping rate (Table 2, both breeds combined: \( R_s = 0.46, \ p = 0.0004, n = 54 \)), kicking rate (Table 2, both breeds combined: \( R_s = 0.29, \ p = 0.034, n = 54 \)), neophobia (Table 2, both breeds combined: \( R_s = 0.37, \ p = 0.007, n = 52 \)), and was weaker for time spent facing the herd (Table 2, both breeds combined: \( R_s = 0.21, \ p = 0.13, n = 51 \)) and vocalization rate (Table 2, both breeds combined: \( R_s = 0.17, \ p = 0.23, n = 51 \)). The model analyzing variation in time spent facing the herd including also age, confirms the above correlations; age had
again a positive effect (Wald statistics = 8.77, p = 0.003), and the previously recorded time spent facing the herd had limited effect (Wald statistics = 0.52, p = 0.47).

Comparing across behavioral responses recorded, we observe positive correlations for the variables stepping rate vs. time spent facing the herd (Table 2, both breeds combined: $R_s = 0.38$, $p = 0.006$, $n = 51$), and for stepping rate vs. vocalization rate (Table 2, both breeds combined: $R_s = 0.32$, $p = 0.024$, $n = 51$), but did not observe significant correlations for other compared variables (Table 2, for variables combined for both breeds: $R_s \leq 0.12$, $p \geq 0.42$).

(Table 2 can be presented for example here)

**Milk Production**

There tended to be some breed differences in milk measures, where Holstein cows tended to produce somewhat more milk in their first lactation ($H = 3.69$, $p = 0.055$, $n_{SRB} = 26$, $n_{Holstein} = 28$, means ± SE, SRB: 27.69 ± 0.58, Holstein: 29.86 ± 0.82), but with less difference between the breeds in current milk production ($H = 2.61$, $p = 0.11$, $n_{SRB} = 24$, $n_{Holstein} = 27$, means ± SE, SRB: 31.40 ± 1.65, Holstein: 34.95 ± 1.35). The relationship between milk measures did not correlate significantly (First lactation ECM vs. Current ECM: $R_s = -0.15$, $p = 0.28$, $n = 52$).

First lactation ECM correlated negatively with stepping rate (Figure 1a), correlated negatively with kicking rate for Holstein cows, tended to correlate positively with kicking rate for SRB (Figure 1b), and correlated negatively with time spent facing the herd (Figure 1c). Current ECM tended to be positively correlated with stepping rate (Figure 1d), and correlated negatively with vocalization rate (Figure 1e). No other behaviors correlated with milk production (Figure 1). In a model including also age, the correlations above were confirmed and time spent facing herd was negatively correlated with early ECM (Wald statistics = 5.37, $p = 0.021$, parameter estimate: $-0.059 \pm 0.03$), while current ECM was not (Current ECM, Wald statistics = 1.21, $p = 0.27$, parameter estimate: $-0.012 \pm 0.01$, age, Wald statistics = 6.07, $p = 0.014$, parameter estimate: $0.0004 \pm 0.0002$).
**DISCUSSION**

We investigated the relationships between behavioral responses during milking and in personality tests of two breeds of dairy cows (Swedish red and white, SRB, and Holstein), with their milk production. We observe limited breed differences in behavior, but the breeds differed in their consistency of behavior over time (Holstein cows were more consistent in their behavior than SRBs), and also in the relationship among behavior, and between behavior and milk traits. Combined for the two breeds, milk production in the cows’ first lactation correlated negatively with stepping rate during milking, and with time spent facing the herd during social isolation. Milk production during first lactation and kicking rate tended to correlate in opposing directions for the two breeds (positively for SRB and negatively for Holstein). Current milk production tended to be positively correlated with stepping rate during milking, and was negatively correlated with vocalization during isolation. Stepping rate during milking correlated positively with time facing the herd and vocalization during isolation. Taken together, the relationships between behavior and milk production differed somewhat dependent on the traits and breed in focus, but overall suggest that cows with stronger behavioral responses produce less milk. Below we discuss; (i) variation in the behavioral variables we scored, (ii) the breed differences we observe, and (iii) the relationships here observed between behavior and milk production.

(i) Variation in behavioral responses used to describe personality traits

Primarily termed ‘temperament’, previous studies have demonstrated that cattle show individual variation in behavioral responses used to describe their personality. While some studies have repeatedly observed the same cows to investigate how consistent over time or context these behavioral responses are, many studies have only observed the cows once. We scored behavioral responses repeatedly (separated by at least 8 weeks) and in several contexts to capture variation in cow personality. We observed that behavior used by other authors to describe variation in cow personality differ in how consistent they are over time and that this also depends on the breed observed. We demonstrate that cows are consistent over time in their behavior during milking, particularly in stepping. Stepping has previously been demonstrated to link with increased heart rate and milk cortisol concentrations, thus capture variation in cows’ personality along a gradient describing variation in nervousness (Wenzel et al., 2003; Rousing et al 2004; Dodzi and Muchenje, 2011, and references therein). Kicking during milking was on the other hand not consistent over time in our focal population.
Previous studies have found both stepping and milking consistent over a short time period, but not over several months as investigated here (van Reenen et al., 2002). Our results do however confirm that variation in kicking during milking was uncorrelated with stepping (Rousing et al., 2004 and references therein). These results together suggest that kicking during milking needs further validation of whether it is actually describing consistent variation among cows, and how this behavior describes variation in their personality.

Although the strength of the correlation coefficients differ somewhat between the two breeds we investigated, our results support the findings of previous studies by showing consistent individual variation in neophobia during exposure to a novel object (Forkman et al., 2007). Fear of novelty thus seem to be a behavior that across studies describe variation in traits describing the personality of also cows (Forkman et al., 2007).

Further, our results confirm the results of previous studies that describe variation among individuals to social isolation (vocalization in calves, van Reenen et al., 2004; 2013; vigilance and vocalization, Müller and Schrader, 2005). Other studies have investigated consistency in behavioral responses to social isolation (e.g., Müller and Schrader, 2005). Our results differ dependent on behavior used and also between cows of the two breeds. This again brings to the attention that consistency in behavioral responses typically used to describe personality traits needs to be investigated. Our results suggest that other factors like habituation and age can influence these responses. In our population older cows were more attracted to the herd when a cow was isolated. Behavioral responses are expected to be dynamic and influenced by experiences, again highlighting the need to verify the consistency over time of the behavioral response used to describe variation in personality. Having said so, in general has cows that vocalize more been suggested to have a stronger response to the stress caused by social isolation (see references in Watts et al., 2001; van Reenen et al., 2004), which in turn may describe variation in sociality in the cows (e.g. van Reenen et al., 2013). The behavioral responses used thus still may describe variation in stress-related responses. However, to improve our understanding of underlying variation and relationship of these responses, causes of variation, flexibility and consistency of them should be further explored.

We interpret that the behavioral responses we scored all captured some aspect of nervousness among the cows. However, apart from stepping during milking which correlated positively with time facing the herd and vocalization during social isolation, our observed behaviors
were not correlated. This suggests that behaviors used to describe variation in personality did not form a behavioral syndrome (Sih et al., 2004), but instead describe variation among individuals for different personality traits (e.g. Müller and Schrader 2005; Gibbons et al., 2009; van Reenen et al., 2013; MacKey et al., 2014). Taken together, this indicates that variation in no single personality trait describes variation in nervousness in cattle. Instead, cows might react to more or less stressful situations with different responses (Boissy, 1995). Responses triggered can differ among situations (although within contexts responses can be relatively consistent), and be passive (freeze), active defense (fight), or active avoidance (flight) (Boissy, 1995).

(ii) Variation among the breeds
We observed some breed differences in the cows’ behavioral responses, and the extent to which previous behavioral responses explain current behavior (i.e. how consistent behavior responses were over time). Previous studies have demonstrated differences among groups or breeds of cows for example in their fearfulness (Waiblinger et al., 2003; Uetake et al., 2004; Dodzi and Muchenje, 2011), nervousness (Gergovaska et al., 2012), and in milk production (Dodzi and Muchenje, 2011; Gergovska et al., 2012). Holstein is the dominant breed in Europe, and has undergone strong selection for production traits (Olenacu and Broom, 2010). In addition, Scandinavian breeds (like SRB) have been selected based on broader breeding objectives (Olenacu and Broom, 2010). As a consequence of this, there is likely more genetic variability in the SRB breed, which may enable also more behavioral flexibility in the situation an individual is exposed to. This may explain why we observe differences in how consistent the cows of the two breeds were (Oltenacu and Broom, 2010). In a recent review of heritability estimates of behavioral responses across breeds, Holstein cows had higher heritability in personality compared to a range of other breeds (Adamczyk et al., 2013). A higher heritability predicts higher consistency in behavioral responses within individuals, which may explain that we find Holstein cows to be more consistent in their behavioral responses compared to SRB. Variation among breeds in behavioral consistency and heritability can in turn have consequences for the potential for further breeding for preferred traits. Additional studies on the correlational nature within and between behavioral responses are therefore encouraged, particularly to explore the potential for selection for specific traits.
(iii) The relationships between behavior and milk production

The main aim of our study was to investigate links between behavior used to describe variation in personality traits and production, in our cow population. We demonstrate that several aspects of nervousness differ in strength but were negatively related to milk production (stepping during milking, time facing the herd and vocalization during isolation). Although previous studies investigating variation in behavior during milking and milk production have found varying results (e.g. Purcell et al., 1988 found no correlation within herds; Uetake et al., 2004 found no relationship between milk yield and stepping-kicking), our results confirm several previous studies. For example, heifers with high flinch – step – kick score during milking (i.e. a combined score of behaviors during milking) had lower milk yields (Breuer et al., 2000; Sutherland and Dowling, 2014). Rousing and co-workers (2004) investigated stepping and kicking separately and found that stepping during milking had a complex relationship with milk yield, where very low yielding cows stepped the most during milking. Further, kicking did not affect milk yield (Rousing et al., 2004). Our results support previous findings to the extent that the relationship between one of the recorded behaviors during milking (stepping) was negatively correlated with milk yield, that stepping and kicking was uncorrelated, and that kicking did not associate strongly with milk production. The overall understanding of observed variation in behavior during milking and milk yield is however still unclear, and more research is warrant to further out understanding of this relationship and its potential underlying mechanisms.

Despite that variation in neophobia is often investigated in cows (Forkman et al., 2007), its association with milk production is on the other hand less often investigated. MacKey and co-workers (2014) recently explored variation in neophobia and milk yield, showing a weak positive relationship between latency to interact with the novel object and milk production. If this relationship in general is only weak, this can explain why we did not detect such a link in our data. Similarly, responses to social isolation are often part of behavioral tests of cattle (e.g. Kilgour et al., 2006), but are not often investigated in relation to milk production (e.g. investigated in calves up to 29 weeks of age, van Reenen et al., 2004). We observed negative relationships for both vigilance and vocalization rate during isolation and milk production. These findings contradict a recent study of van Reenen and co-workers (2013) who found that heifer that vocalized more during isolation had better milk ejection during their first milking. However, later during lactation this pattern became non-significant (Kovalcikova and Kovalcik 1982; van Reenen et al., 2013). Both in our measure of first lactation ECM and
current ECM we observe a negative association with responses to social isolation (although for different milk measures for the different behavioral responses, and of different strength dependent on breed). We did not compare the cows’ first milking, thus the use of different milk measures make the comparison with previous results less straight forward. This, in addition to the discussion above on the lack of consistency in responses to social isolation in our population add further uncertainty to the relationship between responses to social isolation and milk measures.

Inconsistencies among results of different studies can at least partly be due to methodological differences and comparison of different traits (both milk and behavioral traits), together with variation in handling, breed, age and other influences affecting behavioral responses, how consistent these responses actually are and/or milk production. Nevertheless, when trying to draw more general conclusion across patterns observed among behavior and milk production across a broad range of studies, increased nervousness or fearfulness (definitions and descriptions of responses vary among studies) is more often associate negatively with milk production, than positively in these studies (e.g. Rushen et al., 1999; Breuner et al., 2000; Sutherland and Dowling, 2014). This suggests that the current framework of personality and production, which mainly is based on variation in differential allocation over time, and or even life (Stamps, 2007; Wolf et al., 2007), poorly explains associations between personality and milk production. What seem to better explain the patterns emerging for behavior and production in dairy cows is instead the resource allocation theory (Beilharz et al., 1993). According to this theory, reduced production is predicted to associate with stronger responses both behaviorally and stress-related (Rushen et al., 1999; 2001; Breuner et al., 2000; Sutherland and Dowling, 2014). It is a general observation that domesticated animals show higher production traits than their wild ancestors. In addition, they are typically more docile than their wild counter parts (Mignon-Gasteau et al., 2005). For example, when investigating the relationship between social behavior and production, domesticated relatives spend less time on social interactions compared to their wild ancestors (Schütz and Jensen, 2001). This theory therefore seem to offer a useful starting point when investigating variation in personality and production, although the details of the underlying mechanism of such a relationship are still not clear.
(iv) Conclusions
Taken together, we demonstrate that associations observed between behavior used to describe variation in personality traits and production are dependent on the behavior and milk measure compared, and also the breed in focus. However, overall is a negative relationship suggested between behavior that are often used to describe variation in nervousness among cows, and production. The framework to understand a negative relationship between personality and milk production may best be explained by the negative correlations expected by resource allocation theory. Future studies should aim to investigate the factors causing variation in these relationships further, including the underlying mechanisms between variation in personality and production.

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REFERENCES


### Tables

Table 1a. Principle Component Analyses of behaviors of two breeds of dairy cows when exposed to novel objects and social isolation.

<table>
<thead>
<tr>
<th>Behavior</th>
<th>Swedish Red and White</th>
<th></th>
<th>Holstein</th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Observation 1</td>
<td>Observation 2</td>
<td>Observation 1</td>
<td>Observation 2</td>
</tr>
<tr>
<td>Latency to approach the novel object</td>
<td>PC1</td>
<td>PC2</td>
<td>PC1</td>
<td>PC2</td>
</tr>
<tr>
<td>Interaction with novel object (duration)</td>
<td>0.49</td>
<td>0.22</td>
<td>0.43</td>
<td>-0.39</td>
</tr>
<tr>
<td>Interaction with novel object (frequency)</td>
<td>0.59</td>
<td>-0.03</td>
<td>0.52</td>
<td>0.24</td>
</tr>
<tr>
<td>Standing within 2 m from object</td>
<td>0.28</td>
<td>0.15</td>
<td>0.43</td>
<td>-0.29</td>
</tr>
<tr>
<td>Vocalization rate</td>
<td>-0.27</td>
<td>0.60</td>
<td>0.05</td>
<td>0.76</td>
</tr>
<tr>
<td>Time facing the herd</td>
<td>-0.39</td>
<td>0.46</td>
<td>-0.32</td>
<td>0.15</td>
</tr>
<tr>
<td>Eigenvalues</td>
<td>1.94</td>
<td>1.35</td>
<td>2.54</td>
<td>1.41</td>
</tr>
<tr>
<td>% of variance explained</td>
<td>32.3</td>
<td>22.4</td>
<td>42.3</td>
<td>23.4</td>
</tr>
</tbody>
</table>

n = 52. Separate analyses were carried out for each breed, and on responses to the first and second time cows were tested (‘Observation 1’ and ‘Observation 2’, respectively). The first (‘PC1’) and second principle component (‘PC2’) primarily describes variation in neophobia, and responses to social separation, respectively. Variables that load strongly in a component (> 0.4) are highlighted in bold.
Table 1b. Principle Component Analyses of responses by two breeds of dairy cows to a novel object.

<table>
<thead>
<tr>
<th>Behavior</th>
<th>Swedish red and white</th>
<th>Holstein</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Observation 1</td>
<td>Observation 2</td>
</tr>
<tr>
<td>Latency to approach the novel object</td>
<td>-0.47</td>
<td>-0.53</td>
</tr>
<tr>
<td>Interaction with novel object (duration)</td>
<td>0.47</td>
<td>0.43</td>
</tr>
<tr>
<td>Interaction with novel object (frequency)</td>
<td>0.63</td>
<td>0.55</td>
</tr>
<tr>
<td>Standing within 2 m from object</td>
<td>0.40</td>
<td>0.48</td>
</tr>
<tr>
<td>Eigenvalues</td>
<td>1.77</td>
<td>2.37</td>
</tr>
<tr>
<td>% of variance explained</td>
<td>44.3</td>
<td>59.2</td>
</tr>
</tbody>
</table>

Separate analyses were carried out for first vs. second time cows were exposed to a novel object (‘Observation 1’ and ‘Observation 2’, respectively), for each of the two breeds Swedish red and white (n = 24), and Holstein (n = 28). Variables that load strongly in a component (> 0.4) are highlighted in bold.
### Table 2. Correlations among behavioral responses of two breeds of dairy cows.

<table>
<thead>
<tr>
<th></th>
<th><strong>Swedish Red and White</strong></th>
<th></th>
<th><strong>Holstein</strong></th>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Stepping</td>
<td>Kicking</td>
<td>Neophobia</td>
<td>Facing herd</td>
<td>Vocalization</td>
<td>Stepping</td>
<td>Kicking</td>
<td>Neophobia</td>
<td>Facing herd</td>
</tr>
<tr>
<td>Stepping</td>
<td>0.62*</td>
<td>-0.09</td>
<td>-0.11</td>
<td>0.04</td>
<td>0.39</td>
<td>0.42*</td>
<td>0.14</td>
<td>0.01</td>
<td>0.66*</td>
</tr>
<tr>
<td>Kicking</td>
<td>0.05</td>
<td>0.11</td>
<td>-0.33</td>
<td>-0.29</td>
<td>-0.33</td>
<td>0.46*</td>
<td>0.13</td>
<td>-0.12</td>
<td>-0.12</td>
</tr>
<tr>
<td>Neophobia</td>
<td>0.35</td>
<td>-0.22</td>
<td>0.15</td>
<td>0.09</td>
<td>0.40*</td>
<td>0.40*</td>
<td>0.06</td>
<td>0.54*</td>
<td>-0.30</td>
</tr>
<tr>
<td>Facing herd</td>
<td>-0.21</td>
<td>0.09</td>
<td>0.09</td>
<td>0.54*</td>
<td>0.09</td>
<td>0.26</td>
<td>0.06</td>
<td>0.54</td>
<td>0.10</td>
</tr>
<tr>
<td>Vocalization</td>
<td></td>
<td></td>
<td></td>
<td>0.26</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

Swedish Red and White: n = 26, Holstein: n = 28. ‘Stepping’ refers to ‘Stepping rate’, ‘Kicking’ to ‘Kicking rate’, ‘Neophobia’ to an aggregated neophobia score, ‘Facing herd’ to ‘Time spent facing the herd’, and ‘Vocalization’ refers to ‘Vocalization rate’, see main text for details. Rs values are presented, significant correlations are highlighted by the symbol *. For comparison of the same behavior over time, responses from Observation 1 and Observation 2 are used. For comparison between behaviors, responses from Observation 2 are used.
Figure legends

Figure 1. The relationship between personality and milk production for two breeds of dairy cows. (a) Milk production (Energy Corrected Milk in kg, ECM) during first lactation and stepping rate (number of steps per second observed) did not correlate significantly for SRB (Swedish Red and White, grey diamonds, dotted lines, $R_s = -0.07$, $p = 0.73$) and tended to correlate negatively for Holstein (filled circles, solid line, $R_s = -0.35$, $p = 0.077$). Both breeds combined, a negative relationship was observed ($R_s = -0.32$, $p = 0.019$, $n = 52$). (b) ECM during first lactation and kicking rate (number of kicks per second observed) tended to correlate positively for SRB ($R_s = 0.38$, $p = 0.06$) and correlated negatively for Holstein ($R_s = -0.40$, $p = 0.039$). Both breeds combined, the relationship was not significant ($R_s = -0.04$, $p = 0.76$, $n = 52$). (c) ECM during first lactation and time spent facing the herd (seconds facing the herd over seconds observed) tended to correlate negatively for SRB ($R_s = -0.42$, $p = 0.054$) and for Holstein ($R_s = -0.34$, $p = 0.08$). The breeds combined, show a negative relationship ($R_s = -0.40$, $p = 0.0045$, $n = 49$). (d) Current milk production (ECM) and stepping rate tended to correlate positively for SRB ($R_s = 0.36$, $p = 0.087$), but not for Holstein ($R_s = 0.03$, $p = 0.90$). The breeds combined, the relationship tended to be positive ($R_s = 0.23$, $p = 0.09$, $n = 50$). (e) Current ECM and vocalization rate during isolation (number of vocalization over seconds observed) did not correlate significantly for SRB ($R_s = -0.22$, $p = 0.32$), but correlated negatively for Holstein ($R_s = -0.40$, $p = 0.045$). Both breeds combined, the relationship was negative ($R_s = -0.31$, $p = 0.03$, $n = 49$). (Analyses without the outlier in the Holstein data: $R_s = -0.34$, $p = 0.09$; the breeds combined, the relationship was negative: $R_s = -0.29$, $p = 0.048$, $n = 48$). Other combinations of behavior and milk production traits were not correlated ($R_s < \pm 0.11$, $p > 0.60$, but from neophobia and ECM during first lactation: $R_s = -0.22$, $p = 0.11$).
Figures

Hedlund Figure 1.