Some like it varied: individual differences in preference for feed variety in dairy heifers

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Abstract

Motivation to explore is believed to be widespread among animals, but exploratory behaviour varies within populations. Offering variety in feed is one simple way of allowing intensively housed dairy cattle to express exploratory foraging behaviour. Individuals' exploration of different feed types, as with other new stimuli, likely reflects a balance between exploratory motivation and fear of novelty. We tested the degree to which Holstein heifers (n=10) preferred variety in feed vs. a constant, high quality mixed ration, by first providing varying types of forages and then varying flavours of mixed feed. We also investigated individual differences in exploratory behaviour by measuring switching between feed bins. Individual consistency in preferences was assessed between tests, and longer-term consistency was evaluated by comparing

these results with behaviour in novel object and novel feed tests before weaning. On average, the heifers preferred the constant, familiar feed (spending on average just 20% of their time at varied feed bins), but this preference varied among individuals (from 0 to 46% of time eating in the forage trial, and 0 to 93% in the flavour trial). Preference for varied forages correlated positively with intake of novel feed as calves (r_s=0.72, n=9). Preference for varied flavours showed a negative correlation with latency to approach a novel object (r_s=-0.65). It thus appears that preference for variety and exploratory foraging behaviour reflect consistent personality traits. These results suggest that offering novel feeds on a rotating schedule as a supplement to the regular diet may be an effective form of enrichment for at least some individuals within a herd.

Keywords: foraging behaviour; individual differences; neophobia; curiosity; animal welfare; preference

1. Introduction

Animals are often motivated to explore (Berlyne 1960, Hughes 1997, Špinka & Wemelsfelder 2011). It has been demonstrated, for example, that opportunities to explore can be used as reinforcers for learning tasks (Butler 1953: rhesus macaques; Montgomery 1954: rats), and that rats will sometimes choose to explore new locations over visiting known reward locations (Franks et al. 2013). Motivation to explore is presumed to be common across species because it enables gathering of information about resource availability and proximity of potential threats or mates (see e.g. Inglis et al. 1997). Although the tendency to explore varies between species and taxa, with generalist species hypothesized to be more exploratory (see Glickman & Sroges 1966, Mench 1998), some exploration when feeding is expected in all species (e.g. moving between locations to try different feed types). Not only is it useful to find higher quality food patches in the wild, but herbivores must consume more than one type of plant to meet dietary requirements (Villalba et al. 2010).

Modern dairy farms provide few opportunities to perform feed-related exploratory behaviour; they commonly feed an unvarying diet consisting of a mixture of forage and grains to all animals of a given age or production stage, provided in a constant location. Environments with few and unvarying stimuli may be monotonous for the animals and thus potentially reduce welfare (Wood-Gush & Vestergaard 1991, Meagher & Mason 2012). Some evidence suggests that variation in feed is preferred to such uniform diets by other ruminants (e.g. Scott & Provenza 1998). Lambs fed a uniform diet with no opportunity for choice had slower feed intakes than did those allowed to choose between feeds that varied over time, as well as higher cortisol levels and neutrophil to

lymphocyte ratios, suggesting that they might have been experiencing stress (Catanese et al. 2013). Consistent with the hypothesis that cattle prefer variety, all beef heifers tested consumed more than one type of feed when they are offered a choice (Ginane et al. 2002), and calves select different dietary ingredients day to day and at different times of day (Atwood et al. 2001). Cows have approximately 20,000 taste receptors on their tongues, compared to less than 7,000 for humans and 1,700 for dogs (reviewed by Roura et al. 2008), suggesting they may be highly attuned to distinctions in flavour, and perhaps prone to boredom when fed monotonous diets. The first aim of our experiment was therefore to determine whether heifers prefer varied feeds to a nutritionally balanced but unchanging feed.

Exploratory behaviour varies within as well as between species. The expression of this behaviour in response to novelty likely reflects a balance of two competing motivations (reviewed by Russell 1973): fear of novelty (neophobia) and motivation to gain information and/or stimulation (i.e. motivation to explore, sometimes called 'curiosity'; see e.g. Hughes 1997 and Litman 2005 for discussions of different theories of the motivation underlying exploration). Understanding individual differences in such traits is important because it can influence response to experimental treatments, susceptibility to stress, and perhaps health (see e.g. Carere and Eens 2005; Cavigelli 2005). However, little experimental work has been done on this topic in ruminants, and research on feed preferences has typically focused on the group rather than individuals. Our second aim was therefore to determine whether individual differences in preference for varied feed were stable across tests, and the extent to which these differences could be predicted by behaviours associated with fearfulness and curiosity.

2. Methods

2.1 Animal housing and care

This research was approved by the University of British Columbia Animal Care Committee (Protocol A15-0117). The subjects were 10 female Holsteins, housed at the University of British Columbia Dairy Education and Research Centre (Agassiz, BC, Canada). These animals were exposed to behavioural tests as calves and as weaned heifers. As calves, animals were housed individually from birth to 48 ± 3 days of age, in sawdust-bedded pens (1.2 × 2 m). Calves had ad libitum access to water and grain (Hi-Pro Medicated Calf Starter, Chilliwack BC, Canada). For the first 26 d of life, they were fed 8 L of milk per day by bottle, split between two feedings. The amount per feeding was then reduced over two days to a total of 4 L per day. They were then weaned at the time they were moved to a group pen (48 ± 3 d).

As weaned heifers, the animals were housed as a group in a free-stall pen that was deep-bedded with sand, containing 13 lying stalls and 13 headlocks at the feed bunk. All animals had ad libitum access to water. Their regular diet was a total mixed ration (TMR) of corn silage, local fescue and orchardgrass hay, grain, and grass silage (35%, 25%, 22%, and 19% of dry matter, respectively; the overall mixture had an average of 44% dry matter, 17.5% crude protein, 43% neutral detergent fibre, and 0.93 Mcal/kg net energy for gain).

2.2 Feeding behaviour tests

Preference for variety and expression of exploratory foraging behaviour were tested when the heifers were aged 41 to 49 weeks old. During the habituation phase, heifers were introduced to the new feeds to be included in the experiment. Timothy and alfalfa hays, a local tall fescue/orchardgrass hay mixture and chopped rye straw were placed in four different bins at the feed bunk simultaneously. Two heifers at a time were provided access for 20 min each for two days, with feed locations rearranged on the second day. Over the next four days, the same procedure was followed but with access to only one forage type per day. The heifers had no access to their regular TMR during these habituation trials. Heifers were paired during this stage to reduce stress associated with isolation and encourage feeding while the test conditions and feeds were novel.

In the next phase (i.e. the Forage trial), heifers could choose between a feed bin containing the regular TMR and a bin containing one of these four forage types, with the forage varying day-to-day in a pseudorandom order (each forage being presented an equal number of times once all heifers were eating). Tests were conducted following the protocol of Huzzey et al. (2013), in which heifers were allowed to approach the feed bunk one at a time in daily tests, while the other heifers were held in another section of the pen. The heifers were allowed to enter in the order in which they chose to approach the gate. Tests were 10 min long, and began at the typical feed delivery time (approximately 7:30 a.m.) to ensure that the heifers were motivated to eat. Bins were partially covered by a lid to prevent the animals from seeing the contents before they approached, but were always in the same locations (see Figure 1). Bins were refilled between heifers as needed to maintain equal fill. The heifer's first choice of bin (defined

129 by the heifer putting her head in the bin and interacting with the feed) and time spent
130 interacting with the feed at each bin were recorded within each trial. Additionally,
131 number of switches between bins was recorded in each trial, reflecting sampling
132 behaviour (cf. Huzzey et al. 2013; Nielsen et al. 1996), which is a form of exploration
133 (see e.g. Eliassen et al. 2007), and latency to feed on the first day of the habituation
134 phase was recorded as a measure of feed neophobia. These tests were continued for
135 14 days. The first two days of the Forage trial were excluded from analyses of feed
136 preferences because some heifers were not yet consistently eating; the remaining 12
137 days of data included three presentations of each of the four forage types.
138 The Forage preference test provides a naturalistic treatment, but can be criticized
139 because the different forages also varied nutritionally. Thus, in a second test (the
140 Flavour trial), we used the standard TMR but varied flavour using non-nutritive
141 powdered flavours (Essentials Inc., Abbotsford, BC, Canada) added to this mixed ration.
142 Heifers were habituated to the new flavours and a new feeding location over two days in
143 which they only had access to the flavoured TMR (three flavours on Day 1 and two on
144 Day 2), as in the Forage trial. On the following day, all five flavours were presented
145 simultaneously to assess preferences, with heifers tested one at a time. Preferences
146 were again assessed based on time spent at each bin. Starting the next day, heifers
147 were given the choice among three bins: one containing the regular (unflavoured) TMR,
148 one that varied between four flavours (Power Punch [berry flavoured], Peppermint,
149 Banana and Anise essences), and one with a constant flavour (Caramel Toffee). This
150 third option had been highly consumed in a short pilot trial in which another group of
151 heifers was offered all flavours simultaneously. It was provided to test whether heifers

simply preferred TMR with flavour added rather than variety in flavour per se. This might be expected if, for example, the unflavoured TMR had low palatability.

This test was conducted in the alley behind the pen to allow the regular TMR and varied feed to be placed at an equal distance from the entrance to the test area (Figure 2). To control for side biases, we placed the varied feed on the left for half the heifers, and on the right for the other half of the heifers. The constant flavour was available on both sides. The same response variables as above were recorded.

Health was monitored daily during the testing period following standard farm protocols; no heifers required medication for any illnesses during the trial.

2.3 Behavioural tests as calves

Nine of these calves had been given two tests of neophobia and exploratory motivation as part of an earlier study. A novel object test was conducted at 5 weeks (35 ± 3 d) of age. The object (a ball or plastic basket) was lowered into the pen on a rope. Latency to touch the object and time in contact were recorded over the next 10 min. Although both of these measures are likely affected by both motivational systems in question (e.g. previous work has reported that both are correlated with cortisol and influenced by anxiolytic administration: Van Reenen et al. 2005, 2009), latency is most commonly used in assessing fear (see review by Forkman et al. 2007) and contact duration has been used to measure curiosity or exploration in other species (e.g. Glickman & Sroges 1966). When heifers were 6.5 weeks (45 ± 3 d) of age a food neophobia test was conducted. A bucket containing 3.0 kg of TMR (as described above) was put on the front of the individual pen in place of the usual grain. Latency to eat was

recorded from video, and the '*as fed*' amount consumed in 30 min was calculated by weighing the leftover feed. Predictions for the direction of the relationship expected between these behaviours and those assessed in the following trial are given in Table 1, based on the hypothesis that preference for variety reflects exploratory motivation, and that high latencies to eat when the food is first presented reflects fear of novelty.

2.4 Statistical analyses

Preference for variety was assessed within each stage as the proportion of time eating from a varied bin in relation to the total time spent eating, and whether the first bin chosen was varied or stable feed. To test whether varied feed was preferred to normal feed, we calculated the individual means across days within each phase of the study. For the Forage preference trial, a one-sample t-test was used to determine whether the consumption in the last set of tests (the last test for each feed type in the varied bin) differed from zero. This was repeated for the Flavour preference trial, but the data were non-normally distributed according to Shapiro-Wilk tests, and were log-transformed to correct this in further analyses. Due to this non-normality, summary data presented for this trial are medians rather than means. Biases in feeding choices based on feed locations were assessed by calculating binomial probabilities. We also tested whether preferences and levels of exploratory behaviour (switching between feed bins) changed over time within the feeding trials by calculating means for each day across individuals and regressing against test day, since a decrease in exploration might be expected due to decreasing information gain. Changes were considered significant at the P=0.05 level.

To assess whether individual differences in preference for variety reflected lasting differences in fearfulness or exploratory motivation, Spearman rank correlations were calculated between preference in each phase of the study (Forage and Flavour trials) and behaviour in the tests conducted while the subjects were calves. Within the heifer trial, correlations were also calculated between preference for variety in each trial and latency to eat on the first day of the habituation phase (i.e. neophobia), and with switches between bins (exploratory behaviour) in each trial. Correlations were categorized as negligible (<0.3), low (0.3-0.5), moderate (0.5-0.7), high (0.7-0.9) or very high (>0.9) according to Hinkle and colleagues (2003). All analyses were conducted in R (3.2.2, The R Foundation for Statistical Computing).

3. Results

3.1 Group-level feeding preferences

The median time spent eating per session in the Forage trial was 456 s of the 600 s possible (interquartile range: 355 – 530 s). Heifers did not spend more time eating from the varied forage bins than from the familiar TMR; on average, they spent 20% (± 17) of their time feeding from the varied forage bin. The linear regression of proportion of time eating varied forage vs. day showed no change over the 12 days of testing ($r<0.001$, $P=0.943$). Similarly, heifers visited the varied bins first in 28 ± 26% of the trials. The results were similar for the tests using the flavoured TMR: on average, heifers spent just 6% (median; interquartile range: 4-16%) of their total feeding time at the varied bins, and again this did not vary over the 12 days of testing ($r=0.07$, $P=0.399$). Heifers visited these varied bins first in just 12% (median; interquartile range:

2-17%) of trials. In the Flavour trial, heifers spent a median 554 s eating all foods combined (interquartile range: 517 – 580 s).

Heifers showed side preferences in the Flavour trial: on the first day of testing heifers alone, when all flavours were presented simultaneously, nine of ten heifers went to the bins on the left first (binomial probability of this or a more extreme result happening by chance: P=0.022) and only ate from those bins. This preference continued throughout the trial: a median 89% (interquartile range: 44-75%) of feeding time for the fixed flavour, which was present on both sides, was at the bins to the left of the gate. This side bias was less obvious during the Forage trial, although by the end of this trial heifers tended to go to the bins in the half closer to the entry: all nine chose these bins first on day 12 (vs. 5 of 9 on day 1; 62 of 105 across all heifers and days).

The mean number of switches between bins of different feed types did not change over sessions (Forage trial: r=0.13, P=0.251; Flavour trial: r=0.17, P=0.178).

3.2 Individual differences in feeding preferences as heifers

Individual differences in preference were observed throughout the study. In the varied Forage trial, individual averages of the proportion of eating time spent at the varied bins ranged from 0% to 46%. For the Flavour trial, individual differences were influenced by the side bias: the maximum proportion of time eating from the varied bins was only 12% when it was placed on the right, versus 93% when on the left (see Figure 3). The preference for variability showed some consistency between the Forage and Flavour preference trials (r_s= 0.47; Figure 4).

244 *3.3 Relationships within tests*

245 In the calf tests, the two measures taken during the food neophobia tests, latency
246 to eat and amount consumed, were positively correlated (r_s = 0.63). There was a low
247 negative correlation between time in contact with the novel object and latency to make
248 contact (n=8, r_s = -0.31).

249 In the heifer trial, preference for varied feed was not predicted by latency to eat
250 on the first day of the habituation phase (r_s = 0.25 for Forage trial and 0.26 for Flavour
251 trial). There was, however, a low positive correlation between preference for varied feed
252 and the number of times they switched between bins in the Flavour trial (r_s = 0.30), and
253 in the Forage trial (r_s = 0.48).

254

255 *3.4 Relationships between tests*

256

257 In the two tests conducted as calves, neither latency to eat nor intake in the food
258 neophobia test correlated with the latency to touch a novel object (r_s = 0.23 and 0.26,
259 respectively).

260 The relationships between the calf novel object test and behaviour in the feeding
261 trial as heifers are summarized in Table 2. For the purpose of these analyses,
262 preference for variety is expressed as proportion of time eating from the variable bins;
263 this measure was very highly correlated with the first choice of bins (r_s = 0.94 and 0.91
264 in the Forage and Flavour trials, respectively), so using both was unnecessary. There
265 was a high positive correlation between intake of novel feed as calves and preference
266 for varied feed over TMR in the Forage trial. A moderate correlation was found between

latency to touch a novel object and preference for varied flavour over TMR with no flavour added. Since the side of the alley to which the varied feed was assigned affected preferences, the analyses were split by side. We found a high negative correlation with latency to touch the novel object only when varied flavour was tested on the right; when the varied feed was on the left, there was no relationship. Total time spent in contact with a novel object was moderately correlated with preference for varied feed in the Forage trial.

The number of switches between bins, averaged across the Forage and Flavour trials, had a high positive correlation with intake of novel feed as a calf. There was also a moderate correlation between latency to eat the novel forage as a heifer and latency to touch a novel object as a calf; however, this relationship was unexpectedly negative. All remaining correlations were low or negligible.

4. Discussion

On average, heifers did not prefer varied over stable feed, even when there was no energetic or nutritional cost to choosing the varied feed. This finding is surprising given that other work has shown that monotonous flavours are generally less preferred in young animals of another ruminant species, sheep (Scott & Provenza 1998). This finding also contrasts with results from primates that show a preference for varied over monotonous diets (Addessi et al. 2010). The current results are more in keeping with the common wisdom that farms should aim to keep feed as stable as possible (e.g. Stone 2008). Feeding a consistent diet is thought to improve intake and performance (e.g. milk yield: Sova et al. 2014, but see Yoder et al. 2013 for a counterexample) and is

290 hypothesized to be better for health (Sova et al. 2014). Cattle and other domestic
291 ruminants tend to be neophobic with regard to food, i.e. they are reluctant to eat novel
292 food items and tend to sample small amounts at first (see e.g. Launchbaugh et al. 1997;
293 Herskin et al. 2003), likely helping them avoid toxic doses (Launchbaugh 1995). If this
294 neophobia was not fully overcome in the time given, it might explain the greater
295 consumption of familiar feed in the current experiment. The heifers may also not have
296 perceived the TMR as uniform or monotonous since it contained many ingredients.
297 Moreover, individual bites may vary slightly in the exact mixture of elements that the
298 heifer ingests, and their many taste buds may make them sensitive to fine distinctions.
299 Still, most heifers consumed at least some varied feed throughout the Forage trial
300 despite the varied feed having lower average energy and protein content (the two major
301 nutritional needs expected to guide choice; see e.g. Bailey, 1995; Villalba et al. 2015)
302 lower than that of the TMR.
303 There are several reasons why feeding behaviour might not always maximize
304 energy gain (cf. Newman et al. 1992). Optimal foraging theory allows for sampling of
305 different feeds to obtain information about feed quality, and predicts this sampling to be
306 more persistent in changing environments, where past experience is a less effective
307 predictor of current conditions (Stephens & Krebs 1986; Shettleworth 1988). However,
308 in the Flavour trial, all foods offered were consistently of identical high quality and
309 therefore little sampling would be expected (Huzzey et al. 2013). If consumption of
310 varied feed was primarily a form of sampling to gain information about patch quality, we
311 might have expected this to decrease over time as the heifers learned about the feeds.
312 If consumption of the varied feed was limited primarily by feed neophobia rather than

feed value, by contrast, it would have been expected to increase over time. Instead, we found that consumption of the varied feed did not change over time, suggesting that the results reflect a relatively stable preference for some variety in the diet. While the literature on feed preferences often describes 'partial preferences' for consumption of more than one feed as opposed to always choosing a single feed (e.g. McNamara & Houston 1987, Rutter 2010), there is little discussion of how much needs to be consumed for this to qualify as being partially preferred.

Such partial preferences may allow animals to select a more balanced diet (Newman et al. 1992), and choice based on specific nutrients other than energy and protein cannot be absolutely ruled out in the Forage trial here. However, partial preferences can also be seen when there is no evidence of relevant nutritional differences (Newman et al. 1992, Parsons et al. 1994). Preferring feeds that have not been recently consumed, as seen in other ruminants (Parsons et al. 1994, Scott & Provenza 1998; similar phenomena also being reported in other taxa, e.g. Tuttle et al. 1990), may be explained mechanistically by sensory-specific satiety. This is a phenomenon observed in humans, in which foods become subjectively less pleasant as they are consumed, before any physiological consequences of the nutrients can be processed (Rolls 1986). The functional basis for this phenomenon remains unclear, but likely relates to a more general need for sensory change, which has been suggested as one reason for what is called "intrinsic exploration" (Hughes 1997): exploration that appears to be performed for its own sake. This means that opportunities to explore different feeds would be rewarding for individuals with strong exploratory motivation

335 regardless of the nutritional value of those offerings, and the motivation may be possible
336 to meet with non-feed-related stimuli as well.
337 Although the average consumption of varied feed in both the Forage and Flavour
338 trials was low relative to consumption of regular feed, there was large variation in
339 preference among individuals. While the correlation in preference between the Forage
340 and Flavour trials was low, greater individual consistency may have been seen if not for
341 the side bias in the Flavour trial. Moreover, preferences in these trials were correlated
342 with certain behaviours earlier in life, suggesting some consistent individual traits. The
343 directions of many of these correlations were predicted by the hypothesis that
344 preference for variety reflects exploratory motivation, fear of novelty, or both. Calves
345 that spent more time exploring a novel object at 5 weeks of age were more interested in
346 varied feed as heifers (41 weeks and older; Forage trial), and those that ate more novel
347 feed as calves also performed more exploratory behaviour (feed switching) as heifers.
348 Correlations between the calf tests and behaviour in the Flavour trial were weaker,
349 again likely due to the side bias.
350 Novel object latency was a strong predictor of preference in the Flavour trial, with
351 shorter latencies being associated with greater proportional consumption of varied feed,
352 especially when controlling for the side of the alley to which the feeds were assigned.
353 These results are similar to the finding that lambs which show fewer signs of distress in
354 a novel setting consume more of a novel feed (Villalba et al. 2009). In the current
355 experiment, the correlations between latency to eat novel feed during habituation in the
356 heifer trials and behaviour in the calf tests were largely weak and were in the opposite
357 direction to that predicted. The reasons for this need further investigation, but novel feed

latency could reflect a different type of exploration than sampling does, with strategies of exploration differing between individuals (as in birds: Van Overveld & Matthysen 2013). Regardless, the correlations found suggest that preference for varied feed is related to stable personality traits (defined as individual characteristics describing stability of behaviour over time; see Gosling [2008] for discussion of the term).

Progress in understanding personality traits and their significance in cattle is hindered by the lack of reliable, validated measures for the species (see e.g. Meagher et al. 2016; Mackay 2013). To be considered a true measure of personality, an indicator must be repeatable, yet data on repeatability is often limited (see e.g. Svartberg et al. 2005). There has been criticism of some of the common types of test used in animals, because they are done in artificial and potentially stress-inducing settings and might not accurately reflect natural behaviour (Carter et al. 2013; Biro 2013). The types of feeding test used here, by contrast, were relatively naturalistic. If these types of test prove to be valid indicators of motivation to explore and neophobia in cattle, they may prove useful for research as they are quick and easy to conduct, and can be done in the home pen. These tests also seem to be relatively straightforward to interpret since the animals are making an active choice between novel or varied feed and routine feeds, whereas measures such as latency to approach an object are influenced by various competing motivations (e.g. motivation to lie down) which can be difficult to disentangle.

We suggest that offering rarely experienced feeds may provide welfare benefits for at least some individuals by allowing them to express exploratory behaviour. Varied feeds might also function as a reinforcer in training cattle to perform desired behaviours such as entering a robotic milking machine. This use would avoid some of the difficulties

with using varied feed as enrichment in the home pen, such as increased competition, with dominant animals monopolizing access to preferred feeds in group-fed animals (see Mandel et al. 2016). Offering opportunities for choice may also have psychological benefits even if little of the less preferred feed is chosen; this may also be true of choices unrelated to food. Monkeys, for example, “choose to choose”: they prefer to control the order of tasks themselves rather than having this assigned, all else being equal (Perdue et al. 2014). The correlations between choice of varied feed and exploratory behaviour as calves support the conclusion that both relate to a broader exploratory motivation, rather than something specific to the feed such as flavour boredom or motivation for a specific highly palatable food amongst the options, and any opportunities for choice and exploration might improve welfare.

It has also been suggested that allowing individuals to choose their own diets is valuable because physiological needs differ across individuals (Atwood et al. 2001, Manteca et al. 2008). This assumes that animals have some level of ‘nutritional wisdom’ and are able to select feeds based on the nutrients they require; there is some evidence to support this view (Manteca et al. 2008). The importance of personalized diets taking into account individual differences in needs is increasingly recognized in human nutrition (e.g. Noecker & Borenstein 2015), and ways of identifying those needs are currently being studied (e.g. by assessing glycemic responses to meals: Zeevi et al. 2015). Aside from the direct physiological effects of giving animals variety or choice in their diets, there is some evidence that monotonous prescribed diets can cause stress (Catanese et al. 2013) and, in early life, even influence later stress responsiveness

403 (Villalba et al 2012). These effects may result from the animals being unable to act upon
404 their ‘wisdom’.

405 There were a few limitations to the current experiment. The side bias may reflect
406 behavioural lateralization, since cows, like most mammals, do exhibit some laterality,
407 including in their responses to novelty (Robins & Phillips 2010). However, the bias here
408 emerged over time, not being evident during the initial preference tests when all flavours
409 were presented simultaneously, as one might have expected if there was an innate side
410 preference. The bias may be because the preferred bins to the left of the gate were in
411 front of the home pen and therefore closer to their social group, while the others were in
412 front of a neighbouring pen. This preference for being near the home pen may have
413 become stronger over time as social bonds and familiarity with that pen increased.
414 Whatever the reason, this bias complicated the interpretation of the results. Randomly
415 assigning half of the group to each side allowed detection of this problem, but the
416 strength of the side preference was such that it interfered with our investigation of
417 individual differences. Side biases must be taken into consideration when designing
418 similar experiments in future. The effect of timescale should also be considered; this
419 experiment investigated preferences only in short-term tests over a period of 12 days
420 per trial. Preferences might change over time as the degree of novelty of the feed
421 changes (see e.g. Parsons et al. 1994). Testing for only a short period of the day may
422 also result in individuals being ranked differently than they would be in tests of longer
423 duration (Dumont et al. 1995), although this may be less of a concern in this context
424 than when investigating feeding on pastures where factors such as sward height
425 change over time. Finally, replication of this work is needed to confirm the relationships

between feeding preferences and relevant personality traits, and to more clearly distinguish between fear and curiosity or desire for stimulation as underlying motivations.

Future research should also investigate how the early rearing environment influences preference for variety. These heifers had been individually reared in indoor pens, and as such were expected to be less flexible and more afraid of novelty, including novel feeds, than they would be if they had been housed socially and in more complex environments (see Meagher et al. 2015; Costa et al. 2015). The animals had also not been provided much experience with diversity of feed, except in the form of the brief food neophobia tests described. In lambs, early experience with varied diets increases willingness to eat novel feeds or flavours (e.g. Catanese et al. 2012). Average preferences might thus differ in other management systems.

In summary, many of the heifers tested choose to consume standard TMR rather than novel or varied feed, but most individuals exhibited some exploratory feeding behaviour. The range in time devoted to investigating and consuming feed from varied bins, even when there was some energetic cost to this behaviour, suggests that at least some individuals are motivated to obtain variety in their feed. Some individual consistency in animals' responses to novelty across time can be expected based on the relationship between their feeding choices and their behaviour during the milk-feeding period. Offering a choice of feed at least for some portion of the day might improve welfare, particularly on farms or in pens in which the animals show high levels of exploration. Responses to changing feeds may also provide a simple, naturalistic measure of exploratory tendencies for use in future research.

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References

Addessi, E., Mancini, A., Crescimbene, L., Ariely, D., Visalberghi, E., 2010. How to spend a token? Trade-offs between food variety and food preference in tufted capuchin monkeys (Cebus apella). Behav. Processes 83, 267-275.

Atwood, S.B., Provenza, F.D., Wiedmeier, R.D., Banner, R.E., 2001. Influence of free-choice vs mixed-ration diets on food intake and performance of fattening calves. J. Anim. Sci. 79, 3034-3040.

Bailey, D.W., 1995. Daily selection of feeding areas by cattle in homogeneous and heterogeneous environments. Appl. Anim. Behav. Sci. 45, 183-200.

Beilharz, R., Luxford, B., Wilkinson, J., 1993. Quantitative Genetics and Evolution - is our Understanding of Genetics Sufficient to Explain Evolution. Journal of Animal Breeding and Genetics-Zeitschrift Fur Tierzuchtung Und Zuchtungsbiologie 110, 161-170.

Berlyne, D.E., 1960. Conflict, Arousal, and Curiosity. McGraw-Hill, New York.

Biro, P.A., 2013. On the use of rapid assays in personality research: a response to Edwards et al. Anim. Behav. 86, e1-e3.

Butler, R.A., 1953. Discrimination Learning by Rhesus Monkeys to Visual-Exploration Motivation. J. Comp. Physiol. Psychol. 46, 95-98.

Carere, C., Eens, M., 2005. Unravelling Animal Personalities: How and Why Individuals Consistently Differ. Behaviour 142, 1149-1157.

Carter, A.J., Feeney, W.E., Marshall, H.H., Cowlishaw, G., Heinsohn, R., 2013. Animal personality: what are behavioural ecologists measuring? Biological Reviews 88, 465-475.

Catanese, F., Distel, R.A., Provenza, F.D., Villalba, J.J., 2012. Early experience with diverse foods increases intake of nonfamiliar flavors and feeds in sheep. J. Anim. Sci. 90, 2763-2773.

Catanese, F., Obelar, M., Villalba, J.J., Distel, R.A., 2013. The importance of diet choice on stress-related responses by lambs. Appl. Anim. Behav. Sci. 148, 37-45.

Cavigelli, S.A., 2005. Animal personality and health. Behaviour 142, 1223-1244.

Costa, J.H.C., Meagher, R.K., von Keyserlingk, M.A.G., Weary, D.M., 2015. Early pair housing increases solid feed intake and weight gains in dairy calves. J. Dairy Sci. 98, 6381-6386.

Dumont, B., D'hour, P., Petit, M., 1995. The usefulness of grazing tests for studying the ability of sheep and cattle to exploit reproductive patches of pastures. Appl. Anim. Behav. Sci. 45, 79-88.

Eliassen, S., Jørgensen, C., Mangel, M., Giske, J., 2007. Exploration or Exploitation: Life Expectancy Changes the Value of Learning in Foraging Strategies. Oikos 116, 513-523.

Forkman, B., Boissy, A., Meunier-Salauen, M.C., Canali, E., Jones, R.B., 2007. A critical review of fear tests used on cattle, pigs, sheep, poultry and horses. Physiol. Behav. 92, 340-374.

Franks, B., Champagne, F.A., Higgins, E.T., 2013. How Enrichment Affects Exploration Trade-Offs in Rats: Implications for Welfare and Well-Being. PLoS One 8, e83578.

Ginane, C., Baumont, R., Lassalas, J., Petit, M., 2002. Feeding behaviour and intake of heifers fed on hays of various quality, offered alone or in a choice situation. Anim.Res. 51, 177-188.

Glickman, S.E., Sroges, R.W., 1966. Curiosity in zoo animals. Behaviour 26, 151-188.

Gosling, S.D., 2008. Personality in non-human animals. Social and Personality Psychology Compass 2, 985-1001.

Hedlund, L., Løvlie, H., 2015. Personality and production: Nervous cows produce less milk. J. Dairy Sci. 98, 5819-5828.

510 Herskin, M.S., Munksgaard, L., Kristensen, A., 2003. Behavioural and adrenocortical
511 responses of dairy cows toward novel food: effects of food deprivation, milking
512 frequency and energy density in the daily ration. Appl. Anim. Behav. Sci. 82, 251-265.

513 Hinkle, D.E., Wiersma, W., Jurs, S.G., 2003. Applied Statistics for the Behavioral
514 Sciences, 5th Ed. ed. Houghton Mifflin, Boston, USA.

515 Hughes, R.N., 1997. Intrinsic exploration in animals: motives and measurement. Behav.
516 Processes 41, 213-226.

517 Huzzey, J.M., Fregonesi, J.A., von Keyserlingk, M.A.G., Weary, D.M., 2013. Sampling
518 behavior of dairy cattle: Effects of variation in dietary energy density on behavior at the
519 feed bunk. J. Dairy Sci. 96, 247-256.

520 Inglis, I.R., Forkman, B., Lazarus, J., 1997. Free food or earned food? A review and
521 fuzzy model of contrafreeloading. Anim. Behav. 53, 1171-1191.

522 Launchbaugh, K., 1995. Effects of neophobia and aversions on feed intake: why feedlot
523 cattle sometimes refuse to eat nutritious feeds. Intake by Feedlot Cattle: Symposium
524 Proceedings P-942, 36-48.

525 Launchbaugh, K.L., Provenza, F.D., Werkmeister, M.J., 1997. Overcoming food
526 neophobia in domestic ruminants through addition of a familiar flavor and repeated
527 exposure to novel foods. Appl. Anim. Behav. Sci. 54, 327-334.

528 Litman, J.A., 2005. Curiosity and the pleasures of learning: Wanting and liking new
529 information. Cognition & Emotion 19, 793-814.

530 MacKay, J.R.D., 2013. Characterising personality traits in cattle using biotelemetry
531 systems.

532 Mandel, R., Whay, H.R., Klement, E., Nicol, C.J., 2016. Invited review: Environmental
533 enrichment of dairy cows and calves in indoor housing. J. Dairy Sci. 99, 1695-1715.

534 Manteca, X., Villalba, J.J., Atwood, S.B., Dziba, L., Provenza, F.D., 2008. Is dietary
535 choice important to animal welfare? J Vet Behav 3, 229-239.

536 McNamara, J.M., Houston, A.I., 1987. Partial preferences and foraging. Anim. Behav.
537 35, 1084-1099.

538 Meagher, R.K., Mason, G.J., 2012. Environmental Enrichment Reduces Signs of
539 Boredom in Caged Mink. Plos One 7, e49180.

540 Meagher, R.K., Daros, R.R., Costa, J.H.C., von Keyserlingk, M.A.G., Hötzel, M.J.,
541 Weary, D.M., 2015. Effects of Degree and Timing of Social Housing on Reversal
542 Learning and Response to Novel Objects in Dairy Calves. PLoS ONE 10, e0132828.

543 Meagher, R.K., von Keyserlingk, M.A.G., Hötzel, M.J., Weary, D.M., 2016.
544 Inconsistency in dairy calves' responses to tests of fearfulness. Appl Anim Behav Sci
545 185, 15-22.

546 Mench, J.A., 1998. Environmental enrichment and the importance of exploratory
547 behavior, in: Shepherdson, D.J., Mellen, J.D., Hutchins, M. (Eds.). Smithsonian
548 Institution, Washington, DC, USA, pp. 30-46.

549 Montgomery, K.C., 1954. The role of the exploratory drive in learning. J. Comp. Physiol.
550 Psychol. 47, 60-64.

551 Nielsen, B.L., Lawrence, A.B., Whittemore, C.T., 1996. Feeding behaviour of growing
552 pigs using single or multi-space feeders. Applied Animal Behaviour Science 47, 235-
553 246.

554 Newman, J.A., Parsons, A.J., Harvey, A., 1992. Not all sheep prefer clover: diet
555 selection revisited. J Ag Sci Camb 119, 275-283.

556 Noecker, C., Borenstein, E., 2016. Getting Personal About Nutrition. Trends Mol. Med.
557 22, 83-85.

558 Parsons, A.J., Newman, J.A., Penning, P.D., Harvey, A., Orr, R.J., 1994. Diet
559 Preference of Sheep: Effects of Recent Diet, Physiological State and Species
560 Abundance. J. Anim. Ecol. 63, 465-478.

561 Perdue, B., Evans, T., Washburn, D., Rumbaugh, D., Beran, M., 2014. Do monkeys
562 choose to choose? Learning & Behavior 42, 164-175.

563 Rauw, W.M., Kanis, E., Noordhuizen-Stassen, E.N., Grommers, F.J., 1998. Undesirable
564 side effects of selection for high production efficiency in farm animals: a review. Livest.
565 Prod. Sci. 56, 15-33.

566 Robins, A., Phillips, C., 2010. Lateralised visual processing in domestic cattle herds
567 responding to novel and familiar stimuli. Laterality 15, 514-534.

568 Rolls, B.J., 1986. Sensory-specific Satiety. Nutr. Rev. 44, 93-101.

569 Roura, E., Humphrey, B., Tedo, G., Ipharraguerre, I., 2008. Unfolding the codes of
570 short-term feed appetence in farm and companion animals. A comparative oronasal
571 nutrient sensing biology review. Canadian Journal of Animal Science 88, 535-558.

572 Russell, P.A., 1973. Relationships between exploratory behaviour and fear: a review.
573 British Journal of Psychology 63, 417-433.

574 Rutter, S.M., 2010. Review: Grazing preferences in sheep and cattle: Implications for
575 production, the environment and animal welfare. Canadian Journal of Animal Science
576 90, 285-293.

577 Scott, L.L., Provenza, F.D., 1998. Variety of foods and flavors affects selection of
578 foraging location by sheep. Appl. Anim. Behav. Sci. 61, 113-122.

579 Shettleworth, S.J., Krebs, J.R., Stephens, D.W., Gibbon, J., 1988. Tracking a fluctuating
580 environment: a study of sampling. Anim. Behav. 36, 87-105.

581 Sova, A.D., LeBlanc, S.J., McBride, B.W., DeVries, T.J., 2014. Accuracy and precision
582 of total mixed rations fed on commercial dairy farms. J. Dairy Sci. 97, 562-571.

583 Špinka, M., Wemelsfelder, F., 2011. Environmental challenge and animal agency, in:
584 Appleby, M.C., Mench, J.A., Olsson, I.A.S., Hughes, B.O. (Eds.). CAB International,
585 Wallingford, UK, pp. 27-44.

586 Stephens, D.W., Krebs, J.R., 1986. Foraging Theory. Princeton University Press,
587 Princeton, NJ, USA.

588 Stone, B., 2008. Considerations in feed bunk management. Tri-State Dairy Nutrition
589 Conference Proceedings , 113-123.

590 Svartberg, K., 2005. Consistency of personality traits in dogs. Animal behaviour 69,
591 283-291.

592 van Overveld, T., Matthysen, E., 2013. Personality and Information Gathering in Free-
593 Ranging Great Tits. PLoS ONE 8, 1-9.

594 Van Reenen, C.G., O'Connell, N.E., Van der Werf, J.T.N., Korte, S.M., Hopster, H.,
595 Jones, R.B., Blokhuis, H.J., 2005. Responses of calves to acute stress: Individual
596 consistency and relations between behavioral and physiological measures. Physiol.
597 Behav. 85, 557-570.

598 Van Reenen, C.G., Hopster, H., Van der Werf, J.T.N., Engel, B., Buist, W.G., Jones,
599 R.B., Blokhuis, H.J., Korte, S.M., 2009. The benzodiazepine brotizolam reduces fear in
600 calves exposed to a novel object test. Physiol. Behav. 96, 307-314.

601 Villalba, J.J., Manteca, X., Provenza, F.D., 2009. Relationship between reluctance to
602 eat novel foods and open-field behavior in sheep. Physiol. Behav. 96, 276-281.

603 Villalba, J.J., Provenza, F.D., Manteca, X., 2010. Links between ruminants' food
604 preference and their welfare. Animal 4, 1240-1247.

605 Villalba, J.J., Catanese, F., Provenza, F.D., Distel, R.A., 2012. Relationships between
606 early experience to dietary diversity, acceptance of novel flavors, and open field
607 behavior in sheep. Physiol. Behav. 105, 181-187.

608 Villalba, J.J., Provenza, F.D., Catanese, F., Distel, R.A., 2015. Understanding and
609 manipulating diet choice in grazing animals. Animal Production Science 55, 261-271.

610 Wood-Gush, D.G.M., Vestergaard, K., 1989. Exploratory behavior and the welfare of
611 intensively kept animals. Journal of Agricultural and Environmental Ethics 2, 161-169.

612 Yoder, P.S., St-Pierre, N.R., Daniels, K.M., O'Diam, K.M., Weiss, W.P., 2013. Effects of
613 short-term variation in forage quality and forage to concentrate ratio on lactating dairy
614 cows. J. Dairy Sci. 96, 6596-6609.

615 Zeevi, D., Korem, T., Zmora, N., Israeli, D., Rothschild, D., Weinberger, A., Ben-Yacov,
616 O., Lador, D., Avnit-Sagi, T., Lotan-Pompan, M., Suez, J., Mahdi, J., Matot, E., Malka,
617 G., Kosower, N., Rein, M., Zilberman-Schapira, G., Dohnalová, L., Pevsner-Fischer,
618 M., Bikovsky, R., Halpern, Z., Elinav, E., Segal, E., 2015. Personalized Nutrition by
619 Prediction of Glycemic Responses. Cell 163, 1079-1094.

620

Table 1. Predicted direction of correlations between measures of response to novelty as calves and behaviour when offered choice of varied (forage type or flavours) or stable feed as weaned heifers.

Calf Heifer	Novel object latency	Novel object contact duration	Novel feed latency	Novel feed intake
Proportion of eating time spent at varied bin, Forage trial	Negative	Positive	Negative	Positive
Proportion of eating time spent at varied bin, Flavour trial	Negative	Positive	Negative	Positive
Latency to eat novel feed (habituation phase)	Positive	Negative	Positive	Negative
# of switches between bins (average)	Negative	Positive	Negative	Positive

626 **Table 2.** Spearman correlation coefficients for relationships between heifers' behaviour
627 in neophobia tests as calves and their behaviour when offered choices between varied
628 or stable feed as weaned heifers. n=8 for contact durations, n=9 for all other values.
629

Calf **Heifer**	**Novel object latency**	**Novel object contact duration**	**Novel feed latency**	**Novel feed intake**
Proportion of eating time spent at varied bin, Forage trial	-0.26	*0.54*	-0.39	**0.72**
Proportion of eating time spent at varied bin, Flavour trial	*-0.65* **-1** among those with TMR on the left side	0.29	-0.29	-0.24[1]
Latency to eat novel feed (habituation phase before Forage trial)	*-0.60*[1]	0.24[1]	-0.48[1]	0.44[1]
# of switches between bins (average)	-0.08	0.42	*-0.55*	**0.71**

630 Bold text indicates high correlation, italics indicate moderate, according to Hinkle et al.
631 (2003).
632 [1] Values are in the opposite direction of the prediction
633
634

635 **Figures**
636

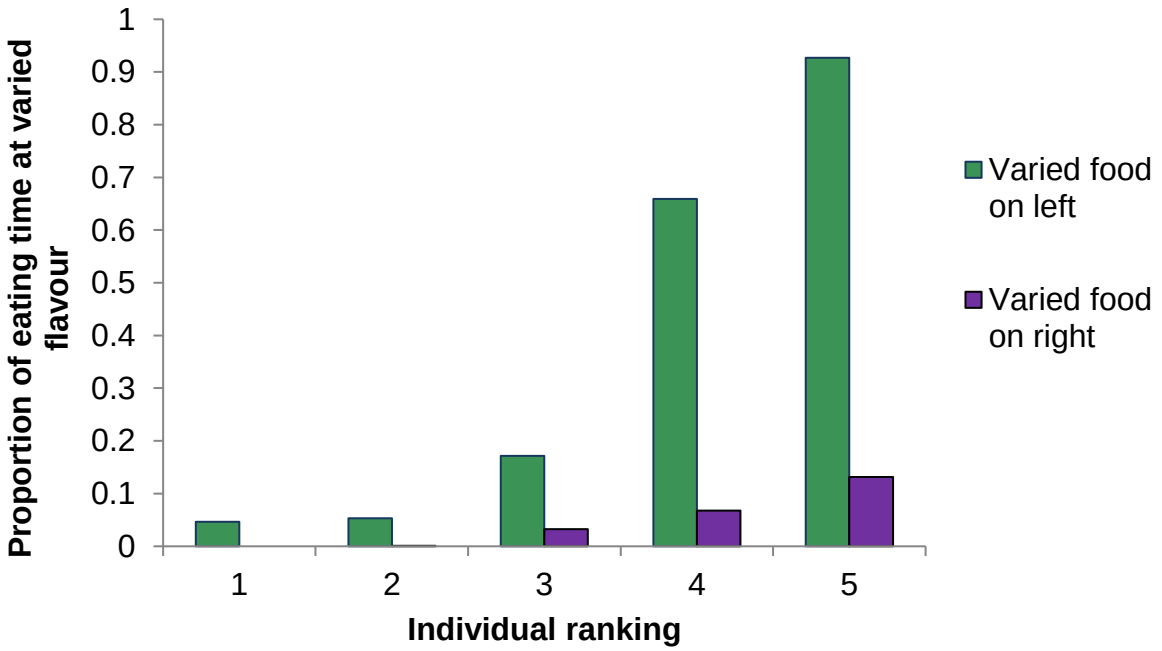
637

638 **Figure 1.** Pen layout for varied forage preference trial. VAR = bins containing a forage
639 that varied day-to-day; TMR = bins containing regular total mixed ration.

640

641 **Figure 2** Pen layout for varied flavour preference trial. For half of the heifers, the
642 positions of the plain (unflavoured TMR) and varied (TMR with one of four flavours
643 added each day) bins were reversed. Fixed flavour bins had the same flavour added
644 each day.

645



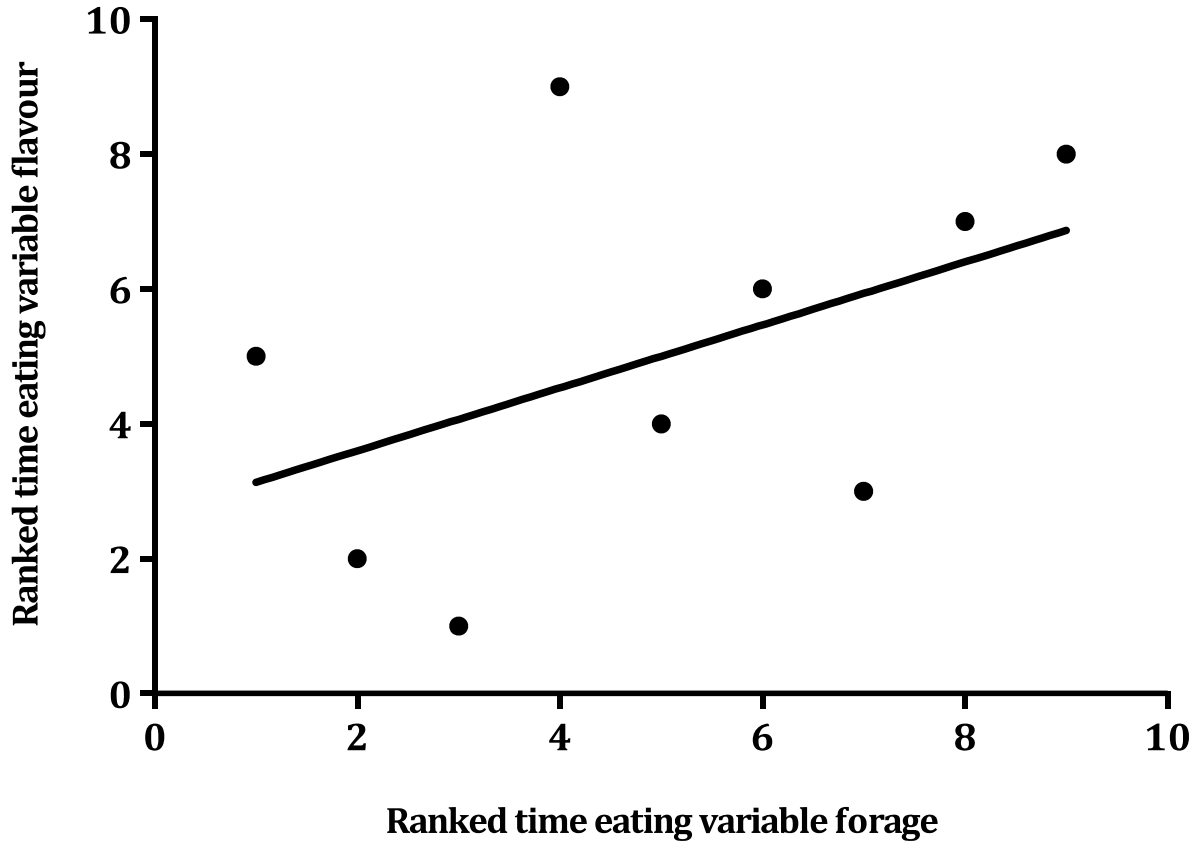
646

647 **Figure 3** Individual differences in the proportion of all time eating heifers spent eating
648 TMR from bins where the flavour varied, split by the side of the alley in which this bin

649 was placed. High numbers on the x-axis indicate higher proportions of varied feed

650 consumed relative to other heifers. n=5 per side.

651



652

653 **Figure 4** Consistency in proportion of eating time individual heifers spent at the varied

654 bin when the feed was varied forage vs. TMR of varied flavours. n=9.