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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 an 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 2 breeds of dairy cattle, Swedish Red and White and Holstein. The milk production parameters investigated were energy-corrected milk (in kg) for the cows' first lactation and energy-corrected milk 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 used, behavior, and breed investigated, supporting that the relationship between behavior and production traits is not straightforward.
Key words: *Bos taurus*, dairy cattle, neophobia, temperament, vocalization

INTRODUCTION

Significant variation exists 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 (i.e., 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 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, whereas 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 particularly 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

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that step more during milking have been described as more nervous (Wenzel et al., 2003; Rousing et al. 2004; Dodzi and Muchenje, 2011), further confirmed by the fact that increased stepping is positively correlated with hearth rate and milk cortisol (Wenzel et al., 2003). Kicking during milking, however, has been used to describe cows that are less fearful or nervous (Rousing et al., 2004). 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 as 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 to social isolation (e.g., Müller and Schrader, 2005). Consistency in stepping and kicking behavior during milking has not yet been demonstrated to our knowledge, despite its common use as a behavioral test in cattle (e.g., Rousing et al., 2004).

Whereas 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 Stamps, 2008), the relationship between fecundity-related traits, such as milk production, and personality is less clear. This is because the relationship seems 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 was noted between milk yield and stepping (Willis, 1983; Uetake et al., 2004), and no relationship was 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 relate to milk production.

In addition to the fact 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). Another 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 the total amount of resources are limited (Beilharz et al., 1993). When individuals are selected for higher production, fewer resources are thus available for other processes (Rauw et al., 1998; Oltenacu and Broom, 2010). As a consequence of investment in production traits, we predicted production and personality would be negatively related overall and that docile individuals would produce more. Within the same framework, stronger stress responses should also link with reduced production (Rushen et al., 1999, 2001; Breuer et al., 2000; Forkman et al., 2007).

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

MATERIALS 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 students. Animals were kept indoors in a loose housing systems designed for 28 animals, with 2 automatic feeders and 4 automatic water cups. The cows were fed roughage ad libitum and an individual amount of concentrated cow feed (Unik72 and Vida from Lantmännen, Stockholm, Sweden) based on lactation status. Cows were milked in a milking parlor every day between 0730 and 0900, 1430 and 1600, and 2130 and 2300 h local time. The cows varied in their stage of pregnancy (days since last successful insemination), age (in days), and current lactation (first to seventh lactation). In total, data from 56 cows were obtained (SRB, n = 27; Holstein, n = 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 2 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 (1430–1600 h) 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 (e.g., Kilgour et al., 2006). The objects used were a blue Pilates ball (diameter = 60 cm), a pink umbrella (diameter = 1 m), and a blue and white plastic bag (60 × 60 × 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 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 m 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 an upright position and being vigilant with head turned in the direction toward 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 (www.norfor.info). Milk quality was scored by a test-milking every month. To investigate the relationship between behavior and milk production, we used the amount of produced milk in kilograms of ECM. 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 5 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 1 mo before, the current month, and 1 mo after the last observation (i.e., observation 2) was carried out (current ECM).

Statistical Analyses

Age and lactation status correlated strongly (Spearman rank correlation coefficient, $\mathbf{R_s} = 0.82$, $P < 0.0001$, n = 54). Thus, only one of the variables, age, was used for further analyses. Age did not differ between breeds (Mann-Whitney U-test, $\mathbf{H} = 1.83$, $P = 0.18$). Age did not affect behavioral responses recorded ($R_s \leq 0.19$, $P \geq 0.16$), but was positively correlated with the behavioral response 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 behaviors 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 principal component analyses (**PCA**) was used to investigate the relationship among behaviors recorded when cows were isolated and exposed to a novel object.

Table 1. Principal component analyses of behaviors of 2 breeds of dairy cows when exposed to novel objects and social isolation[1]

	Swedish Red and White				Holstein			
	Observation 1		Observation 2		Observation 1		Observation 2	
Behavior	PC1	PC2	PC1	PC2	PC1	PC2	PC1	PC2
Latency to approach the novel object	−0.32	**−0.59**	**−0.51**	−0.33	**−0.47**	0.14	**−0.51**	0.14
Interaction with novel object (duration)	**0.49**	0.22	**0.43**	−0.39	**0.43**	**−0.43**	**0.48**	−0.17
Interaction with novel object (frequency)	**0.59**	−0.03	**0.52**	0.24	**0.55**	−0.13	**0.55**	−0.07
Standing within 2 m from object	0.28	0.15	**0.43**	−0.29	0.39	−0.01	0.38	**0.54**
Vocalization rate	−0.27	**0.60**	0.05	**0.76**	0.23	**0.62**	−0.21	−0.31
Time facing the herd	−0.39	**0.46**	−0.32	0.15	0.29	**0.63**	−0.10	**0.74**
Eigenvalues	1.94	1.35	2.54	1.41	2.68	1.39	2.57	1.39
% of variance explained	32.3	22.4	42.3	23.4	44.6	23.1	42.8	23.2

[1]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; n = 52). The first and second principal components (PC) primarily describe variation in neophobia and responses to social separation, respectively. Variables that load strongly in a component (>0.4) are highlighted in bold.

For this analysis, these behavioral variables were entered in separate PCA 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 m from the object, vocalization rate, and time spent facing the herd. Variables describing variation in neophobia all loaded in the first component, whereas time facing the herd and vocalization rate primarily loaded in the second component (Table 1). Time facing the herd and vocalization rate loaded differently for the 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 1 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, and duration standing within 2 m from the object (for observation 1 and observation 2, for each breed separately; Table 2). This aggregated component was used for further analyses.

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 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 was used with the most recent behavioral response as response variable and age (in days) and the previously recorded behavioral response as covariates. For analyses of variation in time spent facing the herd and the 2 milk traits investigated, a generalized linear model 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 Mann-Whitney U-test. For the variable vocalization rate, 1 Holstein cow had a rate around 10-fold 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

Table 2. Principal component analyses of responses by 2 breeds of dairy cows to a novel object[1]

	Swedish Red and White		Holstein	
Behavior	Observation 1	Observation 2	Observation 1	Observation 2
Latency to approach the novel object	**−0.47**	**−0.53**	**−0.50**	**−0.52**
Interaction with novel object (duration)	**0.47**	**0.43**	**0.51**	**0.49**
Interaction with novel object (frequency)	**0.63**	**0.55**	**0.58**	**0.57**
Standing within 2 m from object	**0.40**	**0.48**	**0.40**	**0.40**
Eigenvalues	1.77	2.37	2.49	2.48
% of variance explained	44.3	59.2	62.4	62.0

[1]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 2 breeds Swedish Red and White (n = 24), and Holstein (n = 28). Variables that load strongly in a component (>0.4) are highlighted in bold.

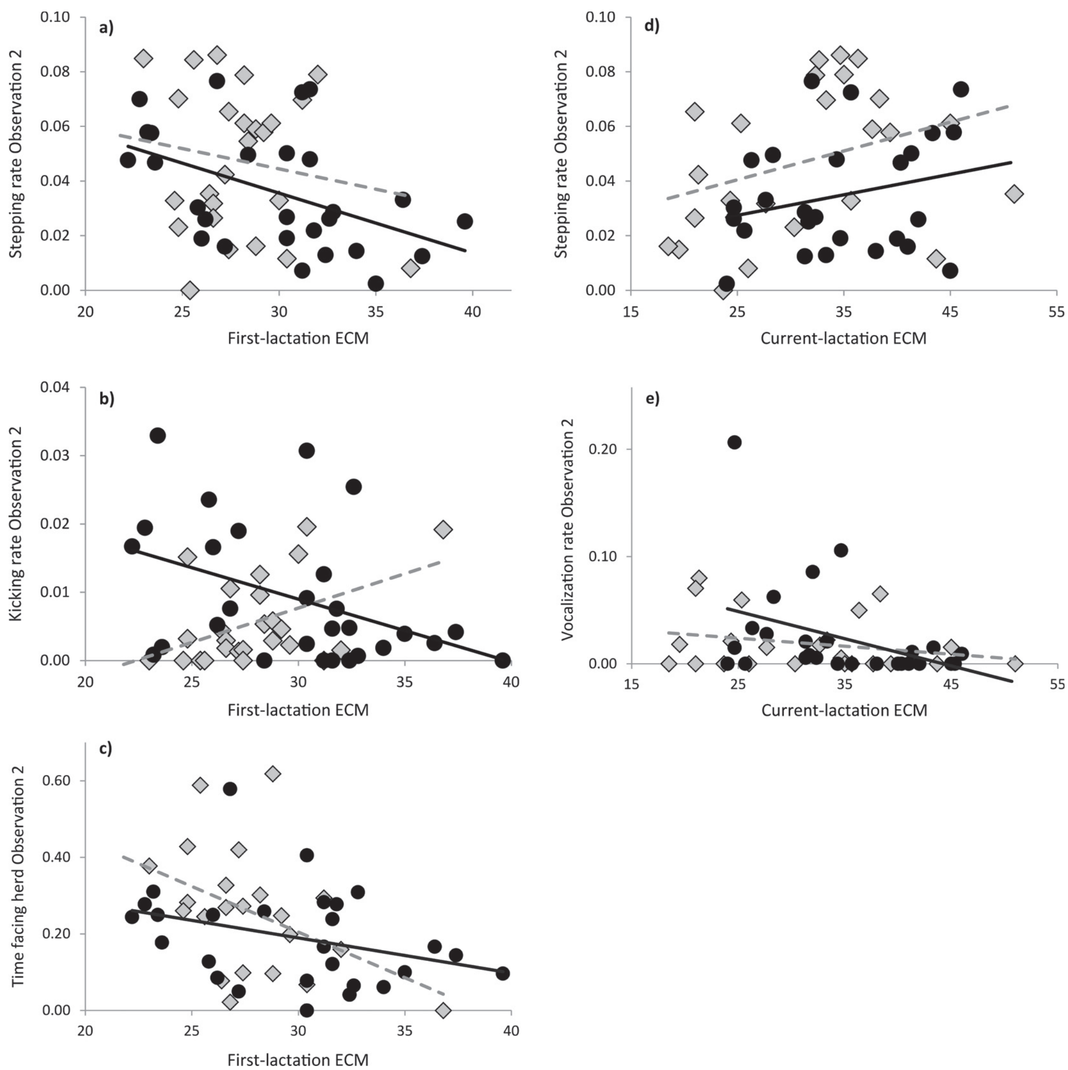

Figure 1. The relationship between personality and milk production for 2 breeds of dairy cows. (a) Milk production (ECM, kg) during first lactation and stepping rate (number of steps per second observed) did not correlate significantly for Swedish Red and White (SRB; gray diamonds, dotted lines, Spearman rank correlation coefficient, $R_s = -0.07$, $P = 0.73$) and tended to correlate negatively for Holstein (filled circles, solid line, $R_s = -0.35$, $P = 0.077$). For both breeds combined, a negative relationship was observed ($R_s = -0.32$, $P = 0.019$, n = 52). (b) Energy-corrected milk production 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 ($R_s = -0.40$, $P = 0.039$). For both breeds combined, the relationship was not significant ($R_s = -0.04$, $P = 0.76$, n = 52). (c) Energy-corrected milk production 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 ($R_s = -0.34$, $P = 0.08$). Both breeds combined, show a negative relationship ($R_s = -0.40$, $P = 0.0045$, n = 49). (d) Current milk production (in ECM) and stepping rate tended to correlate positively for SRB ($R_s = 0.36$, $P = 0.087$), but not for Holstein ($R_s = 0.03$, $P = 0.90$). For both 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 ($R_s = -0.40$, $P = 0.045$). For 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 ($R_s < 0.11$, $P > 0.60$, but from neophobia and ECM during first lactation: $R_s = -0.22$, $P = 0.11$).

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 (StatSoft Inc., Tulsa, OK).

RESULTS

Behavioral Responses

We found limited differences (mean ± SE) between the breeds in their behavioral responses. For example,

Table 3. Correlations among behavioral responses of 2 breeds of dairy cows[1]

	Swedish Red and White					Holstein				
Item[2]	Stepping	Kicking	Neophobia	Facing herd	Vocalization	Stepping	Kicking	Neophobia	Facing herd	Vocalization
Stepping	0.62*	−0.09	−0.11	0.04	0.39	0.42*	0.14	0.01	0.66*	0.27
Kicking		0.05	0.11	−0.33	−0.29		0.46*	0.13	−0.12	0.24
Neophobia			0.35	−0.22	0.15			0.40*	−0.06	−0.30
Facing herd				−0.21	0.09				0.54*	0.10
Vocalization					0.26					0.12

[1]Swedish Red and White: n = 26, Holstein: n = 28. Spearman rank correlation coefficient, R_s, values are presented. 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.

[2]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.

*$P < 0.05$.

for stepping rate (H = 1.69, $P = 0.19$; SRB = 0.046 ± 0.005, n = 26; Holstein = 0.037 ± 0.004, n = 28), kicking rate (H = 3.27, $P = 0.07$; SRB = 0.005 ± 0.001, n = 26; Holstein: 0.011 ± 0.003, n = 28), neophobia (H = 0.0, $P = 1.0$; SRB 0.0 ± 0.29, n = 24; Holstein = 0.068 ± 0.29, n = 28), time facing the herd (H = 1.27, $P = 0.26$; SRB = 0.25 ± 0.031, n = 23; Holstein = 0.20 ± 0.02, n = 28), and vocalization rate (H = 0.02, $P = 0.88$; SRB = 0.02 ± 0.005, n = 24; Holstein = 0.017 ± 0.005, n = 28). Because breed sometimes had some effect on response variables obtained, we present both separate and combined results for the 2 breeds throughout.

Overall, responses obtained at least 8 wk previous explained variation in current observations of cows' behavior, although how much differed between behavior and breeds (Table 3). Correlations within behavior over time were stronger for Holsteins (Table 3), and stronger for stepping rate (Table 3; both breeds combined: R_s = 0.46, $P = 0.0004$, n = 54), kicking rate (Table 3; both breeds combined: R_s = 0.29, $P = 0.034$, n = 54), and neophobia (Table 3; both breeds combined: R_s = 0.37, $P = 0.007$, n = 52), and was weaker for time spent facing the herd (Table 3; both breeds combined: R_s = 0.21, $P = 0.13$, n = 51) and vocalization rate (Table 3; both breeds combined: R_s = 0.17, $P = 0.23$, n = 51). The model analyzing variation in time spent facing the herd including age confirms the correlations; age had a positive effect (Wald statistics = 8.77, $P = 0.003$, parameter estimates: 0.0005 ± 0.0002), and the previously recorded time spent facing the herd had a limited effect (Wald statistics = 0.52, $P = 0.47$, parameter estimate: 0.39 ± 0.55). Comparing across behavioral responses recorded, we observed positive correlations for the variables stepping rate versus time spent facing the herd (Table 3; both breeds combined: R_s = 0.38, $P = 0.006$, n = 51) and for stepping rate versus vocalization rate (Table 3; both breeds combined: R_s = 0.32, $P = 0.024$, n = 51), but did not observe significant correlations for other compared variables (Table 3; for variables combined for both breeds: $R_s \leq 0.12$, $P \geq 0.42$).

Milk Production

There tended to be some breed differences (means ± SE) in milk measures, where Holstein cows tended to produce somewhat more milk in their first lactation (H = 3.69, $P = 0.055$; SRB = 27.69 ± 0.58, n = 26; Holstein = 29.86 ± 0.82, n = 28), but with less difference between the breeds in current milk production (H = 2.61, $P = 0.11$; SRB = 31.40 ± 1.65, n = 24; Holstein = 34.95 ± 1.35, n = 27). 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 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 ± 0.03), whereas current ECM was not correlated (Wald statistics = 1.21, $P = 0.27$, parameter estimate: −0.012 ± 0.01; age, Wald statistics = 6.07, $P = 0.014$, parameter estimate: 0.0004 ± 0.0002).

DISCUSSION

We investigated the relationships between behavioral responses during milking and in personality tests of 2 breeds of dairy cows (SRB and Holstein), with their milk production. We observed 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 SRB) and also in the relationship among behavior and between behavior and milk traits. For the 2 breeds, combined milk production in the cows' first lactation correlated negatively with stepping rate during milking, as well as 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 2 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. Herein we discuss variation in the behavioral variables we scored, the breed differences we observed, and the relationships observed between behavior and milk production.

Variation in Behavioral Responses Used to Describe Personality Traits

Previous studies have demonstrated that cattle show individual variation in behavioral responses used to describe their personality (primarily termed temperament). Whereas some studies have repeatedly observed the same cows to investigate how consistent over time or context these behavioral responses are, many studies only observed the cows once. We scored behavioral responses repeatedly (separated by at least 8 wk) and in several contexts to capture variation in cow personality. We observed that behavior used by other authors to describe variation in cow personality differs in how consistent they are over time and that this also depends on the breed observed. We demonstrated 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 capturing variation in cows' personality along a gradient describing variation in nervousness (Wenzel et al., 2003; Rousing et al. 2004; Dodzi and Muchenje, 2011). 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 in the current study (van Reenen et al., 2002). However, our results do confirm that variation in kicking during milking was uncorrelated with stepping (Rousing et al., 2004). These results together suggest that further validation is needed as to whether kicking during milking is consistently varied among cows and how this behavior describes variation in their personality.

Although the strength of the correlation coefficients differ somewhat between the 2 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). Thus, fear of novelty seems to be a behavior describing variation in traits and the personality of cows across studies (Forkman et al., 2007).

Furthermore, 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 2 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, such as 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. In general, cows that vocalize more have been suggested to have a stronger response to the stress caused by social isolation (Watts et al., 2001; van Reenen et al., 2004), which in turn may describe variation in socialization in the cows (e.g., van Reenen et al., 2013). The behavioral responses used 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 should be further explored.

We interpreted 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; MacKay 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).

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 in their fearfulness (Waiblinger et al., 2003; Uetake et al., 2004; Dodzi and Muchenje, 2011), nervousness (Gergovska 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 (Oltenacu and Broom, 2010). In addition, Scandinavian breeds (such as SRB) have been selected based on broader breeding objectives (Oltenacu and Broom, 2010). As a consequence, more genetic variability likely exists in the SRB breed, which may enable also more behavioral flexibility in the situation to which an individual is exposed. This may explain why we observed differences in how consistent the cows of the 2 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 with a range of other breeds (Adamczyk et al., 2013). A higher heritability predicts higher consistency in behavioral responses within individuals, which may explain why we found Holstein cows to be more consistent in their behavioral responses compared with 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.

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 demonstrated that several aspects of nervousness differed 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, and 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 et al. (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, stepping and kicking was uncorrelated, and kicking did not associate strongly with milk production. However, the overall understanding of observed variation in behavior during milking and milk yield is still unclear, and more research is warranted to further understanding of this relationship and its potential underlying mechanisms.

Although variation in neophobia is often investigated in cows (Forkman et al., 2007), its association with milk production has been investigated less often. MacKay et al. (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 wk 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 et al. (2013), who found that heifers that vocalized more during isolation had better milk ejection during their first milking. However, later during lactations this pattern became nonsignificant (Kovalčikovač and Kovalčik, 1982; van Reenen et al., 2013). Both in our measure of first-lactation ECM and current ECM we observed 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 straightforward. This, in addition to the lack of consistency in responses to social isolation in our population, adds 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, other influences affecting behavioral responses, how consistent these responses actually are, or milk production. Nevertheless, when trying to draw more general conclusions 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 associated negatively with milk production than positively in these studies (e.g., Rushen et al., 1999; Breuer et al., 2000; Sutherland and Dowling, 2014). This suggests that the current framework of personality and production, which is mainly based on variation in differential allocation over time or even life (Stamps, 2007; Wolf et al., 2007), poorly explains associations between personality and milk production. Resource allocation theory seems to better explain the patterns emerging for behavior and production in dairy cows (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., 1999a,b; Breuer 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 counterparts (Mignon-Grasteau et al., 2005). For example, when investigating the relationship between social behavior and production, domesticated relatives spend less time on social interactions compared with their wild ancestors (Schütz and Jensen, 2001). Therefore, this theory seems 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.

CONCLUSIONS

We demonstrated that associations observed between behaviors used to describe variation in personality traits and production are dependent on the behavior and milk measure compared, as well as the breed in focus. However, overall, a negative relationship was suggested between behaviors 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 investigate the factors causing variation in these relationships further, including the underlying mechanisms between variation in personality and production.

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