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Personality is associated with feeding behavior and performance in dairy calves

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ABSTRACT

Performance varies considerably at weaning, perhaps in part because it is associated with the personality traits of the animals. Our objective was to identify calf personality traits using standardized tests and determine whether these were associated with measures of feeding behavior and performance. Fifty-six dairy calves were housed in 7 groups of 8 calves each with access to an automated milk feeder and ad libitum access to water, starter, and hay. We measured starter DMI and the number of unrewarded visits to the automated milk feeder during each of 4 periods: prestep (full milk allowance; 7–41 d of age), step (milk allowance reduced to 50%; 42–50 d of age), weaning (51–54 d of age), and postweaning (55–68 d of age). At 27 and 76 d of age, each calf was subjected to 3 novelty tests: novel environment (30 min), human approach (10 min with an unknown stationary human), and novel object (15 min with a black 140-L bucket). During each of the tests, 7 behaviors were scored: latency to touch and duration of touching the human or object, duration of attentive behavior toward the human or object, number of vocalizations, number of quadrants crossed as a measure of activity, and duration of inactivity, exploration, and playing. Data were averaged across ages and then across tests. Principal component analysis revealed 3 factors (interactive, exploratory–active, and vocal–inactive) that together explained 73% of the variance. Calves that were more exploratory–active began to consume starter at an earlier age and showed greater starter dry matter intake during all experimental periods and greater overall average daily gain. Calves that were more interactive and vocal–inactive had more unrewarded visits to the milk feeder during initial milk reduction. We conclude that personality traits are associated with feeding behavior and performance around weaning.

Key words: temperament, behavioral syndrome, fear, animal welfare

INTRODUCTION

Cattle are known to differ in their individual responses to stressful events. This individual variation may have important consequences for production. Animals that are generally calmer or less reactive have improved growth rates, meat quality, and milk production (reviewed by Haskell et al., 2014), improved immune function (Fell et al., 1999; Hulbert et al., 2011), and decreased physiological responses to stressful events (Curley et al., 2008) compared with excitable or more reactive animals.

Fearfulness and excitability in cattle are often assessed by measuring responses to isolation and handling, activity during restraint (typically in a squeeze chute), flight speed after release from restraint, and responses to milking and handling (Haskell et al., 2014). Responses to handling have received considerable focus given their relationship with performance. For example, excitable beef cattle (measured as reactivity to confinement in a chute and flight speed following release from the chute) have lower growth rates (Müller and von Keyserlingk, 2006; Cafe et al., 2011; Bruno et al., 2016), lower BW (Cziszter et al., 2016), and poor carcass quality such as yield and quality grade, back fat, and marbling score (Nkrumah et al., 2007; Reinhardt et al., 2009) compared with calm cattle. Dairy cattle scored as more reactive in the milking parlor produce less milk (Sutherland and Dowling, 2014; Hedlund and Løvlie, 2015), milk out slower (Sewalem et al., 2011), and have reduced lifetime production efficiency (Neja et al., 2015).

Few studies have focused on personality traits of young cattle and how these relate to performance despite the growing evidence that early-life growth and nutrition are predictive of long-term productivity, such as first-lactation milk yield (e.g., Heinrichs and

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Heinrichs, 2011; Soberon et al., 2012; Van De Stroet et al., 2016), feed intake, efficiency, and body and carcass composition at slaughter (reviewed by Greenwood and Cafe, 2007). Beef calves that were more excitable at weaning had lower BW at weaning, preconditioning, and slaughter (Francisco et al., 2012). Similar results were reported by Torres-Vázquez and Spangler (2016) for weaning and yearling weights. To our knowledge, no studies have related personality traits with performance before the weaning period in young ruminants.

During the first weeks of life, calves need to learn where, how, and what to eat; these skills can have a profound effect on growth rates. For dairy calves, the transition from a milk diet to a solid-feed diet is often associated with delayed growth (De Paula Vieira et al., 2010; Sweeney et al., 2010). To mitigate growth checks at this time, calves should be consuming starter before the onset of weaning. However, the age at which dairy calves begin to consume substantial quantities of starter is variable, with one study reporting a range of 23 to 82 d of age to consume 200 g of starter (de Passillé and Rushen, 2016). This variation in starter intake before weaning is thought to be one reason why weight gains before the weaning period are variable (e.g., from 0.1 to 1.6 kg/d in Soberon et al., 2012). Personality may play an important role in the development of these feeding patterns and, consequently, performance before weaning.

The literature to date has focused on the effects of reactivity on performance in cattle. Previous work examining behavioral responses to a novel object or human has resulted in weak or negligible correlations with performance (e.g., Breuer et al., 2000; Hedlund and Løvlie, 2015), perhaps due to limited characterization of behaviors during these tests. For example, exploration and playfulness are often measured when the individual is exposed to an unfamiliar environment (open field or novel environment tests; de Passillé et al., 1995; Perals et al., 2017), but to our knowledge no study has examined how these traits are associated with feeding behavior measures or performance in cattle.

The objectives of this study were to describe personality traits of preweaned dairy calves using a series of novelty tests and to determine how these traits relate to performance and the development of solid feeding behavior. We also investigated the relationship between personality and behavioral responses to weaning.

MATERIALS AND METHODS

The study was conducted from April to October 2015 at the University of British Columbia (UBC) Dairy Education and Research Centre in Agassiz, British Columbia, Canada. The study was approved under the UBC Animal Care protocol no. A14-0245 and A15-0117.

Housing and Animal Management

Fifty-six Holstein calves (32 females, 24 males) were enrolled in this study. These calves were also used in another experiment investigating how milk allowance affects BW gains (see Rosenberger et al., 2017). Briefly, all calves were separated from the dam within 6 h of birth, weighed, moved into individual sawdust-bedded pens, and fed 4 L of colostrum within 6 h of birth. At 7.5 ± 1.3 d of age, calves were moved to sawdust-bedded group pens with a partially slatted floor. Groups were filled in relation to birth dates of calves, and once group size reached 8 a new group was begun until all 7 groups (56 calves) were formed. Calves were randomly assigned to 1 of 4 milk-feeding allowances (6, 8, 10, or 12 L of milk/d) within each group of 8 calves, with each group containing 2 calves on each allowance. Milk was reduced to 50% of the allowance at 42 d of age and reduced by 20%/d from d 50 until calves were completely weaned at d 55. Calves assigned to the different milk allowances were similar in sex, BW, calving ease, and order of enrollment in the group.

Calves within each group had access to pasteurized whole milk, fed at 40°C using an automated milk feeder (CF 1000 CS Combi; DeLaval Inc., Tumba, Sweden) equipped with 1 teat. Calves could come and go from the milk feeder as they wished. Milk allowance delivered at each visit accrued hourly at a rate of 5% of the daily value every hour from midnight to 2000 h, with a minimum and maximum portion size of 0.5 and 9 L, respectively. Calf starter (Hi-Pro Medicated; Hi-Pro Feeds, Chilliwack, BC, Canada) was fed ad libitum from the same feeder. Only one calf at a time could feed from each of the milk and grain feeders. Intake, time, and duration of each visit for both milk and starter were recorded by the feeder. Farm hay and water were available ad libitum.

Data Recording and Calculations

Daily intake of milk and starter was recorded by the automated feeding system until 68 d of age. We also recorded the number of rewarded (when the calf visited the feeder and received milk) and unrewarded (when the calf visited the feeder but did not receive milk) visits to the milk feeder. Average milk and starter DMI, total DMI (sum of milk and starter DMI), and average number of rewarded and unrewarded visits to the milk feeder were calculated for 5 experimental periods:

prestep (full milk allowance; 7–41 d of age), step (milk allowance reduced to 50%; 42–50 d of age), weaning (51–54 d of age), postweaning (55–68 d of age), and the total experimental period (7–68 d of age). The ADG (kg of BW/d) was calculated for each experimental period, and total weight gain and gain:feed ratio (kg of BW/DMI) was calculated for the total experimental period.

To describe the development of solid feeding behavior, we determined the age (d) when each calf first ate at least 40 g of starter from the feeder (indicating that the calf ate at least the previous 20 g, which is the smallest portion dispensed by the feeder) and the first day of age that each calf met specific starter consumption targets (225, 675, and 1,300 g, corresponding to the targets of 0.5, 1.5, and 3 lb, respectively; Bovine Alliance on Management and Nutrition, 2017). Values were calculated as the average starter consumption over the previous 3 d, with the requirement that each of the previous 3 d met at least 50% of the daily target. To further characterize the behavioral response to weaning, we calculated the total number of unrewarded visits during the postweaning period (55–68 d of age) to reflect how persistent calves were in continuing to attempt to gain milk from the feeder.

Health checks were performed weekly following Costa et al. (2015). Briefly, feces were scored on a scale from 1 (normal feces) to 4 (watery and body temperature ≥39.5°C). Respiratory health was scored on the basis of nasal discharge and pathological sounds suggestive of pulmonary inflammation. Two calves scored high on consecutive health checks for poor respiratory health and were treated with an antibiotic (Resflor Gold; Intervet Inc., Roseland, NJ) according to the farm's standard procedure. Calves were weighed weekly using a portable scale placed at the entrance to the calf pen.

Novelty Tests

The novel environment, human approach, and novel object tests were chosen to assess behavioral responses toward different novel situations, similar to previous studies (e.g., Van Reenen et al., 2004; Lauber et al., 2006). These are the most common tests of fear in farm animals (Forkman et al., 2007), but others have suggested that behaviors in these tests may also reflect a motivation to explore (de Passillé et al., 1995; Perals et al., 2017). Tests were carried out in a test pen that was identical to the home pen but access to the feeding equipment was blocked. At the time of testing, the calf was guided gently into the test pen. Calves were tested individually in 1 test per day in the following order: novel environment, human approach, and novel object test. Testing occurred over 3 consecutive days starting at 27 ± 3 d of age (nominally 27 d, 2 wk before initial milk reduction). Calves were retested in each of these tests starting at 76 ± 3 d of age (nominally 76 d, 3 wk after weaning). Testing order was randomized.

Calves remained in the novel environment, human approach, and novel object tests for 30, 10, and 15 min, respectively. In the human approach test, an unknown person stood immobile at the center of the test pen. The person looked toward the feet of the calf and their hands remained in the pockets of their coveralls. In the novel object test, a black 140-L bucket was placed at the center of the test pen. While in the test pen, the calf was video recorded continuously using 1 camera (WV-CW504SP, Panasonic, Osaka, Japan) positioned 7 m above the test pen. A single observer scored all behaviors in all tests using an ethogram (Table 1) after establishing high interobserver reliability ($\kappa_W > 0.86$) for each test. Vocalizations were recorded for each test by an observer who was seated out of sight of the test arena. The start of a test was considered to be when the calf had all 4 feet inside the test arena.

Statistical Analysis

All analyses were performed using SAS (version 9.4; SAS Institute Inc., Cary, NC) with calf ($n = 56$) as the experimental unit. All feeding and behavior measures were scrutinized using PROC UNIVARIATE and normalized as required using a log10 transformation (vocalizations, latency to touch, and play behavior measures in novelty tests; rewarded visits to the milk feeder during weaning; and unrewarded visits to the milk feeder during prestep) and a square root transformation (starter DM during prestep).

Model residuals were also scrutinized to verify normality and homogeneity of variances. Behaviors recorded as durations were expressed as a percentage of the total test. Bucking, resting, and withdrawals rarely occurred and were excluded from further analysis. For each behavior, measures were averaged across ages (age 27 and 76 d) for each test. Vocalizations and time spent playing (locomotory and object play) were averaged across the 3 novelty tests (novel environment, human approach, and novel object), and latency to touch, time spent touching, and time spent attentive were averaged across the human approach and novel object tests (following Lecorps et al., 2018). This resulted in a total of 5 behavioral responses from the 3 novelty tests (vocalizations, latency to touch, touch, attentive, and play) and 3 additional responses from the novel environment test (active, inactive, and explore).

These 8 behaviors were subjected to a principal component analysis with varimax rotation to condense correlated measures into principal components (following Van Reenen et al., 2004). Three principal components with eigenvalues equal to or larger than 1 accounted for 73% of the variance; these were retained for further analyses (hereafter referred to as factor 1, factor 2, and factor 3).

We first tested whether milk allowance affected these responses. This model tested the fixed effects of milk allowance, sex, birth weight, and birth date (explanatory variables) on each of the 3 factor scores (factor 1, factor 2, or factor 3; response variables), with group as a random effect. We then tested whether personality affected measures of performance and feeding behavior during each of the 5 experimental periods. This model tested the fixed effects of factor score, milk allowance, sex, birth weight, birth date, and the interaction between milk allowance and factor score (explanatory variables) on the following response variables: ADG, gain:feed ratio, milk DMI, starter DMI, total DMI, first day to eat starter, first day to eat each of 225, 675, and 1,300 g of starter, number of daily rewarded and unrewarded visits to the milk feeder, and total number of unrewarded visits after weaning. Group was included as a random effect. The interaction term was dropped when $P > 0.1$. A separate analysis was conducted for each factor (1, 2, and 3) to test the effect of each of these factors on each of the response variables. Sickness, classified as calves with diarrhea score ≥ 3 or pulmonary inflammation on 2 consecutives health checks, was included in the analysis but was never significant and was not included in the final analysis. Significance was declared at $P \leq 0.05$ and a tendency was declared at $P \leq 0.10$.

RESULTS

Principal Component Analysis

The behavioral responses of calves in each of the novelty tests are presented in Table 2, and the loadings for each factor are reported in Table 3. Factor 1 explained 37.3% of the total variance and contained high positive loadings for time spent in contact and playing. There were also high negative loadings for latency to touch and time spent attentive toward the human or novel object. Calves that loaded highly on

Table 1. Ethogram of behaviors scored during each of the 3 novelty tests when calves (n = 56) were tested individually at 27 ± 3 and 76 ± 3 d of age in novel environment, human approach, and novel object tests

Test and behavior	Description
All tests	
Vocalizations	All types of vocalizations, sound emitted from the mouth
Locomotor play	Occurs without head oriented toward and more than 1 body length away from human or object Jumping: both forelegs off the ground and extended forward Running: calf trotting (2 beats) or galloping (3 beats) across or around the enclosure
Bucking	Both hind legs off the ground and extended backward (no. of events)
Resting	Time spent lying down with underside or side of body in full contact with flooring substrate
Withdrawal	Sudden movement backward or sideways (no. of events)
Novel environment test	
Exploration	Time spent with muzzle or tongue in contact with either walls or flooring substrate while moving or stationary
Active	Total number of squares crossed with all 4 feet (test arena divided into 4 equal quadrants)
Inactive	Time spent standing still without sniffing or licking walls or floor
Human approach and novel object tests	
Latency to touch	Time until moment calf touches human or object (muzzle within 5 cm)
Attentive	Time spent with head oriented toward human or object, excluding touching and object play behaviors (close: within 1 body length away; far: more than 1 body length away)
Touching	Time spent with muzzle in contact with human or object (muzzle within 5 cm)
Object play	Butting (head in contact with) human or object, or mock butt where head is oriented downward and toward but not in contact with human or object

Table 2. Behavioral responses (mean ± SD) of calves (n = 56) when tested individually at 27 ± 3 and 76 ± 3 d of age in novel environment, human approach, and novel object tests[1]

Test and behavior	Mean	SD	Range
Novel environment test			
Vocalizations (no.)	24.5	20.1	0–80.5
Active (no. of quadrants crossed)	58.2	19.3	24.5–121
Inactive (% of test time)	25.6	10.3	7.4–55.3
Exploring walls or floor (% of time)	43.7	8.8	24.6–62.6
Locomotor play (% of time)	1.3	1.0	0.06–5.1
Bucking (no.)	2.2	2.0	0–9.5
Human approach test			
Vocalizations (no.)	4.5	5.5	0–21
Latency to touch (s)	224	191	13–600
Time in contact (% of time)	20.3	18.6	0–73.9
Attentive close (% of time)	8.8	4.6	1.1–22.9
Attentive far (% of time)	9.8	9.2	0.3–52.4
Object play (% of time)	4.6	6.4	0–28.8
Locomotor play (% of time)	0.31	0.31	0–1.1
Bucking (no.)	0.44	0.73	0–3
Novel object test			
Vocalizations (no.)	10.0	9.3	0–42.5
Latency to touch (s)	85	151	3–900
Time in contact (% of time)	19.8	9.3	0–38.8
Attentive close (% of time)	7.0	2.4	2.8–12.1
Attentive far (% of time)	3.2	3.2	0.4–22.6
Object play (% of time)	2.5	2.9	0–11.7
Locomotor play (% of time)	0.31	0.34	0–1.3
Bucking (no.)	0.67	1.0	0–4.5

[1]Behaviors were averaged across repeated tests for each calf.

factor 1 were termed "interactive." Factor 2 explained 21.6% of the total variance and had high positive loadings for activity and time spent exploring the arena in the novel environment test. Calves that loaded highly on factor 2 were termed "exploratory/active." Factor 3 explained 14.4% of the total variance and had high positive loadings for vocalizations and inactivity in the novel environment test. Calves that loaded highly on factor 3 were termed "vocal/inactive."

Performance, Feed Intake, and Behavior

Performance, feed intake, development of solid feeding behaviors, and behavior at the milk feeder over the

Table 3. Coefficients (loadings) of the eigenvectors for the first 3 factors extracted by principal component analysis of behavioral measures recorded when calves (n = 56) were tested in novel environment, human approach, and novel object tests[1]

Variable	Factor 1	Factor 2	Factor 3
Vocalizations (no.)	0.25	0.05	**0.80**
Latency to touch human or object (s)	**−0.82**	0.26	−0.23
Time in contact with human or object (% of time)	**0.92**	0.16	0.02
Attentive[2] (% of time)	**−0.79**	0.13	0.001
Time spent playing (% of time)	**0.82**	0.25	0.04
Active[3] (no. of quadrants crossed)	−0.11	**0.84**	0.08
Inactive[3] (% of time)	−0.08	−0.18	**0.84**
Exploring[3,4] (% of time)	0.14	**0.76**	−0.24
Eigenvalues	2.99	1.73	1.15
Variance explained (%)	37.3	21.6	14.4
Interpretation (suggested label)	Interactive	Exploratory/active	Vocal/inactive

[1]Behaviors were averaged across tests except where indicated. High loadings (≥0.70) are indicated in bold. Eigenvalues and proportion of total variation explained by each factor are reported, and suggested labels for each factor are offered.

[2]Calf observes (head oriented toward) human or object; sum of time spent within 1 body length ("close") and more than 1 body length away ("far").

[3]Behavior recorded only in novel environment test.

[4]Time spent sniffing, licking, or with muzzle close to floor or wall surfaces.

Table 4. Performance, feed intake, and feeding behavior measures (mean ± SD) for calves (n = 56) during the preweaning and postweaning experimental period from d 7 to 68

Measure	Mean	SD	Range
Performance			
ADG (kg of BW/d)	0.84	0.15	0.54–1.16
Gain:feed ratio (kg of BW/DMI)	0.71	0.09	0.51–0.98
Feed intake			
Milk DMI (kg/d)	0.60	0.13	0.40–0.91
Starter DMI (kg/d)	0.71	0.24	0.25–1.25
Total DMI[1] (kg/d)	1.30	0.26	0.75–1.89
Development of solid feeding behavior[2]			
First day to eat 40 g of starter (d)	19.0	8.2	4–41
First day to eat 225 g of starter (d)	36.0	7.5	17–50
First day to eat 675 g of starter (d)	42.5	4.9	33–52
First day to eat 1,300 g of starter (d)	47.3	5.0	36–61
Behavior at milk feeder[3]			
Rewarded visits (no./d)	5.9	1.4	3.1–11.3
Unrewarded visits (no./d)	7.1	3.7	1.2–18.1
Persistent return to milk feeder after weaning[4]			
Total unrewarded visits (no.)	89.6	40.4	26–229

[1]Calculated from the sum of milk and starter intake. Hay was offered, but intakes could not be recorded reliably.

[2]Calculated as the average of the previous 3 d, with the requirement that each of the 3 d met at least 50% of the target.

[3]Rewarded refers to a visit where milk was available; unrewarded refers to a visit where milk was not available.

[4]Postweaning period: 55 to 68 d of age.

preweaning and postweaning period (7–68 d of age) are presented in Table 4. A summary of these measures by milk allowance treatment (6, 8, 10, or 12 L/d) is presented in Rosenberger et al. (2017). There was substantial individual variation among calves for weight gains and starter DMI over the experimental period, ranging from 0.5 to 1.2 kg/d of ADG and from 0.25 to 1.25 kg/d of starter DMI. Individual calves also differed in the age they first found and began to consume starter (at least 40 g of grain), ranging from 4 to 41 d of age. Unrewarded visits to the milk feeder ranged from on average 1 to 18 visits/d. This variability was due in part to milk allowance, but even within milk allowance assignment there was considerable variation in ADG (range: 0.54–1.0, 0.54–1.0, 0.64–1.1, and 0.56–1.2 kg of ADG/d), average starter DMI (range: 0.33–1.24, 0.25–1.1, 0.31–1.24, and 0.32–1.0 kg of DM/d), age that starter was first found and consumed (range: 6–29, 8–32, 4–41, and 12–41 d of age), and average number of unrewarded visits (range: 8.4–18.1, 4.5–12.3, 1.9–12.7, and 1.2–7.3/d) for calves allowed 6, 8, 10, and 12 L/d, respectively. This residual variation could be explained by personality traits of the individuals.

Milk allowance did not affect any of the 3 factors. The relationships between the 3 factors and performance and feed intake measures during the prestep, step, weaning, and postweaning periods are presented in Table 5. Factor 2 was related to several performance and feed intake measures; calves loading highly on factor 2 had higher starter and total DMI during all experimental periods and tended to have higher milk DMI during the prestep period. These calves also had greater ADG during the step period and greater overall ADG and tended to have greater gain:feed ratio for the total experimental period. Factor 1 and factor 3 showed more limited associations with these measures. Calves loading highly on factor 1 tended to have reduced ADG during the prestep period, and calves loading highly on factor 3 tended to have greater ADG during the step period and greater gain:feed ratio.

The development of solid feeding behaviors and behavior at the milk feeder during each experimental period was also associated with the factors (Table 6). Calves loading highly on factor 2 met all starter intake targets (40, 225, 675, and 1,300 g) at an earlier age. Calves loading highly on factor 1 also tended to begin to consume starter (40 g) at an earlier age. Neither factor 1 nor factor 3 were associated with any other starter intake targets. However, calves that loaded highly on either of these 2 factors generally had a greater number of rewarded and unrewarded visits to the milk feeder. Factor 3 was positively associated with rewarded visits during prestep and total experimental periods and with unrewarded visits during the step period. Factor 1 was also positively associated with unrewarded visits during the step and total experimental periods.

To characterize the behavioral response to weaning, we also examined the relationship between factor

Table 5. Relationships between factor scores and performance and feed intake measures during each of 5 experimental periods: prestep (full milk allowance; 7–41 d of age), step (milk allowance reduced to 50%; 42–50 d of age), weaning (51–54 d of age), postweaning (55–68 d of age), and the total experimental period (7–68 d of age)[1]

	Factor 1 (interactive)			Factor 2 (exploratory/active)			Factor 3 (vocal/inactive)		
Measure	Effect direction[2]	F-value	P-value	Effect direction	F-value	P-value	Effect direction	F-value	P-value
ADG (kg/d)									
Prestep	–	**3.85**	**0.06**		1.79	0.19		1.90	0.18
Step		0.00	0.97	+	**4.26**	**0.04**	+	**3.06**	**0.09**
Postweaning		0.07	0.80		1.63	0.21		0.79	0.38
Total		0.57	0.46	+	**16.03**	**<0.001**		1.31	0.20
Milk DMI (kg/d)									
Prestep		0.08	0.77	+	**3.38**	**0.07**		1.17	0.29
Step		0.03	0.87		0.44	0.51		0.04	0.83
Weaning		0.14	0.24		0.02	0.89		0.42	0.52
Total		0.02	0.89		2.45	0.13		0.62	0.44
Starter DMI (kg/d)									
Prestep		0.20	0.66	+	**7.68**	**0.008**		0.20	0.66
Step		0.76	0.39	+	**6.33**	**0.02**		0.56	0.46
Weaning		0.12	0.29	+	**5.57**	**0.02**		0.24	0.63
Postweaning		0.73	0.40	+	**6.47**	**0.01**		0.24	0.63
Total		1.0	0.32	+	**8.76**	**0.005**		0.00	0.98
Total DMI[3] (kg/d)									
Prestep		0.13	0.72	+	**9.82**	**0.003**		0.23	0.63
Step		0.90	0.35	+	**6.45**	**0.01**		0.61	0.44
Weaning		1.2	0.28	+	**5.44**	**0.02**		0.29	0.59
Total		0.79	0.38	+	**9.11**	**0.004**		0.03	0.86
Gain:feed ratio (kg of BW/DMI)									
Total		0.40	0.53	+	**3.47**	**0.07**	+	**6.49**	**0.01**

[1]Effect direction is provided when the main effect is $P \leq 0.1$ (in bold).

[2]– = negative; + = positive.

[3]Calculated from the sum of milk and starter intakes. Hay was offered, but intakes could not be recorded reliably.

Table 6. Relationships between factor scores and measures related to the development of solid feeding behavior, behavior at the milk feeder, and behavioral response to weaning[1]

	Factor 1 (interactive)			Factor 2 (exploratory/active)			Factor 3 (vocal/inactive)		
Measure	Effect direction	F-value	P-value	Effect direction	F-value	P-value	Effect direction	F-value	P-value
Age to consume grain target[2] (d)									
At least 40 g	–	**3.78**	**0.06**	–	**2.85**	**0.09**		0.48	0.49
225 g		1.32	0.26	–	**9.03**	**0.004**		0.48	0.49
675 g		0.29	0.59	–	**4.96**	**0.03**		0.04	0.85
1,300 g		0.81	0.37	–	**7.46**	**0.009**		0.06	0.81
Rewarded visits to the milk feeder[3] (no./d)									
Prestep		0.94	0.33		0.76	0.39	+	**4.18**	**0.05**
Step		0.23	0.63		0.57	0.45		2.02	0.16
Weaning		2.03	0.16	+	**6.28**	**0.02**		0.18	0.68
Total		0.82	0.37		1.11	0.30	+	**4.33**	**0.04**
Unrewarded visits to the milk feeder[3] (no./d)									
Prestep		1.87	0.18		0.15	0.71		1.97	0.17
Step	+	**4.65**	**0.04**		0.77	0.39	+	**4.51**	**0.04**
Weaning		0.00	0.99		0.08	0.78		1.32	0.26
Total	+	**5.44**	**0.02**		1.72	0.20		1.56	0.22
Persistent return to milk feeder after weaning									
Total unrewarded visits (no.)		0.60	0.44	–	**8.00**	**0.007**	–	0.80	0.38

[1]Experimental periods were defined as prestep (full milk allowance; 7–41 d of age), step (milk allowance reduced to 50%; 42–50 d of age), weaning (51–54 d of age), postweaning (55–68 d of age), and the total experimental period (7–68 d of age). Effect direction is provided when the main effect is $P \leq 0.1$ (in bold).

[2]Calculated as the average of the previous 3 d, with the requirement that each of the 3 d met at least 50% of the target.

[3]Rewarded refers to a visit where milk was available; unrewarded refers to a visit where milk was not available.

scores and total number of visits to the milk feeder after weaning (Table 6). Calves loading highly on factor 2 engaged in fewer unrewarded visits, suggesting that these calves were less persistent in attempting to gain milk after weaning.

DISCUSSION

This study was the first to investigate personality traits of dairy calves using responses to novelty and the relationship with performance, feed intake, and development of solid feeding behavior around weaning. Calves that were more exploratory and active in the novelty tests (i.e., loaded highly on factor 2) consumed solid feed at an earlier age and ate more grain throughout the preweaning period, resulting in higher ADG. These calves also had fewer visits to the milk feeder after weaning, suggesting that they experienced a smoother transition from milk onto solid feed. In contrast, calves that were more vocal and inactive (i.e., loaded highly on factor 3) had more unrewarded visits to the milk feeder during initial milk reduction, indicating that these calves respond to milk removal by persisting in their unsuccessful behavior rather than searching for other feed sources.

Performance and Feed Intake

We found large variation in weight gains and starter intake among calves, even within milk allowance treatment. Similar variation in weight gains within a given milk feeding regimen was reported by de Passillé et al. (2011); these authors reported a weight gain range of 0.4 to 2.1, −0.4 to 1.9, and 0.3 to 1.8% of BW during the postweaning period for low-milk early-weaning, high-milk early-weaning, and high-milk late-weaning treatments, respectively. Large variability has also been reported for weaning weights (2 different farms: 82.1 ± 10.3 and 84.1 ± 10.8 kg, mean ± SD; Soberon et al., 2012) and weekly starter intake up to 8 wk of age (Van De Stroet et al., 2016).

We predicted that personality would explain some of the variation in weight gain and starter intake. Indeed, we found that calves that were more exploratory (i.e., loaded high on factor 2) had greater weight gains during the step period (when milk was reduced to 50% of allowance), resulting in greater overall weight gains and a tendency to have greater gain:feed ratio for the total experimental period. These calves also consumed more starter DMI and total DMI across all experimental periods and tended to consume more milk DMI before initial milk reduction. Müller and von Keyserlingk (2006) reported similar findings for 8-mo-old heifers tested in a social separation test; increased levels of exploration and activity in the test, such as duration of walking and number of quadrants crossed, were related to ADG. These authors reported that heifers with increased time spent immobile and more frequent vigilance behaviors in the social separation test had reduced ADG. Calves in our study that loaded highly on factor 3 (i.e., reflecting high vocalizations and inactivity) tended to have greater ADG during the first reduction in milk allowance (step period) and a greater overall gain:feed ratio. Improved performance in both the exploratory–active and vocal–inactive calves may be related to feed efficiency; exploratory–active calves may have greater ADG due to increased DMI, whereas vocal–inactive calves may have reduced energy expenditure, leading to greater ADG.

There is growing evidence suggesting a relationship between performance and fear responses to handling in beef cattle (reviewed by Haskell et al., 2014). Studies in beef calves generally report decreased weaning weight or postweaning weight gains in calves that are highly reactive inside the chute (Torres-Vázquez and Spangler, 2016) or have high flight speeds when exiting the chute (Francisco et al., 2012). This evidence suggests that more reactive, fearful, or excitable traits are predictive of poor performance in weaned beef calves. Similar relationships are reported in mature beef cattle for weight gains (e.g., Petherick et al., 2002; Reinhardt et al., 2009; Lockwood et al., 2015) and feed efficiency (Cafe et al., 2011) and in dairy cattle when scored for reactivity to milking or restraint in the chute (e.g., Cziszter et al., 2016). Likewise, cattle showing reduced feed intake at the feedlot also showed increased agitation in the chute (Cafe et al., 2011), high flight speed out of the chute (Nkrumah et al., 2007; Elzo et al., 2009), and high reactivity when isolated in a pen with a handler (Black et al., 2013). No studies have examined how reactivity to handling or restraint is related to performance or feed intake in preweaned beef or dairy calves. However, our study suggests that individuals that are less reactive to novel situations (i.e., are more interactive, active, or exploratory) perform better than individuals that are more reactive (i.e., vocal or inactive).

Recent studies have demonstrated the long-term benefits of increased preweaning weight gains and intakes. For example, Soberon et al. (2012) found that among several early-life performance, nutrition, and management factors that potentially influence long-term productivity, preweaning weight gain had the highest correlation with first-lactation milk production, with every 100-g increase in preweaning ADG resulting in 110 kg more milk during the first lactation. Another large-scale study demonstrated that higher preweaning growth translated to higher BW in mature cattle (Van De Stroet et al., 2016). Furthermore, weaning DMI was related to first-lactation milk yield, where every 1-kg increase in weaning DMI yielded around 280 kg of ME milk yield (Heinrichs and Heinrichs, 2011). Given that the current study indicates that personality traits such as exploration and inactivity influence preweaning and weaning weight gains, we suggest that future work should determine the consistency of these personality traits over the animal's life span and how these traits relate to long-term productivity.

Development of Solid Feeding Behaviors

Irrespective of milk allowance treatment, we observed large variation in the age at which calves first found and began to consume starter. de Passillé and Rushen (2016) reported a range in age from 23 to 82 d when calves met a target of 200 g of starter intake. This variability is notable considering that all calves were allocated the same milk allowance and were housed in the same social environment. Calves in our study showed a similar range in the age at which they met the target of 225 g of starter intake, and this variability was only partly explained by differences in milk allowances (see Rosenberger et al., 2017). Another study by de Passillé and Rushen (2012) reported variability in the duration of weaning that was initiated after the first starter target (200 g) was reached. Interestingly, calves that first reached the 200-g target were not always the first to reach the 1,400-g target, suggesting that there is also individual variation in the rate of increase in starter intake (de Passillé et al., 2011). Together, this evidence indicates that calves vary in their ability to find or willingness to eat solid feed. This behavior is important in preweaning calves; early intakes of starter encourage rumen development and ease the transition from milk onto a solid-feed diet (reviewed by Khan et al., 2016). Around weaning, calves must seek alternative food sources and learn through sampling and postingestive feedback about which novel feeds are appropriate to consume (Provenza and Balph, 1987). An understanding of the mechanisms that drive these individual feeding patterns is lacking.

Our study showed that calves that were more exploratory in the novel environment test tended to begin to eat starter earlier and reached the majority of the targets for starter intake earlier than other calves regardless of milk allowance. Other work provides some evidence that personality traits may explain individual differences in sampling of novel feeds. For example, Meagher et al. (2017) offered feed bins with different forage varieties or flavors and recorded the number of bin switches as a measure of exploratory feed sampling, similar to behavior seen in first-lactation dairy heifers (Huzzey et al., 2013). There was a low-moderate correlation between exploration of the varied or flavored feed and novel object contact duration and a moderate correlation between preference for varied forages (i.e., time spent eating) and novel object contact duration (Meagher et al., 2017). In lambs, Villalba et al. (2009) found that individuals that were less vocal in an open field test were more willing to eat a novel food. Taken together, these studies suggest that some individuals may be more proficient in exploring and sampling novel feeds.

The propensity of an individual to find and sample novel feeds may be a personality trait itself. Food neophobia, in which animals are reluctant to eat unfamiliar foods, is a well-known phenomenon in ruminants (Chapple and Lynch, 1986). This fear of novel diets must be overcome for calves to transition from milk to solid feed. There is limited research on food neophobia in dairy cattle. Costa et al. (2014) performed a series of food neophobia tests and found that tests repeated over time were consistent within individuals, suggesting that this behavior may reflect a stable trait. This food neophobia test has since been used in dairy heifers (Meagher et al., 2017) and mature dairy cattle (Mainardes and DeVries, 2016). Future research should investigate how food neophobia affects the development of solid feeding behavior and weaning success.

The sociability of the calf may also contribute to the development of solid feeding behavior. For example, more affiliative calves may be more likely to learn from others where and how to eat novel feeds. Seeing another calf eating, approaching, or manipulating feed may increase attention toward the feed and subsequently encourage consumption of feed in other calves, a phenomenon known as social facilitation (Zentall and Galef, 1988). Calves may also gain information about novel feeds through a related mechanism called social learning, in which calves learn by observation of, or interaction with, other individuals (Zentall and Galef, 1988). Regardless of the mechanism, there is evidence that social housing of calves from an early age results in increased solid feed intake and improved ability to cope with novelty (Bernal-Rigoli et al., 2012; Costa et al., 2015; Miller-Cushon and DeVries, 2016). In our study, interactivity (i.e., spending more time in contact with and playing with the human or novel object) showed limited relationship with measures of early solid feed consumption. However, these types of interactions with a human or novel object are not necessarily related to a social affinity toward conspecifics; the latter may be more relevant in the development of feeding behaviors.

For example, some evidence indicates a relationship between exploration and activity in a foraging task and sociability in finches (McCowan and Griffith, 2015). Further, sticklebacks that actively explored unfamiliar environments quickly exploited social advantages provided by demonstrators (Nomakuchi et al., 2009), suggesting that the social dimension of personality may play an important role in the development and expression of feeding behavior. Future research should determine whether individuals that are more socially affiliative toward conspecifics are more likely to start and continue to consume solid feed.

Discovering and sampling novel feeds requires some degree of learning. For example, calves must also locate the feeder and, in the case of an automated feeder, learn how to use it. These learning processes may be facilitated by exploration, which has been described as a means of collecting information about the environment (Wood-Gush and Vestergaard, 1989). Thus, exploratory calves may learn environmental information more quickly, aiding in the early exploration and discovery of feed sources in their environment. Some research has investigated a link between learning ability and personality traits. For example, Webb et al. (2015) found no association between fearfulness and learning ability in calves. However, Boissy and Le Neindre (1990) reported that learning ability in heifers was positively influenced by the social affinity of the individual and negatively influenced by the individual's reactivity toward fear-eliciting stimuli.

Behavioral Responses to Weaning

Calves in our study also showed a large range in the number of visits to the milk feeder when milk was unavailable; these unrewarded visits ranged from 1 to 18 visits per day over the experimental period. We could not find any previous study that reported individual variation in unrewarded visits, although several reports describe higher numbers of unrewarded visits in calves fed restricted milk diets (e.g., Jensen and Holm, 2003; Borderas et al., 2009), indicating that these calves are experiencing hunger (De Paula Vieira et al., 2008). Our study shows residual variability in unrewarded visits not explained by milk allowance. Calves that loaded highly as interactive (i.e., spent more time interacting with the human or object and spent more time playing) had more unrewarded visits during the step and total experimental periods; calves loading highly as inactive or vocal also had more unrewarded visits during the step period. More interactive calves may be sensation-seeking individuals and thus search for stimulation in their environment (Raju, 1980). This may take the form of nonnutritive suckling on a teat. Rushen and de Passillé (1995) found that the motivation behind nonnutritive teat suckling was more related to the act of sucking itself rather than milk ingestion.

The motivation for nonnutritive sucking is also associated with milk allowance (de Passillé, 2001). Milk reduction during the step and weaning periods elicits nonnutritive visits (Budzynska and Weary, 2008; De Paula Vieira et al., 2008; Rosenberger et al., 2017). In the current study, the calves loading highly as inactive or vocal may have engaged in more unrewarded visits as a consequence of hunger. This idea is supported by our results showing that inactive or vocal calves also had more rewarded visits (i.e., visits with milk) over the weaning period. Jensen (2004) showed that when calves had their milk allowance divided into 8 rather than 4 portions, the calves remained in the feeder for longer following a milk meal, perhaps reflecting hunger-related motivation. Future research should attempt to disentangle suckling and hunger motivations behind unrewarded visits and how they relate with personality traits of the individual.

Although personality traits explain part of the variability in feeding behavior and performance, we cannot rule out other causes of variation; for example, undiagnosed subclinical illness may have contributed to some of the variation in feeding behavior measures. Also, the specifics of our study may have constrained various measures. For example, the starter feeder used in the present study allowed only 1 calf to feed at a time. In contrast, an open trough allows calves to feed in the company of social companions, perhaps affecting the development of feeding behavior.

Nonetheless, these findings do offer some opportunity for on-farm application. It is important to identify individuals that are struggling to make the transition from milk onto solid feed so that performance and welfare are not compromised. Our study suggests that the characterization of individual personalities at around 3 wk of age can identify animals that are most likely to make this transition smoothly and to identify calves that would benefit from additional assistance. Currently, personality methods are time consuming and likely impractical to implement on farms; future research should identify more practical testing methods. This may include a subset of the measures used in the current study, but we especially encourage new work to consider measures that can be collected automatically—for example, using computerized calf feeders.

CONCLUSIONS

Personality traits explain individual variability in the development of feeding behavior, solid feed intake and weight gains, and behavioral responses around weaning. Further understanding of the mechanisms behind these associations is warranted, including how food neophobia, sociability, and learning processes relate to personality traits relevant in the development of feeding behavior.

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