INDIVIDUAL VARIABILITY IN THE FEEDING BEHAVIOUR OF DAIRY CALVES AND GOATS

by

Heather Whittaker Neave

B.Sc., University of Victoria, 2012

M.Sc., University of British Columbia, 2013

A THESIS SUBMITTED IN PARTIAL FULFILLMENT OF

THE REQUIREMENTS FOR THE DEGREE OF

Doctor of Philosophy

in

THE FACULTY OF GRADUATE AND POSTDOCTORAL STUDIES

(Applied Animal Biology)

THE UNIVERSITY OF BRITISH COLUMBIA

(Vancouver)

July 2019

The following individuals certify that they have read, and recommend to the Faculty of Graduate and Postdoctoral Studies for acceptance, the dissertation entitled:

INDIVIDUAL VARIABILITY IN THE FEEDING BEHAVIOUR

OF DAIRY CALVES AND GOATS

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submitted by Heather Whittaker Neave in partial fulfillment of the requirements for

the degree of Doctor of Philosophy

in Applied Animal Biology

Examining Committee:

Dr. Marina A. G. von Keyserlingk

Supervisor

Dr. Daniel M. Weary

Supervisory Committee Member

Dr. Anita DeLongis

Supervisory Committee Member

Dr. Ronaldo Cerri

University Examiner

Dr. Colin Brauner

University Examiner

Abstract

There is individual variability in the development and expression of feeding behaviours in farm animals. This variation cannot be fully explained by differences in genetics, management practices, body size, or growth rate. The aim of my thesis was to describe how personality traits influence feeding behaviour of dairy calves and adult goats during challenging feeding practices, and to investigate alternatives to traditional feeding practices that could help individuals to cope with these challenges by attending to individual needs and promoting natural behaviour. In Chapter 2, I review the evidence that individual variability in feeding behaviour is associated with personality traits of the individual. In Chapters 3 and 4, I focused on the stressful management practice of weaning in dairy calves (i.e. transition from milk onto solid feed diet), and investigated if personality traits could explain variability in feeding behaviours, feed intake, and performance around weaning. I found that calves that were less reactive (exploratory, interactive) performed better during weaning than calves that were more reactive (vocal, inactive) (Chapter 3). When calves were weaned on an individualized weaning plan, I found that individual characteristics (such as fearfulness and learning ability) could explain variability in weaning age (Chapter 4). In Chapters 5 and 6, I focused on feeding practices on dairy goat farms that limit expression of natural feeding behaviours (feeding at floor level) and restricted space at the feeders leading to high amounts of competition to access feed. I provided goats with elevated feeder heights to promote natural browsing behaviours and found that goats ate more from, and competed to access, these feeders more compared to a traditional floor-level feeder (Chapter 5). Goats also differed in their expression of competitive behaviours at different feeder heights: more 'bold' goats expressed more aggression and more 'fearful' goats avoided competition

(Chapter 6). These studies provide evidence that personality traits can explain individual variability in feeding behaviours during challenging feeding practices for dairy calves and goats, and that alternatives to these feeding practices may provide an improved opportunity for individuals to succeed by attending to individual needs and promoting natural behaviour.

Lay Summary

Personality can influence how individual animals respond to stressors, including those associated with the feeding environment, and this can impact feeding behaviour, feed intake and growth. My thesis determined that personality traits of dairy calves and goats influence how they cope with common farm management practices like weaning (when calves must shift from an entirely milk to an entirely solid feed diet) and restricted feeding space. Individualized weaning programs for dairy calves and opportunities to feed from raised surfaces for dairy goats are examples of alternative feeding practices that attend to individual needs and promote natural behaviour. Understanding how personality traits affect feeding behaviour can help to create tailored management that better meets the needs of different individuals on the farm.

Preface

A version of Chapter 2 has been published as Neave, H. W., D. M. Weary and M. A. G. von Keyserlingk. 2018. Individual variability in feeding behaviour of domesticated ruminants. *animal*, 12(supplement s2): s419-s430. H.W. Neave developed the main ideas for this project and wrote the manuscript. M.A.G. von Keyserlingk and D.M. Weary acted in the typical role of supervisors, providing input and editing drafts. This chapter did not require ethics approval.

A version of Chapter 3 has been published as Neave, H. W., J. H. C. Costa, D. M. Weary, and M. A. G. von Keyserlingk. 2018. Personality is associated with feeding behavior and performance in dairy calves. J. Dairy Sci. 101: 7437-7449. H. W. Neave designed the study, collected all data, and wrote the manuscript. M. A. G. von Keyserlingk and D. M. Weary acted in the typical role of supervisors, helping with statistical analysis, and providing input and editing drafts. This project received UBC Animal Care approval (certificate numbers: # A14-0245 and A15- 0117).

A version of Chapter 4 has been accepted for publication as Neave, H. W., J. H. C. Costa, J. Benetton, D. M. Weary and M. A. G. von Keyserlingk. 2018. Individual characteristics in early life can predict age of weaning when dairy calves are automatically weaned based on solid feed intake. J. Dairy. Sci. (*accepted)*. H. W. Neave designed the study, collected all data, and wrote the manuscript. M.A.G. von Keyserlingk and D.M. Weary acted in the typical role of supervisors, helping with statistical analysis, and providing input and editing drafts. This project received UBC Animal Care approval (certificate numbers: # A14-0245 and A15- 0117).

A version of Chapter 5 has been published as Neave, H. W., M. A. G von Keyserlingk, D. M. Weary, and G. Zobel. 2018. Feed intake and behavior of dairy goats when offered an elevated feed bunk. J. Dairy Sci. 101: 3303-3310. H. W. Neave designed the study, collected all data, and wrote the manuscript. G. Zobel acted as overseas supervisor during my PhD internship and acted helped in the design of the study, statistical analysis, input and editing of manuscript drafts. M.A.G. von Keyserlingk and D.M. Weary acted in the typical role of supervisors, helping with statistical analysis, and providing input and editing drafts. This project received UBC Animal Care approval (certificate number: # A16–0213) and approval from the Ruakura Animal Ethics Committee (Hamilton, New Zealand; certificate number: # AE13930).

A version of Chapter 6 has been submitted for publication as H. W. Neave and G. Zobel. Competitive feeding behaviour of dairy goats is affected by feeder height and personality traits. PLoS ONE. (*in review*). H. W. Neave designed the study, collected all data, and wrote the manuscript. G. Zobel acted as overseas supervisor during my PhD internship and acted in the typical role of supervisor, helping with statistical analysis, input and editing of manuscript drafts. This project received UBC Animal Care approval (certificate number: # A16–0213) and approval from the Ruakura Animal Ethics Committee (Hamilton, New Zealand; certificate number: # AE13930).

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List of Abbreviations and Definitions

ADG = average daily gain

BW = body weight

DM = dry matter

DMI = dry matter intake

NSAID = non-steroidal anti-inflammatory

PCA = Principal Component Analysis

SE = standard error

SD = standard deviation

Starter = grain-based solid feed diet for dairy calves

Acknowledgements

This thesis has come together only with the help of many. I am grateful to my mentors, friends and family for supporting and encouraging me in this journey. Reflecting back I see how far I have come in developing skills and knowledge in the field of animal welfare - this wealth of experience and knowledge comes from the privilege of studying under some of the greatest scientists I know. First, I thank my supervisor Dr. Nina von Keyserlingk for years of advice and guidance in becoming the scientist I am today – you are an inspiration, and I only hope that I can become as much of a role model for my future students as you have been for me. A huge thank you also to Dr. Dan Weary for challenging me to think broadly and critically, bringing my statistics knowledge to where it is now, and pushing me to 'dream big'. The two of you are a force to be reckoned with – my 'big dream' is to have a lab that is as supportive, challenging, fun, productive and successful as yours is. There is a reason that AWP graduates go on to do great things, and that is thanks to your immense dedication to each of our successes. Thank you so much.

There are many other mentors that have helped me along this journey. Thank you to Drs. Jeff Rushen and Anne-Marie de Passille who I had the privilege to work with in their last few years at the Dairy Centre; your weaning research has inspired a part of this thesis. I will never forget your ISAE retirement party in Denmark, 2017 – the feeling of gathering together with the best animal welfare scientists in the world to thank you for all that you have done was like no other. Dr. David Fraser, you never fail to amaze me with your wisdom and teaching expertise that inspires students to become welfare scientists.

Two other individuals in particular have been my mentors for many years now and are a big part of this thesis and the scientist I have become today. Thank you to Dr. Joao Costa for being the first to tell me I should do a PhD when I finished my MSc, and for always reminding me that there are few people in this world that can do what we do. Your years of support, friendship, advice, and challenge have pushed me to be as productive as I have been. Thank you also to Dr. Gosia Zobel for bringing me into the goat world in New Zealand– my future research will definitely include these underappreciated animals with big personalities. You have been a friend and mentor since the moment I stepped foot into the Big House… beyond the research and life advice, I have learned all things technology, cameras, and how to manage people from you.

I also extend a thanks to my farm family that has been a big support network during my time at the Dairy Centre. First, thanks to the best farm staff any farm could ask for – Nelson, Brad, Barry, Ted and Bill! Thank you to all who lived in Blue House at one point or other and fellow PhD students – Tracy, Joao, Rua, Augusto, Ben, Genie, Thomas, Ana Carolina, Laura, Anne-Marieke, Hanna, Jane and Juliana – thank you for the countless memories, laughs and bbqs at Blue House, for friendship and intellectual discussion, and for always keeping Beast and Maui entertained. Thank you to Juliana Benetton and Katrina Rosenberger for your dedication to the calf projects of this thesis and the many health checks. I also extend my thanks to the amazing help from the technicians in New Zealand (Trevor, Ian, Briar, and Frankie) who made the days and drives extra entertaining. Outside of the farm, thank you to Jen Buchanan for being my long-time friend from Vic and your years of support when I show up to dinner or your house smelling like cow and needing to talk.

To my family, I could not have asked for more love and support from Mom, Dad, Fraser and Alysse. I would not be where I am today without such an amazing and encouraging family –

I hope I won't end up too far away from home, but I trust you'll always be there with family dinners and birthday cakes over Skype.

Finally, I thank the many calves and goats with their unique personalities for providing endless fascination and entertainment – in return I hope this thesis will shed light on the importance of providing for your needs.

Chapter 1: Introduction

Feed intake is critical for farm animals, and is affected by feeding behaviour of the individual (Grant and Albright, 2000; von Keyserlingk and Weary, 2010). Individuals vary in feeding behaviour, including in the expression of distinct and consistent feeding patterns (e.g. Melin et al., 2005). These feeding patterns develop from an early age (Provenza and Balph, 1987), and can be influenced by a number of management factors. For instance, the availability of preferred forages or habitats, the frequency of pasture rotation, and the distribution and quality of forage influence feeding behaviour in grazing herds (cattle: Launchbaugh and Howery, 2005; goats: Goetsch *et al*., 2010; sheep: Rutter, 2006). In confined systems, the timing and frequency of feed delivery, and feed bunk structure and space allowance, are important features of the feeding environment that affect feeding behaviour of ruminants (cattle: von Keyserlingk and Weary, 2010; goats: Jørgensen et al., 2007). Domesticated ruminants are generally social, so social interactions between group mates, including competition for resources and learning from social partners, can also affect feeding behaviour (Forbes and Kyriazakis, 1995; Proudfoot and Habing, 2015).

Other factors that impact feeding behaviour include common but stressful management practices. The chapters of this thesis will focus specifically on dairy animals (dairy cattle and dairy goats) and common management practices associated with these systems. These species undergo similar routine practices involving changes to the nutritional, physical and social aspects of their feeding environment; examples include diet, feeding space available for each individual, and social regrouping changes. These practices can lead to disruptions in behaviour, emotional state, and biological functioning of the individual, compromising the animal's welfare.

Individuals within a group may cope differently with these challenges. For instance, some individuals may fail or take longer to learn where, how or what to eat, and others may be unable to cope within their social environment and thus fail to gain access to food resources. Both situations can result in animals that do not achieve their growth and production potential, perhaps due to inappropriate behavioural responses to the environment and pervasive negative emotional states such as frustration, anxiety, or panic.

There is limited understanding of why individuals within a herd differ in feeding behaviour and whether these differences are stable. Knowing why characteristic feeding patterns develop and persist may help tailor management to the needs of the individual, especially given the development of technologies (e.g. precision nutrition; González et al., 2018) that allow for management at the individual rather than herd level. Authors have often focused on external factors such as season, climate, health, genetics, or feeding and housing practices as potential explanations for individual variability in feed intake and growth (e.g. Place et al., 1998; Heinrichs and Heinrichs, 2011; Shivley et al., 2018); rarely are individual differences in behavior considered as a contributing factor. A look at how individuals behave in response to situations outside of a feeding context may offer some insight. For instance, some individuals may be highly reactive to handling in a chute, when restrained in a head locker or to milking procedures, some may be particularly aggressive with other animals when accessing a desired resource, and others may be especially docile, friendly or social towards humans or herd mates. This consistent variability in behaviour between individuals in different contexts is termed 'personality', and specific aspects of the behavioural repertoire are referred to as personality 'traits', using terms such as fearful, aggressive, and docile (for detailed reviews on animal personality refer to: Réale et al., 2007; Stamps and Groothuis, 2010; Carter et al., 2013; personality specific to farm animals: Koolhaas and Van Reenen, 2016).

There is growing evidence that personality traits such as exploration, reactivity and sociability are associated with growth and productivity in ruminants (Dodd et al., 2012; Haskell et al., 2014). Individual variability in feeding behaviour, and the way in which individuals respond to their feeding environment, may also be related to the personality of the individual. I therefore review the literature on this topic in Chapter 2. The findings of this review illustrate major gaps in our understanding of how individuals cope with stressful management practices and why they differ, and thus served as a basis for the empirical work in the following chapters in dairy calves (Chapter 3 and 4) and in dairy goats (Chapter 5 and 6). In particular, these chapters focus on two common practices associated with feeding: 1) weaning in dairy calves, and 2) restricted feeding space in dairy goats. In the remainder of this chapter, I introduce the topics that will be discussed in these empirical chapters and present the research questions of this thesis.

1.1 Weaning in dairy calves

Initially the young calf is entirely dependent upon milk, consuming between 8 to 13 L daily when left with the dam (de Passillé and Rushen, 2006); however, in commercial systems that remove calves from the dam, calves are typically restricted to lower milk allowances of 4 to 6 L/d (USDA, 2016). One of the most important processes that a dairy calf experiences during the rearing period is weaning, undergoing a transition from an entirely milk-based diet to one comprised entirely of solid feed (forage and calf starter). In natural and semi-natural environments, this process occurs much later and over a longer period of time than when commercial farming systems impose it; a study on extensively managed cattle reported weaning age ranged from 7 to 14 months (Reinhardt and Reinhardt, 1981), while weaning age on most commercial farms in North America occurs much earlier at around 6 to 8 wk of age, with some farms weaning as early as 4 to 5 wk of age (Vasseur et al., 2010; USDA, 2011).

During the transition from milk to solid feed (hereafter referred to as weaning), the calf undergoes rapid structural, physiological and microbiological transformations in the rumen and gastro-intestinal tract that prepare the young calf to become a functional ruminant (see Meale et al., 2017). It is critical for calves to be consuming large amounts of solid feed before weaning (milk removal) occurs; those that have poor solid feed intakes at the time of weaning are much more likely to have poor growth and experience prolonged hunger (de Passillé et al., 2011) after weaning. One method to encourage early solid feed intake is to gradually wean calves off milk (Sweeney et al., 2010). Gradual weaning methods, such as the step-down technique (Khan et al., 2007; Rosenberger et al., 2017), also help to reduce the number of fruitless visits to the milk feeder and maintain growth during the weaning transition, contributing to improved welfare.

However, there is large individual variability in how early calves begin to consume solid feed and in how much they are consuming at the time of weaning, despite rearing under similar conditions. For instance, de Passillé and Rushen (2016) reported that calves consumed 200 g/d of grain between 23 and 82 d of age, and 1.4 kg/d of grain (target amount before complete weaning) between 58 and 94 d of age when fed 12 L/d of milk. Similarly, Roth et al. (2009) found calves took between 45 to 98 d to consume 2 kg/d of grain when fed 6 L/d of milk. This variability in intakes suggests that calves differ in how well they cope with weaning, yet there is little understanding of the source of this variation. Given the findings of my review in Chapter 2, I investigated in Chapter 3 if personality traits could explain this individual variability in solid feed intakes around weaning, and if these traits could also explain variability in performance and other feeding behaviours during weaning.

Furthermore, there is currently only limited discussion of opportunities to manage weaning at the individual level. This is surprising given that farm management is moving toward data-driven and technology-based decision making allowing for individualized management (see review by Rutten et al., 2013). For example, Roth et al. (2008, 2009) and de Passillé and Rushen (2016) demonstrated how calves could be individually weaned when they reached specific solid feed intake targets using automated milk and grain feeders. It would be advantageous to be able to predict from an early age which calves are suitable candidates for early weaning; this would allow expensive milk resources to be removed earlier from these calves and allocated toward calves that require more time on milk before weaning. Individual characteristics of calves at an early age may be easy measures to identify calves that will wean early or late. Therefore in Chapter 4 I therefore investigated which individual characteristics (including personality traits) measured in the first month of age could predict when calves would complete weaning based on solid feed intake. Overall, Chapters 3 and 4 are the first studies to investigate if individual characteristics and personality traits of dairy calves can explain variability in feeding behaviour, performance and weaning age.

1.2 Restricted feeding space in dairy goats

The feeding behaviour of goats classifies them as both grazers (like cattle and sheep) and browsers. Browsing behaviour includes selection of foliage, buds, flowers and stems of shrubbery (termed ‘browse’) from variable heights, involving the use of a range of body positions such as ground-level grazing to eye-level feeding and rearing onto the hind legs to access forage high above the head (Sanon et al., 2007; Tölü et al., 2012). Several reports indicate that goats will include browse in a large portion of their diet when possible (Askins and Turner, 1972; Sanon et al., 2007). Goats are highly flexible in what they consume, changing their diet selection under different conditions. For example, extensively managed Argentinian Creole goats included grasses in their diet when they were available in the summer, but shifted to a diet of 98% shrubs and trees in winter when grasses dwindled (Egea et al., 2014).

Generally indoor-housing systems for goats provide little consideration for opportunities to express these natural feeding behaviours (reviewed in Zobel et al., 2018). Most commercial goat farms provide feed at ground level, although some elevated feeding surfaces may be offered in the form of hay racks or by raising the drive alley where feed is dispensed to allow for head-level feeding (Zobel et al., 2018). To my knowledge, no research has investigated the feeding behaviour and feed intake of dairy goats when offered different commercial feeder designs that promote feeding postures more typical of their natural feeding environment. Therefore, in Chapter 5 I investigated the preference of goats to feed from floor-level, head-level and elevated-level feeder heights.

In addition to the traditional practice of feeding at floor-level, commercial farms often provide limited space at the feeder. The minimum space recommendation for milking goats at the feeder is between 33 and 40 cm/head (Norway: Jørgensen et al., 2007; New Zealand: MPI, 2018) but is often reported to be lower (e.g. Norway: Muri et al., 2013; Italy: Battini et al., 2016). Feeder space below this (i.e. one feeding space for two or three goats) results in high levels of competition to access the feeder while feeding (Jørgensen et al., 2007). Examples of competitive behaviours include physical displacements from the feeder, frontal clashes (rearing onto the hind legs and descending forcefully onto the front legs to deliver a strike to the head of the receiver), butting the head or body of another goat, and chasing another goat (Nordmann et al., 2011). These behaviors involve considerable stress for both initiators and recipients (Aschwanden et al., 2008a; Nordmann et al., 2011), and constitute a welfare concern. Feeder designs that provide protection during feeding (such as head partitions or palisades that provide more physical separation; Nordmann et al., 2011, 2015) or platforms to separate goats in vertical space (Aschwanden et al., 2009a) are effective at reducing competition. Feeding posture is an important consideration in feeder designs to ensure goats are comfortable while feeding (Keil et al., 2017). I describe competitive behaviours of goats offered an elevated feeder height that promoted a natural browsing feeding posture (compared to head- and floor-level feeders) when provided unrestricted (Chapter 5) and restricted (Chapter 6) space allowance at the feeder.

Similar to other ruminant species, individual traits of dairy goats are expected to influence how animals cope with challenges and affect their feeding behavior expression. Feeding behaviour of goats has been shown to be highly variable, especially when feeding space is limited. For instance, Jørgensen et al. (2007) showed that 30% of goats reduced their feeding time by more than 40%, and a few goats reduced their feeding time by more than 80%, when space was decreased at the feeder. This variability in feeding behaviour suggests that goats respond to challenges differently, with some adjusting their behaviour according to the changing feeding conditions. Furthermore, goats that engaged in different types and frequencies of social interactions (e.g. aggressive or affiliative behaviours) differed in their feeding success (Miranda-de la Lama et al., 2011). Therefore, an additional objective of Chapter 6 was to investigate if personality traits can explain variability in the expression of competitive behaviours at different feeder heights when goats are provided restricted feeding space.

1.3 Thesis objectives

The overall aims of this thesis were to: 1) describe how personality traits influence the feeding behaviour of dairy calves and goats during common feeding management practices that are expected to be challenging, and 2) investigate alternatives to traditional feeding practices that attend to individual needs, promote natural behavior, and allow animals to cope with these feeding practices. These feeding practices include weaning in dairy calves and restricted feeding space in dairy goats.

I hypothesized that personality traits could explain variability in feeding behaviour, feed intake and performance of dairy calves around weaning (Chapter 3), and that personality traits could also predict weaning age of calves when weaned on an individual basis (Chapter 4). Furthermore, I hypothesized that dairy goats would prefer to consume feed from a feeder height that promoted their natural feeding posture compared to a traditional feeder design (Chapter 5), and that personality traits could explain variability in competitive feeding behaviours at these different feeder designs when experiencing restricted feeder space (Chapter 6).

Chapter 2: Individual variability in feeding behaviour of domesticated ruminants

A version of this chapter has been published: Neave, H. W., D. M. Weary and M. A. G. von Keyserlingk. 2018. Review: Individual variability in feeding behaviour of domesticated ruminants. animal. 12(supplement s2): s419-s430. doi: https://doi.org/10.1017/S1751731118001325

2.1 Introduction

The overall aim of this review is to critically examine the available literature describing individual variability in feeding behaviour of ruminants, and how personality traits of the individual may explain some of this variability. I will focus especially on 'exploratory' and 'sociability' personality traits that have received limited attention compared to more commonly cited 'fear' (Forkman et al., 2007) and 'reactivity' traits (Haskell et al., 2014). I first describe how variability in development and expression of feeding behaviour may contribute to differences in growth and productivity, and how several key personality traits may play an important role in how individuals interact with and respond to challenges faced in the feeding environment. Throughout I review evidence in both grazing (e.g. extensively raised on rangeland or intensively raised on pasture) and confined (e.g. raised indoors or finished on feedlots) farming systems, offer suggestions for future research, and draw upon evidence from other species to provide better insight into our understanding of feeding behaviour in ruminants.

2.2 Individual variability in feeding behaviour

2.2.1 Development of feeding behaviour

The young ruminant relies initially on milk and begins sampling solid feed within the first weeks after birth (Nicol and Sharafeldin, 1975). The timing of the transition from nursing to a solid diet is highly variable among individuals; for example, natural weaning in domestic cattle was reported to be between 7 and 14 months after birth (Reinhardt and Reinhardt, 1981). Young ruminants will begin to graze by learning from social models such as the mother and conspecifics or learning by trial and error, leading to individual preferences and aversions to plants, and individual differences in ability to forage efficiently (Provenza and Balph, 1987; Kyriazakis et al., 1999). Even at an older age, social models may be useful when introducing naïve animals to new feeding systems; when dairy heifers were turned out to pasture for the first time without an experienced companion, some individuals took over three hours to begin to graze compared to just one hour for those that were pastured with an experienced grazer (Costa et al., 2016a).

In most dairy cattle production systems, calves are raised apart from their mother. Dairy farms vary in how much and how often milk is delivered to the calves and in opportunities for social learning (Vasseur et al., 2010; Hötzel et al., 2014; USDA, 2016); both factors may influence the development of feeding behaviours (reviewed by Miller-Cushon and DeVries, 2015). For example, calves reared individually must learn on their own where, how and what to eat. The lack of a social model may be particularly important during the transition from milk onto a solid diet, especially given that weaning occurs much earlier than in nature (Enríquez *et al*., 2011; reviewed by Khan *et al*., 2016).

Young ruminants vary in the amount of milk that they choose to consume when milk is provided *ad libitum*. This variability can contribute to differences in growth rates during the pre-weaning period. For example, de Passillé *et al*. (2016) reported a large range in milk intakes during the first 2 to 4 d of age in Holstein dairy calves, ranging from 2.4 L to 12 L per day (7 to 30% of body weight), resulting in differences in body weight gains (ranging from 0.07 to 1.2 kg/d in the first month of age). Similar variability in milk feeding patterns were reported for artificially-reared lambs, ranging from 0.3 to 2.9 L/d milk consumption (David *et al*., 2014).

Dairy calves raised indoors are typically introduced to a concentrate diet soon after birth. Considerable variability in concentrate consumption was reported by de Passillé and Rushen (2016). Calves fed 12 L/d of milk first consumed 200 g/d of grain at between 23 to 82 d of age and first reached a daily grain consumption of 1400 g/d at between 58 to 94 d of age. Calves fed less milk typically begin to consume more grain at an earlier age; however, Roth *et al*. (2009) showed that even when calves were fed just 6 L of milk/d, the age range when they first consumed 2000 g/d of grain was between 45 and 98 d of age. Furthermore, when group-housed calves were offered free choice of milk replacer, concentrate, maize silage, hay and straw, there was large individual variability in intake of each component, suggesting that calves develop diet preferences from a young age (Webb et al., 2014). These preferences may also arise from associations between sensory properties and nutritional value of the diet (Forbes and Kyriazakis, 1995), the experiences associated with the first encounter with the feedstuff, or the physical properties of the diet that are important for stimulating ruminal development (Baumont, 1996).

This evidence highlights the variation in feeding behaviour among individuals from a young age. It is well known that reduced milk intake or reluctance to transition to solid feed can result in impaired growth during the pre-weaning and weaning periods in young ruminants (e.g.

dairy calves: de Passillé *et al*., 2016; goat kids: Warmington and Kirton, 1990; lambs: Greenwood *et al*., 1998). Furthermore, early-life nutritional disadvantages have been shown to affect future foraging behaviour in other species (e.g. Andrews *et al*., 2015). Understanding how and why some individuals develop feeding patterns that result in better or worse performance is important if we are to help all animals thrive.

2.2.2 Expression of feeding behaviour

Characteristic feeding patterns that develop from an early age in ruminants appear to also be present in adulthood. The rearing environment, as well as morphological and physiological differences, will have a profound impact on how individuals express their feeding preferences and patterns as adults (Provenza and Balph, 1987). Individuals within a herd can show feeding patterns that are widely variable between individuals, but remain relatively consistent over time within individuals (Melin *et al*., 2005). This is not to say that feeding behaviour is inflexible, but rather that the degree of flexibility in feeding patterns generally remains consistent within individuals over time.

The selection of, and preference for, plants to graze or browse will depend on the individual's nutritional needs and on prior experience with these food sources and ability to cope with toxins (Provenza *et al*., 2003). Ruminants are known to make trade-offs in selecting diets that meet the requirements of their internal state (e.g. hunger, and physiological state such as pregnancy) while reducing costs in the selection of the diet (e.g. environmental or social pressures) (Kyriazakis *et al*., 1999; Arsenos *et al*., 2000). Thus an individual's diet selection is flexible with changing internal state, with changes in diet dependent upon any nutritional deficiency and post-ingestive feedback from ingested foods (e.g. Tolkamp *et al*., 1998). Day *et* *al*. (1998) proposed that food selection is also influenced by a motivation to explore the feeding environment, which functions to identify new food items and to monitor and update information on existing food sources; individuals are able to modify their feeding behaviour if needed.

Foraging animals must choose between continuing to exploit an existing site or searching for a superior foraging site (see Giraldeau and Caraco, 2000). One approach to understanding this dichotomy is the producer-scrounger model, originally developed to describe the feeding strategies of sparrows (Barnard and Sibly, 1981). ‘Producers’ take the role of finding higher food quality food patches. These individuals benefit from first access to the new patch, but pay the cost of lost foraging opportunities (and perhaps increased predation) while searching for new patches (Giraldeau and Caraco, 2000). Other individuals adopt a ‘scrounger’ strategy of following ‘producers’ to exploit their findings rather than searching for food themselves. This framework has been applied to foraging strategies in goats (Stears *et al*., 2014) and sheep (Hewitson, 2002). Individuals within a herd may also adopt ‘leader’ and ‘follower’ roles in making decisions when to move between feeding locations including cattle (Dumont *et al*., 2005), sheep (Squires and Daws, 1975), goats (Escós *et al*., 1993) and buffalo (Prins, 1996). ’Producers’ may be more likely to be ‘leaders’ but this line of research has yet to be explored.

Given the evidence of individual variability in diet selection of foraging animals (Kyriazakis *et al*., 1999; Arsenos *et al*., 2000), it follows that there would be similar variability in the feeding patterns of confined ruminants. For instance, Melin *et al*. (2005) found that as much as 84-98% of the variation in feeding patterns could be attributed to individual differences between dairy cows. Several studies have shown substantial between-cow variability for meal frequency (e.g. ranging from 5 to 9 meals/day) and feeding time (dairy cattle: 250 to 450 min/d; beef cattle: 8 to 90 min/d or 86 to 120 min/d) (Schwartzkopf-Genswein *et al*., 2002; DeVries *et* *al*., 2003). Such feeding patterns have been attributed more to phenotypic than to genetic variation among individuals (Løvendahl and Munksgaard, 2016).

Studies have also shown that some individuals will adjust their feeding behaviour in response to social or environmental changes. Crossley *et al*. (2017) reported that when dairy cows competed for access to a feeding area, there was an increase in variability in feeding time, feeding rate and meal duration. In a companion study, increasing feeding frequency did not reduce variability in feeding time, feeding rate or dry matter intake (Crossley *et al*., 2018). This variability is likely due to individual motivations to access the feed bunk; some animals reduce feeding time and others strive to maintain feeding times even under high levels of competition (dairy cattle: Val-Laillet *et al*., 2008b; goats: Jørgensen *et al*., 2007). Some individuals will also respond more negatively than others when experiencing environmental changes. For instance, Rice *et al*. (2016) found that 18% of lambs entering a feedlot spent less than 30 min/d feeding, lost weight during the first week, and were more likely to visit the feeder when no other lambs were present. This evidence suggests that the feeding behaviour of some individuals will change in response to social or environmental pressure.

In summary, there is wide individual variability in feeding behaviour from an early age. Understanding why feeding behaviour is variable among individuals will be the focus of the remainder of this review, particularly how personality traits such as exploration, fear or reactivity, and sociability affect how ruminants interact with their feeding environment.

2.3 Exploration of the feeding environment

2.3.1 Foraging strategies

Studies on the personality characteristics of individuals adopting producer-scrounger or leader-follower foraging strategies often profile animals along an exploration-avoidance or boldness-shyness axis, and individuals that are more exploratory or bold are thought to be more likely be leaders or producers by searching for food rather than relying on others (Kurvers *et al*., 2012). For example, sheep that were more exploratory in an unfamiliar arena with novel objects were also more likely to move away from conspecifics while grazing, enabling them to explore more of the pasture area (Sibbald *et al*., 2009). Sheep that were more exploratory were also more likely to split into smaller subgroups, indicating these animals made the trade-off to explore their feeding environment rather than to remain together as a cohesive group (Michelena *et al*., 2009). Domestic deer that spent more time close to or investigating novel objects made a similar trade-off, spending less time engaged in vigilant behaviours and more time investigating a novel food (Bergvall *et al*., 2011). In addition, beef heifers that spent more time interacting with a novel object tended to be positioned at the front of the herd (Ramseyer *et al*., 2009). These studies suggest that more exploratory individuals (as indicated by greater investigation of novel objects or food) adopt riskier foraging behaviour and that this results in increased opportunities to forage.

In confined farming systems, ruminants are typically provided uniform diets at specific times of the day, reducing the need for deciding when and where to forage. Indoor-housed animals will still perform exploratory behaviour, particularly when the feed quality is variable (Huzzey *et al*., 2013). Meagher *et al*. (2017) offered feed bins with different forage varieties or flavours along a feed bunk and recorded the number of bin switches as a measure of exploratory feed sampling. Heifers that spent more time in contact with a novel object in a previous test also spent more time exploring and eating the varied feed. Moreover, those that were quicker to reach a novel food in the individual test also spent more time at the varied feed and switched between bins more often. Collectively this evidence indicates that some individuals are more proficient in exploring and sampling varied or novel feeds.

2.3.2 Feed sampling and sorting behaviour

Dairy cows are known to preferentially sort for concentrate and against long forage components in a mixed ration but this type of behaviour is highly variable among individuals, with some even sorting against the typically preferred finer particles (Leonardi and Armentano, 2003). Interestingly, sorting behaviour did not decrease when cows were fed in a competitive feeding environment (Hosseinkhani *et al*., 2008), suggesting that individuals engaging in this behaviour are motivated to do so even when access to feed is limited. A possible explanation for this finding is that individuals that continued to sort in a competitive environment were also higher in social rank and thus could maintain their position at the feed bunk (see Favati *et al*., 2014).

Sorting is also likely a learned behaviour, related to post-ingestive feedback mechanisms (Provenza, 1995), and familiarity of feed from an early age (Miller-Cushon and DeVries, 2011). Consequently, young dairy calves are able to sort a mixed ration and will adjust this behaviour in response to the availability of grain (Costa *et al*., 2016b). Feed sorting is seen as a risk factor for ruminal acidosis in adult cows (Cook *et al*., 2004), so farms often strive to prevent this type of behaviour. If indeed the motivation behind sorting behaviour stems from a desire to explore the feeding environment, management practices may be able to redirect this behaviour by offering other opportunities for environmental exploration or manipulation. To our knowledge no work to date has explored such opportunities.

Overall, individuals differ in how much they explore their feeding environment. Some individuals are producers or scroungers, and some are leaders or followers when it comes to deciding how and where to find food. In confined housing these foraging differences have yet to be documented, but individuals that sample their feeding environment have been shown to be more exploratory and bold in novel situations. Individuals that are more reactive in response to novelty (rather than exploratory or bold) also show differences in their feeding behaviour; this will be the focus of the next section.

2.4 Coping with stress: response patterns and emotional reactivity

Domestic ruminants experience many stressors; differences in the behavioural responses of individuals toward these stressors are called ‘coping styles’ (Benus *et al*., 1991; Koolhaas *et al.*, 1999). Individuals also differ in their level of fear when responding to a stressful event, where more fearful individuals typically show stronger behavioural responses (e.g. Boissy, 1995). The quality (i.e. coping style) and magnitude or quantity of the response (i.e. fearfulness) may reflect two independent dimensions that together describe how individuals respond to a particular stressor (Koolhaas *et al*., 2007). This framework is supported by the multivariate analysis of the behavioural responses of dairy heifers exposed to different stressors including a novel environment, stationary human, novel object and restraint (Van Reenen *et al*., 2002, 2005).

However, a two-dimensional approach may not fully describe the degree of variability in how individuals respond to stressors. A multidimensional framework has also been proposed, suggesting that other traits (such as sociability) are dimensions along which individuals will vary, in addition to the dimensions of qualitative and quantitative responses to a challenge (Koolhaas and Van Reenen, 2016). Thus, the way in which an animal responds to a stressor is likely mediated by multiple traits (such as the 'Big Five': neuroticism, extraversion, agreeableness, openness and conscientiousness; Gosling and John, 1999) and position of an animal in this multidimensional space indicates its capacity to cope with a stressor, rather than position along a single dimension.

For some individuals, adjustments to their feeding behaviour may be a coping mechanism in response to changes in the feeding environment or other stressors. There is growing evidence in ruminants that feeding behaviour, including feed intake, may be reduced when individuals that are particularly fearful experience stressful events such as changes in the environment or feed type, or handling and restraint by humans. We will review this evidence in the next sections.

2.4.1 Reactivity to novel environments

Dairy heifers are known to differ in their responses when first introduced to the milking parlour; Van Reenen *et al*. (2002) showed that some individuals had consistently higher physiological (i.e. cortisol) and behavioural reactivity (i.e. stepping and kicking) during milking preparation and teat cup attachment. Heifers habituated to the milking parlour for several weeks before calving had improved feed intake compared to those that were not habituated (Daniels *et al*., 2007). Thus changes in feeding behaviour may be an indication of individuals that are especially affected by novel processes like milking.

Several authors have reported individual variability in physiological stress responses in cattle (e.g. Loerch and Fluharty, 1999; Eitam *et al*., 2010) and lambs (Rice *et al*., 2016b) when introduced to a feedlot. Lambs with a high cortisol response during the first week in this new environment were also more reactive during isolation and restraint tests, and had a greater number of feeding bouts likely due to a high number of displacements.

Some personality traits may drive consistent behavioural responses across a range of situations, while other traits may only manifest under specific contexts (Sloan Wilson *et al*., 1994; Beausoleil *et al*., 2012). For instance, lambs that spent less than 30 min/d feeding in the first week after arriving at the feedlot (termed 'shy-feeders') had no relationship with behavioural responses during isolation and restraint (Rice *et al*., 2016a). However, this study used a standardized test that elicited a fear response specific to isolation which may be unrelated to responses to stressors encountered in a highly social feeding environment. Future work should aim to identify personality traits that are specific to individuals that show changes in their feeding behaviour when introduced to new environments and how modifications to that environment may be beneficial.

2.4.2 Food neophobia

Food neophobia, defined as a reluctance to eat unfamiliar foods (Chapple and Lynch, 1986), is well-known in ruminants and is thought to help animals avoid toxic plants (Provenza and Balph, 1987). This fear of novel diets must be overcome for livestock to transition to different feed types (Launchbaugh *et al*., 1997). When this transition is coupled with a change in environment, food neophobia is greater compared to when animals remain in familiar environments (Burritt and Provenza, 1997). Individuals will even consume familiar foods containing toxins over novel feeds when in an unfamiliar environment (Burritt and Provenza, 1997). However, early exposure to a diversity of foods can increase acceptance of novel foods especially in unfamiliar locations (Villalba *et al*., 2012).

Variability in feeding behaviour may be due in part to differences in food neophobia. For instance, Rice *et al*. (2016a) suggested that highly reduced feeding times in some lambs ('shy-feeders') may be due to individual differences in food neophobia. This reluctance to sample novel feeds can be consistent over time and in different contexts. For example, Costa *et al*. (2014) demonstrated that dairy calves were consistent across days in their willingness to sample two types of novel foods (carrots and hay), and heifers that were quick to find and eat more of a novel food in an arena also spent more time eating flavoured and varied forages offered at the feed bunk (Meagher *et al*., 2017). In lambs, individuals that were more food neophobic were also more fearful in a novel arena and exhibited more stress-induced hyperthermia (Villalba *et al*., 2009), suggesting that the test of food neophobia reflects fearfulness. These experimental findings were recently supported in a study of pair-housed calves on a commercial farm that consumed nearly 3 times as much novel food compared to isolated calves (Whalin *et al*., 2018). No studies have investigated how food neophobia is related to other personality traits, such as exploration and sociability.

2.4.3 Reactivity to handling

Individuals differ in their reactivity to handling and restraint. Many such interactions occur in farm animal production including vaccinations, dehorning, branding or castrating. With the advances of automated management technologies, opportunities for positive interactions and habituation to humans may be limited (Rushen *et al*., 1999; Butler *et al*., 2012). Poor handling and fear of humans is expected to alter the behaviour of the animals, including changes in feeding behaviour. For instance, beef cattle that are especially reactive when in the chute or isolated in a pen with a handler (i.e. nervous, vigorous or violent movement, or attempts to escape), and have high flight speeds exiting the chute, also have reduced feed intake (Black *et al*., 2013) and reduced feeding times (Cafe *et al*., 2011). Similar effects on feeding behaviour have been shown in physiologically more reactive cattle (e.g. high cortisol response when in the chute; Llonch *et al*., 2016). However, other studies have not found a relationship between reactivity and feed intake (Petherick *et al*., 2002; Francisco *et al*., 2015) or feeding time (Nkrumah *et al*., 2007). These inconsistent results may be related to how personality measures were analysed [e.g. categorical, such as 'adequate' versus 'excitable' in Francisco *et al*. (2015), or continuous, such as scoring personality from 1 to 5 in Cafe *et al*. (2011)] or may be related to the degree of negative experiences associated with humans (e.g. blood samples were taken before personality measures were scored in the chute; Cafe *et al*., 2011).

Apart from feed intake and feeding time, no studies have examined how reactivity to handling influences other aspects of feeding behaviour in ruminants. However, work on other farm animals shows an association. For example, reactivity during weighing was associated with more visits to the feeder and less intake per visit in pigs (Ros-Freixedes *et al*., 2014). Rohrer *et al*. (2013) found that pigs that struggled more during restraint in the supine position (i.e. 'reactive' pigs) tended to have fewer daily meals and these were of longer duration compared to 'proactive' pigs. 'Reactive' pigs also preferred to eat at times when the feeder was less occupied. These studies suggest that active movement during restraint may be related to active avoidance of social conflict at the feeder.

Stress from prolonged or repeated unpleasant handling can lead to impaired growth and productivity (e.g. Lensink *et al*., 2000). Whether growth is reduced due to changes in feeding behaviour that limit feed intake, or due to poorer feed efficiency, remains unknown. Recent research has shown that human presence can have a profound impact on goat behaviour; even changes in a human's head position can alter the behaviour of goats (Nawroth *et al*., 2015). Thus, the behaviour of stockpersons during management practices may elicit stress responses that in turn affect feeding behaviour. Together this evidence suggests that reactive individuals may be more prone to changes in feeding behaviour.

In summary, individuals differ in the way they respond to stressful events on farms. Feeding behaviour and feed intake can be impaired in individuals that are particularly reactive to a change in environment (feedlot, milking parlour), change in diet (food neophobia) and handling by humans (e.g. restraint in a chute). Aspects of the social environment may also be stressful for some individuals, and the way in which individuals respond to stressors may be related to the social relationships within the herd. We turn to this topic in the following section.

2.5 Social relationships: Dominance and sociability

Most farm animals are housed in groups, resulting in a feeding environment that also involves interactions with other individuals. This can be a source of stress for some individuals, especially when the number of animals exceeds resource availability and results in competition for food (Proudfoot and Habing, 2015). The social context, including social relationships among individuals, has a major effect on behaviour. These social relationships can be agonistic (e.g. dominant-subordinate) or affiliative (e.g. sociability).

2.5.1 Dominant-subordinate relationships

Domestic ruminants are gregarious and will organize themselves into social hierarchies with dominant and subordinate individuals (e.g. cattle: Bouissou *et al*., 2001; goats: Miranda-de la Lama and Mattiello, 2010). An individual's position in the hierarchy is often expressed through agonistic interactions when gaining or maintaining access to resources (Miller and Wood-Gush, 1991; Barroso et al., 2000a). For grazing ruminants on rangeland, where space is less limited, this hierarchy is related to priority of access to high quality grazing areas (Barroso et al., 2000a), which can be expressed as a an 'avoidance order'; whereby, subordinate animals avoid conflict with dominant ones (Sárová *et al*., 2010).

Feeding behaviour is related to social rank of the individual with dominant individuals typically having priority access to food. This is especially evident when forage is limited and low in quality. For example, higher-ranking goats will out-compete subordinates to consume preferred shrubs (Barroso et al., 2000a) and dominant individuals are often more efficient foragers (e.g. Thouless, 1990), likely due to less selection required when given priority access to feed resources. To achieve these foraging advantages, dominant animals position themselves toward the front of the herd and cover shorter distances relative to subordinates during periods of foraging (Sárová *et al*., 2010). Consequently, subordinates are often forced to graze areas of lower quality; these individuals could move away from the group in search of improved grazing opportunity but risk increased exposure to predators (Thouless, 1990; Barroso et al., 2000a). Indeed, the slower bite rate of subordinates is thought to reflect the trade-off between grazing and maintaining vigilance for predators and dominant animals, in addition to the increased necessity to select forage (Thouless, 1990). Interestingly, subordinates also reduce bite rate when dominant individuals are nearby, and cease grazing altogether to avoid neighbouring dominant animals (Thouless, 1990). Together this evidence indicates that dominant-subordinate relationships are important drivers of foraging behaviour in grazing systems.

Dominant-subordinate relationships in confined housing systems also influence feeding behaviour. Subordinate individuals may fail to gain access to the feed bunk and eat at times that are less preferred (Huzzey *et al*., 2006), and even sacrifice higher quality feed to avoid feeding near a dominant (Rioja-Lang *et al*., 2009). These effects may be exacerbated when competition for feed increases (e.g. Jørgensen *et al*., 2007). Although dominance rank is often scored as the number and outcome of agonistic interactions between dyads (Galindo and Broom, 2000), displacements at the feeder by cattle has been reported to be bi- or tri-directional and nonlinear with subordinate cows occasionally displacing dominants (Val-Laillet *et al*., 2008a). Of most interest is that high-ranking cows do not necessarily have the longest feeding times; dominance at the feed bunk may be related to individual motivation to gain access to feed or to defending the resource (Val-Laillet et al., 2008b; a).

Variability in social behaviour at the feeder cannot be explained entirely by dominance. For example, Miranda-de la Lama *et al*. (2011) described four social strategies or 'identity profiles' in goats: 'passive' goats (submissive but made no attempt to avoid or engage in agonistic behaviour) spent the least time at the feeder while 'avoider' goats (submissive and avoided both agonistic and even non-agonistic behaviour) spent the most time feeding. Goats that were 'aggressive' (highly dominant and mediated other social conflicts) and 'affiliative' (average dominance and engaged in socio-positive behaviours) were similar in time spent at the feeder but intermediate to 'avoider' and 'passive' goats. Thus individuals can share similar dominance ranks yet adopt different social strategies that impact feeding behaviour.

Temporal feeding patterns and other measures of feeding behaviour such as feeding rate can further our understanding of how individuals are able to maintain or adjust feeding time under competitive conditions when adopting different social strategies. Zobel *et al*. (2011) noted that beef heifers varied in how they responded to a highly competitive feeding environment; some individuals actively engaged in competition while maintaining a relatively stable feeding rate, but others appeared to actively avoid competition and shifted their feeding until after peak feeding time. Still others appeared to adopt a ‘get-in-and-get-out’ strategy characterized by increased feeding rate and avoidance of agonistic interactions. Indeed, Nielsen (1999) noted that changes in feeding rate could be a valuable indicator of social pressure experienced by individuals in group feeding environments.

These results suggest avenues for future research. Given that individuals differ in their responsiveness to environmental change (i.e. behavioural plasticity; reviewed in Dingemanse *et al*., 2010), we might expect that some individuals will adjust their social behaviour at the feed bunk in response to a change in social environment (e.g. reduce aggression when there is low stocking density or when there are many other dominant individuals), while others will remain consistent across different social environments (e.g. maintain aggression despite plenty of space to access feed). This research would help to advance our understanding of, and opportunities for management of, the social grouping of ruminants in both grazing and confined feeding environments.

2.5.2 Affiliative relationships and sociability

Herd-living animals also have affiliative relationships, and these are also likely to influence social behaviour in the feeding environment. The formation of affiliative relationships among individuals has been reported among domestic ruminants, including cattle (Bouissou *et al*., 2001), goats (Miranda-de la Lama and Mattiello, 2010) and sheep (Lynch *et al*., 1992). Dairy cows form and maintain preferred partnerships from an early age (Raussi *et al*., 2010) with large within- and between-cow variability in the frequency of social interactions and time spent in close proximity to partners (Gutmann *et al*., 2015). This variability in sociability has been proposed as a distinct personality trait underlying how individuals respond to environmental challenges (Koolhaas and Van Reenen, 2016). Sociability can be defined as the motivation to remain close to conspecifics (Sibbald et al., 2006), and appears to be linked with feeding patterns of grazing animals that must make trade-offs between social and feeding motivations. For example, when high quality forage is distributed in patches, the intake and diet composition of each individual depends on their willingness to move away from the herd to graze preferred patches (Sibbald and Hooper, 2003). In a subsequent paper these authors (Sibbald and Hooper, 2004) demonstrated that more sociable sheep (i.e. those that spent the most time in close proximity to other sheep) were less likely to move away from the group to access a preferred grazing patch.

These foraging trade-offs appear to be influenced by the strength of relationships with herd mates. Dumont and Boissy (2000) reported that ewes penned with familiar companions chose to graze away from the group for longer periods, vocalized less and were less vigilant than those grazing with unfamiliar companions. Brahman steers were also more willing to leave a familiar companion to approach a food bowl, but did not do so when housed with an unfamiliar companion (Patison *et al*., 2010). These authors suggested that a combination of a lack of social support and fear of isolation motivated individuals to remain close to unfamiliar companions. Sociability is also related to group movements between foraging sites. Ramseyer *et al*. (2009) demonstrated that heifers with limited affiliative partnerships and ewes that often grazed away from the group were those that most often initiated group movement.

In confined housing systems there is also evidence that individual differences in sociability influence feeding behaviour. Gibbons *et al*. (2010) found that dairy cows who took longer to return to the group following separation at the end of a passageway had more limited partner associations, were less synchronized with the group, and did not feed during peak feeding times. The strength and type of partner associations appears to affect feeding behaviour. Individuals housed together for longer periods were more likely to be preferential partners during feeding (dairy cattle: Gutmann *et al*., 2015; goats: Aschwanden *et al*., 2008), and these feeding partners showed more positive social contact such as allogrooming (Val-Laillet *et al*., 2008a).

These studies suggest that preferential associations among individuals can influence feeding behaviour in both grazing and confined herds. Future research should aim to understand how the quality and quantity of relationships between individuals influences how individuals make foraging decisions and affect feeding patterns. For instance, individuals that develop close social bonds may become more reliant on a social partner to find high quality food in a grazing system. Furthermore, individuals with strong social bonds or many social partnerships may be better able to cope with stressful feeding environments given that social partners often mediate stress responses in farm animals (Rault *et al*., 2011).

2.5.3 Social facilitation and social learning

Social companions are important sources of information for making foraging decisions in both grazing and confined housing systems. Social facilitation and social learning play important roles in the development of foraging behaviour in neonatal ruminants on pasture (Launchbaugh and Howery, 2005). Social facilitation is the phenomenon where the stimulus of another animal eating, approaching or manipulating feed may increase attention toward the feed, and subsequently encourage consumption of feed by others, while social learning describes the mechanism of learning through observation of others (Zentall and Galef, 1988).

Young ruminants learn from their mother and conspecifics the location of food, water, and shelter, and consequently develop diet and habitat use patterns that resemble those of social models (Provenza and Balph, 1987). For instance, individuals that were conditioned to avoid a particular plant when grazing alone began to consume this plant when grazing with others that had not learned to avoid this plant (cattle: Ralphs *et al*., 1994; lambs: Provenza and Burritt, 1991). Social models can be influential in learning how to graze; naïve beef calves had increased grazing activity when turned out to pasture with experienced companions compared to those without an experienced social model (Hessle, 2009).

For young ruminants that are raised in confinement, social facilitation and social learning may influence how quickly individuals begin to use feeding equipment. Lambs were quicker to learn to drink milk from a teat when grouped with lambs that had previously learned this behaviour (Veissier and Stefanova, 1993). Dairy calves raised with a social partner consumed more starter during the milk feeding period (Costa *et al*., 2015), were quicker to first visit a new concentrate feeder when regrouped after weaning (de Paula Vieira *et al*., 2010) and had more frequent concentrate meals before and during weaning (Miller-Cushon and DeVries, 2016) compared to calves raised alone. Consequently, socially-housed calves have improved feed intake and weight gains (reviewed by Costa *et al*., 2016c). Together the evidence in both grazed and housed ruminant species suggests that learning about the feeding environment is influenced by the presence of social models.

Social foraging theory suggests that obtaining information by observing others is less costly than gaining the same information personally (Galef and Laland, 2005). An exciting area of research is how individuals differ in their use of social information, such that some may be more likely to learn from social information in a feeding context. Sih and Bell (2008) suggest that more sociable individuals may be more likely to acquire social information, given their close proximity and increased interactions among group mates compared to less sociable individuals. Indeed, the development and extent of social relationships among individuals in a grazing herd of cattle has been shown to be critical in the efficiency of information transfer (Launchbaugh and Howery, 2005). Similarly, the development of solid feeding behaviour in young ruminants requiring the discovery and exploitation of a novel food resource may be influenced by the sociability of the animal such that strong affiliations may lead to increased attention to social cues. Naïve observers may pay more attention to experienced demonstrators if they share a particular relationship (see review by Nicol, 1995).

The personality of the demonstrator may also suggest to observers within the herd that they are a reliable source of information. For instance, observers may watch and learn from the foraging behaviour of more exploratory or dominant individuals (Nicol, 1995). Indeed, there is evidence suggesting that the feeding behaviour of dominant individuals is copied by subordinates (Laland, 2004). This line of research has been tested in some ruminants. In sheep, dominance status of both the observer and demonstrator affected decisions to leave a food patch for a potentially better foraging opportunity (Hewitson *et al*., 2007); subordinate sheep would only follow a dominant when the expectation for discovering high-quality food was high. In contrast, Baciadonna *et al*. (2013) found that the use of social information by goats to locate a food patch was not dependent upon the dominance rank of the demonstrator. However, these authors also found that goats favoured the use of personal rather than social information to locate food. Reliance upon personal information may be more important when foraging in a variable or patchy environment.

These studies illustrate how social status affects the use of information when making foraging decisions. However, no work in ruminants has explored the effects of affiliative relationships on the use of social information. In addition, efforts could be made to understand if some personality types utilize or convey social information more than others.

In summary, the social environment influences feeding behaviour in grazing and confined housing systems. Dominant-subordinate and affiliative relationships affect how individuals forage, gain access to feed, and adjust feeding patterns when the social environment changes.

2.6 Implications for management and animal welfare

This review has highlighted the wide variability in feeding behaviour among individuals, and how personality differences can explain why some individuals struggle to learn about their feeding environment or fail to adapt to changes in their nutritional, social or physical environment. Using the associations between personality traits and feeding behaviour that have emerged throughout this review I provide suggestions for how changes in management may improve feeding behaviour and intake in farmed ruminants.

In grazing herds, managers can take advantage of foraging strategies where individuals favour searching for new food sources themselves rather than relying upon others. ‘Producers’ are more likely to widen their grazing distribution and explore new habitats, while the more sociable individuals that tend to remain close to herd members are likely to follow the grazing patterns of the ‘producers’ (Launchbaugh and Howery, 2005). Individuals with exploratory, bold, or dominant personalities, or those with strong affiliative or familiar relationships, are known to be especially influential in directing the grazing patterns of the herd. Managers may be able to guide habitat use by cueing or training these individuals where to graze, and subsequently may direct the grazing movements of the whole herd through information flow through the group.

In confined systems where the feed bunk is a highly social and often competitive environment, management of these social dynamics should be targeted. Farms that tend to overstock at the feed bunk, or have groups with many highly dominant or aggressive individuals, are likely to see more variable feeding patterns due to individuals adopting different social strategies to gain or maintain access to the feed bunk (e.g. Miranda-de la Lama *et al*., 2011; Zobel *et al*., 2011). Consequently, some individuals will be forced to increase their feeding rate, reduce feeding time, or access the feed bunk at non-peak feeding times, potentially leading to limited or lower-quality feed intake. Managers should aim to provide ample space at the feed bunk and ensure pens have few highly dominant individuals that may monopolize access to the feed bunk; these strategies will help all individuals of the herd to express their preferred feeding patterns.

Farmed ruminants must adjust to stressors such as dietary and environmental transitions, including introduction to unfamiliar environments like the feedlot or milking parlour, novel foods, or exposure to handling or restraint devices that often occur in conjunction with negative experiences. Negative responses to novelty that potentially impact feeding behaviour could be reduced by, for example, introducing novel diets before movement to a new feeding facility, or by pairing movement through a restraining device with a food reward. This is likely to be especially beneficial for individuals that are most reactive to stressful events. However, it is important to remember that all individuals require time to adapt to change.

Managers should also consider providing an experienced social model, especially when moving animals to new pens requiring the use of different feeding equipment (e.g. headlocks) or when introducing novel feeds (e.g. when artificially weaning young ruminants from milk onto a solid-feed diet). We suggest that individuals that are particularly calm in response to stressors may be effective social models for those that are more reactive, even if they are not knowledgeable or experienced; however, the social model must be familiar to the group to avoid an added stressor.

Some farms already allow for individuals to adapt to transition periods at their own pace. For instance, automated calf feeders have been used to wean calves individually when they reach specific grain consumption targets rather than applying one weaning program to all animals (e.g. de Passillé and Rushen, 2016). Heifers may also be kept in a separate lactating group after calving since they are often of lower social rank and subject to aggression when mixed with the main herd (Neisen *et al*., 2009). Managing these vulnerable individuals appropriately may improve access to the feed bunk and feeding time (Krohn and Konggaard, 1979).

2.7 Conclusions

This review has illustrated the variability in feeding behaviour of domesticated ruminants and has argued that personality differences can explain why some individuals struggle to learn about, or fail to adapt, to changes in their feeding environment. The propensity of individuals to explore their feeding environment, the reactivity of individuals in response to common management stressors, dominance status, and degree of sociability in the herd all affect the ability of individuals to access feed. With a better understanding of how personality influences feeding behaviour, individual management may improve the welfare of individuals, particularly those that have difficulty learning where and what to eat, are typically last to gain access to feed, or expend more effort maintaining access to feed.

Chapter 3: Personality is associated with feeding behaviour and performance in dairy calves

A version of this chapter has been published: Neave, H. W., J. H. C. Costa, D. M. Weary, and M. A. G. von Keyserlingk. 2018. Personality is associated with feeding behavior and performance in dairy calves. J. Dairy. Sci. 101: 7437-7449. doi: https://doi.org/10.3168/jds.2017-14248

3.1 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 to 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 to 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 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 impact on growth rates. For dairy calves, the transition from a milk 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 intakes 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 pre-weaned 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.

3.2 Materials and methods

The study was conducted from April to October 2015 at the UBC Dairy Education and Research Centre in Agassiz, BC, Canada. The study was approved under the UBC Animal Care protocol # A14-0245.

3.2.1 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 one of 4 milk-feeding allowances (6, 8, 10 or 12 L/d of milk) within each group of 8 calves, with each group containing 2 calves on each allowance. Milk was reduced to 50% of the allowance at d 42 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 enrolment 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 one 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, with a minimum and a maximum portion size of 0.5 L and 9 L. Calf starter (Hi-Pro Medicated; 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*.

3.2.2 Data recording and calculations

Daily intake of milk and starter were recorded until 68 d of age by the automated feeding system. 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: pre-step (full milk allowance; d 7 to d 41 of age), step (milk allowance reduced to 50%; d 42 to d 50 of age), weaning (d 51 to d 54 of age), post-weaning (d 55 to d 68 of age) and the total experimental period (d 7 to d 68 of age). 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 starter from the feeder (indicating 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 g, 675 g, and 1300 g, corresponding to the targets of 0.5 lb, 1.5 lb, and 3 lb, respectively, provided by the 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 post-weaning period (d 55 to d 68 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) and included a measure of rectal body temperature. 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, USA) according to the farm's standard procedure. Calves were weighed weekly using a portable scale placed at the entrance to the calf pen.

3.2.3 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 one 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 re-tested 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 each of the tests for 30, 10 and 15 min for the novel environment, human approach and novel object tests, respectively. In the human approach test, an unknown person stood immobile at the center of the test pen. The person looked towards 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 one 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 3.1**) after establishing high inter-observer reliability ($\kappa_W > 0.86$) for each test. Vocalizations were recorded for each test by an observer that was seated out of sight of the test arena. The start of a test was considered to be when the calf had all four feet inside the test arena.

Table 3.1. Ethogram of behaviors scored during each of the three novelty tests. Calves (n=56) were tested individually at 27 ± 3 d and 76 ± 3 d of age in a novel environment, human approach and novel object tests.

Test / Behavior	Description
All Tests	
Vocalizations	All types of vocalizations, sound emitted from the mouth
Locomotor Play	Occurs without head oriented toward and more than one body length away from human or object. *Jumping:* both forelegs off the ground and extended forwards (number of events) *Running:* calf trotting (2 beats) or galloping (3 beats) across or around the enclosure (number of events)
Bucking	Both hind legs are off the ground and extended backwards (number of events)
Resting	Time spent lying down with underside or side of body in full contact with flooring substrate
Withdrawal	Sudden movement backwards or sideways (number of events)
Novel Environment Test	
Explore	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 four 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 the human or object (muzzle within 5 cm)
Attentive	Time spent with head oriented toward human or object, excluding touching and object play behaviors
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

3.2.4 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 pre-step) and a square-root transformation (starter DM during pre-step). 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) for each test, following verification of significant correlation over time using PROC CORR. 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 (measures were verified for significant correlation across tests using PROC CORR, and 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 (PCA) 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 1300 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 and/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 at $P \leq 0.10$.

3.3 Results

3.3.1 Principal component analysis

The behavioral responses of calves in each of the novelty tests are presented in **Table 3.2**, and the loadings for each factor are reported in **Table 3.3**. 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 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, with high positive loadings for vocalizations and inactivity in the novel environment test. Calves that loaded highly on Factor 3 were termed ‘vocal/inactive’.

Table 3.2. Behavioral responses of calves in each of the novelty tests.
Calves (n = 56) were tested individually in each test. Behaviors were averaged across repeated tests for each calf.

Test / Behavior	Mean	SD	Range
Novel Environment Test			
Vocalizations (no.)	24.5	20.1	0 – 80.5
Active (no. 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 (% time)	0.31	0.34	0 – 1.3
Bucking (no.)	0.67	1.0	0 – 4.5

Table 3.3. Coefficients (loadings) for the first 3 factors of the principal component analysis. Behavioral measures of calves were recorded in the three novelty tests. 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.

Variable	Factor 1	Factor 2	Factor 3
Vocalizations (no.)	0.25	0.05	**0.80**
Latency to touch human/object (s)	**-0.82**	0.26	-0.23
Time in contact with human/object (% of time)	**0.92**	0.16	0.02
Attentive (% of time) [1]	**-0.79**	0.13	0.001
Time spent playing (% of time)	**0.82**	0.25	0.04
Active (no. quadrants crossed) [2]	-0.11	**0.84**	0.08
Inactive (% of time) [2]	-0.08	-0.18	**0.84**
Exploring (% of time) [2, 3]	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] Calf is observing (head oriented toward) human/object (sum of time spent within 1 body length (‘close) and more than 1 body length away (‘far’)
[2] Behavior recorded only in novel environment test
[3] Time spent sniffing, licking or muzzle close to floor or wall surfaces

3.3.2 Performance, feed intake and behavior

Performance, feed intake, development of solid feeding behaviors, and behavior at the milk feeder over the pre-weaning and post-weaning period (from d 7 to d 68 of age) are presented in **Table 3.4**. A summary of these measures by milk allowance treatment (6, 8, 10 or 12 L/d) is presented in Rosenberger et al. (2017).

Table 3.4. Performance, feed intake, and feeding behavior measures.
Mean ± SD and range of measures for calves (n = 56) during the total experimental period (d 7 to d 68).

Measure	Mean	SD	Range
Performance			
ADG (kg BW/d)	0.84	0.15	0.54 – 1.16
Gain:feed ratio (kg 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 (kg/d) [1]	1.30	0.26	0.75 – 1.89
Development of solid feeding behavior [2]			
First day to eat 40 g starter (d)	19.0	8.2	4 – 41
First day to eat 225 g starter (d)	36.0	7.5	17 – 50
First day to eat 675 g starter (d)	42.5	4.9	33 – 52
First day to eat 1300 g starter (d)	47.3	5.0	36 – 61
Behavior at milk feeder			
Rewarded visits (no./d) [3]	5.9	1.4	3.1 – 11.3
Unrewarded visits (no./d) [3]	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] Post-weaning period: d 55 to d 68 of age

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 ADG and from 0.25 to 1.25 kg/d in 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 per day. This variability was due in part to milk allowance, but even within milk allowance assignment there was considerable variation in ADG (range 0.54

to 1.0, 0.54 to 1.0, 0.64 to 1.1 and 0.56 to 1.2 kg/d ADG), average starter DMI (range 0.33 to 1.24, 0.25 to 1.1, 0.31 to 1.24, 0.32 to 1.0 kg DM/d), age that starter was first found and consumed (range 6 to 29, 8 to 32, 4 to 41, 12 to 41 d of age), and average number of unrewarded visits (range 8.4 to 18.1, 4.5 to 12.3, 1.9 to 12.7, 1.2 to 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 three factors. The relationships between the three factors and performance and feed intake measures during each of pre-step, step, weaning and post-weaning periods are presented in **Table 3.5**. Factor 2 was related to a number of 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 pre-step period. These calves also had greater ADG during the step period, 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 pre-step 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 were also associated with the factors (**Table 3.6**). Calves loading highly on Factor 2 met all starter intake targets (40, 225, 675 and 1300 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 was associated with any other starter intake targets. However, calves that loaded highly on either of these two factors generally had a greater number of rewarded and unrewarded visits to the milk feeder. Factor 3 was positively associated with rewarded visits during pre-step 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 scores and total number of visits to the milk feeder after weaning (**Table 3.6**). 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.

Table 3.5. Relationship between factor scores and performance and feed intake measures. Results are reported for each of 5 experimental periods: pre-step (full milk allowance; d 7 to d 41 of age), step (milk allowance reduced to 50%; d 42 to d 50 of age), weaning (d 51 to d 54 of age), post-weaning (d 55 to d 68 of age) and the total experimental period (d 7 to d 68 of age). Effect direction is provided when the main effect is P ≤ 0.1 (in bold).

Measures	Factor 1 ('interactive')			Factor 2 ('exploratory/active')			Factor 3 ('vocal/inactive')		
	Effect	F-value	P-value	Effect	F-value	P-value	Effect	F-value	P-value
ADG (kg/d)									
Pre-step	-	**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**
Post-weaning		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)									
Pre-step		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)									
Pre-step		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
Post-weaning		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 (kg) [1]									
Pre-step		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] Calculated from the sum of milk and starter intakes. Hay was offered but intakes could not be recorded reliably.

Table 3.6. Relationship between factor scores and development of solid feeding behavior, behavior at the milk feeder, and behavioral response to weaning.
Results are reported for each of 5 experimental periods: pre-step (full milk allowance; d 7 to d 41 of age), step (milk allowance reduced to 50%; d 42 to d 50 of age), weaning (d 51 to d 54 of age), post-weaning (d 55 to d 68 of age) and the total experimental period (d 7 to d 68 of age). Effect direction is provided when the main effect is P ≤ 0.1 (in bold).

Measures	Factor 1 ('interactive')			Factor 2 ('exploratory/active')			Factor 3 ('vocal/inactive')		
	Effect	**F-value**	**P-value**	**Effect**	**F-value**	**P-value**	**Effect**	**F-value**	**P-value**
Age to consume grain target (d) [1]									
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
1300 g		0.81	0.37	**-**	**7.46**	**0.009**		0.06	0.81
Rewarded visits to the milk feeder (no.) [2]									
Pre-step		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 (no.) [2]									
Pre-step		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] 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
[2] Rewarded refers to a visit where milk was available; unrewarded refers to a visit where milk was not available

3.4 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 pre-weaning 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 these calves respond to milk removal by persisting in their unsuccessful behavior rather than searching for other feed sources.

3.4.1 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 regime were 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 % BW during the post-weaning 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 (two 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 weeks 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, while '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 post-weaning 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 pre-weaned 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 pre-weaning weight gains and intakes. For example, Soberon et al. (2012) found that among several early-life performance, nutrition and management factors potentially influencing long-term productivity, pre-weaning weight gain had the highest correlation with first-lactation milk production, with every 100 g increase in pre-weaning average daily gain resulting in 110 kg more milk during the first lactation. Another large-scale study demonstrated that higher pre-weaning 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 pre-weaning and weaning weight gains, we suggest future work should determine the consistency of these personality traits over the animal's lifespan and how these traits relate to long-term productivity.

3.4.2 Development of solid feeding behaviors

Irrespective of milk allowance treatment we observed large variation in the age that 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 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 1400 g target, suggesting 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 pre-weaning 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 post-ingestive 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 is a well-known phenomenon in ruminants, in which animals are reluctant to eat unfamiliar foods (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 repeated tests over time were consistent within individuals, suggesting 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 with a social affinity towards conspecifics; the latter may be more relevant in the development of feeding behaviors. For example, some evidence indicates a relationship between exploration/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 if 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 towards fear-eliciting stimuli.

3.4.3 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 a number of reports describe higher numbers of unrewarded visits in calves fed restricted milk diets (e.g. Jensen and Holm, 2003; Borderas et al., 2009), indicating 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 non-nutritive suckling on a teat. Rushen and de Passillé (1995) found that the motivation behind non-nutritive teat suckling were more related to the act of sucking itself rather than milk ingestion.

The motivation for non-nutritive sucking is also associated with milk allowance (de Passillé, 2001). Milk reduction during the step and weaning periods elicits non-nutritive visits (Budzynska and Weary, 2008; De Paula Vieira et al., 2008; Rosenburger 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, these 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.

While 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 one 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 application on-farm. 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.

3.5 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.

Chapter 4: Individual characteristics in early life relate to variability in weaning age, feeding behavior, and weight gain of dairy calves

A version of this chapter has been accepted for publication: Neave, H. W., J. H. C. Costa, J. B. Benetton, D. M. Weary and M. A. G. von Keyserlingk. Individual characteristics in early life relate to variability in weaning age, feeding behavior and weight gain of dairy calves. J. Dairy. Sci (*accepted).*

4.1 Introduction

Individual variability in milk and grain intakes before and after weaning has been observed across a number of studies (e.g. Nielsen et al., 2008; de Passillé and Rushen, 2016; Neave et al., 2018a in Chapter 3). Some calves begin to consume grain at a young age (Neave et al., 2018a; Chapter 3), and others take up to 11 wk to consume just 200 g/d of grain (de Passillé and Rushen, 2016). Calves are also variable in when they are able to complete weaning based on intake of grain, with some weaning as early as 6 wk (Roth et al., 2009; Benetton et al., 2019) or as late as 13 wk of age (de Passillé and Rushen, 2016). This variability in grain intake and age of weaning likely contributes to the variability in weight gains seen across studies (e.g. 0.1 to 1.6 kg/d; Soberon et al., 2012), which can have important consequences. For example, high pre-weaning DMI and weight gains have been linked to improved milk production and reproductive outcomes (e.g. Raeth-Knight et al., 2009; Gelsinger et al., 2016).

There is limited understanding of why calves vary when fed and housed under similar conditions. Some authors have attributed variability to differences in season of birth, parity of the dam, management factors, genetics or health (Place et al., 1998; Heinrichs and Heinrichs, 2011).

Shivley et al. (2018) found a number of factors affecting pre-weaning ADG on US dairy operations, including measures related to calving, colostrum, feeding and housing practices, nutrient intake composition, climate and disease. However, their models did not include behavioral factors known to contribute to pre-weaning calf performance. For instance, Gilbert et al. (2017) showed that drinking speed and fearfulness (response to human contact and movement on a weigh scale) were negatively associated with weight gain in veal calves, and Neave et al. (2018a; Chapter 3) found that personality traits in dairy heifers (such as interactive, exploratory, and vocal responses when exposed to novel situations) were related to feeding behavior and performance before and during weaning. Behavioral measures in these studies were taken when calves were several weeks to several months of age; it is possible that other behaviors recorded at an early age may explain variability in feeding behavior, growth, and suitability to wean early.

One of the first measures available is vitality at birth and in the first few hours of life (reviewed by Murray and Leslie, 2013). Calves with low vitality have reduced weight gain at 14 d of age (Furman-Fratczak et al., 2011; Murray et al., 2015), take longer to learn to use automated milk feeders and have reduced milk intake in the first 2 wk of life (Fujiwara et al., 2014). Calves that required more time to learn to drink from the milk feeder had reduced weight gain at 30 d of age (Medrano-Galarza et al., 2018). These characteristics may also influence how individuals cope with environmental stressors such as weaning, and thus how early calves will wean. Differences in individual traits such as fearfulness, sociability and exploration can also explain why some individuals struggle to adapt to changes in their feeding environment (for review Neave et al., 2018b; Chapter 2).

Dairy calves are normally weaned at a set age (e.g. Canada: Vasseur et al., 2010; Brazil: Hötzel et al., 2014; Czech Republic: Staněk et al., 2014; USA: Shivley et al., 2018), but automated milk and grain feeders can be used to wean calves based on individual grain intakes (Roth et al., 2009; de Passillé and Rushen, 2012, 2016). In this way computer-controlled feeders can be used to allocate milk resources away from calves that begin to consume grain early, and toward calves requiring more time on milk before weaning (Benetton et al., 2019). However, it is not clear how best to predict which calves are suitable candidates for early weaning. No study to date has investigated which measures can predict suitability of dairy calves for early weaning when allowed to wean based on solid feed intake.

The first objective of this study was to describe individual characteristics of dairy calves measured in the first 30 d of life and their relationship with weaning age, feeding behavior, and performance when weaned based on individual intake of solid feed. The second objective of this study was to identify which other measures in the first 30 d of age (such as automatically recorded feeding behavior, or growth) are the best predictors of weaning age.

4.2 Materials and Methods

The study was conducted from July 2017 to March 2018 at the UBC Dairy Education and Research Centre in Agassiz, BC, Canada, and was approved under the UBC Animal Care protocol # A14-0245.

4.2.1 Housing and animal management

Detailed animal management, housing, and weaning protocols for this experiment can be found in Benetton et al. (2019). Briefly, 48 Holstein calves (45 females and 3 males) were enrolled in this study. Calves remained with their dam for 5 h after birth, and were then separated, weighed (mean 40.3 ± 5.9 kg) and moved into individual pens where 4 L of colostrum was fed using a nipple bottle within 6 h after birth. At the next AM or PM feeding following the colostrum meal, 4 L of whole milk was fed through a nipple bottle in the individual pen. Calves were moved into a sawdust-bedded group pen (4.87 x 7.31 m) 1 h before their second milk meal (nominally 1 d of age). Group pens were filled to 8 calves based on birth date, and then a new pen was started (for a total of 6 group pens). After their first milk meal in the group pen (24 to 30 h after colostrum feeding), a blood sample was collected from the jugular vein for serum analysis using a Reichert AR 200 Digital Handheld Refractometer (Reichert, Depew, NY, USA). All calves achieved passive transfer as identified by serum total protein > 5.2 g/dL.

4.2.2 Feeding and weaning program

Each group pen was equipped with an automated milk feeder (CF 1000 CS Combi; DeLaval Inc., Tumba, Sweden) with one teat providing access to pasteurized whole milk. The milk feeder delivered milk in 0.5 L portions. The milk allowance accrued hourly at a rate of 5% of the daily value every hour from midnight to 2000 h. Calves were otherwise allowed to split their milk allowance in as many visits as they wish. Calf starter (Trouw Nutrition; Chilliwack, BC, Canada) was fed *ad libitum* from the same feeder. The feeder recorded intake, time and duration of each milk and starter visit. Farm hay and water were available *ad libitum* from automatic feeders (RIC; Insentec B. V., Marknesse, the Netherlands).

All calves were assigned to a weaning plan that combined two weaning techniques: a step-down reduction in milk at 30 d, and subsequent milk reduction based on individual starter intake. Calves were offered 12 L/d of milk from d 1 until nominally d 30 of age (mean 31.3 ± 1.15 d). On d 31, milk was reduced by 25% relative to each individual's average milk intake over the previous 3 d. The timing of subsequent 25% reductions in milk were based upon when the calf consumed specific amounts of starter: 225 g/d, 675 g/d, and 1300 g/d of starter (approximately 0.5, 1.5 and 3 lbs, respectively, as recommended by the Bovine Alliance on Management and Nutrition, 2017). To qualify for the milk reduction, the calf needed to consume the target starter consumption on average across the preceding 3 d, but with a daily minimum of 50% of the target. Calves were permitted up to d 84 of age to reach all 3 intake targets; if a calf did not consume 1300 g/d of starter by d 84, the calf was gradually weaned by reducing the milk over 7 d, beginning from the calf's current milk allowance until weaning was completed at d 91. Calves remained in their group pen until the last calf from the group reached 105 d of age.

Milk samples were collected and analyzed for components once per week (Pacific Milk Analysis Lab, Chilliwack, BC, Canada). Starter and hay samples were analyzed as reported in Benetton et al. (2019).

4.2.3 Health measures

Health examinations were performed as described in Benetton et al. (2019) for purposes of controlling for the effect of illness on outcome measures (health was not considered an outcome measure). Calves with severe diarrhea (score = 4) were treated with electrolytic solutions (Hydrafeed, EXL Laboratories, Minneapolis, MN, USA), and calves failing to respond to treatment within 2 d were administered a NSAID (Metacam 20 mg/mL, Boehringer Ingelheim, Burlington, ON, Canada), according to our farm's standard procedure. Calves showing nasal discharge and pathological sounds of pulmonary infection were treated with antibiotic drugs (Resflor GOLD®, Intervet Inc. Roseland, NJ, USA or Draxxin®, Zoetis Inc., Parsippany, NJ, USA). Calves were also visually examined twice per day (morning and afternoon) and any calves that were seen to have diarrhea or ill thrift (unresponsive to human presence at the front of the pen, head or ears down) were given a complete health examination and treatment was administered as necessary.

4.2.4 Measures of feeding behavior, weaning age and growth

Daily milk and solid feed intake, and the number of rewarded (when the calf visited the feeder and received milk) and unrewarded visits (when the calf visited the feeder but did not receive milk) to the milk feeder were recorded by the automated feeding system. Each of these measures was calculated as a daily average for 4 experimental periods: pre-weaning (full milk allowance; d 1 to d 30 of age), weaning (from initial milk reduction to end of required weaning period; d 31 to d 91), post-weaning (d 92 to d 105 of age), and the total experimental period (d 1 to d 105 of age). Additional measures for the total experimental period included cumulative milk and starter intake, ADG (kg of BW/d), and final weight at completion of the experiment at d 105.

We described the development of solid feeding behavior and behavioral response to weaning for each calf following Neave et al. (2018a; Chapter 3). Early solid feed intake measures included the age (d) that each calf first ate at least 40 g solid feed from the feeder (indicating the calf ate at least the previous 20 g, which is the smallest portion dispensed by the feeder), and the age that each calf met each of the solid feed intake targets (225 g, 675 g, and 1300 g). Weaning age was the age that calves consumed 1300 g/d of solid feed (or d 91 for those calves that failed to reach this target). To describe the behavioral response to weaning for each calf, the total number of unrewarded visits during the first week after weaning was calculated (i.e. from the day of weaning to 7 d post-weaning); this measure was meant to capture how persistent the calf was in attempting to gain milk from the feeder.

4.2.5 Measures of individual characteristics

Vitality

During the 5 h that the calf remained with the dam, video was recorded continuously using 4 cameras (WV-CW504SP, Panasonic, Osaka, Japan) positioned above the maternity pen. The latency to reach sternal recumbency, attempt standing, stand, walk and suckle the dam were recorded from video following an ethogram (**Table 4.1**). Longer latencies indicate lower vitality (Murray and Leslie, 2013). After separation from the dam, the calf was transported to the calf barn where additional vitality measures were taken (**Table 4.2**; adapted from Vannucchi et al., 2012; Murray, 2014), including respiration rate, heart rate, standing with or without stimulation, reflex and rectal temperature. Scores were tallied such that a higher total indicated higher vitality.

Drinking ability

Immediately following vitality scoring, calves were offered 4 L of colostrum from 2 2-L nipple bottles. Calves were scored for drinking response during this feeding (strong, medium or weak sucking; following an ethogram described in **Table 4.2**), and during a second colostrum feeding (offered 15 min after first attempt if the 4 L was not fully consumed). If more than 3.5 L of colostrum was consumed, calves were not tubed (score 1) and if less than 3.5 L of colostrum was consumed calves were tube-fed the remainder of the colostrum (score 0). A 'colostrum drinking score' was tallied for a maximum score of 4, with a higher score indicating a stronger suck. At the first milk feeding after colostrum feeding, a total of 4 L of whole milk was offered in 2 2-L nipple bottles; drinking score for this first milk meal was scored identically to that for colostrum feeding, and 'First milk meal drinking score' was tallied for a maximum score of 4, with a higher score indicating a stronger suck. Total milk consumption from the first milk meal was also recorded.

Table 4.1. Ethogram of behaviors scored with the dam and during the three novelty tests. Behaviours were scored from video. Calves (n = 43) remained with the dam for 5 h before separation and were tested individually at 25 ± 2 d of age in 3 novelty tests (novel environment, novel object and human approach test).

Test and behavior	Description
Vitality at birth	
Latency to sternal recumbency	Time from birth to time when calf is lying on sternum. Legs may be tucked underneath body, with head held up
Latency to standing attempt	Time from birth to time when calf is supported by two or more legs
Latency to stand	Time from birth to time when all four legs are fully supporting the calf. Legs fully extended
Latency to walk	Time from birth to time when calf is in standing position and takes 3 or more steps
Latency to suckle	Time from birth to time when calf's head is under dam's lower abdomen, and pointing up towards udder for more than 2 s
All Novelty Tests	
Vocalizations	All types of vocalizations, sound emitted from the mouth
Locomotor Play	Occurs without head oriented toward and more than one body length away from human or object *Jumping:* both forelegs off the ground and extended forwards (number of events) *Running:* calf trotting (2 beats) or galloping (3 beats) across or around the enclosure (number of events)
Bucking	Both hind legs are off the ground and extended backwards (number of events)
Resting	Time spent lying down with underside or side of body in full contact with flooring substrate
Withdrawal	Sudden movement backwards or sideways (number of events)
Novel Environment Test	
Explore	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 four 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 the human or object (muzzle within 5 cm)
Attentive	Time spent with head oriented toward human or object, excluding touching and object play behaviors
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 4.2. Scoring sheet for calf vitality and drinking ability.
Vitality measures were scored after removal from the dam and immediately after transport to the calf facility and tallied for a maximum score of 10. Colostrum drinking ability was scored during colostrum feeding within 6 h after birth and tallied for a maximum score of 4. First milk meal drinking ability was scored during the first AM or PM feeding after colostrum feeding and tallied for a maximum score of 4. Adapted from Vannucchi et al. (2012) and Murray (2014).

Variable	**Score**			
	0	1	2	3
Vitality score				
Respiration rate	Fast (> 36 rrpm)	Slow (< 24 rrpm)	Normal (24 – 36 rrpm)	
Heart rate	Slow (< 80 bpm)	Fast (> 100 bpm)	Normal (80 – 100 bpm)	
Initiation of movement	Unable to stand	Standing after stimulation	Standing without stimulation	
Response to straw in nasal cavity	No response	Twitches or flinches	Moves head away	Shakes head vigorously
Rectal temperature	Abnormal (< 38 or > 39.5)	Normal (> 38 and < 39.5)		
Colostrum drinking score [1]				
First feeding	Weak suck (must open mouth to place nipple, stops to drink often or does not drink at all)	Medium suck (takes several breaks)	Strong suck (minimal breaks)	
Secondary feeding	Required	Not required		
Tube feeding	Required	Not required		
First milk meal drinking score [2]				
First bottle	Weak suck (must open mouth to place nipple, stops to drink often or does not drink at all)	Medium suck (takes several breaks)	Strong suck (minimal breaks)	
Second bottle	Weak suck (must open mouth to place nipple, stops to drink often or does not drink at all)	Medium suck (takes several breaks)	Strong suck (minimal breaks)	

[1] First colostrum feeding involved attempting to feed all 4 L of colostrum to the calf in the first 15 min. If the calf did not complete the first feeding, there was a 15 min wait period before beginning the second feeding. If after 10 min the calf still had not finished at least 3.5 L of colostrum, the calf was tube-fed
[2] Calves were offered 4 L of milk for their first milk meal, divided into two bottles of 2 L each

Learning ability

Once calves entered the group pen they were trained to drink from the milk feeder following a training protocol. Human assistance was offered for each calf twice per day at 0900 h and 1700 h until learning was achieved (2 L of milk consumed between feedings without human assistance). When calves first entered the group pen they were permitted 1 h to attempt to access and drink from the milk feeder on their own before assistance was offered. At each feeding (0900 and 1700 h), if a calf had not yet visited the feeder on her own and consumed at least 2 L of milk, the trainer entered the calf pen and stood next to the milk feeder; if the calf did not enter the feeder and begin to drink on her own, the trainer approached the calf and offered her hand (without permitting suckling) to guide the calf into the feeder. If the calf did not follow, the human gently pushed the calf into the feeder while allowing the calf to suck her fingers. Once in the feeder, the calf was permitted 10 s to find the teat on her own. If the calf was unable to find the teat, the trainer allowed the calf to suck her fingers and guided the calf's mouth onto the nipple. This action was tallied as a teat demonstration. If the calf stopped sucking on the teat it was permitted 5 s to re-locate the teat before assistance was again offered (as described earlier). This pattern was repeated until the calf consumed at least 2 L of milk. If the calf did not begin to suck on the teat after 5 teat demonstrations, a nipple bottle was offered while inside the milk feeder to stimulate a suckling response. Once the calf was successfully sucking from the nipple bottle, the calf was transferred back to the milk feeder teat following the above protocol. The total number of teat demonstrations until 2 L of milk was consumed (including the number of demonstrations required using a nipple bottle) was tallied per feeding, and then a grand total of teat demonstrations across all feedings requiring human assistance was calculated. The number of feedings requiring human assistance was also tallied.

Responses to novelty

Standardized personality tests (novel environment, human approach and novel object tests) were used following (Neave et al., 2018a; Chapter 3). Briefly, calves were tested individually in a sawdust-bedded pen similar to the home pen except that the feeding equipment was inaccessible. Testing occurred over 3 consecutive days in the week before initial milk reduction (nominally 25 d of age, 25.3 ± 2.3 d). At the time of testing, the calf was guided gently into the test pen. Each calf remained in the test arena for 30, 10 and 10 min for the novel environment, human approach and novel object tests, respectively. The novel environment test consisted of an empty arena. In the human approach test, a human female, unknown to the calf and dressed in dark coveralls with hands in the coverall pockets, stood immobile at the center of the test pen looking towards the feet of the calf. In the novel object test, a black 140-L bucket was placed at the center of the test pen. The calf was video recorded continuously using one camera (WV-CW504SP, Panasonic, Osaka, Japan) positioned 7 m above the test pen. A single observer scored all behaviors after establishing high inter- and intra-observer reliability ($\kappa_W > 0.81$) for each test. Vocalizations were recorded by an observer that was out of sight of the test arena. Calves that never touched the human or object were assigned the maximum latency (10 min).

4.2.6 Statistical analysis

All analyses were performed using SAS (version 9.4; SAS Institute Inc., Cary, NC, USA) with calf as the experimental unit. Three calves failed to wean (did not meet the final starter intake target before 12 wk of age), and were excluded due to a low sample size for this weaning outcome, leaving 43 calves in our final analyses.

Behaviors recorded as durations in the personality tests were expressed as a percentage of the total test time. Bucking, resting and withdrawals rarely occurred during the tests and were excluded from further analysis. Behaviors recorded in both novel object and human approach tests were averaged across tests (following Neave et al., 2018a in Chapter 3, and Lecorps et al., 2018), resulting in 5 behavioral measures (number of vocalizations, latency to touch, and duration of touching, playing, and attentive) and a further 3 behavioral measures for the novel environment test (duration of active, inactive, and exploring). All measures of individual characteristics, feeding behavior, and performance, were verified for normality using the PROC UNIVARIATE procedure and probability distribution plots. All variables deemed not normal, were normalized as required using log10 or square-root transformations. Model residuals were also scrutinized to verify normality (using box, distribution, and probability plots) and homogeneity of variances. Calves were classified as sick if they had a score of 3 or higher for diarrhea, had a score of 2 for lung consolidation, were treated with NSAID or antibiotics, or had any combination of the above at any point during the experiment.

To address our first objective, we subjected the response variables to a Principal Component Analysis (PCA) with varimax rotation to condense correlated measures into principal components. These 20 response variables reflected individual characteristics of calves in early life including measures of vitality (6 measures: latency to reach sternal recumbency, first standing attempt, stand, walk and suckle from the dam, and vigor score), drinking ability (4 measures: colostrum drinking score, first milk meal drinking score, first milk meal intake, average milk intake during first week), learning ability (2 measures: total number of feedings, and number of teat demonstrations required to learn to drink from the automated milk feeder), and personality measures (8 measures, described above). We retained 5 principal components following examination of the scree plot of eigenvalues; these 5 principal components (referred to as Factor 1 through 5 hereafter) had eigenvalues > 1.5 and explained 66% of the variance. High loadings on each principal component were considered greater than ± 0.50. We tested whether each of these factors (reflecting particular individual characteristics) affected weaning age (i.e. age to eat 1300 g/d of solid feed), and feeding behavior and performance during each of the 4 experimental periods (pre-weaning, weaning, post-weaning, and total experiment). Using PROC MIXED, a single analysis was conducted to test for the effects of each Factor (1, 2, 3, 4 and 5) on milk intake, starter intake, total DMI, rewarded visits, unrewarded visits, persistent unrewarded visits in the week after weaning, ADG, final BW, age to first eat solid feed, age to eat 225 and 675 g/d of solid feed, and weaning age. Initially the model included the fixed effects of each factor score, birth weight, order of entry into the group pen, and sickness (dichotomous variable: sick or healthy), with group as a random effect. Weaning age was also included as a fixed effect for all variables except for the models with outcome measures in the pre-weaning period, age to first eat 225 and 675 g/d of solid feed, and weaning age (1300 g/d of solid feed). Order of entry into the group pen and sickness were dropped from the model if $P > 0.30$; birth weight and weaning age were retained in all models.

To address our second objective, we performed a multiple regression analysis with backward elimination using PROC MIXED to identify which combination of variables were best able to predict weaning age in the automated weaning program based on solid feed intake. Explanatory variables initially included were the 5 Factors derived from the PCA (reflecting early individual characteristics) and 7 variables reflecting feeding behavior and performance in the pre-weaning period (during the first 30 d of age): total milk and starter intakes, total rewarded and unrewarded visits to the milk feeder, drinking speed, ADG, and age to first eat solid feed. Birthweight, order of entry into the group pen and sickness were also included in the model. A backward elimination procedure was conducted to identify the best predictors of weaning age. The criterion for a variable to remain in the model was $\alpha < 0.15$, with Type 1 sum of squares. Group was specified as a random effect.

4.3 Results

4.3.1 Principal component analysis

Measures of vitality, drinking ability, learning ability, and behavioral responses of calves in each of the novelty tests are presented in **Table 4.3**, and the loadings for each factor are reported in **Table 4.4**. Factor 1 explained 23.7% of the total variance, and contained high positive loadings for all latency measures in the maternity pen (time to sternal recumbency, standing attempt, standing, walking, and suckling dam); thus, we labeled Factor 1 ‘low vitality’. Factor 2 explained 14.3% of the total variance, and had high positive loadings for latency to touch the human or object and time spent attentive and high negative loadings for time spent playing and touching the human or object; thus, we labeled Factor 2 ‘fearful’. Factor 3 explained 11.7% of total variance, with high positive loadings for drinking score (colostrum and first milk meal) and for first milk meal intake; Factor 3 was labeled ‘strong drinker’. Factor 4 explained 9% of the total variance, with high positive loadings for number of feedings and demonstrations required to learn to use the group feeder and high negative loading for milk intake in the first week; Factor 4 was labeled ‘slow learner’. Finally, Factor 5 explained 7.6% of the total variance, with high positive loadings for time spent exploring and active, and number of vocalizations; this was labelled ‘exploratory-active’.

Table 4.3. Measures of vitality, drinking and learning ability, and responses to novelty. Mean ± SD and range of measures for n = 43 calves.

Variable	Mean	SD	Range
Vitality at birth [1]			
Latency to sternal recumbency (min)	8.8	10.4	0.62 – 65.3
Latency to standing attempt (min)	13.8	11.6	3.5 – 71.8
Latency to stand (min)	64.8	43.2	18.2 – 234.2
Latency to walk (min)	80.2	57.8	20.4 – 300.0
Latency to suckle (min)	138.6	86.3	29.9 – 300.0
Vitality score (score 0 - 10)	6.6	0.98	4 – 9
Drinking ability [2]			
Colostrum drinking score (score 0 - 4)	2.2	1.6	0 – 4
First milk meal drinking score (score 0 - 4)	1.5	1.4	0 – 4
Total first milk meal intake (L)	1.7	1.4	0.0 – 4.0
Average daily milk intake during first week (L/d)	7.0	1.7	3.3 – 11.2
Learning ability [3]			
Total demonstrations required to learn to drink from feeder (no.)	23.8	27.2	0 – 126
Total feedings to learn to drink from feeder (no.)	5.0	3.5	0 – 17
Responses to novelty [4]			
Novel environment test			
Vocalizations (no.)	5.2	8.2	0 – 39
Active (no. quadrants crossed)	42.8	20.9	12 – 113
Inactive (% of test time)	32.3	15.4	3.4 – 67.8
Exploring walls or floor (% of time)	37.2	12.5	10.3 – 64.4
Locomotor Play (% of time)	2.5	1.5	0 – 5.8
Human approach test			
Vocalizations (no.)	0.67	1.5	0 – 7
Latency to touch (s)	241.5	238.7	4 – 600
Time in contact (% of time)	14.6	19.8	0 – 75.0
Attentive close (% of time)	18.4	9.4	3.0 – 43.0
Attentive far (% of time)	55.8	19.2	17.3 – 85.2
Object play (% of time)	1.7	4.5	0 – 25.8
Locomotor play (% of time)	0.86	1.3	0 – 5.3

Variable	Mean	SD	Range
Novel object test			
Vocalizations (no.)	2.4	4.1	0 – 19
Latency to touch (s)	145.3	173.9	11 – 600
Time in contact (% of time)	13.6	13.1	0 – 50.7
Attentive close (% of time)	18.1	15.4	3.0 – 80.2
Attentive far (% of time)	55.7	18.3	12.2 – 83.5
Object play (% of time)	0.083	0.20	0 – 0.88
Locomotor play (% time)	0.21	0.46	0 – 2.6

[1] Measured using video recordings when the calf remained with the dam for the first 5 h after birth. Calves that never performed a behavior were assigned the maximum latency of 300 min (5 h). Vitality scoring was performed immediately after separation and after transport to the calf rearing facility.
[2] Measured during colostrum feeding (5-6 h after birth) and during first milk meal (first AM or PM feeding after colostrum feeding).
[3] Measured beginning from the first entry to the group pen at 1 d of age until the calf learned to use the automated milk feeder in the group pen without human assistance.
[4] Calves were tested individually in a separate arena from their home pen at 25 ± 2 d of age in a novel environment test (30 min), novel object test (10 min) and human approach test (10 min).

Table 4.4. Coefficients (loadings) for the first 5 factors of the principal component analysis. Calves (n = 43) were scored across a series of characteristics broadly covering measures of early vitality, drinking and learning ability, and personality traits scored in novel environment, human approach and novel object tests. Behaviors were averaged across tests except where indicated. High loadings (≥ 0.50) are indicated in bold. Eigenvalues and proportion of total variation explained by each factor are reported, and suggested labels for each factor are offered.

Variable	Factor 1	Factor 2	Factor 3	Factor 4	Factor 5
Latency to sternal recumbency (min)	**0.70**	-0.03	0.28	-0.29	-0.30
Latency to stand attempt (min)	**0.68**	-0.16	0.10	-0.14	-0.35
Latency to stand (min)	**0.92**	0.20	0.022	0.04	0.01
Latency to walk (min)	**0.90**	0.17	0.14	0.06	0.10
Latency to suckle dam (min)	**0.75**	0.09	0.29	0.07	0.17
Vitality score	-0.28	0.28	0.13	-0.22	-0.10
Colostrum drinking score	0.27	0.11	**0.72**	0.04	0.08
First milk meal drinking score	0.14	-0.03	**0.89**	-0.11	-0.26
First milk meal intake (L)	0.22	-0.11	**0.87**	0.09	-0.21
Milk intake first week (L/d)	-0.05	0.28	0.34	**-0.68**	0.05
Feedings to learn to use group feeder (no.)	-0.02	0.00	0.24	**0.84**	-0.04
Teat demonstrations to learn to use group feeder (no.)	-0.07	0.01	-0.22	**0.74**	0.08
Exploring (% of time) [1,2]	0.13	-0.35	-0.14	-0.09	**0.56**
Active (no. quadrants crossed) [2]	-0.15	0.06	0.15	0.18	**0.66**
Inactive (% of time) [2]	0.02	-0.22	-0.40	0.27	-0.1
Vocalizations (no.)	0.02	0.03	-0.22	-0.12	**0.72**
Latency to touch object or human (s)	0.16	**0.81**	0.01	-0.17	-0.20
Time spent playing (% of time)	0.02	**-0.62**	-0.09	0.04	0.45
Time spent touching object or human (% of time)	-0.07	**-0.87**	-0.17	0.01	0.05
Attentive (% of time) [3]	0.12	**0.83**	-0.17	-0.01	0.19
Eigenvalues	4.75	2.86	2.34	1.80	1.53
Variance explained (%)	23.7	14.3	11.7	9.0	7.6
Interpretation (suggested label)	Low vitality	Fearful	Strong drinker	Slow learner	Exploratory-active

[1] Time spent sniffing, licking or muzzle close to floor or wall surfaces
[2] Behavior recorded only in novel environment test
[3] Calf is observing (head oriented toward) human/object (sum of time spent within 1 body length ('close) and more than 1 body length away ('far')

4.3.2 Characteristics associated with feeding behavior, weaning age, intake and performance

Development of solid feeding behaviors, weaning age, behavior at the milk feeder, feed intake, and performance for calves during the experimental period (d 1 to 105 of age) are presented in **Table 4.5**.

Table 4.5. Development of solid feeding behaviours, weaning age, feeding behavior, intake and growth measures.
Mean ± SD and range for n= 43 calves during the total experimental period (d 1 to d 105 of age).

Measure	Mean	SD	Range
Development of solid feeding behavior [1]			
Age to eat 40 g solid feed (d)	36.0	12.8	18 – 75
Age to eat 225 g/d solid feed (d)	47.2	10.9	33 – 78
Age to eat 675 g/d solid feed (d)	53.4	10.4	37 – 81
Weaning age (eat 1300 g/d solid feed) (d) [2]	59.1	9.6	44 – 84
Behavior at milk feeder [3]			
Rewarded visits (total no.)	407.8	116.4	212 – 737
Unrewarded visits (total no.)	491.4	197.0	211 – 1160
Drinking speed (L/min)	0.65	0.16	0.30 – 1.1
Persistent return to milk feeder during first wk after weaning			
Unrewarded visits (total no.)	89.0	35.8	37 – 197
Total feed intake			
Milk DMI (kg)	47.0	11.4	28.1 – 76.8
Starter DMI (kg)	141.7	36.5	58.3 – 257.2
Growth			
ADG (kg BW/d)	1.0	0.11	0.75 – 1.2
Final weight (kg)	147.3	15.8	118.7 – 186.8

[1] 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
[2] Calves that failed to meet the intake target of 1300 g/d by d 84 of age were forced to wean over a 7-d period and are not included here.
[3] Rewarded refers to a visit where milk was available; unrewarded refers to a visit where milk was not available

As expected, calves differed in when they began to eat solid feed (mean 36 d, range 18 to 75 d of age) and when they completed weaning at 1300 g/d of solid feed intake (mean 59 d, range 44 d to 84 d of age). **Figure 4.1** shows the distribution of weaning ages using 8 wk as a cut-point, given that the majority of farms in North America wean calves between 6 to 8 wk of age (Vasseur et al., 2010; USDA, 2016). Calves also varied in their motivation to access milk, with some showing more than 1000 unrewarded visits to the milk feeder during the experimental period (mean 491 total visits).

There was also individual variation in total feed intake and performance over the experimental period, with calves consuming between 28 and 77 kg DM of milk (mean 47 kg; see **Figure 4.2**) and between 58 and 257 kg DM of solid feed (mean 142 kg); calves also varied in ADG, from 0.75 to 1.2 kg/d (mean 1.0 kg/d).

Figure 4.1. Distribution of weaning ages.
Calves successfully completed weaning based on solid feed intake (1300 g/d of grain) at a range of ages. A weaning age of 8 wk was used as a cut-point for descriptive purposes, since the majority of farms in North America wean calves between 6 to 8 wk of age. 18 calves weaned before 8 wk (green bars), and 25 weaned between 8 and 12 wk of age (blue bars). 3 calves failed to complete weaning by 12 wk of age (did not consume 1300 g/d of grain, and thus were forced to wean over 7 d) (red bars). Calves that failed to wean were not considered in further analyses.

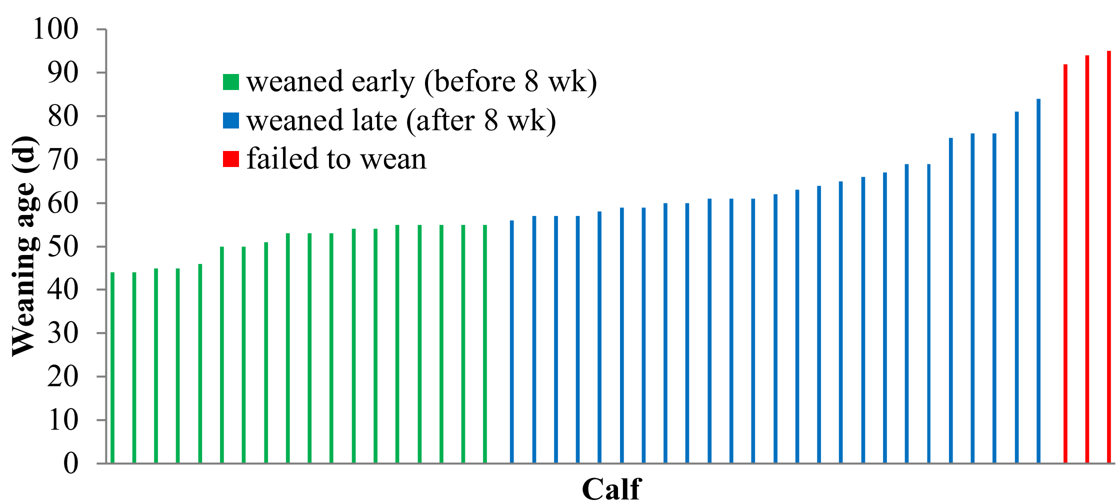
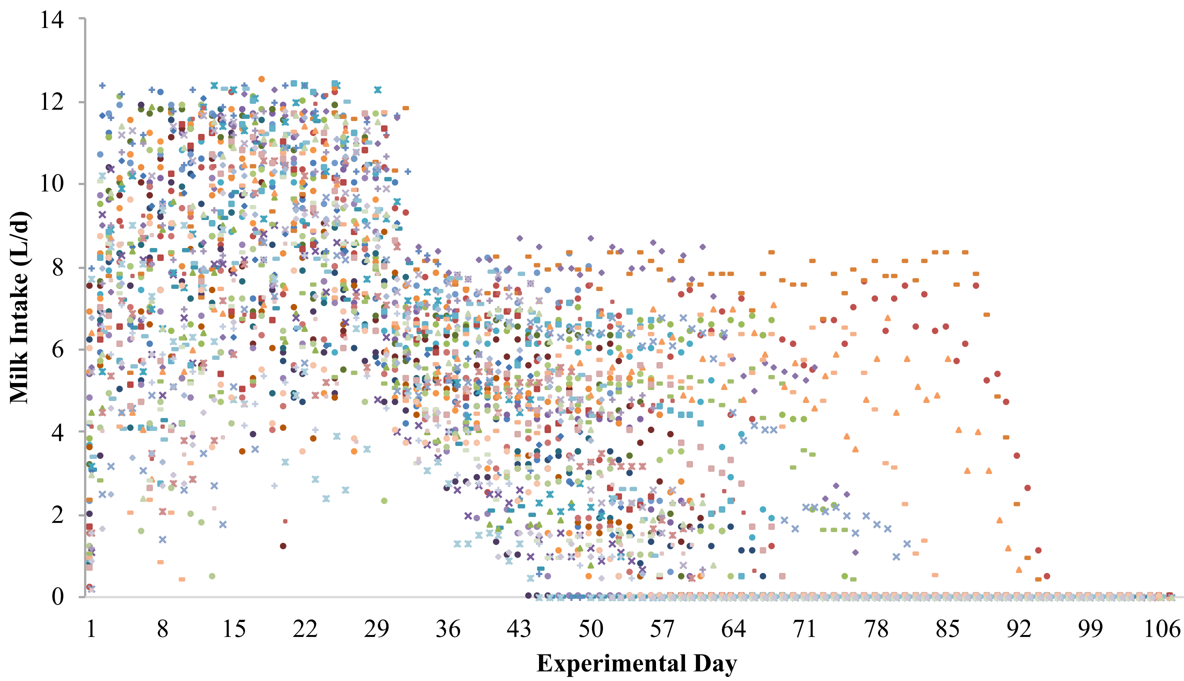


Figure 4.2 Individual variability in milk intakes over the experimental period.
Milk intake of calves during the experimental period (d 1 to 105 of age), where each calf is represented by a symbol (n = 43). All calves received 12 L/d until d 30. Milk was then reduced by 25% of each individual's milk allowance at d 31, and then a further 25% when each calf reached each target of starter intake (225, 675 and 1300 g/d) until complete weaning at 1300 g/d of starter, resulting in variable weaning ages. (Figure published in Benetton et al., 2019)



Some of this variation in solid feeding behaviors and weaning age could be explained by early individual characteristics and personality traits. The associations between the 5 factors identified in the PCA and solid feeding behaviors, weaning age, and behavior at the milk feeder during each period (pre-weaning, weaning, post-weaning, and total experiment) are presented in **Table 4.6**. Calves that scored highly on Factor 4 ('slow learner') tended to wean at a later age, but there were no other associations with early solid feed intake. These calves also had fewer pre-weaning and total rewarded visits to the milk feeder, reduced pre-weaning drinking speed, and tended to have fewer unrewarded visits before weaning and in the week after weaning, suggesting these calves were less persistent in attempting to gain milk. In contrast, calves scoring highly on Factor 2 ('fearful') tended to wean earlier, and also had reduced drinking speed before weaning. The remaining factors had no associations with development of solid feeding behaviors or weaning age. However, Factor 5 ('exploratory-active') was positively associated with pre-weaning and total rewarded visits to the milk feeder, while Factor 1 ('low vitality') and Factor 3 ('strong drinker') were negatively associated with these measures.

We also investigated the associations between the factors and feed intake and performance measures during each period (**Table 4.7)**. Calves that scored highly on Factor 4 ('slow learner') had reduced pre-weaning and overall DMI, driven primarily by reduced milk intake, resulting in a tendency for reduced pre-weaning ADG. Calves that scored highly on Factor 5 ('exploratory-active') had increased pre-weaning, weaning and total ADG, resulting in increased final BW; however, this improved growth did not appear to be due to greater milk or starter intakes. In contrast, calves that scored highly on Factor 1 ('low vitality') had reduced pre-weaning ADG, likely driven by a tendency for reduced pre-weaning milk intake. Factor 3 ('strong drinker') was negatively associated with weaning ADG, but had no associations with milk or starter intake. Factor 2 ('fearful') had no association with feed intake or performance.

4.3.3 Predicting weaning age

When all variables were included in the regression model this could account for approximately 76% of the variance in weaning age. After backward elimination, 5 explanatory variables were retained in the model: age to start eating grain ($P < 0.01$), total pre-weaning grain intake ($P < 0.01$), Factor 4 ('slow learner', $P < 0.01$), Factor 2 ('fearful', $P = 0.03$) and total unrewarded visits ($P = 0.08$). Together these variables explained 67% of the variance. This regression equation (illustrated in **Figure 4.3**) was: *weaning age = 48.4 + 0.39 (age to start eating) – 6.98 (total pre-weaning grain intake) + 1.45 (Factor4) – 2.23 (Factor2) – 0.039 (total pre-weaning unrewarded visits)*.

Table 4.6. Relationships between factor scores and development of solid feeding behavior, weaning age, behavior at the milk feeder, and behavioral response to weaning.
Results are reported for each of 5 experimental periods: pre-weaning (full milk allowance; d 1 to d 30 of age), weaning (d 31 to d 91 of age), post-weaning (d 92 to d 105 of age) and the total experimental period (d 1 to d 105 of age). Calves were weaned based on their individual intake of solid feed, and thus completed weaning at different ages. Effect direction is provided when the main effect is $P \leq 0.1$ (in bold).

Measures	**Factor 1 (Low vitality)**			**Factor 2 (Fearful)**			**Factor 3 (Strong drinker)**			**Factor 4 (Slow learner)**			**Factor 5 (Exploratory-active)**		
	Effect	**$F_{1,29}$**	***P***	**Effect**	**$F_{1,29}$**	***P***	**Effect**	**$F_{1,29}$**	***P***	**Effect**	**$F_{1,29}$**	***P***	**Effect**	**$F_{1,29}$**	***P***
Age to consume solid feed intake target (d)															
At least 40 g		0.67	0.42		0.50	0.48		2.0	0.17		0.80	0.34		0.08	0.78
225 g/d		0.54	0.47		0.46	0.50		0.27	0.61		1.5	0.23		0.0	0.96
675 g/d		0.05	0.82		0.24	0.63		0.40	0.53		1.4	0.24		0.01	0.93
Weaning age (1300 g/d)		0.44	0.51	**-**	**2.9**	**0.10**		0.15	0.70	+	**3.6**	**0.07**		0.20	0.66
Rewarded visits to milk feeder (no./d)															
Pre-weaning	**-**	**5.3**	**0.03**		1.8	0.19	**-**	**5.4**	**0.03**	**-**	**11.3**	**<0.01**	+	**6.5**	**0.01**
Weaning		0.67	0.42		1.7	0.20		0.01	0.93		2.1	0.16		2.5	0.13
Total	-	**4.7**	**0.04**		2.3	0.14	-	**3.1**	**0.09**	**-**	**8.81**	**<0.01**	+	**7.1**	**0.01**
Unrewarded visits to milk feeder (no./d)															
Pre-weaning		1.2	0.28		0.01	0.91		0.23	0.63	**-**	**2.7**	**0.10**	+	**2.7**	**0.10**
Weaning		0.0	0.96		0.07	0.79		0.0	0.99		0.21	0.65		1.7	0.20
Post-weaning		0.68	0.42		2.0	0.17		0.12	0.74		0.41	0.53		0.56	0.46
Total		0.02	0.88		0.18	0.67		0.02	0.88		0.50	0.49		2.0	0.17

Measures	Factor 1 (Low vitality)			Factor 2 (Fearful)			Factor 3 (Strong drinker)			Factor 4 (Slow learner)			Factor 5 (Exploratory-active)		
	Effect	**$F_{1,29}$**	***P***	**Effect**	**$F_{1,29}$**	***P***	**Effect**	**$F_{1,29}$**	***P***	**Effect**	**$F_{1,29}$**	***P***	**Effect**	**$F_{1,29}$**	***P***
Drinking speed (L/min)															
Pre-weaning		1.1	0.30	**-**	**4.0**	**0.05**		1.2	0.29	**-**	**4.0**	**0.05**		0.0	0.99
Weaning		0.23	0.63		0.09	0.78		0.10	0.75		0.84	0.37		0.19	0.67
Total		0.82	0.37		0.89	0.35		0.25	0.62		2.1	0.16		0.04	0.84
Persistent return to milk feeder during first wk after weaning															
Total unrewarded visits (no.)		0.21	0.65		0.51	0.48		0.93	0.34	**-**	**2.9**	**0.10**		0.58	0.45

[1] 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
[2] Rewarded refers to a visit where milk was available; unrewarded refers to a visit where milk was not available

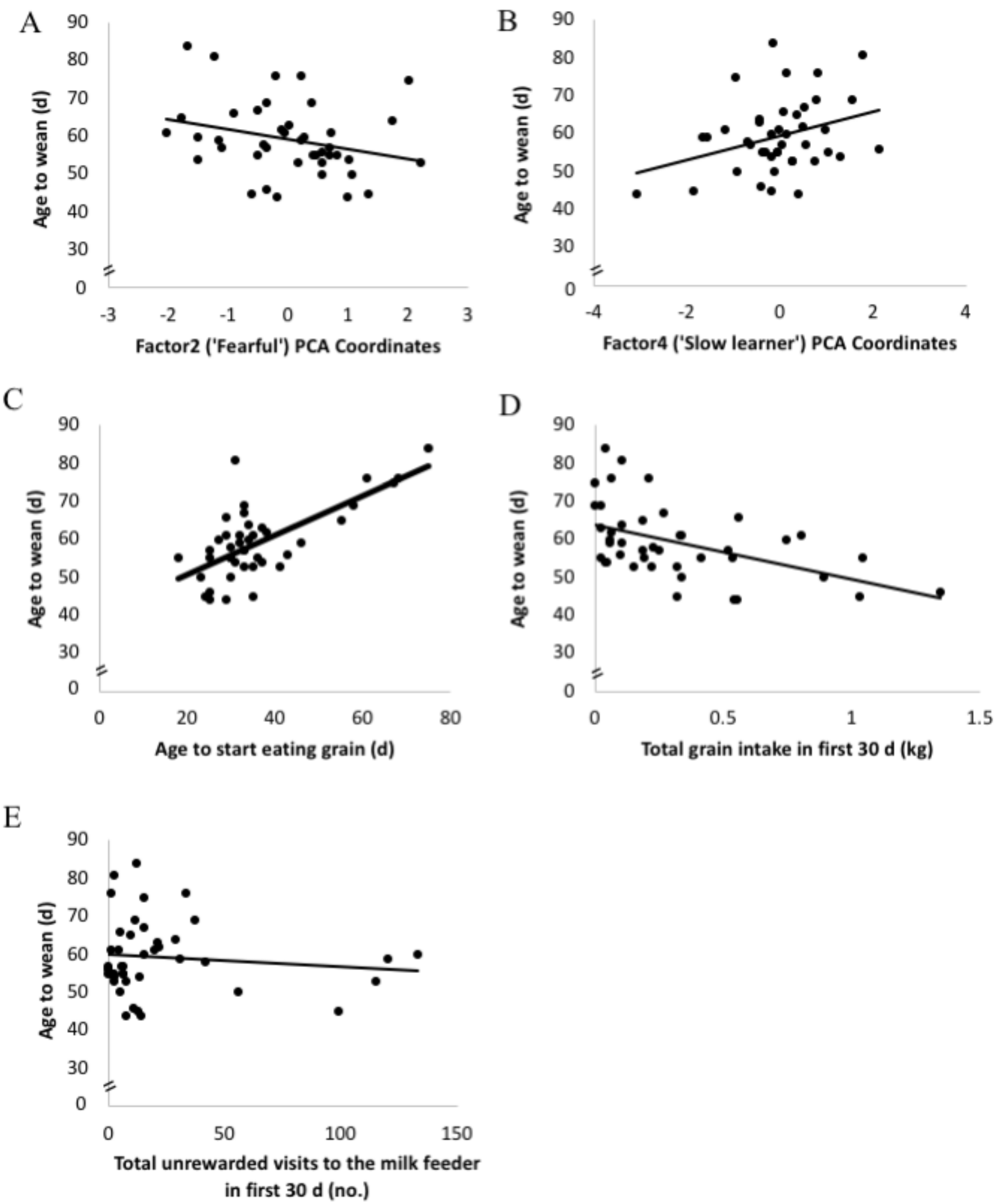
Table 4.7. Relationships between factor scores and feed intake and growth measures.
Results are reported for each of 5 experimental periods: pre-weaning (full milk allowance; d 1 to d 30 of age), weaning (d 31 to d 91 of age), post-weaning (d 92 to d 105 of age) and the total experimental period (d 1 to d 105 of age). Calves were weaned based on their individual intake of solid feed, and thus completed weaning at different ages. Effect direction is provided when the main effect is $P \leq 0.1$ (in bold).

Measures	**Factor 1 (Low vitality)**			**Factor 2 (Fearful)**			**Factor 3 (Strong drinker)**			**Factor 4 (Slow learner)**			**Factor 5 (Exploratory-active)**		
	Effect	**$F_{1,29}$**	***P***	**Effect**	**$F_{1,29}$**	***P***	**Effect**	**$F_{1,29}$**	***P***	**Effect**	**$F_{1,29}$**	***P***	**Effect**	**$F_{1,29}$**	***P***
Milk intake (L/d)															
Pre-weaning	**-**	**3.0**	**0.09**		0.37	0.54		1.7	0.20	**-**	**6.0**	**0.02**		1.7	0.20
Weaning		0.24	0.62		0.51	0.48		0.31	0.58	**-**	**3.6**	**0.06**		0.21	0.65
Total		1.9	0.18		0.27	0.61		0.28	0.60	**-**	**6.5**	**0.01**		1.0	0.32
Solid feed intake (kg/d)															
Pre-weaning		0.63	0.44		0.72	0.40		1.5	0.23		0.02	0.89		0.07	0.80
Weaning		0.86	0.36		0.90	0.35		0.61	0.44		0.59	0.45		0.07	0.79
Post-weaning		0.21	0.65		0.32	0.58		0.24	0.62		1.3	0.26		1.1	0.30
Total		0.56	0.46		0.0	0.99		0.0	0.97		1.3	0.26		0.64	0.43
Total DMI (kg) [1]															
Pre-weaning		2.1	0.16		0.00	0.97		1.8	0.19	**-**	**5.5**	**0.03**		1.5	0.22
Weaning		0.13	0.73		0.01	0.93		0.0	0.95		1.9	0.18		0.22	0.64
Total		0.03	0.85		0.05	0.82		0.01	0.91	**-**	**3.1**	**0.09**		1.0	0.32

Measures	Factor 1 (Low vitality)			Factor 2 (Fearful)			Factor 3 (Strong drinker)			Factor 4 (Slow learner)			Factor 5 (Exploratory-active)		
	Effect	**$F_{1,29}$**	***P***	**Effect**	**$F_{1,29}$**	***P***	**Effect**	**$F_{1,29}$**	***P***	**Effect**	**$F_{1,29}$**	***P***	**Effect**	**$F_{1,29}$**	***P***
ADG (kg/d)															
Pre-weaning	**-**	**9.1**	**<0.01**		0.54	0.47		0.18	0.68	**-**	**2.7**	**0.10**	+	**3.0**	**0.09**
Weaning		0.58	0.45		0.12	0.72	**-**	**3.3**	**0.08**		0.19	0.67	+	**3.4**	**0.07**
Post-weaning		0.59	0.44		0.13	0.72		0.40	0.53		0.64	0.43		1.6	0.21
Total		2.2	0.15		0.02	0.88		1.0	0.31		1.1	0.30	+	**7.9**	**<0.01**
Final weight (kg) [2]		0.76	0.39		0.40	0.52		0.20	0.66		0.94	0.34	+	**6.1**	**0.02**

[1] Calculated from the sum of milk and solid feed intakes. Hay was offered but intakes could not be recorded reliably.
[2] Final weight was measured at d 105 of age.

Figure 4.3. Relationship between weaning age and explanatory variables.
(A) Factor 2 ('fearful'), (B) Factor 4 ('slow learner'), (C) age to start eating grain, (D) total grain intake in the first 30 d of age, and (E) total unrewarded visits to the milk feeder in the first 30 d of age. These variables were retained following a multiple regression analysis with backward elimination that initially included 12 measures of individual characteristics, feeding behavior and growth in the first 30 d of age; the final model explained 67% of the variance in weaning age.



4.4 Discussion

These results build upon our previous work that identified a number of associations between personality traits and feed intake, behavior, and performance around weaning (Neave et al., 2018a; Chapter 3). The key difference in the current study is that we used an automated and individualized method of weaning, where calves were allowed to progress through weaning as they consumed increasing amounts of solid feed, resulting in variable weaning ages. This study is also the first to investigate the relationship between individual characteristics measured in early life (vitality at birth, drinking and learning ability, and personality traits) and weaning age, feeding behavior, and performance when calves are weaned automatically based on their intake of solid feed. We also investigated if individual measures in the first 30 d of life could predict weaning age.

4.4.1 Individual variability in weaning age, feeding behavior and performance

Solid feed intake early in life facilitates weaning from milk, yet few studies describe the variability in solid feeding behavior in pre-weaned calves. We found a large range in ages when calves first began to consume solid feed (between 18 and 75 d of age) and when calves reached 225 and 675 g/d of solid feed (between 33 and 81 d of age), a result consistent with that reported in earlier studies (Benetton et al., 2019; Neave et al., 2018a in Chapter 3; de Passillé and Rushen, 2016). In the current study, some calves weaned as early as 44 d while others were as old as 84 d before they met the final solid feed intake target. Weaning age ranged considerably in previous studies that weaned calves based on intake of solid feed, both when calves received *ad libitum* or restricted allowances of milk (Roth et al., 2009; de Passillé and Rushen, 2012, 2016). Collectively this body of work highlights that calves vary in their intake of solid feed in ways that affect success at weaning.

We also found individual variability in milk and grain intake, feeding behaviors, and performance. Variability in pre-weaning milk intakes has been shown in other studies that fed calves high amounts of milk (de Passillé et al., 2016; Dennis et al., 2018). Measures of feeding behavior at the milk feeder, including the frequency of visits to the milk feeder and drinking speed, were highly variable across calves, a finding that to our knowledge has not previously been reported. These individual differences likely contribute to the variability in pre-weaning weight gains. In the current study, pre-weaning ADG ranged from 0.3 to 1.3 kg/d. This result corresponds well with results from earlier work reporting 0.3 to 1.3 kg/d to d 50 of age (Soberon et al., 2012) and 0.07 to 1.2 kg/d to d 30 of age (de Passillé et al., 2016).

Efforts to understand the source of this individual variation have typically focused on external factors such as housing, feeding, health and climate (e.g. Place et al., 1998; Shivley et al., 2018), but internal factors have been largely overlooked. Neave et al. (2018a; Chapter 3) showed that personality differences among calves could explain variability in weight gains, and de Passillé and Rushen (2016) suggested differences in weaning age (when weaned based on solid feed intake) may be related to gastrointestinal differences, taste preferences, or ability to recognize a new food source. To add to this body of work, we measured a number of calf behaviors in the first few weeks of life and predicted that these individual characteristics would explain some of the variability in weaning age, feeding behavior, and performance of calves.

4.4.2 Vitality at birth

Calves with a longer duration to reach sternal recumbency, attempt to stand, stand, walk and suckle the dam in the hours after birth were identified as having 'low vitality' in the PCA. Our findings did not indicate that 'low vitality' calves show delayed solid feed intakes and weaning. However, 'low vitality' was associated with reduced pre-weaning milk intake.

Longer latencies to reach sternal recumbency and to suckle from the dam after birth have been attributed to a difficult birth (Barrier et al., 2012; Murray and Leslie, 2013), and may contribute to reduced colostrum intake (Vasseur et al., 2009), failure of passive transfer and reduced weight gain (Furman-Fratczak et al., 2011). We found that 'low vitality' calves had reduced pre-weaning weight gains, but this is unlikely to be related to inadequate colostrum intake since all our calves received at least 4 L of colostrum and achieved passive transfer. This finding may be related to calves having a difficult calving, but we did not standardize recording of this measure. In other work, low vitality is negatively associated with early milk intake (Fujiwara et al., 2014; de Passillé et al., 2016) but the association is less clear for weight gain (positive association: Murray et al., 2015; no association: de Passillé et al., 2016). The differences across these studies may be related to the timing of measurements (either at birth, or several days later).

4.4.3 Drinking ability

Calves that had high colostrum and first-milk-meal drinking scores (i.e. quickly consumed their full meal), and consumed more milk during their first milk meal, were termed 'strong drinkers' in the PCA. We found no association between this trait and the development of solid feeding behavior, weaning age, feed intake, or growth. Similarly, de Passillé et al. (2016) found that milk intake at d 2 to 3 of age was not related to energy intake or weight gain in the first month of life, although milk intake at d 4 did have some associations with these later measures. Although we did not identify a relationship between drinking ability at d 1 of age and later drinking speed, the ‘strong drinkers’ did have fewer pre-weaning visits to the milk feeder and reduced weight gain during weaning. We speculate that these calves may have been more motivated to consume high milk volumes and thus were more distressed when milk was removed. High early milk intake or drinking strength may be an indicator that calves need assistance when weaned based on solid feed intake. These calves may perform better on a weaning program that removes milk more gradually at each solid feed intake target.

4.4.4 Learning ability

Calves that required extensive training to learn to use the automated milk feeder and had reduced milk intake in the first week were termed ‘slow learners’ in the PCA. We found that these ‘slower learners’ weaned at a later age. These calves also had reduced milk intake, drinking speed, visits to the milk feeder, and growth before weaning, and fewer unrewarded visits to the milk feeder in the week after weaning; this result suggests that these calves were less persistent in attempting to gain milk from the feeder, which may indicate a reduced motivation to drink milk. Other work has shown a negative correlation between latency to drink unassisted from the automated feeder and milk intake in the first two weeks (Fujiwara et al., 2014) and weight gain in the first month (Medrano-Galarza et al., 2018). We speculate that these ‘slow learners’ may be less resourceful when it comes to maximizing milk intake during the milk-feeding period and solid feed intake in the later stages of weaning, resulting in a later weaning age when weaned based on solid feed intake. These calves may also have difficulty learning from social cues of other calves about their feeding environment, as the development of feeding behaviors can be enhanced through social facilitation and learning from other members of the herd (reviewed in Launchbaugh and Howery, 2005).

The training required for calves to learn to use the milk feeder may be measured relatively easily, as automated feeders can be programmed to alarm if calves fail to come to the feeder on their own. Further research is necessary to understand why some calves struggle to learn to use the milk feeding equipment; for instance some work has found that the stall design around the milk feeder may delay learning time (Wilson et al., 2018). Improved training methods may contribute to improving feed intake, behavior and weaning age.

4.4.5 Fearful and exploratory-active personality traits

The PCA identified two main personality traits based on the behavior expressed during the standardized novelty tests: fearful (Factor 2) and exploratory-active (Factor 5). ‘Fearful’ calves tended to wean at an earlier age but were not associated with other measures of development of solid feeding behaviors. This was contrary to our hypothesis that more fearful calves (i.e. more reactive to a novel object and human) would also be more reactive to a change in their feeding environment during our weaning program (i.e. milk removal based on increasing intake of solid feed). ‘Fearful’ calves were more attentive in the novelty tests, which may indicate they are more attentive and responsive to changes in their environment (e.g. by increasing solid feed intake in response to milk removal to complete weaning earlier). Research on lambs has shown that fear responses do not translate to a feeding context (Rice et al., 2016). We found that ‘fearful’ calves had reduced pre-weaning drinking speed, which may be an indication of low feeding motivation or reflect a preferred feeding rate that is characteristic for these calves (Nielsen, 1999), so these calves may not see milk removal as particularly stressful. We encourage further work to understand why 'fearful' calves appear to wean earlier than others and how these specific personality traits influence how calves cope with other management changes.

The personality trait 'exploratory-active' was not associated with the development of solid feeding behaviors or weaning age in this study. This finding contrasts with our previous work that found that 'exploratory' calves consumed more solid feed at earlier ages when weaned at a fixed age (Neave et al., 2018a; Chapter 3). However our 'exploratory-active' calves had improved weight gain throughout the experiment resulting in greater final weight, similar to our previous study and other work in beef heifers (Müller and von Keyserlingk, 2006). The improved weight gain observed in these calves was not associated with increased milk or grain intake, suggesting that these calves may cope well with the weaning transition. We speculate these results are related to the weaning method since the current study removed portions of milk as each individual reached a solid feed intake target; individuals clearly differed in how they responded to this method of milk removal (either by continuing to increase solid feed intake, or trying to regain milk and delaying solid feed intake), resulting in variable weaning ages. Further research should investigate how different personality traits respond to different methods of milk removal during gradual weaning so that appropriate methods of weaning can be identified for different individuals.

Overall, we found that calves differed in how they responded to an automated weaning program; 'slow learner' and 'fearful' characteristics were associated with weaning age (and thus age to consume 1300 g/d of solid feed), which could be used to identify calves from an early age that may do well or struggle during weaning. However, the characteristics measured in this study had limited associations with the early development of solid feeding behaviors. Other characteristics such as sociability and food neophobia explain some variability in feeding behaviors of ruminants (Neave et al., 2018b; Chapter 2) and may be related to early intake of solid feed. In addition, there is a need to identify automated methods of characterizing dairy calves, especially for exploration-activity and fearfulness, as currently it is likely not feasible to collect these measures on-farm. Automated activity monitors (Swartz et al., 2016), and the response to an approaching human during feeding (Lensink et al., 2003; Rousing et al., 2005), are examples of practical assessment methods that should be verified for associations with weaning age, feeding behavior, and performance.

4.4.6 Predicting weaning age

It would be advantageous to identify calves at an early age that are able to wean earlier, especially on farms that still manually feed and wean their calves; milk is an expensive resource that could be better allocated toward calves that need more time to make the transition to solid feed. We found that early measures of grain intake (age to begin eating grain, and total grain intake in the first 30 d of age) were the best predictors of weaning age, explaining a large portion of the variability in weaning age. These measures are relatively easy to monitor in manually-fed calves. About 30% of the variation in weaning age remained unexplained by the measures collected in this study. Future research should integrate multiple technologies and machine learning models (e.g. Borchers et al., 2017) to better identify calves that require more time before weaning (e.g. rumination activity or rumen pH).

4.5 Conclusions

Weaning age is variable when calves are weaned based on their intake of solid feed. Some individual characteristics measured in early life (slow to learn to use the automated milk feeder, and fearful personality), and measures of early grain intake, can identify calves that will wean earlier or later. Low vitality at birth, drinking ability and exploratory-active personality are also associated with feed intake, behavior, and performance. Future work should investigate additional animal-based measures (especially those that can be automatically monitored and feasibly measured on-farm) that can identify calves from an early age that are likely to do well or struggle during weaning.

Chapter 5: Feed intake and behaviour of dairy goats when offered an elevated feed bunk

A version of this chapter has been published: Neave, H. W., M. A. G von Keyserlingk, D. M. Weary, and G. Zobel. 2018. Feed intake and behavior of dairy goats when offered an elevated feed bunk. J. Dairy. Sci. 101: 3303-3310. doi: https://doi.org/10.3168/jds.2017-13934

5.1 Introduction

Goats are selective foragers of 'browse' (e.g. foliage, buds, flowers, and stems of shrubbery) (Askins and Turner, 1972). While this browsing behavior can include some low-level feeding, different body positions are used to access the browse when located at variable heights; these positions include eye-level feeding and rearing onto the rear legs (Tölü et al., 2012). The inclusion of browsing behavior allows for an expansion of the foraging area by accessing browse above head level. There is a wealth of evidence indicating that when goats are faced with a variety of browse, forbs and grasses in their environment, they will consume a diet containing much more browse than sheep or cattle (reviewed by Goetsch et al., 2010; Solaiman, 2010). Sanon et al. (2007) reported that goats browsed forage that was located on average at a height of 1.65 m (maximum 2.1 m), more than double their body height. Goats have also been reported to climb trees when given the opportunity (El Aich et al., 2007). Feeding with the head elevated may aid in predator detection; grazing with the head lowered is known to limit visual identification of threats (Beauchamp, 2015). Feeding at head- or elevated- level may also reduce the risk of infection, as parasite eggs are typically situated at or near ground-level (Lu, 1988).

Extensively managed goats housed in complex naturalistic environments will browse for a considerable portion of their daily feeding time. However, when intensively managed on commercial farms, goats are typically fed using a floor-level feeder. In cattle, different feed bunk designs can impact aggression (DeVries and von Keyserlingk, 2006), feeding time (Huzzey et al., 2006) and access to the feed bunk for subordinate animals (Endres et al., 2005). There have been limited studies on feeder design for goats. Aschwanden et al. (2009) showed reduced aggression between goats when partitions between feeding places were provided; however, it has been suggested that some partitions may restrict goat mobility into and out of the feed bunk (Nordmann et al., 2011).

Few studies have investigated the effect of feeder height on feeding and social behavior of goats. Aschwanden et al. (2009a) allowed goats to feed from a vertically elongated hayrack, that required them to stand on a platform, and found decreased agonistic behavior and increased feeding time compared to feeding at floor-level. In a companion study, Aschwanden et al. (2009b) found that goats provided housing containing structural elements, including elevated platforms for feeding, had longer feeding bouts and fewer interrupted resting bouts. The structure of feed bunks has also been adjusted to allow for a comfortable posture and reach while feeding (Keil et al., 2017). However, these studies did not offer elevated feeders that resemble heights found in natural browsing situations, nor did they allow multiple goats to feed together from the same height. Elevated feeding areas that resemble how goats naturally forage may be preferred and promote increased feed intake.

The objective of this study was to determine if goats prefer to feed from a browsing position. We predicted that goats would consume more feed and spend more time feeding from feeders that permit a browsing position. Furthermore, we expected that more competitive displacements would occur at the higher feeders, as a result of the preference for these feeding positions. Overall our aim was to evaluate the effects of offering dairy goats an elevated surface for feeding.

5.2 Materials and methods

The study was conducted in August 2016 at the Ruakura Research Centre in Hamilton, New Zealand. All procedures were approved by the Ruakura Animal Ethics Committee, Hamilton, New Zealand (#AE13930) under the New Zealand Animal Welfare Act 1999 and by the University of British Columbia Animal Care Committee, Vancouver, Canada (#A16-0213).

5.2.1 Animals, housing and diet

Thirteen non-lactating, nulliparous, non-pregnant and disbudded Saanen X dairy goats were enrolled from the AgResearch herd at approximately 13 mo of age with a mean (± SD) body weight of 37.6 ± 3.6 kg. Goats were previously housed on pasture as a single group, and were given 6 d to habituate to the indoor facility; this began with an initial period of indoor housing at night only, followed by 5 d of continuous indoor housing. Goats were then housed as a single group for the next 24 d in a home pen with plywood walls measuring 11.3 x 3.0 m (offering 2.6 m^2/goat); half of the pen was equipped with a plywood box bedded 40 cm deep with wood shavings (offering 1.3 m^2/goat) and the other half of the pen floor was metal grating (**Figure 5.1**). In the home pen, goats were fed *ad libitum* alfalfa silage (Fibre Protect, Fibre Fresh Feeds, New Zealand), top-dressed with 3 kg of pellets (0.23 kg/goat; Fibre Grow, Dunsan Horse Feeds Ltd, New Zealand) twice daily at 0800 and 1600 (as per requirements for 40 kg non-lactating goat; NRC, 2007). Feed was provided from one of three feeder heights (floor-, head-, and elevated-levels; see **Figure 5.2** for design details). Each morning at 0800, the feeder height was changed to a different feeder height following a randomized schedule such that only one feeder height was offered during a given 24-h period. After 24 d in the home pen, all goats had experienced 8 repetitions of each feeder height. Goats received fresh water from a wall-mounted waterer and *ad libitum* hay was provided and replenished daily at 1200 in two hayracks positioned at 72 cm above the pen floor at either end of the pen.

Figure 5.1. Layout of the test and home pens.
The home pen contained a single feeder 175 cm in length; each day the height of this feeder was varied (floor-level, head-level and elevated-level) to familiarize the goats with the three feeding positions. The test pen contained three smaller feeders, one of each feeder height. Each was 58 cm long, mounted 11.5 cm apart and centered along the length of the pen.

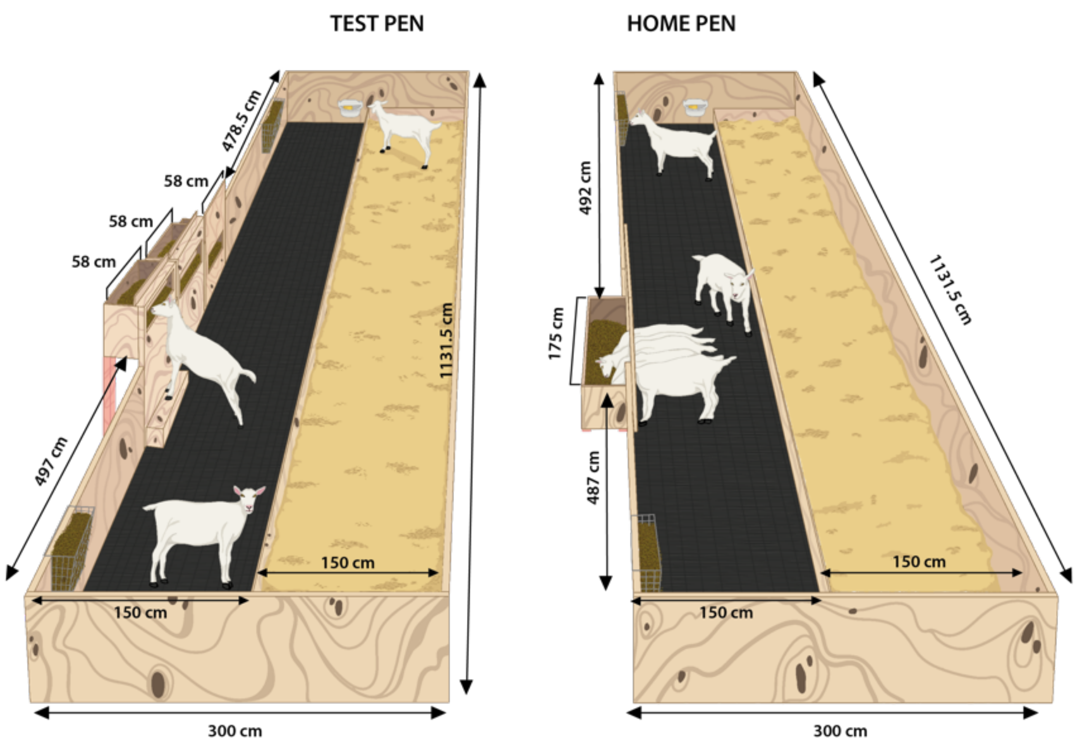
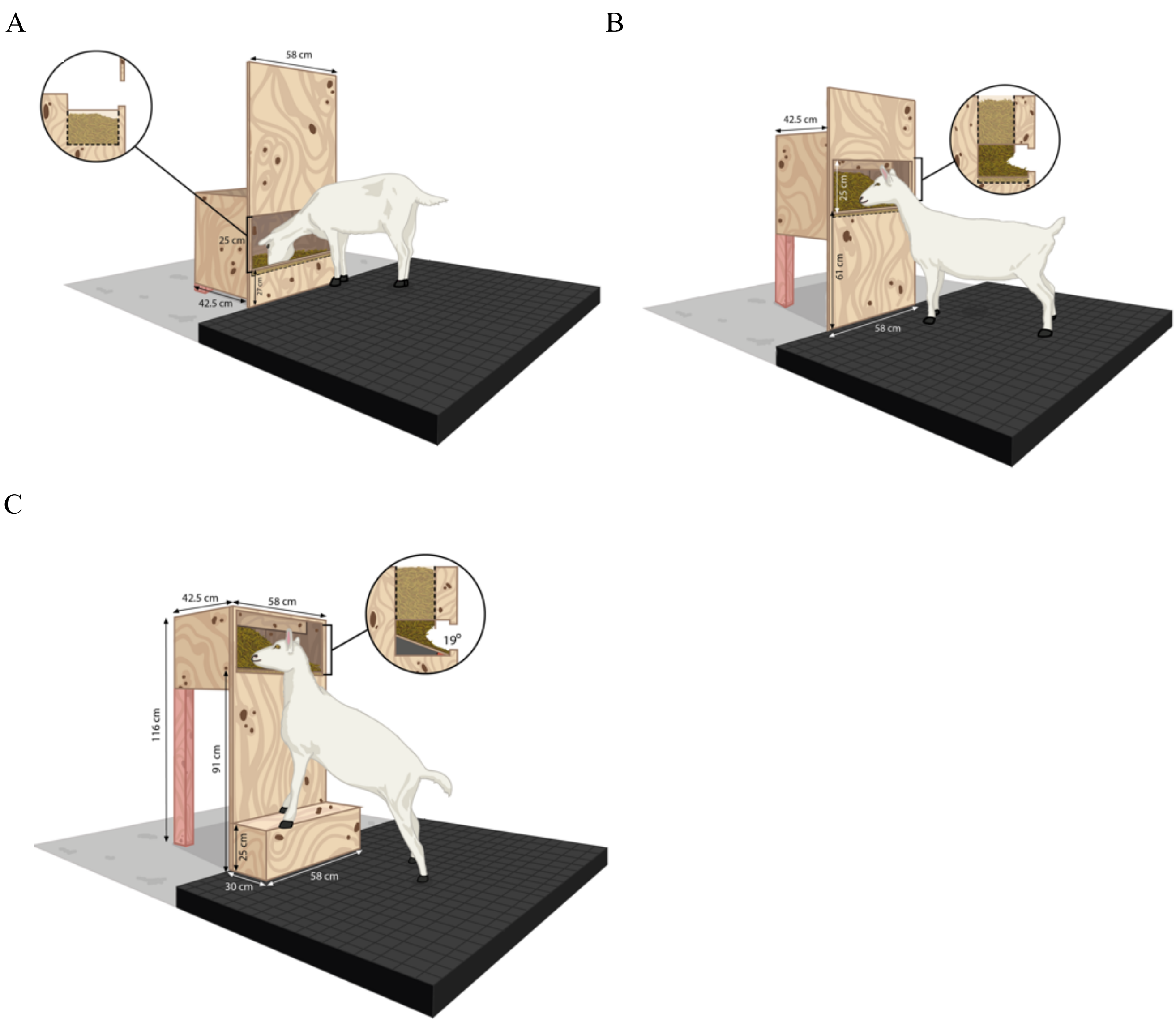


Figure 5.2. Detailed schematics for the three feeders used in the test pen.
A) Floor-level (goat's head is lowered to the ground when feeding to mimic grazing; feeder opening 27 cm from pen floor; feed table at hoof-level); B) Head-level (goat's head is level and parallel to the pen floor when feeding to mimic browsing; feeder opening and feed table 61 cm from pen floor); C) Elevated-level (goat's head and body is angled upward with the front two hooves standing on a raised wooden step attached at the base of the feeder, designed to mimic browsing; feeder opening 91 cm from pen floor; feed table angled at 19°). All feeders were fitted with a wooden frame through which the goats could access feed. For the floor-level feeder the wooden frame also acted as a neck-rail, similar to that used in studies of feeding behavior (Nordmann et al., 2011) and on some commercial farms.



5.2.2 Experimental design

Following 24 d in the home pen, individual preference for feed bunk height was tested over 10 d; on the first day, all goats were moved as a group to the test pen for 24 h of habituation. The test pen was identical to the home pen except that all three feeder heights were offered simultaneously. Goats were able to choose which feeder to feed from, and could feed alongside other goats if they wished (offering 20 cm of feeding space per goat per feeder). Feed offered in the test pen was identical to the home pen, with each feeder providing *ad libitum* chopped alfalfa silage top-dressed with 0.23 kg/goat of pellets refreshed at 0800 and 1600 each day.

Following the 24 h habituation period in the test pen, all the goats were returned to the home pen and over the next 9 d, three goats were selected each morning before feeding to enter the test pen where they remained for 24 h. Goats were selected pseudo-randomly such that all goats entered the test pen as a triad at least twice, but no goat remained in the test pen for two consecutive days and all triads were unique. The order of feeder heights presented from left to right was changed each morning; order was randomized such that each combination was presented at least once and no more than twice over the 9 d testing period. At each feeding, feed refusals from inside each feeder were collected and weighed to calculate feed intake. Any feed that fell out of the feeder was collected from a tray that was placed underneath each feeder under the metal grating of the pen and added to the total refusals calculation. Samples of offered feed from each feeder height were collected daily. All samples were frozen prior to nutrient analysis (Hill Laboratories, Hamilton, New Zealand). Nutritional content of silage offered did not differ among floor-level (DM: 41.8 ± 1.7%, CP: 18.5 ± 1.0% DM, ADF: 34.7 ± 2.6% DM, NDF: 43.7

± 3.6% DM, and ME: 8.9 ± 0.5 MJ/kg DM), head-level (DM: 41.9 ± 1.8%, CP: 18.7 ± 1.0% DM, ADF: 34.4 ± 2.6% DM, NDF: 42.9 ± 3.3% DM, and ME: 9.0 ± 0.5 MJ/kg DM) and elevated-level (DM: 42.0 ± 1.9%, CP: 18.8 ± 0.7% DM, ADF: 34.0 ± 2.0% DM, NDF: 42.6 ± 2.7% DM, and ME: 9.1 ± 0.4 MJ/kg DM) feeders over the duration of the experiment.

5.2.3 Behavioral measures

Behavior at each feeder was recorded using video cameras (DS-2CD2432F-I(W), HikVision, Zhejiang, China) attached to a HikVision NVR (DS-7732N1-14/16P, HikVision, Zhejiang, China). Goats were colour marked on their back (Tell Tail paint, FIL NZ Ltd, Mount Maunganui, New Zealand) to identify individuals for behavioral observations on video recordings. One goat of each triad was randomly selected as the focal animal for observation on each day using a random number generator, resulting in a total of 9 focal goats; no goat was a focal animal more than once. Feeding time at each feeder height (i.e. muzzle of the goat was inside the feeder) and the total number of displacements at the feeder (i.e. the number of times the feeding focal goat physically displaced another goat from the feeder + the number of times the feeding focal goat was physically displaced from the feeder by another goat) were continuously recorded for 24 h for each focal goat. Since a goat needed to be present at the feeder to be involved in a displacement event, we report the number of displacements at each feeder height as a ratio of feeding time at that particular feeder height (i.e. number of displacements per min of feeding time). Feeding rate was calculated from total feed intake and feeding time. When the goat removed its muzzle from the feeder for longer than 2 s, a new visit was counted, and we recorded the total number of feeding visits for each goat.

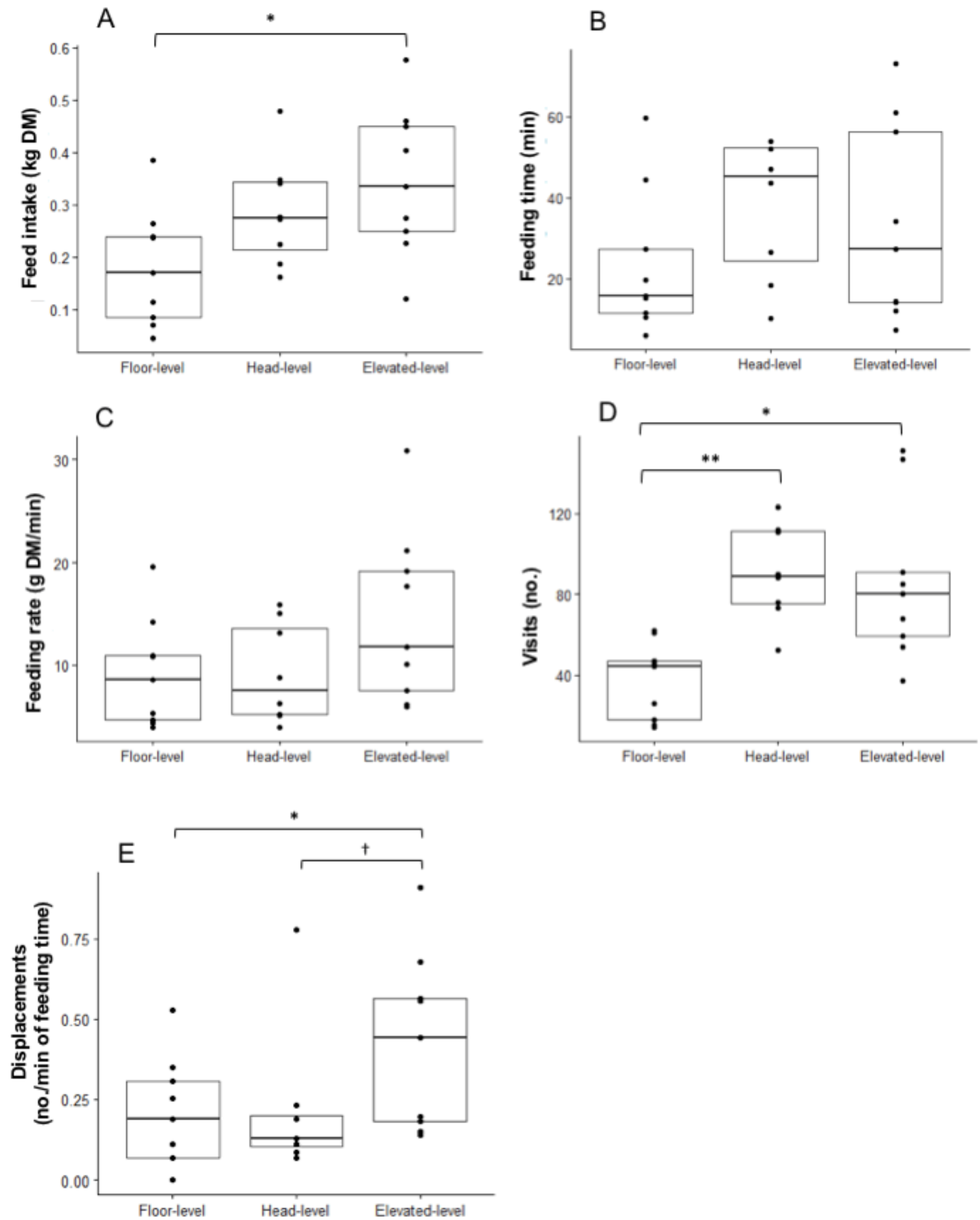
5.2.4 Statistical analysis

All statistical analyses were performed with SAS (version 9.4; SAS Inst. Inc., Cary, NC) using goat or triad as the experimental unit. All the variables were screened using the UNIVARIATE procedure using box, distribution and probability plots and confirmed for normality. Feed intake for each triad over the 24 h observation period was calculated on a DM basis and averaged per goat (kg DM). Total feeding time (min), feeding rate (g DM/min), number of visits (no.), and number of displacements after adjusting for feeding time (no./min of feeding time) were summarized for each focal goat for the 24 h period. All outcome variables were analyzed in a mixed model with the fixed effects of feeder height (floor-, head- and elevated-level), body weight (average weight of the triad for the feed intake variable; focal goat weight for behavior variables), and feeder presentation order (6 combinations). The covariates body weight and feeder presentation order were dropped from the model if $P > 0.1$. Group was specified as a random effect. Treatment differences between all pairwise comparisons of feeder heights were tested using a Bonferroni adjustment. Results are reported as least squares means and SE. Significance was set at $P \leq 0.05$ and tendency at $0.05 < P \leq 0.1$.

5.3 Results

Feed intake (kg DM) increased with increasing feeder height ($F_{2,16} = 4.42$; $P = 0.03$), such that intake was highest at the elevated-level compared to the floor-level but did not differ between elevated- and head-level feeders or between head- and floor-level feeders (**Figure 5.3a**). Feeding time (min) did not vary with feeder height ($F_{2,16} = 1.39$; $P = 0.3$; **Figure 5.3b**).

Figure 5.3. Feeding and social behavior at each feeder height.
Measures over a 24 h observation period when goats were housed in triads (n = 9 triads) and offered one of each feeder height (floor-level, head-level, and elevated-level). Results are shown separately for A) dry matter intake (kg DM), B) feeding time (min), C) feeding rate (g DM/min), D) visits to the feeder (no.), and E) displacements (no./min of feeding time). Significant differences between feeder heights are indicated by ** ($P \leq 0.01$) and * ($P \leq 0.05$), and tendencies are indicated by † ($0.05 < P \leq 0.1$). The median is indicated by a solid black line.



Feeder height tended to affect feeding rate (g DM/min) ($F_{2,15} = 2.7$; $P = 0.1$), such that goats ate more quickly when using the elevated-level feeder compared to head-level and floor-level feeders (**Figure 5.3c**). The number of visits to the feeder was affected by feeder height ($F_{2,16} = 6.7$; $P < 0.01$), with the lowest number of visits at the floor-level feeder compared to head- and elevated-level feeders (**Figure 5.3d**). Feeder height also affected the number of displacements (no./min of feeding time) at each feeder ($F_{2,16} = 4.28$; $P = 0.03$), with the greatest number of displacements at the elevated level (**Figure 5.3e**).

5.4 Discussion

This study examined how providing goats a choice between different feeding heights can affect feeding and social behavior. We found that goats consumed more feed, at a higher feeding rate, from the elevated feeders. Goats were least likely to visit the floor-level feeder and were most likely to competitively displace one another at the highest feeder, suggesting that the animals were motived to feed from higher locations. In contrast with the findings of the current study, Dziba et al. (2003) found no difference in DMI when foliage branches of different heights were offered indoors; however, this finding should be viewed with caution given that goats were only observed for a 3-min period.

Consistent with the results of our study, Dziba et al. (2003) found that intake rate increased with increasing feeding height. Intake rate was primarily driven by increased bite size at higher feeding heights. Neither study found differences in feeding time at higher feeder heights. Increased intake without changes in feeding time at the elevated-level feeder in the current study may be explained by the increased feeding rate. Other work has shown that goats generally consumed more DM when foliage is hanging compared to in a trough, with no differences in feeding time (Van et al., 2005).

An increase in bite rate at higher feeding heights may be explained by the natural browsing behavior and oral morphology of goats. In their natural environment, goats will typically browse on shrub species that have tender small leaves; this type of foraging requires successive bites to sever the leaves rather than in a single bite (Mellado et al., 2007). Goats have a narrow mouth, a mobile upper lip and shorter jaws (relative to many other ruminant species) that allow them to be highly selective while foraging and chew faster (Pérez-Barbería and Gordon, 1999; Mellado et al., 2007). Thus feeding at increased feeding heights may promote natural selective foraging behavior, resulting in increased intake per unit time.

We also observed more displacements at the elevated feeder. Other studies have reported social behavior of indoor goats that could feed from platforms. Aschwanden et al. (2009) housed goats in dyads where one goat could feed at ground level and the other by standing on top of a platform ranging from 25 cm to 80 cm high. The rate of agonistic interactions was lower on higher platforms (50 cm and 80 cm), perhaps because these platforms increased the physical distance between feeding goats and provided limited standing room making it difficult for multiple goats to stand together. In our study, the elevated-level feeder could be accessed by multiple goats, all from a stable standing position with limited risk of falling. However, if all three goats were at a single feeder, this resulted in just 20 cm of feeding space per animal, below the suggested recommendation of 50 cm for hornless goats (Loretz et al., 2004). This feeding environment may have inflated the number of displacements observed at each of the feeders in our experiment; we suggest that elevated feeders do not increase displacements *per se*, but rather that the increased competition reflects the motivation to access this limited resource. This finding highlights the importance of offering adequate space to allow for all individuals to feed when and where they want at the feed bunk; ample feeding space may be especially important in cases where goats are more likely to engage in aggressive behavior, such as if goats are horned or if goats are mixed as adults (Loretz et al., 2004; Aschwanden et al., 2008b).

An elevated feeder allows for quadrupedal browsing, a natural foraging behavior by goats. When managed on rangeland, Angora goats spent a third of their time grazing and the remaining time browsing (Askins and Turner, 1972). Sanon et al. (2007) reported that goats browsed for more than 60% of their feeding time during the rainy season, and for more than 90% of their feeding time during the dry season when the herbaceous component began to decline (Sanon et al., 2007). In non-pregnant and non-lactating goats, browse comprised the majority of reported dietary intake (Mellado et al., 2005). One study showed that the majority of browsing time was spent in the quadrupedal position (Pfister et al., 1988). These authors reported 46, 20 and 44% of foraging time was spent in the quadrupedal position during the mid-dry, late-dry and wet seasons, respectively. Goats spent as much as 8% of their foraging time in the bipedal position during the wet season, despite abundant forage sources in lower strata (Pfister et al., 1988). We suggest that this type of natural foraging behavior should be considered when designing indoor commercial feeding systems.

The feeders in our experiment mimicked a commercial feeding system allowing animals to move freely along the feed bunk. This design may permit greater displacements between feeding goats compared to other commercial feeding systems (Nordmann et al., 2011). Other work investigating modified feed bunk designs showed that the feed table must be raised at least 10 cm to allow for goats to feed in a relaxed posture while also reaching all of the feed in the manger (Keil et al., 2017). Head- or elevated- feeder designs can feasibly be implemented in commercial settings by lowering the pen floor relative to the feed bunk; in fact, some commercial systems have implemented such designs (**Figure 5.4**).

Figure 5.4. Schematic drawing of a head- or elevated-level feed bunk design used on some commercial farms.
Primary features include a driving alley with a ramp up to an elevated feed bunk, and the pen floor lowered relative to the feed bunk. Goats are able to feed with their head and feet raised. Image design based on a commercial farm in Ontario, Canada (Henry & Anja van der Vlies and family).

A notable design feature of our feeders was the use of a wooden frame above the goat's head, which was intended to reduce potential distractions outside the pen. While many commercial farms use a wooden frame as a neck rail, it is less common to have a solid frame above the goat's head. We recognize that this design feature may have had some influence on the feeding behaviour of the goats. We encourage future work to develop and test different designs of elevated feeders that consider ease of feed delivery for the farmer, and minimize competitive interactions and maximize appropriate feeding posture and comfort for the goats.

5.4.1 Conclusions

In conclusion, goats will choose to eat from a variety of feeder heights but show a preference for an elevated feeder height. Dairy goats may benefit from the availability of raised feeders that promote natural browsing behaviors.

Chapter 6: Competitive feeding behaviour of dairy goats is affected by feeder height and personality traits

A version of this chapter has been submitted for publication: Neave, H. W. and G. Zobel. Competitive feeding behaviour of dairy goats is affected by feeder height and personality traits. PLoS ONE. (*in review)*.

6.1 Introduction

The natural feeding behavior of goats includes a mixture of grazing and browsing, involving selection of forages at various heights (Lu, 1988; Goetsch et al., 2010). Free-ranging goats will often be seen feeding at head-level (Lu, 1988) or with a bipedal stance, reaching branches high above their heads by rearing onto their hind legs (Sanon et al., 2007; Tölü et al., 2012). Goats have also been reported to engage in 'aerial grazing' where they climb into and browse in trees (El Aich et al., 2007). These feeding postures allow goats to feed on a variety of grasses, shrubbery and woody stems (e.g. browse materials) (Ngwa et al., 2000). Studies have reported that goats in some situations will include high proportions of browse in their diet (98%, Egea et al., 2014; 70%, Askins and Turner, 1972; 52%, Sanon et al., 2007). In contrast, commercial indoor-housed dairy goats are fed almost exclusively at ground-level, and are rarely offered opportunities to feed using postures typical of browsing (see review by Zobel et al., 2018). In Chapter 5 of this thesis, I found that goats ate more from an elevated feeder that mimicked a browsing posture than from feeders at floor- or head-level, suggesting that commercial dairy goats may benefit from feeding from an elevated surface.

The feed bunk is a place of high competition; physical displacements, frontal clashing, chasing, and head butting are common, especially when space is limited (Jørgensen et al., 2007). Modifications to the design of the feed rail (Nordmann et al., 2011) or providing head partitions (Nordmann et al., 2015) can reduce agonistic behaviors during feeding. Allowing goats to feed at different levels relative to the ground has also been successful in decreasing competitive feeding behaviors. For instance, goats provided with an elevated platform to feed from had decreased agonistic behaviors and increased feeding time (Aschwanden et al., 2009a), and longer feeding bouts with fewer interrupted resting bouts (Aschwanden et al., 2009b). These studies provide some evidence that elevated feeding can reduce competition, but these studies did not directly manipulate the feeding posture of the goat to mimic natural grazing and browsing positions. An elevated feeding posture (with head and feet raised) may either promote or reduce competition compared to a feeding posture with head lowered to the ground. For instance, in Chapter 5 of this thesis I found that goats were displaced more often from an elevated feeder even when ample feeding space was provided from a floor-level and head-level feeder; this increase in competition at the elevated- compared to floor-level feeder may be related to a natural motivation to feed in such browsing positions (Zobel et al. 2018). Alternatively, an elevated feeding posture may reduce competition by allowing individuals to feed in a relaxed position (Keil et al., 2017) and allow for visual monitoring of others with an unrestricted backward view while feeding (Nordmann et al., 2011). The types of competitive behaviors expressed at different feeder heights may also differ (e.g. aggression while feeding that may or may not result in displacement from the feeder, or agonistic behaviors around the feeder but not while feeding); given that individual goats varied in how much displacement behavior they expressed (in Chapter 5), there is likely similar variability in the types of competitive behaviors performed around the feeder.

Individual variability in feeding behavior is seen across a variety of ruminant species, and reflects the individuality of the animal and how it is responding to the environment (see Chapter 2 of this thesis; Neave et al., 2018b). For instance, feeding time is variable among individual goats, particularly when space is limited. Jørgensen et al. (2007) showed that 30% of goats reduced their feeding time by more than 40% when space was decreased at the feeder, and a few goats reduced their feeding time by more than 80%. This variability suggests that goats respond to challenges differently. This individual variability in feeding behavior may be related to personality traits of the individual (Chapter 2 of this thesis; Neave et al., 2018b). Miranda-de la Lama et al. (2011) found that goats with different personalities during agonistic or affiliative interactions (i.e. 'aggressive', 'affiliative', 'passive' and 'avoider') differed dramatically in feeding success; goats that avoided social interactions had the highest feeding time while passive goats had the lowest feeding time. This work identified goat personalities during a social setting, but other personality traits of farm animals such as fearfulness are most commonly measured as individual responses to novelty or potentially fearful situations (Forkman et al., 2007). There is little understanding of how the frequency and expression of competitive feeding behaviors is related to personality traits measured using standardized individual novelty and fear tests.

The objectives of this study were to determine whether feed bunk height affects competitive feeding behaviors, and if personality traits can account for some of the individual variability found in competitive feeding behaviors at different feed bunk heights. In contrast to the study in Chapter 5 of this thesis, we provided goats with limited space at the feed bunk to create a more competitive feeding environment. Under these feeding conditions, we hypothesized that competitive behaviors would be highest at the floor-level feeder compared to the head- and elevated-level feeders, and that a fearful personality trait would be associated with fewer initiations and more recipients of competitive interactions. We also hypothesized that the influence of personality traits would be dependent on feed bunk height, with a stronger influence occurring at the floor-level feeder where competition was expected to be greatest.

6.2 Materials and methods

This study was conducted from July to September 2016 at the Ruakura Research Centre in Hamilton, New Zealand. The animals, management and feed bunk designs were similar to our previous study (Neave et al., 2018c; Chapter 5) so we briefly describe these methods below. All procedures were approved by the Ruakura Animal Ethics Committee, Hamilton, New Zealand (AE13930) and by the University of British Columbia Animal Care Committee, Vancouver, Canada (A16-0213).

6.2.1 Animal management and diet

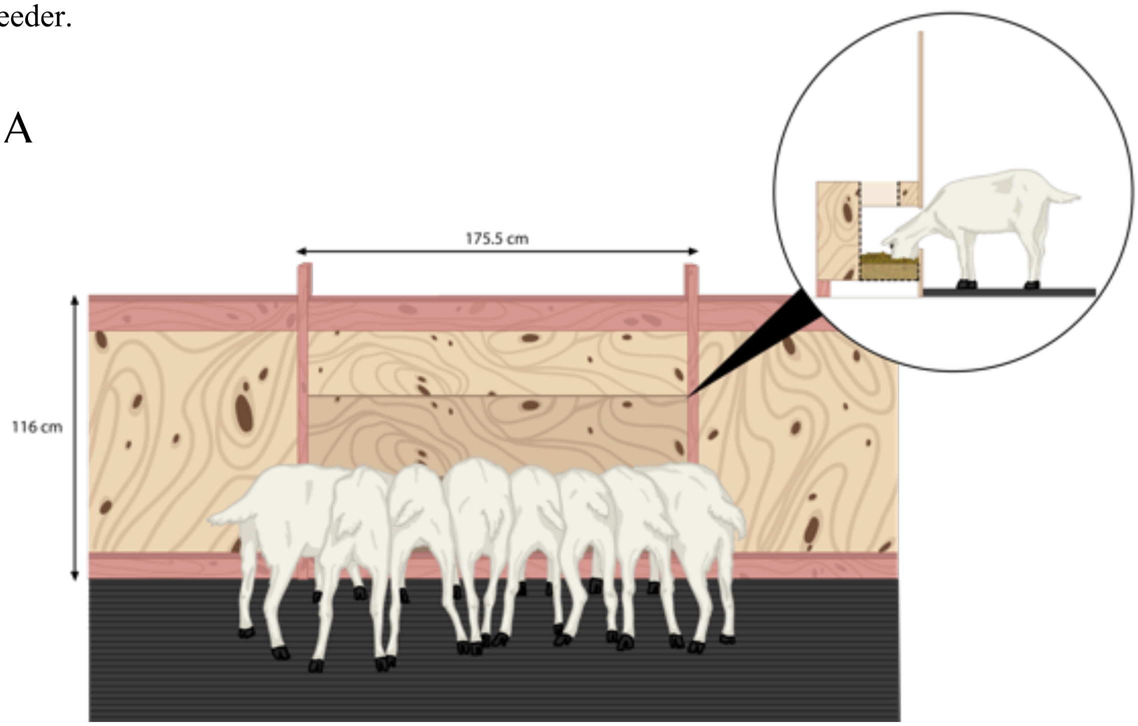
Thirteen non-lactating, nulliparous, and non-pregnant dairy goats (approximately 13 mo of age) were enrolled in this study. Goats were weighed at the beginning and end of the experiment, with an average ± SD weight of 37.6 ± 3.6 kg. Goats were previously housed on pasture as a single group and were transitioned into the indoor facility over a 6 d period (1 d of indoor housing at night only, followed by 5 d of continuous indoor housing and use of the feeding facility). Goats were housed together in one pen measuring 11.5 x 3.0 m (offering 2.65 m^2/goat) with plywood walls. Half of the pen contained a plywood box (11.5 x 1.5 m) bedded with woodchip (40 cm deep) and the other half of the pen had metal grating flooring (for details see Neave et al., 2018c; Chapter 5). Flooring was power washed daily and woodchip bedding was topped up once per week prior to afternoon feeding. Goats received fresh water from a wall-mounted waterer and hay was provided and replenished daily at 1200 in two hay racks at either end of the pen. Goats were fed *ad libitum* alfalfa silage (Fibre Protect, Dunsan Horse Feeds Ltd, New Zealand) top-dressed with 3 kg of pellets (0.23 kg/goat; Fibre Grow, Dunsan Horse Feeds Ltd, New Zealand) from a feed bunk (design described below); feed was replaced twice daily at 0800 and 1600.

6.2.2 Feed bunk design and behavioral measures

For the duration of the experiment, feed was provided each day in one of three feeder heights: floor-level (the goat's head is lowered to the ground when feeding; feeder opening 27 cm from pen floor), head-level (the goat's head is level with the rest of its body when feeding; feeder opening 61 cm from pen floor) or elevated-level (the goat's head and body is angled upward when the front two hooves are standing on a 25 cm high wooden step attached at the base of the feeder; feeder opening 91 cm from pen floor) (see **Figure 6.1).**

Figure 6.1. Schematics of feeder designs offered in the home pen.
(A) Floor-level, (B) head-level, and (C) elevated-level feeders offered to goats (n = 13) housed together and fed from a single feeder providing restricted feeding space of 13.5 cm/head. One of each feeder height was offered each day. Inset shows the side-profile of head positioning at each feeder.

A



B

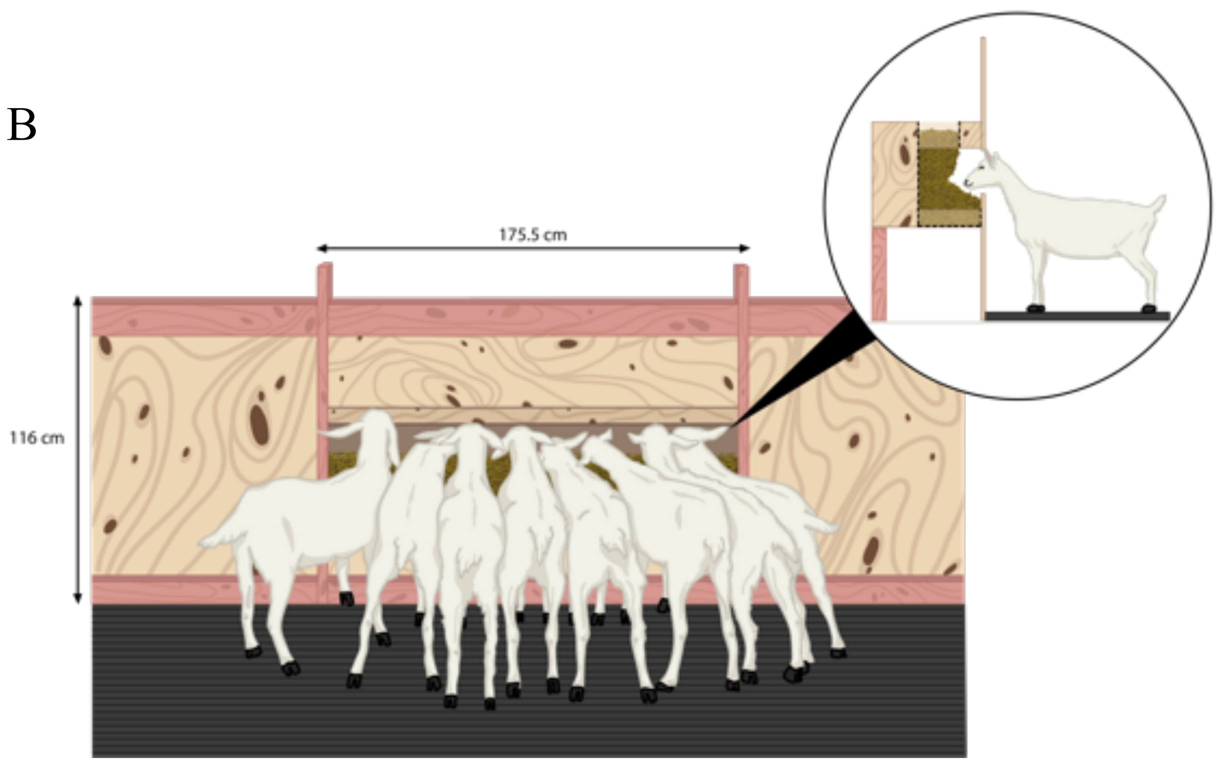
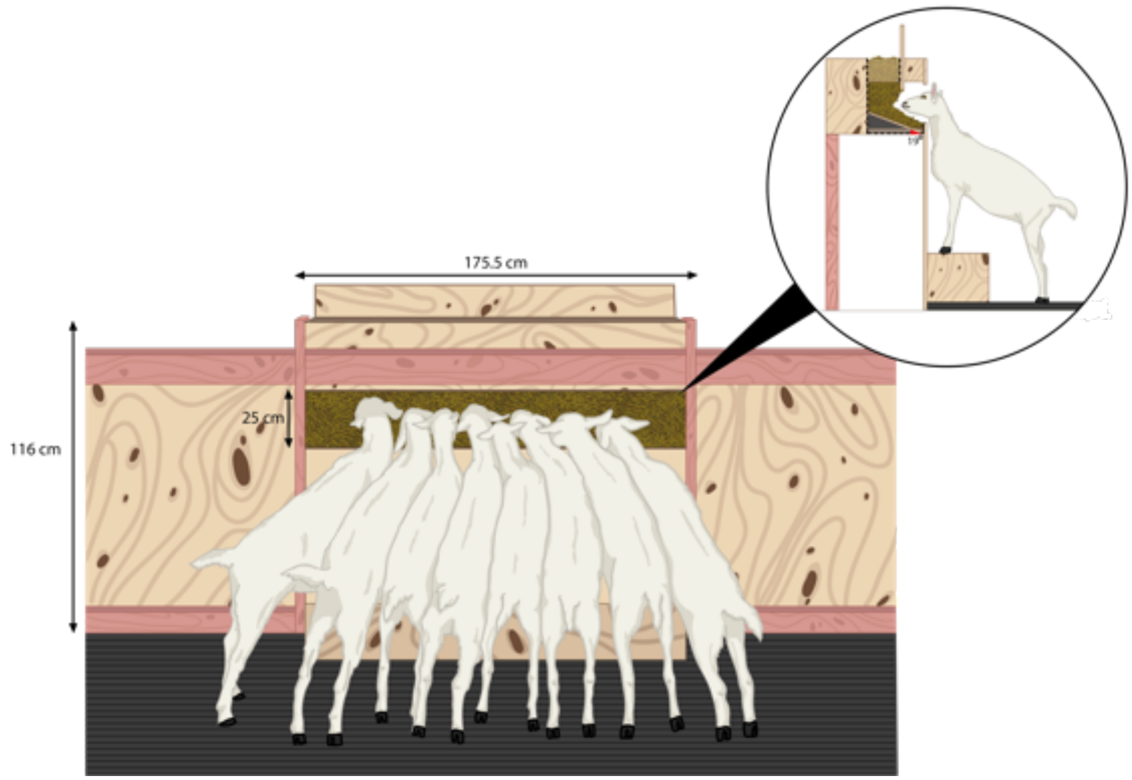


Figure 6.1 (continued). Schematics of feeder designs offered in the home pen.

C



The base of the elevated-level feeder was angled at 19 degrees, and the head-level and elevated-level feeders had two thin wooden strips on the base to prevent feed from sliding out of the feeder. Each feeder was centered along the length of the pen and was intentionally designed to create a competitive feeding environment, providing 13.5 cm of feed bunk space per goat. Recommendations in New Zealand for feed bunk length typically are 40 cm/head for milking goats (MPI, 2018). Each morning at 0800, the feeder height was changed to a different height and remained for 24 h. Order of feeder height presentation was pseudo-randomized such that the same feeder height was never presented for two consecutive days, for a total of 4 repetitions of each feeder height over 12 d.

Goats were habituated to this feeding management procedure for 18 d (6 presentations of each feeder height) before behavioral data collection began over 12 consecutive days. Feeding and competitive behaviours were recorded for 4 replications of each feed bunk height using video cameras (DS-2CD2432F-I(W), HikVision, Zhejiang, China) mounted above the feed bunk and which were recorded using a HikVision NVR and software (DS-7732N1-14/16P, HikVision, Hangzhou, China). Behaviors were coded from video according to an ethogram (**Table 6.1**) during the first 90 min after fresh feed delivery in both the morning and the afternoon. Competitive behaviors were only recorded at and immediately behind and to the sides of the feeder.

Samples of offered feed were collected daily. All samples were frozen prior to nutrient analysis using wet chemistry (Hill Laboratories, Hamilton, New Zealand). Nutritional content of silage at each feed bunk height over the experiment was: floor-level (DM: 43.3 ± 1.0%, crude protein (CP): 17.7 ± 0.5% DM, acid detergent fibre (ADF): 35.4 ± 2.5% DM, neutral detergent fibre (NDF): 43.6 ± 3.4% DM, and metabolizable energy (ME): 8.8 ± 0.3 MJ/kg DM), head-level (DM: 42.7 ± 0.7%, CP: 19.1 ± 0.76% DM, ADF: 31.5 ± 2.0% DM, NDF: 39.1 ± 1.8% DM, and

ME: 9.7 ± 0.3 MJ/kg DM) and elevated-level (DM: 42.5 ± 0.3%, CP: 18.4 ± 0.6% DM, ADF: 32.7 ± 1.6% DM, NDF: 39.9 ± 2.0% DM, and ME: 9.4 ± 0.2 MJ/kg DM). Nutritional content of pellets was 86.4 ± 0.4 % DM, 16.9 ± 0.8 % CP, 19.5 ± 0.99 % ADF, 34.5 ± 1.9 % NDF, and 11.6 ± 0.07 MJ/kg DM.

Table 6.1. Ethogram of feeding and competitive behaviors.
Behaviours were scored from video during the first 90 min following fresh feed delivery at 0800 and 1600. Goats (n = 13) were offered one of three feeder heights each day: floor-level, head-level and elevated-level. Actor and reactor goats refer to the initiator and recipient of the behavior, respectively.

Behaviour	Description
Feeding	Individual is standing at the feeder with head in trough
Waiting to gain access to feeder	Head and body oriented towards the feed barrier, standing behind other goats, or at the side of the feed bunk, on the metal grating. Goat may move behind other feeding goats with head/body oriented toward feed bunk.
Feeding aggression (with or without displacement)	Forced pushing of the head towards the head or body of another goat while feeding. Record as displacement if reactor goat stops to feed. Record actor and reactor goats.
Pushing to gain access to feeder (with or without displacement)	Forward motion that exerts pressure on another goat or multiple goats in order to gain access to the feed bunk. Can occur from behind by pushing in between two individuals or can occur from the side by pushing against one individual. Record as displacement if neighbor goat stops to feed. Record actor and reactor goats.
Clash	Goat is rearing onto the hind legs with the head and torso twisted followed by descending forcefully onto the front legs delivering a powerful strike forward and downwards reaching the head of another goat. Cannot occur while at the feeder. Record actor and reactor goats.
Butting	Forced pushing of the head towards the head or body of another goat (not during feeding). Cannot occur while at the feeder. Record actor and reactor goats.
Chasing	Moving quickly after another goat that tries to escape (does not require physical contact). Cannot occur while at the feeder. Record actor and reactor goats.

6.2.3 Personality tests

Goats were tested in a series of standardized personality tests that were chosen to assess behavioral responses toward different novel situations (novel environment and novel object), and toward putatively fearful situations (sudden and loud movement inducing a startle response, and appearance of a dog). These are the most common tests of fear in farm animals, but can also measure motivation to explore (Forkman et al., 2007; Perals et al., 2017). Goats were individually exposed to 2 novelty tests (novel environment and novel object) followed by 2 fear tests (startle and dog), with one test performed each day. Tests were always done in the same order, but goat order of entry into each test was randomized. Goats were tested beginning 6 d after habituation (repetition 1) to their indoor home pen, and retested 4 wk later (repetition 2).

Procedures for the novelty tests (novel environment and novel object tests) were adapted from other work in goats (Briefer et al., 2015; Nawroth et al., 2017), and procedures for the fear tests (startle and dog tests) were adapted from work in sheep (Désiré et al., 2004; Lee et al., 2016). All tests were conducted from 1130 to 1400 each day in an initially unfamiliar testing arena (4.89 x 3.5 m) with 2.4 m high plywood walls and cement flooring. Goats were gently led individually from their home pen into the testing arena through a door opening at the front left corner of the arena and the goat remained in the test arena for 5 min. Vocalizations were recorded by two observers seated out of sight outside the arena. All goats were colour marked on their back (Tell Tail paint, FIL NZ Ltd, Mount Maunganui, New Zealand) to identify individuals for behavioural observations. The same video recording system was used as for the home pen. Behaviours during each personality test were recorded following an ethogram (**Table 6.2**). The frequency and duration of behaviours in the startle and dog tests were recorded only during the first 60 s after the occurrence of the stimulus (umbrella opening in the startle test; appearance of dog in dog test);

however, vocalizations and latency to return to the food bucket were recorded for the full 5 min duration of the test.

Table 6.2. Ethogram of behaviors in the personality tests.
Behaviours were scored from video in 2 novelty tests (novel environment, novel object) and 2 fear tests (startle, dog). Goats were tested individually in 1 test per day for 5 min in each test. Tests were repeated 4 wk apart.

Test and behaviour	Description
All tests	
Vocalizations	Any sound emitted from the mouth
Standing	All four feet are stationary. Continue to code as standing if just one foot moves forward.
Walking	At least two front feet move forward from initial standing position.
Rearing	Goat reared with 1 or both front hooves on wall of arena
Tail raised	Tail is raised in vertical position or beyond vertical so that tip of tail is toward spine
Novel environment test	
Exploring	Sniffing or licking floor or walls of arena. Head needs to be lowered to the floor or muzzle in contact with wall.
Novel object test	
Far	Standing or walking more than one body length away from object
Close	Standing or walking within one body length away from object
Touching	Any part of body is in contact with object
Attentive	Head oriented towards the object without touching
Climbing	Goat standing with 2 or 4 hooves on object
Startle and dog tests	
Approach umbrella or dog	Standing or walking in area between food bucket and umbrella or dog (more than 0.5 m in front of food bucket)
Touch or eat from food bucket	Any part of body is in contact with food bucket, including muzzle inside food bucket.
Attentive toward umbrella (startle test only)	Head oriented towards the umbrella (only recorded after umbrella opens)
Attentive toward dog door (dog test only)	Head oriented towards the dog door (only recorded after dog door opens)

The novel environment test consisted of exposure to a barren unfamiliar arena. The day after the novel environment test, goats were re-introduced individually to the arena for another 5 min with a familiar red 2 L bucket containing 2 kg of pellets (the same pellet provided at feeding time described above) placed at the center of the arena. After all goats had re-entered the arena individually, all goats were brought into the arena for another 5 min and pellets were scattered along the floor of the arena. This procedure was done to habituate the goats to the arena to ensure that the responses toward being in an unfamiliar arena were minimized as much as possible in the following personality tests; no behaviors were recorded during this second novel environment test.

The first novel object repetition consisted of a 1 m high platform with plastic slatted flooring (1.33 x 1.95 m) placed in the back right corner of the testing arena. The platform had a 30-degree ramp that allowed the goat to climb on top of the platform. The second novel object repetition (4 wk after the first) consisted of two wooden electrical spools (each 1 m-diameter, 0.5 m-high) placed side-by-side in the back right corner of the arena; the goat could climb on top of the spools if she chose.

Two days after the completion of the novelty tests, goats were exposed over two consecutive days to the 2 fear tests. In the startle test, a closed black 1 m diameter umbrella was placed through a hole in the wall 1 m above the floor of the upper centre quadrant of the arena. A red familiar bucket of pellets (1 kg) was placed at the end of the umbrella tip. At the moment the goat either placed her head in the food bucket or touched the umbrella, the umbrella was opened. The umbrella remained open until the end of the test. If the goat did not touch either the food bucket or the umbrella after 5 min, the umbrella was opened regardless of the location of the goat and the response recorded for an additional 1 min (2 goats in the second repetition). The same umbrella was used in the first and second repetitions to ensure responses were related to the fear of the sudden visual and auditory stimulus rather than toward a new object.

In the dog test, a dog (breed: New Zealand Heading Dog) was hidden behind a sliding door in the wall opposite to where the goat entered the arena, and a red familiar bucket of pellets (1 kg) was placed at the centre of the arena. At the moment the goat placed her head in the food bucket, the sliding door opened to reveal the dog for 5 s but the dog was not permitted to enter the arena or interact with the goat. Once the sliding door closed, the dog remained behind the wall, but was silent. If the goat did not touch the food bucket after 5 min, the dog door was opened regardless of the location of the goat and the response recorded for an additional 1 min (1 goat in the first repetition, 4 goats in the second repetition). The same dog was used in the first and second repetitions. The dog test was performed last to ensure that potential carry-over effects of exposure to the dog did not affect responses to subsequent tests.

6.2.4 Statistical analysis

Total frequency of competitive behaviours (feeding aggression, pushing to gain access to feeder, butting, chasing, and clashes) and total duration of feeding behaviors (feeding, and waiting to gain access to feeder) for each goat were summed for each day (i.e. the two 90-min observation periods at each feeding) at each feeder height. We distinguished between the frequency of initiating (actor) and receiving (reactor) each of the competitive behaviours. Butting, chasing, and clashes were summed to reflect total agonistic behavior for each of actor and reactor (following Aschwanden et al., 2009). Reported values for competitive feeding behaviors use the units of frequency or duration per day for simplicity, however, it should be noted that these are the sum of observations over the two 90-min feeding periods. All variables were screened using the

UNIVARIATE procedure of SAS (version 9.4; SAS Institute Inc., Cary, NC, USA) using box, distribution and probability plots. Feeding and competitive behaviour measures were normalized as required using a log10 transformation. Total duration or frequency of behaviors in each of the personality tests were calculated for each goat, and averaged across the two test repetitions. The same behavioral measures (e.g. vocalizations in each of the tests) that were significantly positively correlated across tests (using the CORR procedure of SAS) were also averaged across the novelty tests (vocalizations, standing inactive, rearing, climbing) and across the fear tests (vocalizations, latency to return to food bucket, touching, and eating from food bucket) following the procedure in Neave et al., 2018a; Chapter 3). This resulted in a total of 20 measures reflecting behavioural responses in the novelty tests (9 measures) and fear tests (11 measures).

Underlying personality traits were identified using a principal component analysis (PCA). Behavioural measures were log10 or square-root transformed as required to achieve normality. To account for the high dimensionality created by a high number of variables compared to the number of subjects, a sparse PCA using R (version 3.5.2; R Core Team, 2018) with the MixOmics package from the project package BiocManager (Morgan, 2018) was used. Multiple iterations of the sparse PCA were conducted to determine the least number of input variables and least number of retained principal components to maximize the cumulative variance explained; this resulted in the selection of 10 input variables and 4 principal components, explaining a cumulative 62.6% of the variance. Input variables were standardized to mean = 0 and unit variance = 1. Variables with non-zero values were considered have a high loading on the principal component.

A leave-one-out cross-validation procedure (total 13 iterations) was conducted for each of the 4 principal components to verify stability. For each component, the number of iterations that each variable appeared with a high loading was tallied and compared to the original modeled component. A variable with a high (non-zero) loading on the original modeled component and with 9 or more iterations (> 70%) with a high loading in the cross-validation procedure indicated good stability (i.e. factor consistently had similar loadings across multiple iterations). A variable with zero loading on the original modeled component and 4 or fewer iterations (< 30%) with high (non-zero) loadings in the cross-validation procedure indicated good stability. The original modeled components are hereafter referred to as Factor 1, Factor 2, Factor 3 and Factor 4.

To test whether feeder height and personality traits affected competitive feeding behaviours, and whether the effect of personality traits was dependent on feeder height, we used a mixed repeated measures model (PROC MIXED; SAS version 9.3; SAS Inst. Inc., Cary, NC, USA) with goat as the experimental unit. Response variables were the total frequency of being an actor or reactor in each of feeding aggression, pushing to gain access to the feeder and total agonistic behaviors, as well as feeding time and bouts, and waiting time and bouts to gain access to the feeder. The model included the fixed effects of factor score (Factor 1, Factor 2, Factor 3, and Factor 4), feeder height (floor-, head- and elevated-level), the interaction of each factor score with feeder height, and body weight. Initially, repetition of feeder height (1 to 4) was included, but since it was not significant for any outcome measure, measures were averaged for each feeder height for the final models. Feeder height was a repeated measure with goat as subject and compound symmetry covariance structure. When the main effect of feeder height or interaction term was $P \leq 0.10$, differences between pairwise comparisons of feeder heights, and between slopes of feeder heights for the interaction, were tested using a Bonferroni adjustment and results are reported as t-statistics. All model residuals were verified for normality and homogeneity of variances. Significance was declared at $P \leq 0.05$ and a tendency at $P \leq 0.10$.

6.3 Results

6.3.1 Effect of feeder height on competitive feeding behaviours

The frequency of feeding aggression, pushing to gain access to the feeder, and total agonistic behaviors at each feeder height are shown in **Figure 6.2**. There was large individual variability in the expression of competitive behaviors; goats ranged from an average of 3 to 60 events of feeding aggression, 6 to 41 events of pushing to gain access to the feeder, and 10 to 75 events of agonistic behavior. Goats were also variable in feeding time (ranging from 21 to 88 min each day) and in time spent waiting to gain access to the feeder (ranging from 3 to 18 min each day). Some of this variability in competitive feeding behaviors was associated with feeder height.

Feeding aggression at the elevated- and head-level feeders was greater than at the floor-level feeder ($t_{1,16} = 4.2$, $P < 0.01$; $t_{1,16} = 6.0$, $P < 0.001$, respectively; **Figure 6.2a**). There was no difference in feeding aggression between elevated- and head-level feeders ($t_{1,16} = 1.8$, $P = 0.27$). Pushing to gain access to the elevated-level feeder was similar to the head-level ($t_{1,16} = 2.1$, $P = 0.15$) and floor-level feeders ($t_{1,16} = 0.3$, $P = 0.78$), but tended to be higher at the head-level feeder compared to the floor-level feeder ($t_{1,16} = 2.4$, $P = 0.08$; **Figure 6.2b**). Total agonistic behaviors at the elevated-level feeder were similar to the head-level ($t_{1,16} = 1.9$, $P = 0.22$) and floor-level feeders ($t_{1,16} = 1.3$, $P = 0.68$), and were highest at the floor-level feeder compared to the head-level feeder ($t_{1,16} = 3.2$, $P = 0.02$; **Figure 6.2c**).

Feeding time was similar between elevated- and floor-level feeders ($t_{1,16} = 0.4$, $P = 1.0$), but feeding time at each of these feeders was lower compared to the head-level feeder ($t_{1,16} = 4.7$, $P < 0.001$; $t_{1,16} = 4.3$, $P < 0.01$, respectively; **Figure 6.2d**). Feeding bouts at the elevated-level feeder was intermediate between floor-level ($t_{1,16} = 2.6$, $P = 0.06$) and head-level feeders ($t_{1,16} =$

2.8, $P = 0.04$; **Figure 6.2e**). Time spent waiting to access the feeder ($F_{1,16} = 1.6$, $P = 0.24$; **Figure 6.2f**) and waiting bouts were similar across feeder heights ($F_{1,16} = 0.35$, $P = 0.71$; **Figure 6.2g**).

Figure 6.2. Competitive feeding behavior of goats at each feeder height.
Behaviours were observed over two 90-min observation periods following fresh feed delivery. Goats (n = 13) were housed together and offered one of each feeder height (floor level, head level, and elevated level) each day. Box-plots are shown separately for (A) aggressive feeding behaviors (no./d), (B) pushing to access feeder (no./d), (C) total agonistic behaviors (no./d), (D) feeding time (min/d), (E) feeding bouts (no./d), (F) time spent waiting to access feeder (min/d), and (G) waiting bouts (no./d). Significant differences between feeder heights are indicated by ** ($P \leq 0.01$) and * ($P \leq 0.05$), and tendencies are indicated by † ($0.05 < P \leq 0.1$). The mean is indicated by a red diamond and the median by a solid black line.

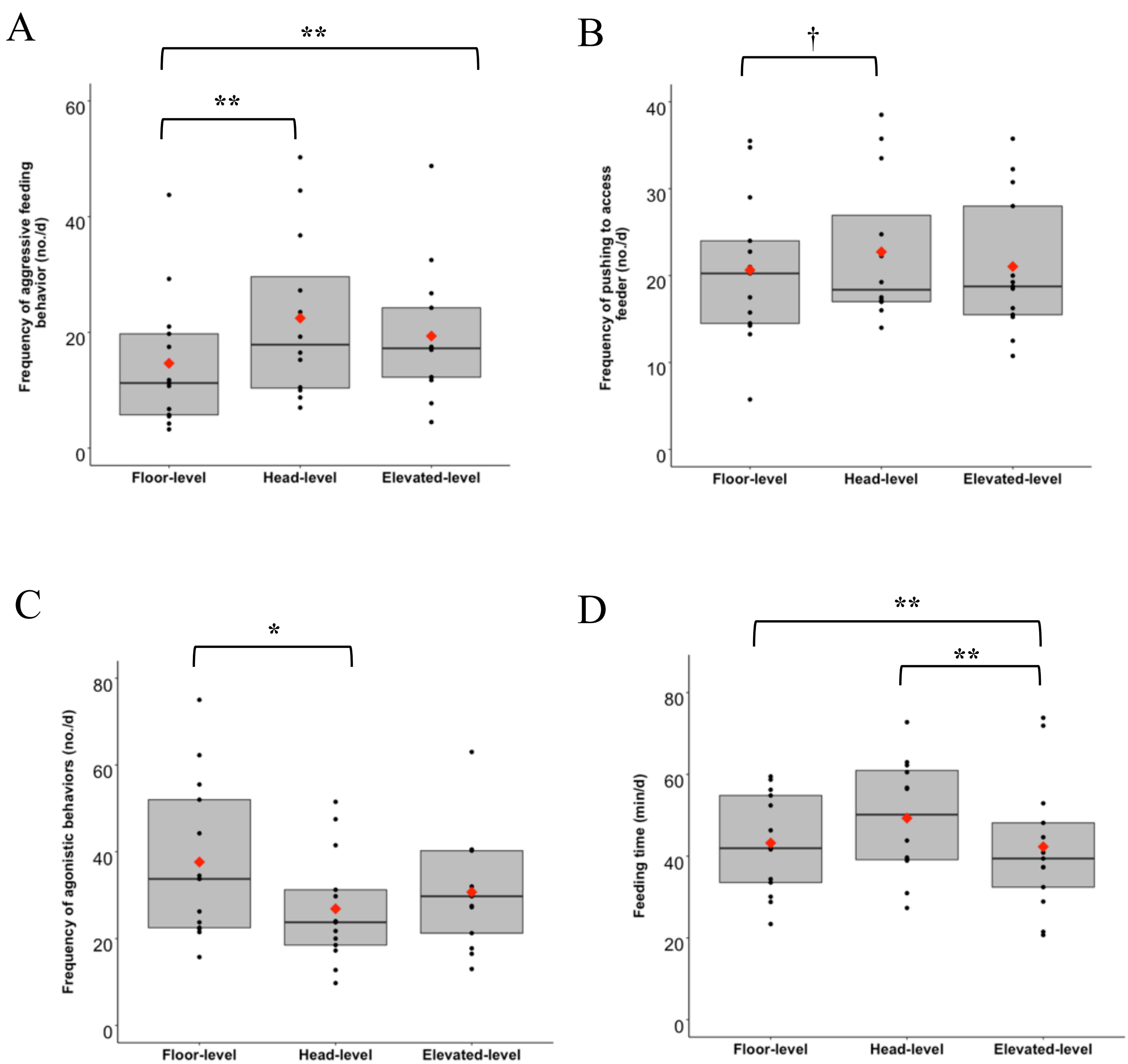
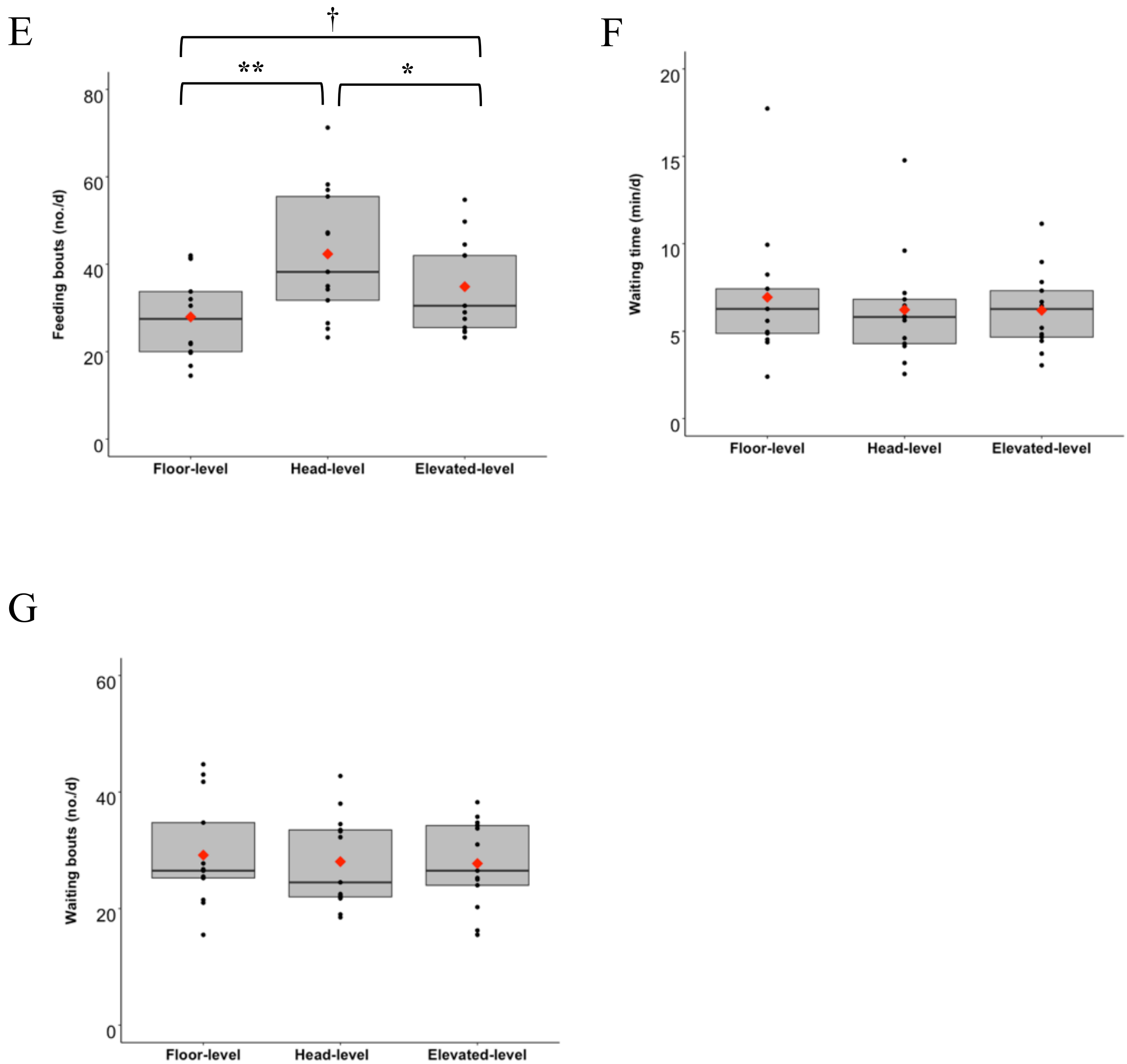


Figure 6.2 (continued). Competitive feeding behaviors of goats at each feeder height.



6.3.2 Personality traits

Behavioral responses of goats in each of the novelty and fear tests are presented in **Table 6.3**, and the loadings for each extracted principal component (factor) are reported in **Table 6.4**. Factor 1 explained 26.6% of the variation and had high positive loadings for vocalizing in the novelty and fear tests, latency to touch the object, latency to return to the food bucket in the fear tests, standing inactive in the dog test, and rearing in the startle test. This factor also had high negative loadings for touching and climbing the object, touching or eating from the food bucket in the fear tests, and standing inactive in the startle test. Goats scoring highly on Factor 1 were labeled 'fearful-avoid'.

Factor 2 explained 16.8% of the variation and had high positive loadings for standing inactive in the novelty tests, attentive toward the object, and approaching the dog and rearing in the dog test. This factor also had high negative loadings for rearing in the novelty tests, exploring in novel environment test, latency to touch the object, climbing the object, attentive toward the dog, and standing inactive in the dog test. Goats scoring highly on Factor 2 were labeled 'bold-approach'.

Factor 3 explained 14.4% of the variation and had high positive loadings for standing inactive in the novelty and dog tests, attentive toward the object and the dog, and approaching the umbrella. This factor also had high negative loadings for vocalizing and rearing in the novelty tests, exploring in the novel environment test, and touching and climbing the object. Goats scoring highly on Factor 3 were labeled 'exploratory'.

Factor 4 explained 10.5% of the variation and had high positive loadings for rearing in the novelty tests, latency to touch the object, attentive toward the object and dog, and standing inactive and rearing in the startle test. There were also high negative loadings for climbing and remaining close to the object, vocalizing in the fear tests, and standing inactive in the dog test. Goats scoring highly on Factor 4 were labeled ‘attentive-cautious'.

Overall, the principal components and their loadings were considered to have good stability based upon the leave-one-out cross-validation procedure (**Table 6.4**). Of the 20 input variables, 19 variables in Factor 1, 17 variables in Factor 2 and Factor 3, and 14 variables in Factor 4 met the stability criteria (i.e. factor consistently had similar loadings across multiple iterations).

Table 6.3. Behavioural responses in the personality tests.
Mean ± SD and range of behaviours of goats (n = 13) tested individually in 2 novelty tests (novel environment, novel object) and 2 fear tests (startle, dog) for 5 min each. Tests were repeated 4 wk apart and measures were averaged across repetitions.

Variable	Mean	SD	Range
Novel environment test			
Vocalizations (no.)	98.8	25.5	55 – 130.5
Standing inactive (s)	187.7	23.0	145.9 – 218.5
Exploring walls or floor (s)	41.3	18.0	13.7 – 75.2
Rearing (no.)	3.5	5.3	0 – 17.9
Novel object test			
Vocalizations (no.)	70.6	23.3	28 – 103.5
Standing inactive (s)	154.4	46.6	73.1 – 246.7
Latency to touch (s)	98.7	91.1	8.4 – 256.4
Touching (s)	9.4	6.2	1.6 – 21.4
Climbing (s)	57.5	64.3	0 – 178.2
Attentive toward object (s)	60.6	21.1	29.8 – 106.2
Close to object (s)	198.3	57.5	117.8 – 263.8
Rearing (no.)	3.5	5.3	0 – 17.9
Startle test [1]			
Vocalizations (no.)	22.5	18.2	1 – 61.5
Standing inactive (s)	45.6	4.9	37.3 – 54.2
Latency to return to food bucket (s)	106.2	114.6	8.2 – 300
Touching or eating from bucket (s)	11.2	10.1	0 – 27.8
Attentive toward umbrella (s)	19.5	6.4	11.7 – 31.1
Approach umbrella (s)	0.27	0.94	0 – 3.4
Rearing (no.)	0.54	1.1	0 – 3.3
Dog test [1]			
Vocalizations (no.)	30.1	24.7	3.0 – 82.0
Standing inactive (s)	48.6	5.4	40.0 – 58.0
Latency to return to food bucket (s)	104.9	106.1	7.6 – 300
Touching or eating from bucket (s)	4.0	4.9	0 – 11.8
Attentive toward dog (s)	24.5	8.2	6.8 – 34.3
Approach dog (s)	2.6	3.6	0 – 11.5
Rearing (no.)	0.21	0.38	0 – 1.0

[1] Measures are reported for the first 60 s after the occurrence of the stimulus (umbrella opening in the startle test; appearance of dog in dog test). Vocalizations and latency to return to the food bucket are reported for the full 5-min test duration.

Table 6.4. Coefficients (loadings) for the first 4 factors of the sparse PCA.
High loadings on each factor are indicated in bold (any non-zero value). Results of the leave-one-out cross validation are presented in parentheses next to the coefficient loading. [1]

Variable	Factor 1	Factor 2	Factor 3	Factor 4
All novelty tests [2]				
Vocalizations	**0.27** (11)	0.0 (1)	**0.41** (13)	0.0 (5)
Standing inactive	0.0 (2)	**0.21** (10)	**-0.51** (12)	0.0 (3)
Rearing	0.0 (4)	**-0.02** (6)	**0.24** (9)	**0.50** (12)
Novel environment test only				
Exploring arena	0.0 (2)	**-0.27** (11)	**0.43** (11)	0.0 (2)
Novel object test only				
Latency to touch object	**0.12** (10)	**-0.11** (12)	0.0 (4)	**0.18** (9)
Touching object	**-0.25** (13)	0.0 (2)	**0.19** (9)	0.0 (6)
Climbing object	**-0.13** (12)	**-0.36** (13)	**0.03** (6)	**-0.28** (10)
Attentive toward object	0.0 (1)	**0.06** (7)	**-0.29** (12)	**0.05** (5)
Close to object	0.0 (0)	0.0 (5)	0.0 (3)	**-0.72** (13)
All fear tests [3]				
Vocalizations [3]	**0.12** (8)	0.0 (0)	0.0 (2)	**-0.29** (11)
Touching and eating from food bucket	**-0.53** (13)	0.0 (0)	0.0 (1)	0.0 (2)
Latency to return to food bucket	**0.39** (13)	0.0 (0)	0.0 (2)	0.0 (6)
Startle test only				
Attentive toward umbrella	0.0 (2)	0.0 (2)	0.0 (5)	0.0 (2)
Standing inactive	**-0.41** (13)	0.0 (1)	0.0 (9)	**0.05** (6)
Approach umbrella	0.0 (0)	0.0 (5)	**-0.41** (9)	0.0 (3)
Rearing	**0.44** (13)	0.0 (1)	0.0 (2)	**0.13** (12)
Dog test only				
Attentive toward dog	0.0 (1)	**-0.51** (11)	**-0.17** (9)	**0.07** (6)
Standing inactive	**0.14** (10)	**-0.31** (12)	**-0.11** (5)	**-0.05** (9)
Approach dog	0.0 (1)	**0.54** (12)	0.0 (4)	0.0 (5)
Rearing	0.0 (1)	**0.31** (11)	0.0 (3)	0.0 (3)
Variance explained (%)	26.6%	16.8%	14.4%	10.5%
Interpretation (suggested label)	Fearful, avoid	Bold, approach	Exploratory	Attentive, cautious

[1] Variables with high (non-zero) loading in bold and with a high number of iterations (out of 13 iterations) in parentheses indicates good stability. Variables with zero loading and with a low number of iterations in parentheses indicates good stability.
[2] Variables are the average across the novelty tests (novel environment and novel object tests)
[3] Variables are the average across the fear tests (startle and dog tests)

6.3.3 Effect of personality traits on competitive feeding behaviors

Some of the individual variability in competitive feeding behaviors was associated with feeder height, and additional variation was associated with goat personality traits, and their interaction with feeder height. The relationships between each factor (personality trait) and competitive feeding behaviors are presented in **Table 6.5** (Factor 1 and 2) and **Table 6.6** (Factor 3 and 4).

Goats scoring highly on Factor 1 (more 'fearful-avoid') were less involved in aggressive feeding interactions (neither initiating or receiving), and were consistent across feeder heights in how frequently they received aggressive interactions. Goats that scored lower on Factor 1 (less 'fearful-avoid') received more aggressive interactions at the head-level feeder compared to the floor-level feeder (slope: $t_{1,16} = 2.2$, $P = 0.04$; **Figure 6.3a**). More 'fearful-avoid' goats were also more often displaced from the feeder when another goat pushed to access the feeder. Feeding time was negatively impacted in these goats, with a greater decrease in feeding time with increasing score on 'fearful-avoid' at head- and elevated-level feeders compared to floor-level feeders (slope: $t_{1,16} > 3.3$, $P < 0.01$; **Figure 6.3b**). Factor 1 was not associated with total agonistic behaviors (butting, chasing, clashes) or time spent waiting to gain access to the feeder.

Goats scoring highly on Factor 2 (more 'bold-approach') initiated more feeding aggression. More 'bold-approach' goats were more consistent across feeder heights in how often they received feeding aggression, but goats that scored low on Factor 2 (less 'bold-approach') received more feeding aggression at the head- and elevated-level feeders compared to the floor-level feeder (slope: $t_{1,16} > 3.0$, $P < 0.01$; **Figure 6.3c**). 'Bold-approach' goats also pushed to gain access to the feeder more often, and engaged in more agonistic behaviors at the floor-level feeder compared to the elevated-level feeder (slope: $t_{1,16} = 2.2$, $P = 0.04$; **Figure 6.3d**). Overall these goats had more feeding and waiting bouts.

Goats scoring highly on Factor 4 (more 'attentive-cautious') tended to receive more feeding aggression, but this was dependent on feeder height; more 'attentive-cautious' goats were consistent in how often they received feeding aggression across feeder heights, but goats scoring low on Factor 4 (less 'attentive-cautious') received less feeding aggression at the floor-level feeder compared to the head- and elevated-level feeders (slope: $t_{1,16} > 2.1$, $P < 0.06$; **Figure 6.3e**). More 'attentive-cautious' goats engaged in more agonistic behavior (butting, chasing, clashes) at the floor-level feeder compared to head- and elevated-level feeders (slope: $t_{1,16} > 1.8$, $P < 0.09$; **Figure 6.3f**). Factor 4 was not associated with measures of feeding or waiting time.

Factor 3 ('exploratory') was not associated with any competitive behaviors, feeding time or time spent waiting to gain access to the feeder.

Table 6.5. Relationship between Factor 1 and Factor 2 and competitive feeding behaviors. Goats (n = 13) were offered one of three feeder heights each day: floor-level, head-level and elevated-level. Effect direction is provided when the main effect of factor score is $P \leq 0.1$ (in bold).

Measures	**Factor 1 (fearful-avoid)**				**Factor 2 (bold-approach)**			
	Effect [1]	$F_{1,7}$	***P***	**Interaction with feeder height (*P*)**	**Effect**	$F_{1,7}$	***P***	**Interaction with feeder height (*P*)**
Feeding aggression (no.)								
Actor	**-**	**4.1**	**0.08**	0.72	+	**8.9**	**0.02**	0.55
Reactor		2.7	0.15	0.11 [2]		0.17	0.69	**< 0.01**
Pushing to gain access to feeder (no.)								
Actor		0.38	0.56	0.76	+	**10.3**	**0.02**	0.66
Reactor	+	**6.3**	**0.04**	0.97		0.01	0.94	0.59
Total agonistic behaviors (no.) [3]								
Actor		0.22	0.66	0.54		0.90	0.37	0.12 [2]
Reactor		0.10	0.76	0.75		0.13	0.73	0.41
Feeding time (min)	**-**	**6.2**	**0.04**	**< 0.01**		0.79	0.41	0.23
Feeding bouts (no.)		0.29	0.60	0.72	+	**10.9**	**0.01**	0.61
Waiting time (to gain access to feeder, min)		2.5	0.16	0.26		0.91	0.37	0.55
Waiting bouts (to gain access to feeder, no.)		1.5	0.26	0.78	+	**5.6**	**0.05**	0.33

[1] negative effect direction (relationship between Factor and behavior) denoted by - ; positive effect direction denoted by +
[2] interaction was explored using pre-planned contrasts; results of these interactions are reported in text
[3] sum of butting, chasing and clashes

Table 6.6. Relationship between Factor 3 and Factor 4 and competitive feeding behaviors. Goats (n = 13) were offered one of three feeder heights each day: floor-level, head-level and elevated-level. Effect direction is provided when the main effect of factor score is $P \leq 0.1$ (in bold).

Measures	**Factor 3 (exploratory-interested)**				**Factor 4 (attentive-cautious)**			
	Effect [1]	$F_{1,7}$	***P***	**Interaction with feeder height (*P*)**	**Effect**	$F_{1,7}$	***P***	**Interaction with feeder height (*P*)**
Feeding aggression (no.)								
Actor		0.08	0.78	0.78		2.6	0.15	0.45
Reactor		0.88	0.38	0.23	+	**4.0**	**0.09**	**0.03**
Pushing to gain access to feeder (no.)								
Actor		0.04	0.85	0.66		2.0	0.20	0.98
Reactor		0.01	0.92	0.30		1.3	0.30	0.93
Total agonistic behaviors (no.) [2]								
Actor		0.08	0.78	0.47		0.0	0.98	**0.02**
Reactor		0.23	0.64	0.84		0.29	0.61	0.23
Feeding time (min)		0.05	0.83	0.28		2.0	0.20	0.16
Feeding bouts (no.)		0.12	0.74	0.68		2.3	0.18	0.64
Waiting time (to gain access to feeder, min)		0.30	0.60	0.37		0.08	0.78	0.47
Waiting bouts (to gain access to feeder, no.)		0.37	0.56	0.74		0.97	0.36	0.48

[1] negative effect direction denoted by - ; positive effect direction denoted by +
[2] sum of butting, chasing and clashes

Figure 6.3. Interactions of personality traits with feeder height for competitive behaviours. Mixed multiple regression model of the interaction between personality traits and feeder height on competitive feeding behavior outcome measures. The personality trait Factor 1 interacted with feeder height for (A) receiving aggressive feeding behaviors, and (B) feeding duration. Factor 2 interacted with feeder height for (C) receiving aggressive feeding behaviors, and (D) total agonistic behaviors. Factor 4 interacted with feeder height for (E) receiving aggressive feeding behaviors, and (F) total agonistic behaviors. Factor 3 had no interaction with feeder height and is not shown. Shaded bands around each line indicate 95% confidence limits.

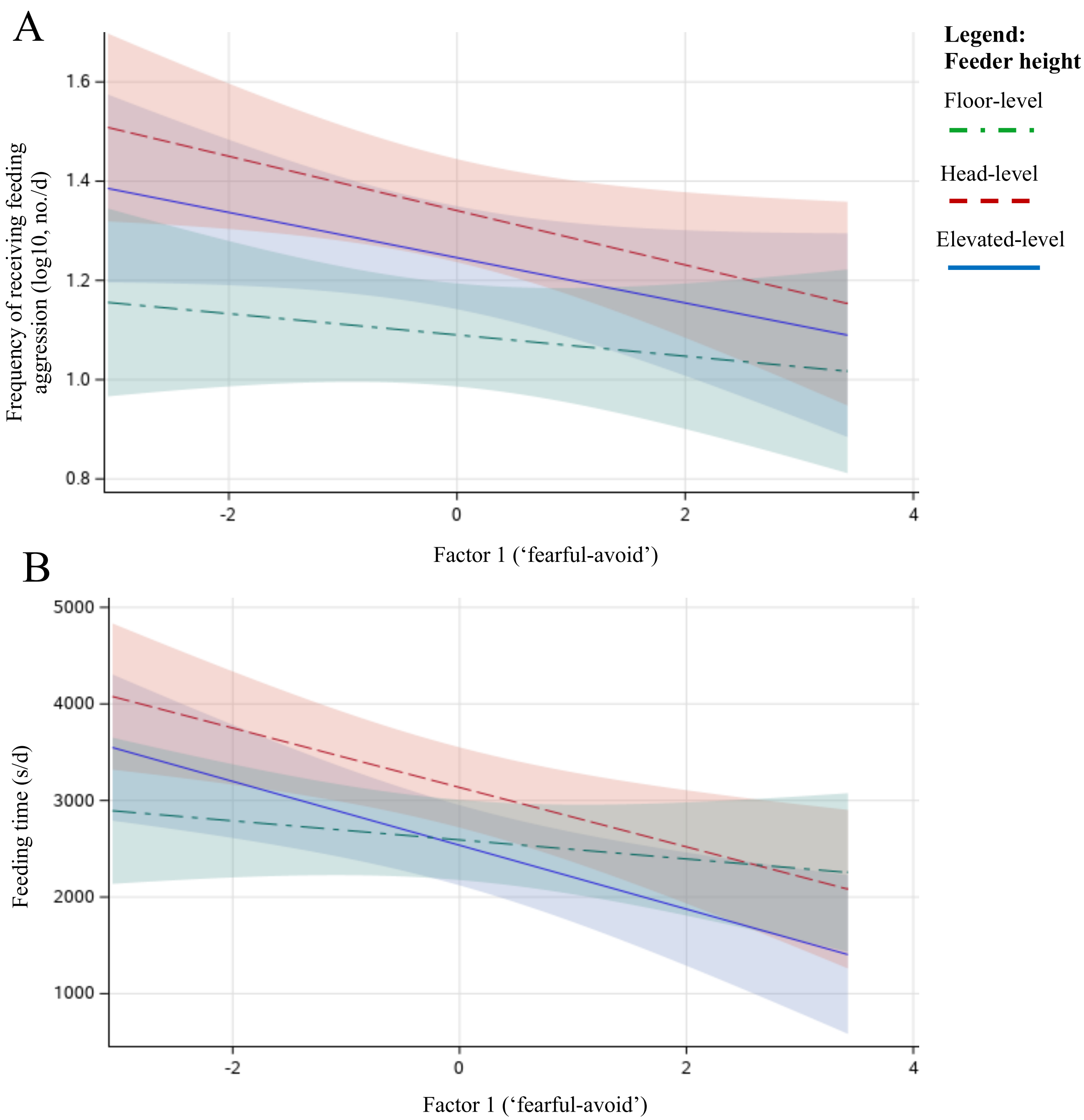


Figure 6.3 (continued). Interactions of personality traits with feeder height for competitive behaviours.

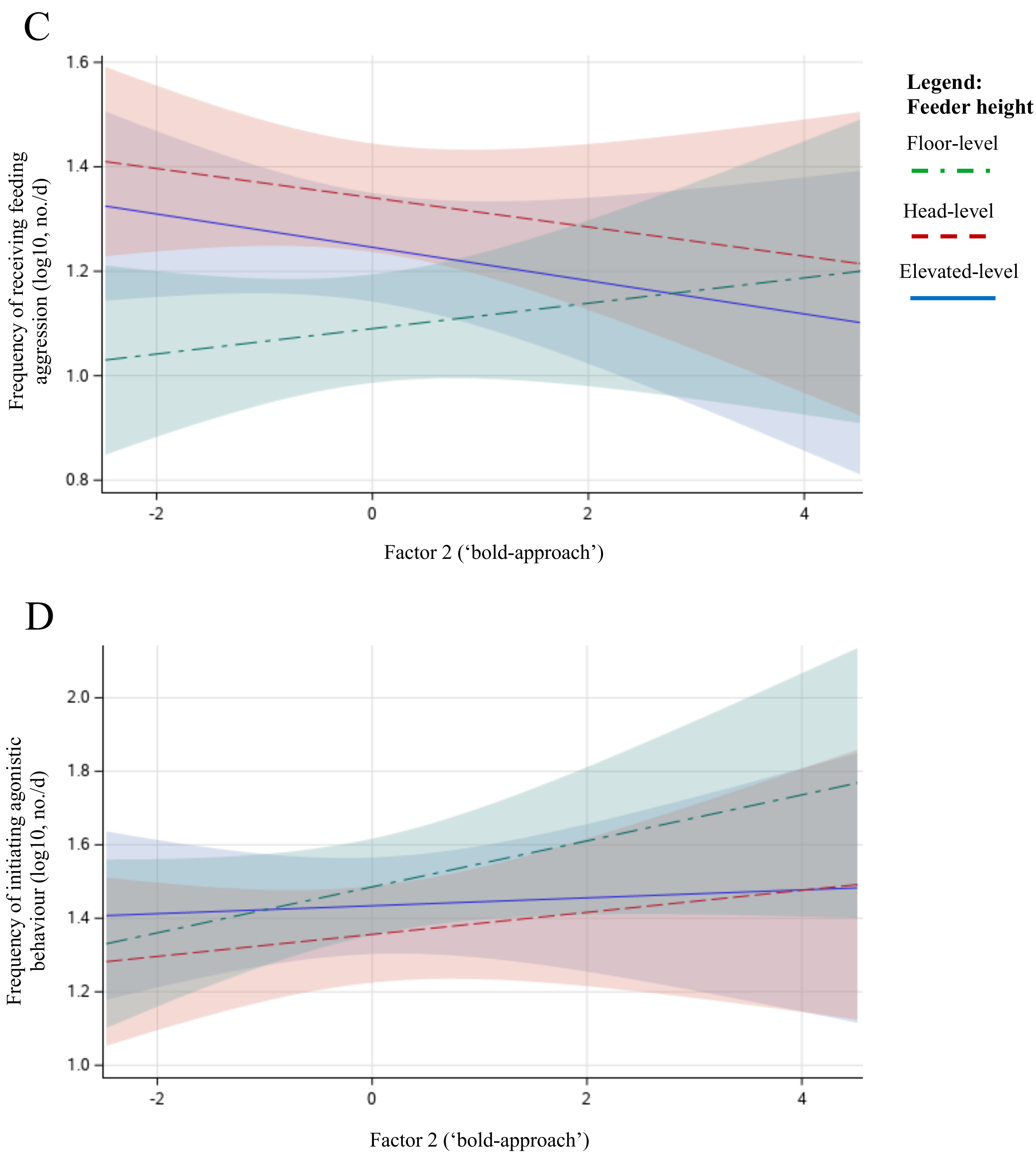
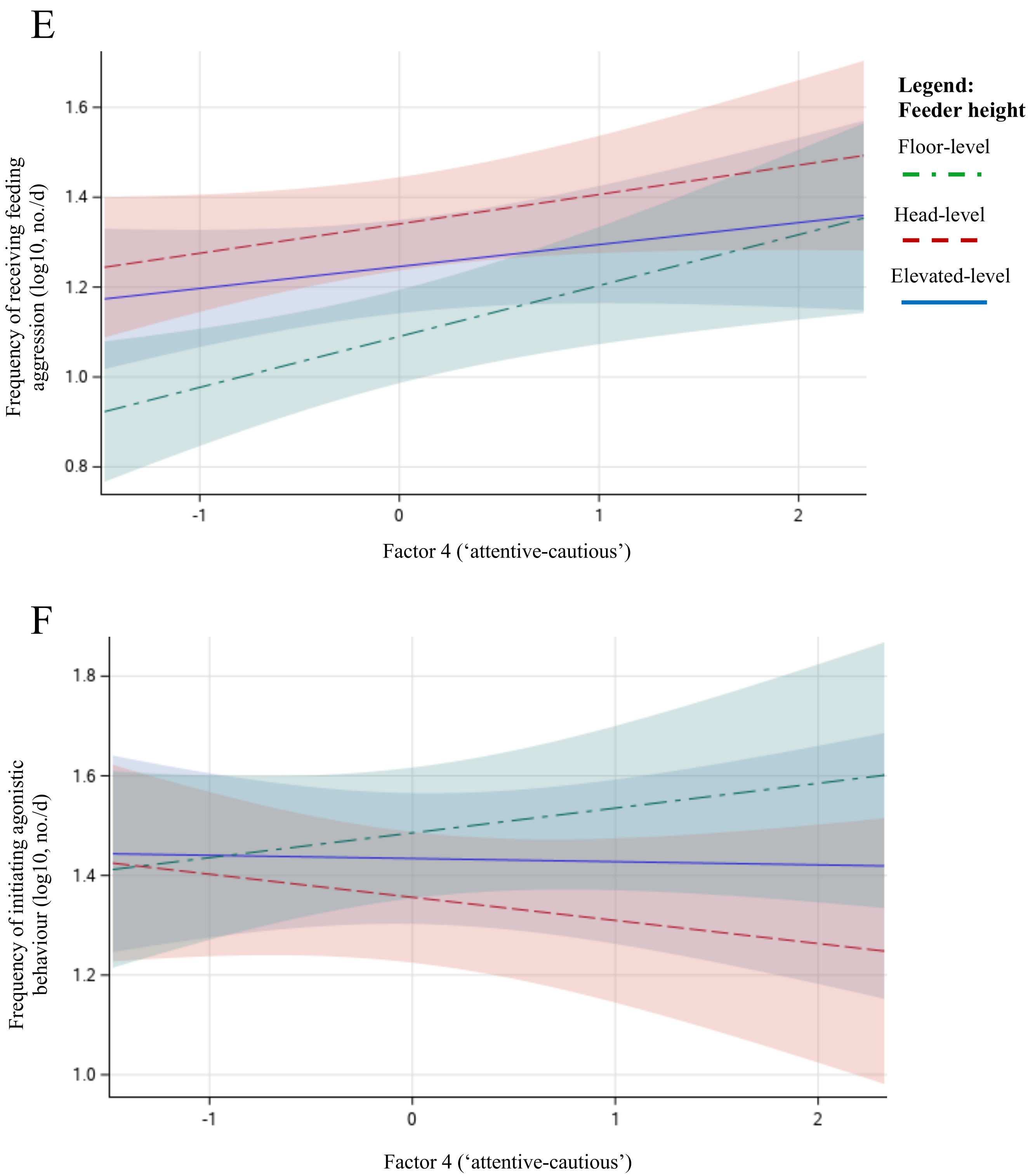


Figure 6.3 (continued). Interactions of personality traits with feeder height for competitive behaviours.



6.4 Discussion

6.4.1 Effect of feeder height on competitive feeding behaviours

The highly overstocked feed bunk created more feeding aggression (i.e., butting that may or may not result in displacement from the feeder) and less agonistic behaviors behind and to the sides of the feeder (i.e., butting, chasing and frontal clashes) at the head- and elevated-level feeders compared with the floor-level feeder. In our previous study, we reported that when goats were given a choice between each of these feeder heights, they also displaced goats more often from the elevated-level feeder despite having sufficient space to feed together (Neave et al., 2018b in Chapter 5). This displacement behavior may occur more often at the elevated-feeder because goats are defending a preferred feeding position. Competition is known to increase with limited resources (Barroso et al., 2000b); since feed in this study was available *ad libitum*, it may be that the goats considered the opportunity to feed from a preferred position to be a limited resource (as they only received each height one-third of the time), and therefore increased their feeding aggression to maintain their position at these feeders. Alternatively, the design of the head- and elevated-level feeders may have permitted more aggression. Feeder design is known to affect feeding aggression; in floor-level neck-rail systems without physical separations, more physical contact and displacements occur since animals can move freely from side to side (Nordmann et al., 2011; dairy cattle: Endres et al., 2005). Interestingly, the same type of system has been suggested to reduce aggression by providing a better backwards view for subordinate goats to avoid dominant approaching animals (Nordmann et al., 2011). In our study, all feeders used a neck-rail design, but instead of it being open above the rail, a solid wood frame above the head was used; this frame likely restricted the backward view when goats lowered their head to floor-level, but not when their heads were at head- or elevated- level. Therefore, the latter types of feeders may have allowed goats to respond more quickly to the movements of neighboring or approaching goats.

The body position required to feed from the ground links to lower feeding aggression. Previous work has shown that goats must splay their legs to reach feed that is at ground level, so the feed table should be raised by 10 cm to allow goats to feed in a relaxed position (Keil et al., 2017). Since we mimicked a commercial feeding system, we did not raise the feed table. It is possible that this uncomfortable position, coupled with a need to maintain position at the feeder, made expression of aggression difficult. Conversely, a more relaxed feeding posture at the head- and elevated-level feeders allowed goats to shift some of their focus to gaining access to or defending their position at the feeder. We caution that our results are specific to feeding conditions where goats are overstocked at the feed bunk; we encourage future work to investigate if competitive behaviors at elevated feed bunks can be reduced by allowing goats to feed at their preferred distances from others (see Aschwanden et al., 2008b).

Decreased feeding aggression at the floor-level feeder was contrasted by increased agonistic behaviors behind and to the sides of the floor-level feeder compared with the other feeder heights. Other work has reported an increase in these behaviors when space at a floor-level feed bunk was reduced to 2 or 3 goats per feeding place (Jørgensen et al., 2007). Space allowance in our study was the same across feeder heights (13.5 cm/goat), yet the body posture of goats at the floor-level feeder permitted fewer goats to feed simultaneously compared with the postures at head-level and while feeding from a step at elevated-level feeders. It was not possible to measure leg splay, but if goats needed to do this to reach the floor-level feed (Keil et al., 2017), it would limit the physical space and the number of goats that could access the feeder at any one time. This would in turn increase the likelihood of agonistic interactions between goats that are waiting for feeder access. Offering elevated platforms for feeding can reduce agonistic behaviors (Aschwanden et al., 2009a; b), but this work did not distinguish whether added space allowance, separation from neighboring goats, or some aspect of the height itself contributed to fewer agonistic interactions.

Feeding time was lower at the elevated- and floor-level feeders compared with the head-level feeder. This may be a consequence of more feeding aggression and agonistic behaviors at each of these feeders, respectively, since feeding time is known to decrease when competition at the feeder is high (Jørgensen et al., 2007). Conversely, greater feeding time at the head-level feeder may be due to a greater number of feeding bouts and increased frequency of pushing to access this feeder. Our previous study showed that goats consumed more feed from the elevated-level feeder despite similar feeding times across feeder heights (Neave et al., 2018b in Chapter 5), suggesting that the altered feeding time in the current study may have resulted in increased feeding rate.

Overall different feeder heights did not reduce competition; rather they produced different behaviors. Resource competition is a social stressor that has serious negative behavioral and health consequences (dairy cattle: Proudfoot et al., 2018); however, the specific aspects of competitive interactions that are most stressful are unknown. For instance, frontal clashes involve significant head-to-head contact, but in nature, horns evolved to be stress-bearing organs that absorb impact during fighting (Geist, 1966; Alvarez, 1990). With the removal of horns in commercially-housed goats, frontal clashes now involve more skull impact. Therefore, efforts to minimize the occurrence of these behaviors, which occurred most at the floor-level feeder, may be especially beneficial.

6.4.2 Effect of personality traits on competitive feeding behaviors

This is the first study to show that personality traits of goats affect how they respond to a challenging feeding environment. Four traits ('fearful-avoid', 'bold-approach', 'exploratory', 'attentive-cautious') described the majority of the variation in behavioral responses toward novel and fearful stimuli in standardized personality tests. These traits were associated with individual differences in the frequency of competitive feeding behaviors, and in some cases, showed a degree of plasticity in relation to different feeder heights.

In a number of species (e.g., rodents, fish, birds and farm animals), differential behavioral response patterns to environmental challenges have most often been described as proactive versus reactive coping styles, or boldness versus shyness (Coppens et al., 2010). A proactive or bold behavioral response pattern is often characterized by a fight-or-flight strategy toward a stressor, with individuals being novelty seekers and aggressive in social and non-social contexts (Benus et al., 1991; Koolhaas et al., 1999, 2007). We suggest that this response pattern was reflected in our 'bold-approach' goats responding to the presence of novelty and fearful stimuli. Alternatively the 'reactive' behavioral response pattern is characterized by withdrawal, immobility and avoidance of a stressful stimulus (Koolhaas et al., 1999, 2007). Following observations of animals in social conflict, some have suggested distinct types of submissive individuals – those that actively try to escape, and those that are unresponsive to attacks or threats from the dominant individual (tree shrews: von Holst, 1986; rats: Stefanski, 1998). We suggest that these two 'reactive' response patterns were also seen among our goats: those that avoided the novel object, vocalized and tried to escape from the pen ('fearful-avoid'), and goats that were more passive, directing attention toward the novel object and dog without vocalizing ('attentive-cautious'). Our goats with different behavioral response patterns toward novelty and fearful stimuli also differed in their responses to the competitive feeding environment.

Goats that were more ‘bold-approach’ (quick to approach the novel object and dog in the standardized tests) were generally more aggressive at the feeder, initiating more feeding aggression, pushing more often for access, and engaging in more agonistic behaviors, especially around the floor-level feeder. Similar findings exist in other farm animal species. Piglets that struggled more during restraint (high-reactivity or ‘proactive’ piglets) responded to an unfamiliar social environment by initiating more fights, spending more time fighting, and chasing surrendering piglets (Bolhuis et al., 2005; Melotti et al., 2011); such piglets were also more aggressive during a food competition test (Ruis et al., 2000). Furthermore, pigs that approached a novel human more quickly were found to have more lesions (an indication of aggression) after mixing with other pigs (Brown et al., 2009). Our ‘bold-approach’ goats maintained high levels of initiating and low levels of receiving aggression across feeder heights, suggesting that they did not adjust this behavior when the feeding environment changed. Similarly, Bolhuis et al. (2005) found high-reactivity piglets were consistently highly aggressive regardless of their success in these encounters. In bird species, highly aggressive individuals tend to be inflexible in their behavior, where they do not adjust their behavior with changing contexts (referred to as plasticity, see Dingemanse et al., 2010). When ‘bold-approach’ goats were not feeding, they engaged in more agonistic behavior around the floor-level feeder compared with the other feeders. This may have been in response to the presence of more non-feeding goats, since fewer were able to access the floor-level feeder. Interestingly, more feeding and waiting bouts did not translate to increased feeding time for ‘bold-approach goats’, despite high amounts of aggression both at and behind the feeder, suggesting aggression is a tactic for these goats when defending or accessing a resource.

Our ‘fearful-avoid’ goats generally avoided aggressive interactions at the feeder (i.e., they were neither initiators nor recipients) and had reduced feeding time. Miranda-de la Lama et al. (2011) found contrary results, where such goats had increased feeding time; this difference may be because we only observed goats for 90 min after feed delivery, so our ‘fearful-avoid’ goats may have compensated for the loss in feeding time during peak periods by feeding later in the day (e.g., beef cattle: Zobel et al., 2011). This idea is supported by Rohrer et al. (2013) who reported that pigs that struggled more during restraint (i.e., active escape attempts), avoided social interactions at the feeder and preferred to eat when the feeder had less occupants. Other work has shown that fearful cattle (e.g., showing nervousness, vigorous movement, escape attempts during weighing or during isolation) have reduced feeding time (Cafe et al., 2011), and pigs that vocalized more while on a weigh scale were more likely to receive aggression after mixing (D’Eath et al., 2009). Our ‘fearful-avoid’ goats were moderately flexible in their behavior, consistently receiving less aggression during feeding across feeder heights, but decreasing feeding time at the head- and elevated-level feeders. This may be because more feeding aggression generally occurred at the head- and elevated-level feeders, resulting in these goats avoiding these feeders more during peak periods. Non-aggressive individuals are more flexible and adaptable under changing conditions, responding only when needed (Van Oortmerssen et al., 1990; Natarajan et al., 2009).

We described ‘attentive-cautious’ goats based on their increased attention toward the novel object and dog. This type of attention bias toward negative stimuli has been described as reflecting anxiety in humans and other species including sheep and cattle (reviewed by Lee et al., 2016, 2017; Crump et al., 2018). We therefore expected that these goats would be more attentive toward potential threats during competition, thus avoiding aggressive interactions; while ‘attentive-cautious’ goats did not initiate aggression while feeding, we did find that they were recipients.

These goats were passive under competitive feeding conditions – neither removing themselves from the situation nor responding to aggression. This type of social behavior has been described in other goat studies, where 'passive' individuals were involved in less aggressive or affiliative behaviors, and were neither conflict mediators nor supporters (Miranda-de la Lama et al., 2011; Pascual-Alonso et al., 2013). Several studies in other species have shown that animals under stress will reduce their attention toward a threat. For instance, chronically-stressed sheep showed reduced vigilance behavior and were quicker to approach a food bucket after the appearance of a dog (Verbeek et al., 2019), and monkeys that had just experienced a stressful event (i.e., veterinary examination) shifted their attention away from aggressive faces while control monkeys sustained attention toward these faces (Bethell et al., 2012). During a challenging competitive computer task, humans will disengage attention toward negative words (Ellenbogen et al., 2002). Therefore, we speculate that 'attentive-cautious' goats in our stressful feeding environment were less attentive toward aggressive goats while feeding and thus were more likely to receive aggression. When not feeding, these goats initiated more agonistic behavior at the floor-level feeder but initiated less at the head-level feeder. The level of challenge experienced in these contexts may lead to differential attention and response toward threats.

Finally, goats that scored highly on the 'exploratory' trait showed no relationship with measures of competitive feeding behaviors. The trait 'exploration' is often described as having similar characteristics to 'boldness'. Both traits refer to a tendency to undertake risky behavior; Réale et al. (2007) suggests that exploratory traits should be reserved for responses toward novelty while bold traits should refer to responses toward a predator. Given its link with boldness, it follows that particularly exploratory individuals may be more aggressive than individuals that are not exploratory (e.g., Jones and Godin, 2010; Blight et al., 2016). Exploratory traits have also been linked with competitive feeding success in birds (David et al., 2011; Cole and Quinn, 2012). The level of exploration (e.g., superficial versus thorough) has also been used to describe personality (Verbeek et al., 1994). Superficial or 'fast explorer' birds were more aggressive and obtained either dominant or subordinate positions (Verbeek et al., 1999), while thorough or 'slow explorer' birds often did not start fights and achieved intermediate hierarchy positions (Marchetti and Drent, 2000). 'Reactive' piglets were slower to approach a novel object, but carefully inspected and explored it once they did (Hessing et al., 1994; Ruis et al., 2000), and these piglets achieved similar social rank as 'proactive' piglets (Bolhuis et al., 2005). This work suggests that the lack of relationship between competitive feeding behaviors and 'exploration' in our goats may relate to the social rank of these animals, where they are both initiators and recipients of aggression at the feed bunk.

6.5 Conclusions

Personality traits can explain why some goats express different levels of aggression around feeding and why some have reduced feeding time. These individual behavioral differences also explain why previous work in goats has shown that restricted feeder space leads to large variability in feeding time among individuals. Since goats show a tendency to feed from a variety of heights and postures, we suggest that when designing feeders, reducing competition should not be the only focus. Feeding practices should take into consideration the needs of all individuals within the herd; this may include offering different feeder heights to provide opportunities for individuals of various personalities to express their feeding preferences.

Chapter 7: General Discussion and Conclusions

7.1 Thesis findings

The overall objective of my research was to contribute to the understanding of individual variability in the feeding behaviour of dairy calves and goats, particularly during challenging feeding circumstances such as weaning and when space is restricted at the feeder. My research also investigated alternatives to traditional weaning programs (for dairy calves) and feeder designs (for adult goats) that are thought to better allow for individual differences and promote natural behaviour.

My review of the literature on individual variability in the development and expression of feeding behaviour of ruminants outlined how differences in personality traits such as exploration, reactivity, and sociability can explain why some individuals are more successful than others in responding to changes in their nutritional, social or physical environment. I identified a number of gaps in our understanding of why and how individuals respond differently to changes in their feeding environment. Some of these gaps were addressed in the subsequent empirical chapters.

One critical management practice during the rearing of dairy calves is weaning (i.e. when calves are transitioned from milk to solid feed). In Chapter 3, I investigated this transition and showed how personality traits of calves (‘exploratory’, ‘interactive’, and ‘vocal’) were associated with feeding behaviour, feed intake, and performance at weaning. I found that calves that were less reactive to novel situations performed better than those that were more reactive. In the follow-up study in Chapter 4, I investigated other individual characteristics that were more feasible for farm staff to collect (early vitality, drinking and learning ability) that might explain variability in feeding behaviour and performance around weaning. Chapter 4 also examined individual variability in behaviour and performance of calves that were weaned on an individual basis according to their intake of solid feed, permitting animals to wean at different ages as they became familiar with solid feed. An important finding of this chapter was that early intake of solid feed and less training time to learn to use the milk feeding equipment were predictors of early weaning age. The work in Chapters 3 and 4 contribute to our understanding of why some calves perform well and others poorly during weaning, and provides a starting point for how to tailor weaning practices to enable calves the best chance for success during this challenging period.

In Chapters 5 and 6 I focused on challenging feeding practices prevalent on intensive dairy goat farms: feeding at floor-level (which limits the expression of the natural browsing behaviour of goats), and providing restricted space at the feeder (which leads to high levels of competition to access feed). In Chapter 5, I tested the preference of goats to feed from two alternative feeder designs (head-level and elevated-level, promoting a natural browsing feeding posture) compared to a traditional floor-level feeder. I found that goats ate more from, and competed for access to, the elevated-level feeder compared to the other feeders. In Chapter 6, I investigated the competitive behaviours of goats at each of these feeder designs when under restricted feeding conditions; goats expressed more feeding aggression at the head- and elevated-level feeders, but more agonistic behaviours (chasing, butting and clashes) at the floor-level feeder. Individual variability in these competitive behaviours at different feeder heights was associated with personality traits; 'fearful' goats generally avoided competition and 'bold' goats initiated aggression. The findings presented in these chapters offer insight into the use of elevated feeder height designs to promote natural feeding postures and feed intake. This work also encourages consideration for individual differences in competitive feeding behaviours when designing feeders; goats may benefit from the opportunity to feed from a variety of feeder heights.

The studies in this thesis collectively provide evidence that individual characteristics such as personality traits can explain individual variability in feeding behaviours, and that alternative approaches to stressful feeding practices such as weaning and restricted feeding space may provide an opportunity for all individuals to succeed by attending to individual needs and promoting natural behaviour. More broadly, my work contributes to improving the welfare of commercially-housed dairy cattle and dairy goats in two of the prominent global dairy industries. In Canada in particular, the dairy cattle industry is the second largest of the agriculture sectors, comprising nearly 1 million cattle and generating $2.4 billion annual income (FAO, 2019). The dairy goat industry of Canada is growing, with the number of dairy goats doubling in the last 30 years to a total of 200,000 goats, yielding an annual $41 million (Canadian Dairy Information Centre, 2017). Thus it is expected that both dairy cattle and dairy goat industries will continue to be prominent in Canada, requiring increased attention toward the welfare of the animals in these systems.

In the remainder of this chapter, I describe some of the limitations of my work and provide suggestions for future research.

7.2 Limitations and future research directions

7.2.1 Weaning transition in dairy calves

The studies presented in Chapters 3 and 4 provided the first evidence in any ruminant species that personality traits are associated with feeding behaviour, feed intake and performance before, during and after weaning; these traits could identify individuals that are most likely to perform well or poorly during this critical period on commercial farms. The methodology to measure personality traits in these studies is well used across species; behavioural responses to novel stimuli in these standardized tests (novel environment, novel object, novel human) are used as an indicator of fear or exploration (Forkman et al., 2007; Perals et al., 2017). The findings in these two chapters align well with another report in young beef cattle using a similar methodology to measure exploration, in which more exploratory heifers had improved weight gains (Müller and von Keyserlingk, 2006). However, the assessment of personality in beef cattle (often referred to as temperament) is more often measured in terms of reactivity to handling or restraint, where more reactive or nervous individuals have impaired feed intake, feeding behaviour and growth (see review by Haskell et al., 2014). While my studies did not include tests for reactivity during handling or restraint, the results do suggest that individuals that are less reactive toward novelty (i.e. interactive, exploratory or active) perform better than more reactive individuals (i.e. inactive, vocal). In the future, it would be worthwhile to include tests for handling and restraint in pre-weaned dairy calves to assess the relationship with early feeding behaviour and performance, given that dairy cattle experience considerable handling in commercial systems.

A limitation of how personality traits were measured in my studies is that they are time consuming and impractical for implementing on commercial farms. This motivated the inclusion of other measures in Chapter 4 that could characterize individuals from a young age; calf vitality and drinking ability are observations that can be made practically by the staff on farms when separating the calf from the dam or feeding colostrum and first milk meals. Handlers must also train calves to use the automated milk feeder and may be able to assess learning ability at this time; this measure is specific to those using automated feeders, but I argue it may also apply to calves learning to drink from a nipple bottle on farms that manually feed milk. Learning ability emerged as an especially important measure in predicting weaning age, where calves that took longer to learn to use the feeder weaned at a later age. Nonetheless, personality traits identified using the standardized tests in Chapters 3 and 4 proved important in their associations with early solid feed intake and growth, negative behavioural response to weaning, and earlier weaning age. Thus there may be benefits to identify quick or automated methods of assessing personality traits in dairy calves. For instance, inactivity in the novelty tests may translate to inactivity in the home environment, which could be monitored automatically using wearable activity monitors (Swartz et al., 2016). Fear may be assessed as the response to an approaching human during feeding in the home pen (Lensink et al., 2003; Rousing et al., 2005). These examples of practical assessment methods should be verified for their associations with feeding behavior, performance, and weaning age.

Other than personality traits (Chapter 3) and individual characteristics like calf vitality, drinking or learning ability (Chapter 4), there may be additional factors that could explain variability in feeding behaviours during the pre-weaning period. For instance, individual differences in early solid feed intake may be related to taste preferences or ability to recognize a food source other than milk (Forbes and Kyriazakis, 1995; Kyriazakis et al., 1999). This latter point may be affected by social facilitation or social learning, where individuals are more likely to encounter and begin to eat solid feed by observing others do the same (Zentall and Galef, 1988). There may be individual differences in the use of social information to locate food sources (e.g. Sih and Bell, 2008). Furthermore, ruminants are particularly prone to food neophobia (i.e. the fear of novel foods; Chapple and Lynch, 1986), and this has been reported in dairy calves (Costa et al., 2014); individuals may differ in how quickly they overcome this fear.

Early consumption of solid feed initiates rumen maturation; there may be individual differences in ruminal enzymatic activity or ruminal pH that may stimulate this early intake of solid feed and prepare some calves for weaning at earlier ages (Rey et al., 2012; Meale et al., 2017). If this is the case, automated technologies such as rumen pH bolus (Penner et al., 2009) or blood collection to test for serum beta hydroxybutyrate concentrations (Deelen et al., 2016) may be other useful methods to identify individuals that may not be prepared for early weaning. Each of these factors warrant investigation to determine their contribution to individual differences in feeding behaviours around weaning.

An obvious follow-up question from Chapter 3 is how to make the weaning transition easier for those individuals that appear to struggle during this period. The individualized weaning program used in Chapter 4 aimed to allow calves to progress through weaning at their own pace as they became familiar with solid feed, resulting in variable weaning ages. A few lessons were learned from the use of this individualized weaning program. In a companion paper (Benetton et al., 2019), we found that calves weaned on this individualized method had substantially more unrewarded visits to the milk feeder (i.e. visits where milk was unavailable) compared to a weaning program based on age; this type of behaviour is an indicator of hunger (de Paula Vieira et al., 2008) and may be a result of the successive abrupt removals of milk when each solid feed intake target was reached. Therefore, the method of milk removal used in the individualized weaning program of Chapter 4 may not have been an ideal method for some calves. I encourage future work to investigate how individuals of different personalities respond to different methods of milk removal. The use of feeder technologies can automate the weaning process (as was used in Chapter 4) and would facilitate the use of different weaning methods that permit all calves to cope well with weaning. Another lesson from Chapter 4 was that there were a few calves on the individualized method that never began to eat large amounts of solid feed, despite having up to 12 wk to complete weaning (average weaning age was 8 wk). These calves are the most likely to struggle during weaning even at later ages, so future work should explore techniques that encourage early solid feed intake, such as flavoured additives to increase palatability (Montoro et al., 2011) or providing older social models that are already experienced with eating solid feed (de Paula Vieira et al., 2012).

A gap in the existing literature is that we do not know the longer term effects of different weaning methods, particularly for individuals that perform well or poorly during the transition. In a companion paper (Benetton et al., 2019), we followed calves that were reared in Chapter 4 until 19 wk of age and found that calves weaned later were unable to make up for their lower body weight compared to calves that weaned earlier. This finding suggests that some calves may have stronger negative responses to weaning (Chapter 3), or calves that wean at later ages (Chapter 4) may also perform poorly when faced with other challenging management practices at later stages in the heifer-rearing period, such as other diet transitions, pen and equipment changes, or regrouping with unfamiliar animals. The ability of individuals to cope with these events after weaning, and other events that occur into young adulthood (such as breeding, onset of lactation and introduction to the milking parlour), may explain why calves with high pre-weaning feed intake and weight gains have greater first lactation milk yield (Gelsinger et al., 2016). I encourage future work to explore these links between performance during weaning and individual responses to other challenging practices on farm.

7.2.2 Restricted feeding space for dairy goats

The work presented in Chapters 5 and 6 is the first to explore the use of elevated feed bunk designs for dairy goats compared to a traditional floor-level feeder, and how personality traits can account for individual variability in competitive feeding behaviours at these feeders. In Chapter 5, I found that when goats were given a choice between three different feeder heights, goats preferred to eat more from the elevated feeder compared to the floor-level feeder. Interestingly, goats chose to eat at least a portion of their diet from each of the feeder heights, suggesting they did not reject the floor-level feeder; this highlights the importance of providing multiple options to allow goats a choice of feeding surfaces that may also promote natural behavior and improve their welfare. However, a drawback of the study described in Chapter 5 is the use of a design that provided goats a choice between several alternatives; this design can be used to draw inferences about preferences, but not the strength of these preferences (Kirkden and Pajor, 2006). Future work should investigate the motivation of goats to access elevated feeder heights, and to determine if this motivation is related to the feeding posture (Tölü et al., 2012), the type of feed offered (since browsing behaviour in nature involves foraging on leaves, buds and shrubbery instead of grasses; Sanon et al., 2007), or being raised off the ground (e.g. aerial feeding in trees; El Aich et al., 2007). Determining the strength of the motivation to feed from elevated feeders would provide more insight into the importance of providing this option on commercial farms.

A major finding of the work in Chapter 6 is that feeder height affected the frequency and type of competitive behaviours. While we provided the same amount of feeding space at each feeder (13.5 cm/head), we observed that fewer goats were able to feed simultaneously at the floor-level feeder compared to the head- and elevated-level feeders. Therefore, we appeared to have confounded to some extent feeder height with available space per head. I speculated that goats had to splay their legs to reach the feed at the floor-level feeder (Keil et al., 2017), leading to reduced available space for other goats to access this feeder. This finding, however, highlights the need to consider feeder designs that allow goats to feed comfortably, and also suggests that space allowances at the feeder may need to be tailored to feeder design. Future work should offer different feeder heights with unrestricted feeding space (e.g. greater than 40 cm/head) to determine if the frequency and types of competitive behaviours at each feeder height in Chapter 6 are independent of space available.

Personality also affected competition at the feeder (Chapter 6). It remains to be seen whether those personalities that avoided and engaged in aggression would do the same, and to the same extent, with unrestricted feeding space. Future work should manipulate space allowance while maintaining the same feeder design to investigate how different personalities respond to increasing or decreasing competitive pressure. This work would inform the design of feeders that meet the needs of different individuals and minimize competition in the herd.

Our understanding of the extent to which competition and feeding behaviours are affected by personality and feeder height is limited to our observation period of 90 min after fresh feed delivery (Chapter 6). The effects of restricted feeder space and high competition on feeding behaviour beyond this observation period are unknown. For instance, fearful goats may make up for their reduced feeding time at later periods of the day (as reported in beef cattle: Zobel et al., 2011). Furthermore, it would be valuable to understand how competition affects measures of individual feed intake, and consequently milk production, in goats of different personalities.

7.2.3 Other literature gaps for future research consideration

There were some literature gaps identified in the review of Chapter 2 that I was unable to address in this thesis. In the remainder of this chapter I briefly discuss 3 important areas for future research that address the influence of personality in commercially managed dairy animals: 1) social relationships and effects on feeding behaviour, 2) feeding strategies and their impact on performance, and 3) consistency of behavioural responses to management practices over time and strategies to mitigate any negative responses.

Sociability (i.e. motivation to be close to other individuals) was a key personality trait discussed in Chapter 2 that had important links with feeding patterns of ruminants; however, the empirical work in this thesis did not include a measure of this personality trait. It is likely that some variation in feeding behaviours can be accounted for by this measure. For instance, in Chapters 3 and 4, sociability of dairy calves may have influenced early grain intake or visits to the milk feeder if these calves are more attentive to social information; these calves may therefore be more susceptible to social facilitation or social learning that increases the occurrence of these behaviours (see Sih and Bell, 2008). In Chapters 5 and 6, goats with more preferential affiliative relationships (i.e. high sociability) may have chosen to avoid conflict at the feeder, especially under high competitive pressure. This prediction is supported by Miranda-de la Lama et al. (2011), who found that affiliative goats were less involved in conflicts between two individuals and more likely to perform non-agonistic behaviours in support of one of the contenders. Future work should explore how sociability affects how individuals interact with their feeding environment and cope with challenging management practices.

Individual variability in feeding behaviour when in the same environmental conditions and management practices may also give rise to variability in the growth and productivity of individuals on commercial farms. In Chapters 3 and 4, I showed that personality traits of calves could account for variability in weight gains around weaning. However, there is little understanding of how personality affects other aspects of performance during later rearing and into maturity. There is evidence in beef cattle that more reactive individuals have compromised growth, finishing weight, carcass quality, and reproductive performance (reviewed by Haskell et al., 2014), but no studies have documented similar associations in dairy animals (apart from milk yield in dairy cattle; Sutherland and Dowling, 2014). This variability in performance measures may also be related to individuals adopting particular feeding strategies, with implications for the quality and quantity of feed consumed. For instance, goats with different social profiles (such as aggressive, affiliative, passive and avoider) had remarkably different feeding success (Miranda-de la Lama et al., 2011; Pascual-Alonso et al., 2013). I recommend future work to focus on how different personality types adopt different feeding strategies, and the relative success of these strategies in terms of quantity and quality of feed consumed. There may also be important associations with performance measures such as feed efficiency, reproductive success, and immune status (see work in beef cattle: Hulbert et al., 2011; Cooke et al., 2017). I see this information helping to inform which individuals may be at risk for culling (i.e. leaving the farm for sale or slaughter) given that 25 to 30% of cows (USDA, 2016) and 15 to 20% of goats (USDA, 2009) are culled each year, most due to production, fertility or health issues (Pinedo et al., 2010).

The empirical chapters of this thesis focused on just two of the many potentially challenging conditions that dairy cattle and goats experience during their lives on commercial dairy farms. Weaning, as described in Chapters 3 and 4, is one important stressor that calves and goats experience early in life, and how they respond to this stressor may offer insight into how these individuals will respond to other stressful situations later in life. There is merit in understanding if some individuals consistently respond poorly to stressors; there may be strategies to help mitigate negative responses to stressful practices. For instance, changes such as introduction to the milking parlour or feed lot, novel foods, or exposure to handling or restraint devices often occur in conjunction with negative experiences. Negative responses may be reduced by introducing novel diets before movement to a new feeding facility, or by pairing the experience of a restraining device with a food reward. Providing an experienced social model when moving animals to new pens may help naïve individuals (and perhaps those individuals that are most social) adjust more quickly to new feeding equipment (e.g. headlocks, electronic feed bins) or to new diets (e.g. during weaning). Individuals that are particularly calm in response to stressors may be effective social models for those that are more reactive, even if they are not knowledgeable or experienced. Such techniques are likely to be especially beneficial for individuals that are most reactive to stressful events. Alternatively, early identification of individuals that respond poorly to management practices may be a useful selection tool for determining which replacement heifers or kids to raise and which should be sold (since most farms do not rear all animals to enter the lactating herd; Hadley et al., 2006).

7.3 General conclusions

Throughout this thesis I have described the variability in feeding behaviour among individuals, and how personality differences can explain why some individuals do better than others when adjusting to changes in their feeding environment. I described how personality traits of dairy calves and goats can account for individual differences in feeding behaviour during stressors like weaning (Chapter 3 and 4) and feed competition (Chapter 6). I also investigated the use of alternatives to traditional feeding practices, such as an individualized weaning method for calves (Chapter 4), and the provision of elevated feeder heights for goats (Chapter 5). The work in this dissertation emphasizes a need for further work to understand how challenging management practices affect individuals of different personalities, and the possible implications for quality and quantity of feed intake, performance and welfare of these individuals during rearing and into lactation. Alternatives to traditional feeding practices that attend to individual needs and promote natural behaviour may provide the best opportunity for all individuals to succeed on the farm.

References

Alvarez, F. 1990. Horns and fighting in male Spanish Ibex, Capra pyrenaica. J. Mammal. 71:608–616. doi:10.2307/1381801.

Andrews, C., J. Viviani, E. Egan, T. Bedford, B. Brilot, D. Nettle, and M. Bateson. 2015. Early life adversity increases foraging and information gathering in European starlings, Sturnus vulgaris. Anim. Behav. 109:123–132. doi:10.1016/J.ANBEHAV.2015.08.009.

Arsenos, G., G.C. Emmans, and I. Kyriazakis. 2000. Variation between individuals and the consequences for diet selection by groups of animals. Anim. Behav. 60:811–820. doi:10.1006/anbe.2000.1544.

Aschwanden, J., L. Gygax, B. Wechsler, and N.M. Keil. 2008a. Cardiac activity in dairy goats whilst feeding side-by-side at two different distances and during social separation. Physiol. Behav. 95:641–648. doi:10.1016/J.PHYSBEH.2008.09.016.

Aschwanden, J., L. Gygax, B. Wechsler, and N.M. Keil. 2008b. Social distances of goats at the feeding rack: Influence of the quality of social bonds, rank differences, grouping age and presence of horns. Appl. Anim. Behav. Sci. 114:116–131. doi:10.1016/J.APPLANIM.2008.02.002.

Aschwanden, J., L. Gygax, B. Wechsler, and N.M. Keil. 2009a. Structural modifications at the feeding place: Effects of partitions and platforms on feeding and social behaviour of goats. Appl. Anim. Behav. Sci. 119:180–192. doi:10.1016/J.APPLANIM.2009.04.004.

Aschwanden, J., L. Gygax, B. Wechsler, and N.M. Keil. 2009b. Loose housing of small goat groups: Influence of visual cover and elevated levels on feeding, resting and agonistic behaviour. Appl. Anim. Behav. Sci. 119:171–179. doi:10.1016/J.APPLANIM.2009.04.005.

Askins, G.D., and E.E. Turner. 1972. A behavioral study of Angora goats on West Texas range. J. Range Manag. 25:82-. doi:10.2307/3896790.

Baciadonna, L., A.G. McElligott, and E.F. Briefer. 2013. Goats favour personal over social information in an experimental foraging task. PeerJ 1:e172. doi:10.7717/peerj.172.

Barnard, C.J., and R.M. Sibly. 1981. Producers and scroungers: A general model and its application to captive flocks of house sparrows. Anim. Behav. 29:543–550. doi:10.1016/S0003-3472(81)80117-0.

Barrier, A.C., E. Ruelle, M.J. Haskell, and C.M. Dwyer. 2012. Effect of a difficult calving on the vigour of the calf, the onset of maternal behaviour, and some behavioural indicators of pain in the dam. Prev. Vet. Med. 103:248–256. doi:10.1016/J.PREVETMED.2011.09.001.

Barroso, F.G., C.L. Alados, and J. Boza. 2000a. Social hierarchy in the domestic goat: effect on food habits and production. Appl. Anim. Behav. Sci. 69:35–53. doi:10.1016/S0168-1591(00)00113-1.

Barroso, F.G., C.L. Alados, and J. Boza. 2000b. Social hierarchy in the domestic goat: effect on food habits and production. Appl. Anim. Behav. Sci. 69:35–53. doi:10.1016/S0168-1591(00)00113-1.

Battini, M., S. Barbieri, S. Waiblinger, and S. Mattiello. 2016. Validity and feasibility of human-animal relationship tests for on-farm welfare assessment in dairy goats. Appl. Anim. Behav. Sci. 178:32–39. doi:10.1016/j.applanim.2016.03.012.

Baumont, R. 1996. Palatability and feeding behaviour in ruminants: a review. Ann. Zootech. 45:385–400.

Beauchamp, G. 2015. Animal Vigilance: Monitoring Predators and Competitors. Academic

Press, San Diego, CA.
Beausoleil, N.J., D. Blache, K.J. Stafford, D.J. Mellor, and A.D.L. Noble. 2012. Selection for temperament in sheep: Domain-general and context-specific traits. Appl. Anim. Behav. Sci. 139:74–85. doi:10.1016/j.applanim.2012.02.020.
Benetton, J., H. Neave, J. Costa, M. von Keyserlingk, and D. Weary. 2019. Automatic weaning based on individual solid feed intake: Effects on behavior and performance of dairy calves. doi:10.3168/jds.2018-15830.
Benus, R.F., B. Bohus, J.M. Koolhaas, and G.A. van Oortmerssen. 1991. Heritable variation for aggression as a reflection of individual coping strategies. Experientia 47:1008–1019. doi:10.1007/BF01923336.
Bergvall, U.A., A. Schäpers, P. Kjellander, and A. Weiss. 2011. Personality and foraging decisions in fallow deer, Dama dama. Anim. Behav. 81:101–112. doi:10.1016/j.anbehav.2010.09.018.
Bernal-Rigoli, J.C., J.D. Allen, J.A. Marchello, S.P. Cuneo, S.R. Garcia, G. Xie, L.W. Hall, C.D. Burrows, and G.C. Duff. 2012. Effects of housing and feeding systems on performance of neonatal Holstein bull calves. J. Anim. Sci. 90:2818–2825. doi:10.2527/jas.2011-4722.
Bethell, E.J., A. Holmes, A. Maclarnon, and S. Semple. 2012. Evidence that emotion mediates social attention in rhesus macaques. PLoS One 7:e44387. doi:10.1371/journal.pone.0044387.
Black, T.E., K.M. Bischoff, V.R.G. Mercadante, G.H.L. Marquezini, N. DiLorenzo, C.C. Chase, S.W. Coleman, T.D. Maddock, and G.C. Lamb. 2013. Relationships among performance, residual feed intake, and temperament assessed in growing beef heifers and subsequently as 3-year-old, lactating beef cows. J. Anim. Sci. 91:2254–2263. doi:10.2527/jas.2012-5242.
Blight, O., G. Albet Díaz-Mariblanca, X. Cerdá, and R. Boulay. 2016. A proactive–reactive syndrome affects group success in an ant species. Behav. Ecol. 27:118–125. doi:10.1093/beheco/arv127.
Boissy, A. 1995. Fear and fearfulness in animals. Q. Rev. Biol. 70:165–91.
Boissy, A., and P. Le Neindre. 1990. Social influences on the reactivity of heifers: Implications for learning abilities in operant conditioning. Appl. Anim. Behav. Sci. 25:149–165. doi:10.1016/0168-1591(90)90077-Q.
Bolhuis, J.E., W.G.P. Schouten, J.W. Schrama, and V.M. Wiegant. 2005. Individual coping characteristics, aggressiveness and fighting strategies in pigs. Anim. Behav. 69:1085–1091. doi:10.1016/j.anbehav.2004.09.013.
Borchers, M., Y. Chang, K. Proudfoot, B. Wadsworth, A. Stone, and J. Bewley. 2017. Machine-learning-based calving prediction from activity, lying, and ruminating behaviors in dairy cattle. doi:10.3168/jds.2016-11526.
Borderas, T.F., J. Rushen, M.A.G. von Keyserlingk, and A.M. de Passillé. 2009. Automated measurement of changes in feeding behavior of milk-fed calves associated with illness.. J. Dairy Sci. 92:4549–4554. doi:10.3168/jds.2009-2109.
Bouissou, M., A. Boissy, P. Le Neindre, and I. Veissier. 2001. The social behaviour of cattle. J.. Keeling and H.. Gonyou, ed. CABI Publishing, New York, NY.
Bovine Alliance on Management and Nutrition. 2017. A Guide to Feeding and Weaning Healthy and Productive Dairy Calves. Accessed November 5, 2017. https://www.aphis.usda.gov/animal_health/nahms/dairy/downloads/bamn/BAMN17_GuideFeeding.pdf.

Breuer, K., P.H. Hemsworth, J.L. Barnett, L.R. Matthews, and G.J. Coleman. 2000. Behavioural response to humans and the productivity of commercial dairy cows. Appl. Anim. Behav. Sci. 66:273–288.

Briefer, E.F., F. Tettamanti, and A.G. McElligott. 2015. Emotions in goats: Mapping physiological, behavioural and vocal profiles. Anim. Behav. 99:131–143. doi:10.1016/j.anbehav.2014.11.002.

Brown, J.A., C. Dewey, C.F.M. Delange, I.B. Mandell, P.P. Purslow, J.A. Robinson, E.J. Squires, and T.M. Widowski. 2009. Reliability of temperament tests on finishing pigs in group-housing and comparison to social tests. Appl. Anim. Behav. Sci. 118:28–35. doi:10.1016/J.APPLANIM.2009.02.005.

Bruno, K.A., E.S. Vanzant, K.A. Vanzant, and K.R. McLeod. 2016. Relationships of a novel objective chute score and exit velocity with growth performance of receiving cattle. J. Anim. Sci. 94:4819. doi:10.2527/jas.2016-0438.

Budzynska, M., and D.M. Weary. 2008. Weaning distress in dairy calves: Effects of alternative weaning procedures. Appl. Anim. Behav. Sci. 112:33–39. doi:10.1016/j.applanim.2007.08.004.

Burritt, E.A., and F.D. Provenza. 1997. Effect of an unfamiliar location on the consumption of novel and familiar foods by sheep. Appl. Anim. Behav. Sci. 54:317–325. doi:10.1016/S0168-1591(97)00005-1.

Butler, D., L. Holloway, and C. Bear. 2012. The impact of technological change in dairy farming: Robotic milking systems and the changing role of the stockperson. J. R. Agric. Soc. Engl. 173:1–6.

Cafe, L.M., D.L. Robinson, D.M. Ferguson, B.L. Mcintyre, G.H. Geesink, and P.L. Greenwood. 2011. Cattle temperament: Persistence of assessments and associations with productivity, efficiency, carcass and meat quality traits. J. Anim. Sci. 89:1452–1465. doi:10.2527/jas.2010-3304.

Canadian Dairy Information Centre. 2017. Goat Milk Production in Canada. Accessed July 6, 2019. https://www.dairyinfo.gc.ca/index_e.php?s1=dff-fcil&s2=farm-ferme&s3=prod&s4=gc.

Carter, A.J., W.E. Feeney, H.H. Marshall, G. Cowlishaw, and R. Heinsohn. 2013. Animal personality: What are behavioural ecologists measuring?. Biol. Rev. 88:465–475. doi:10.1111/brv.12007.

Chapple, R.S., and J.J. Lynch. 1986. Behavioural factors modifying acceptance of supplementary foods by sheep. Res. Dev. Agric. 3:113–120.

Cole, E.F., and J.L. Quinn. 2012. Personality and problem-solving performance explain competitive ability in the wild. Proc. R. Soc. B Biol. Sci. 279:1168–1175. doi:10.1098/rspb.2011.1539.

Cook, N.B., K.V. Nordlund, and G.R. Oetzel. 2004. Environmental influences on claw horn lesions associated with laminitis and subacute ruminal acidosis in dairy cows. J. Dairy Sci. 87:E36–E46. doi:10.3168/jds.S0022-0302(04)70059-4.

Cooke, R.F., K.M. Schubach, R.S. Marques, R.F. G Peres, L.G. T Silva, R. SCarvalho, R.S. Cipriano, D.W. Bohnert, A. V Pires, and J.L. M Vasconcelos. 2017. Effects of temperament on physiological, productive, and reproductive responses in Bos indicus beef cows 1. J. Animal Sci 95:1–8. doi:10.2527/jas2016.1098.

Coppens, C.M., S.F. de Boer, and J.M. Koolhaas. 2010. Coping styles and behavioural

flexibility: towards underlying mechanisms. Philos. Trans. R. Soc. B Biol. Sci. 365:4021–4028. doi:10.1098/rstb.2010.0217.
Costa, J.H.C., N.A. Adderley, D.M. Weary, and M.A.G. von Keyserlingk. 2016a. Short communication: Effect of diet changes on sorting behavior of weaned dairy calves. J. Dairy Sci. 99:5635–5639. doi:10.3168/jds.2015-10052.
Costa, J.H.C., W.G. Costa, D.M. Weary, L.C.P. Machado Filho, and M.A.G. von Keyserlingk. 2016b. Dairy heifers benefit from the presence of an experienced companion when learning how to graze. J. Dairy Sci. 99:562–568. doi:10.3168/jds.2015-9387.
Costa, J.H.C., R.R. Daros, M.A.G. von Keyserlingk, and D.M. Weary. 2014. Complex social housing reduces food neophobia in dairy calves. J. Dairy Sci. 97:7804–7810. doi:10.3168/jds.2014-8392.
Costa, J.H.C., M.A.G. von Keyserlingk, and D.M. Weary. 2016c. Invited review: Effects of group housing of dairy calves on behavior, cognition, performance, and health. J. Dairy Sci. 99:2453–2467. doi:10.3168/jds.2015-10144.
Costa, J.H.C., R.K. Meagher, M.A.G. von Keyserlingk, and D.M. Weary. 2015. Early pair housing increases solid feed intake and weight gains in dairy calves. J. Dairy Sci. 98:6381–6386. doi:10.3168/jds.2015-9395.
Crossley, R., A. Harlander-Matauschek, and T. DeVries. 2018. Mitigation of variability between competitively fed dairy cows through increased feed delivery frequency. J. Dairy Sci. 101:518–529. doi:10.3168/jds.2017-12930.
Crossley, R.E., A. Harlander-Matauschek, and T.J. DeVries. 2017. Variability in behavior and production among dairy cows fed under differing levels of competition. J. Dairy Sci. 100:3825–3838. doi:10.3168/JDS.2016-12108.
Crump, A., G. Arnott, E. Bethell, A. Crump, G. Arnott, and E.J. Bethell. 2018. Affect-driven attention biases as animal welfare indicators: Review and methods. Animals 8:136. doi:10.3390/ani8080136.
Curley, K.O., D.A. Neuendorff, A.W. Lewis, J.J. Cleere, T.H. Welsh, and R.D. Randel. 2008. Functional characteristics of the bovine hypothalamic–pituitary–adrenal axis vary with temperament. Horm. Behav. 53:20–27. doi:10.1016/j.yhbeh.2007.08.005.
Cziszter, L.T., D. Gavojdian, R. Neamt, F. Neciu, S. Kusza, and D.-E. Ilie. 2016. Effects of temperament on production and reproductive performances in Simmental dual-purpose cows. J. Vet. Behav. Clin. Appl. Res. 15:50–55. doi:10.1016/j.jveb.2016.08.070.
D'Eath, R.B., R. Roehe, S.P. Turner, S.H. Ison, M. Farish, M.C. Jack, and A.B. Lawrence. 2009. Genetics of animal temperament: Aggressive behaviour at mixing is genetically associated with the response to handling in pigs. Animal 3:1544–1554. doi:10.1017/S1751731109990528.
Daniels, K.J., S.S. Donkin, S.D. Eicher, E.A. Pajor, and M.M. Schutz. 2007. Prepartum milking of heifers influences future production and health. J. Dairy Sci. 90:2293–2301. doi:10.3168/jds.2005-881.
David, I., F. Bouvier, E. Ricard, J. Ruesche, and J.-L. Weisbecker. 2014. Feeding behaviour of artificially reared Romane lambs. Animal 8:982–990. doi:10.1017/S1751731114000603.
David, M., Y. Auclair, and F. Cézilly. 2011. Personality predicts social dominance in female zebra finches, Taeniopygia guttata, in a feeding context. Anim. Behav. 81:219–224. doi:10.1016/j.anbehav.2010.10.008.
Day, J.E.L., I. Kyriazakis, and P.J. Rogers. 1998. Food choice and intake: towards a unifying

framework of learning and feeding motivation. Nutr. Res. Rev. 11:25–43.
Deelen, S.M., K.E. Leslie, M.A. Steele, E. Eckert, H.E. Brown, and T.J. DeVries. 2016. Validation of a calf-side β-hydroxybutyrate test and its utility for estimation of starter intake in dairy calves around weaning. J. Dairy Sci. 99:7624–7633. doi:10.3168/jds.2016-11097.
Dennis, T.S., F.X. Suarez-Mena, T.M. Hill, J.D. Quigley, R.L. Schlotterbeck, R.N. Klopp, G.J. Lascano, and L. Hulbert. 2018. Effects of gradual and later weaning ages when feeding high milk replacer rates on growth, textured starter digestibility, and behavior in Holstein calves from 0 to 4 months of age. J. Dairy Sci. 101:9863–9875. doi:10.3168/JDS.2018-15319.
Désiré, L., I. Veissier, G. Després, and A. Boissy. 2004. On the way to assess emotions in animals: do lambs (Ovis aries) evaluate an event through its suddenness, novelty, or unpredictability?. J. Comp. Psychol. 118:363–74. doi:10.1037/0735-7036.118.4.363.
de Passillé, A.M. 2001. Sucking motivation and related problems in calves. Appl. Anim. Behav. Sci. 72:175–187. doi:10.1016/S0168-1591(01)00108-3.
de Passillé, A.M., T.F. Borderas, and J. Rushen. 2011. Weaning age of calves fed a high milk allowance by automated feeders: Effects on feed, water, and energy intake, behavioral signs of hunger, and weight gains. J. Dairy Sci. 94:1401–1408. doi:10.3168/jds.2010-3441.
de Passillé, A.M., M. Rabeyrin, and J. Rushen. 2016. Associations between milk intake and activity in the first days of a calf's life and later growth and health. Appl. Anim. Behav. Sci. 175:2–7. doi:10.1016/j.applanim.2014.10.002.
de Passillé, A.M., and J. Rushen. 2012. Adjusting the weaning age of calves fed by automated feeders according to individual intakes of solid feed. J. Dairy Sci. 95:5292–5298. doi:10.3168/jds.2012-5521.
de Passillé, A.M., and J. Rushen. 2016. Using automated feeders to wean calves fed large amounts of milk according to their ability to eat solid feed. J. Dairy Sci. 99:3578–3583. doi:10.3168/jds.2015-10259.
de Passillé, A.M., J. Rushen, and F. Martin. 1995. Interpreting the behaviour of calves in an open-field test: a factor analysis. Appl. Anim. Behav. Sci. 45:201–213. doi:10.1016/0168-1591(95)00622-Y.
de Passillé, A.M.B., and J. Rushen. 2006. Calves' behaviour during nursing is affected by feeding motivation and milk availability. Appl. Anim. Behav. Sci. 101:264–275. doi:10.1016/J.APPLANIM.2006.02.007.
de Paula Vieira, A., V. Guesdon, A.M. de Passillé, M.A.G. von Keyserlingk, and D.M. Weary. 2008. Behavioural indicators of hunger in dairy calves. Appl. Anim. Behav. Sci. 109:180–189. doi:10.1016/j.applanim.2007.03.006.
de Paula Vieira, A., M.A.G. von Keyserlingk, and D.M. Weary. 2010. Effects of pair versus single housing on performance and behavior of dairy calves before and after weaning from milk. J. Dairy Sci. 93:3079–3085. doi:10.3168/jds.2009-2516.
de Paula Vieira, A., M.A.G. von Keyserlingk, and D.M. Weary. 2012. Presence of an older weaned companion influences feeding behavior and improves performance of dairy calves before and after weaning from milk. J. Dairy Sci. 95:3218–3224. doi:10.3168/jds.2011-4821.
DeVries, T.J., and M.A.G. von Keyserlingk. 2006. Feed stalls affect the social and feeding behavior of lactating dairy cows. J. Dairy Sci. 89:3522–3531. doi:10.3168/jds.S0022-0302(06)72392-X.
DeVries, T.J., M.A.G. von Keyserlingk, D.M. Weary, and K.A. Beauchemin. 2003. Measuring

the feeding behavior of lactating dairy cows in early to peak lactation. J. Dairy Sci. 86:3354–3361. doi:10.3168/jds.S0022-0302(03)73938-1.
Dingemanse, N.J., A.J.N. Kazem, D. Réale, and J. Wright. 2010. Behavioural reaction norms: animal personality meets individual plasticity. Trends Ecol. Evol. 25:81–89. doi:10.1016/j.tree.2009.07.013.
Dodd, C.L., W.S. Pitchford, J.E. Hocking Edwards, and S.J. Hazel. 2012. Measures of behavioural reactivity and their relationships with production traits in sheep: A review. Appl. Anim. Behav. Sci. 140:1–15. doi:10.1016/j.applanim.2012.03.018.
Dumont, B., and A. Boissy. 2000. Grazing behaviour of sheep in a situation of conflict between feeding and social motivations. Behav. Processes 49:131–138. doi:10.1016/S0376-6357(00)00082-6.
Dumont, B., A. Boissy, C. Achard, A.M. Sibbald, and H.W. Erhard. 2005. Consistency of animal order in spontaneous group movements allows the measurement of leadership in a group of grazing heifers. Appl. Anim. Behav. Sci. 95:55–66. doi:10.1016/j.applanim.2005.04.005.
Dziba, L., P. Scogings, I. Gordon, and J. Raats. 2003. The feeding height preferences of two goat breeds fed Grewia occidentalis L. (Tiliaceae) in the Eastern Cape, South Africa. Small Rumin. Res. 47:31–38. doi:10.1016/S0921-4488(02)00234-1.
Egea, A. V., L. Allegretti, S. Paez Lama, D. Grilli, C. Sartor, M. Fucili, J.C. Guevara, and C. Passera. 2014. Selective behavior of Creole goats in response to the functional heterogeneity of native forage species in the central Monte desert, Argentina. Small Rumin. Res. 120:90–99. doi:10.1016/j.smallrumres.2014.04.005.
Eitam, H., J. Vaya, A. Brosh, A. Orlov, S. Khatib, I. Izhaki, and A. Shabtay. 2010. Differential stress responses among newly received calves: Variations in reductant capacity and Hsp gene expression. Cell Stress Chaperones 15:865–876. doi:10.1007/s12192-010-0195-9.
El Aich, A., N. El Assouli, A. Fathi, P. Morand-Fehr, and A. Bourbouze. 2007. Ingestive behavior of goats grazing in the Southwestern Argan (Argania spinosa) forest of Morocco. Small Rumin. Res. 70:248–256. doi:10.1016/j.smallrumres.2006.03.011.
Ellenbogen, M.A., A.E. Schwartzman, J. Stewart, and C.-D. Walker. 2002. Stress and selective attention: The interplay of mood, cortisol levels, and emotional information processing. Psychophysiology 39:723–732. doi:10.1017/S0048577202010739.
Elzo, M.A., D.G. Riley, G.R. Hansen, D.D. Johnson, R.O. Myer, S.W. Coleman, C.C. Chase, J.G. Wasdin, and J.D. Driver. 2009. Effect of breed composition on phenotypic residual feed intake and growth in Angus, Brahman, and Angus x Brahman crossbred cattle. J. Anim. Sci. 87:3877–3886. doi:10.2527/jas.2008-1553.
Endres, M.I., T.J. DeVries, M.A.G. von Keyserlingk, and D.M. Weary. 2005. Short Communication: Effect of feed barrier design on the behavior of loose-housed lactating dairy cows. J. Dairy Sci. 88:2377–2380. doi:10.3168/jds.S0022-0302(05)72915-5.
Enríquez, D., M.J. Hötzel, and R. Ungerfeld. 2011. Minimising the stress of weaning of beef calves: a review.. Acta Vet. Scand. 53:28. doi:10.1186/1751-0147-53-28.
Escós, J., C.L. Alados, and J. Boza. 1993. Leadership in a domestic goat herd. Appl. Anim. Behav. Sci. 38:41–47. doi:10.1016/0168-1591(93)90040-V.
FAO. 2019. Faostat, Livestock Primary. Accessed July 5, 2019. http://www.fao.org/faostat/en/?#data/QL.
Favati, A., O. Leimar, H. Løvlie, F. Weissing, and S. Winberg. 2014. Personality predicts social dominance in male domestic fowl. PLoS One 9:e103535.

doi:10.1371/journal.pone.0103535.
Fell, L.R., I.G. Colditz, K.H. Walker, and D.L. Watson. 1999. Associations between temperament, performance and immune function in cattle entering a commercial feedlot. Aust. J. Exp. Agric. 39:795–802. doi:10.1071/EA99027.
Forbes, J.M., and I. Kyriazakis. 1995. Food preferences in farm animals: why don't they always choose wisely?. Proc. Nutr. Soc. 54:429–440. doi:10.1079/PNS19950012.
Forkman, B., A. Boissy, M.C. Meunier-Salaün, E. Canali, and R.B. Jones. 2007. A critical review of fear tests used on cattle, pigs, sheep, poultry and horses. Physiol. Behav. 92:340–374. doi:10.1016/j.physbeh.2007.03.016.
Francisco, C.L., R.F. Cooke, R.S. Marques, R.R. Mills, and D.W. Bohnert. 2012. Effects of temperament and acclimation to handling on feedlot performance of Bos taurus feeder cattle originated from a rangeland-based cow-calf system. J. Anim. Sci. 90:5067–5077. doi:10.2527/jas.2012-5447.
Francisco, C.L., F.D. Resende, J.M.B. Benatti, A.M. Castilhos, R.F. Cooke, and A.M. Jorge. 2015. Impacts of temperament on Nellore cattle: physiological responses, feedlot performance, and carcass characteristics. J. Anim. Sci. 93:5419–5429. doi:10.2527/jas.2015-9411.
Fujiwara, M., J. Rushen, and A.M. de Passillé. 2014. Dairy calves' adaptation to group housing with automated feeders. Appl. Anim. Behav. Sci. 158:1–7. doi:10.1016/J.APPLANIM.2014.06.011.
Furman-Fratczak, K., A. Rzasa, and T. Stefaniak. 2011. The influence of colostral immunoglobulin concentration in heifer calves' serum on their health and growth. J. Dairy Sci. 94:5536–5543. doi:10.3168/JDS.2010-3253.
Galef, B.G., and K.N. Laland. 2005. Social learning in animals: Empirical studies and theoretical models. Bioscience 55:489. doi:10.1641/0006-3568(2005)055[0489:SLIAES]2.0.CO;2.
Galindo, F., and D.M. Broom. 2000. The relationships between social behaviour of dairy cows and the occurrence of lameness in three herds. Res. Vet. Sci. 69:75–79. doi:10.1053/rvsc.2000.0391.
Geist, V. 1966. The evolution of horn-like organs. Behaviour 27:175–214.
Gelsinger, S.L., A.J. Heinrichs, and C.M. Jones. 2016. A meta-analysis of the effects of preweaned calf nutrition and growth on first-lactation performance. J. Dairy Sci. 99:6206–6214. doi:10.3168/JDS.2015-10744.
Gibbons, J.M., A.B. Lawrence, and M.J. Haskell. 2010. Measuring sociability in dairy cows. Appl. Anim. Behav. Sci. 122:84–91. doi:10.1016/j.applanim.2009.11.011.
Gilbert, M.S., J.J.G.C. van den Borne, C.G. van Reenen, and W.J.J. Gerrits. 2017. Only 7% of the variation in feed efficiency in veal calves can be predicted from variation in feeding motivation, digestion, metabolism, immunology, and behavioral traits in early life. J. Dairy Sci. 100:8087–8101. doi:10.3168/JDS.2016-12390.
Giraldeau, L.A., and T. Caraco. 2000. Social Foraging Theory. Princeton University Press, Princeton, NJ.
Goetsch, A.L., T.A. Gipson, A.R. Askar, and R. Puchala. 2010. Invited review: Feeding behavior of goats. J. Anim. Sci. 88:361–373. doi:10.2527/jas.2009-2332.
González, L.A., I. Kyriazakis, and L.O. Tedeschi. 2018. Review: Precision nutrition of ruminants: approaches, challenges and potential gains. animal 12:s246–s261. doi:10.1017/S1751731118002288.

Gosling, S.D., and O.P. John. 1999. Personality Dimensions in Nonhuman Animals. Curr. Dir. Psychol. Sci. 8:69–75. doi:10.1111/1467-8721.00017.

Grant, R.J., and J.L. Albright. 2000. Feeding Behaviour. J.P. Felix D'Mello, ed. CABI, New York, NY.

Greenwood, P.L., and L.M. Cafe. 2007. Prenatal and pre-weaning growth and nutrition of cattle: long-term consequences for beef production. Animal 1:1283–1296. doi:DOI: https://doi.org/10.1017/S175173110700050X.

Greenwood, P.L., A.. Hunt, J.W. Hermanson, and A.. Bell. 1998. Effects of birth weight and postnatal nutrition on neonatal sheep: I. Body growth and composition, and some aspects of energetic efficiency. J. Anim. Sci. 76:2354–2367.

Gutmann, A.K., M. Špinka, and C. Winckler. 2015. Long-term familiarity creates preferred social partners in dairy cows. Appl. Anim. Behav. Sci. 169:1–8. doi:10.1016/j.applanim.2015.05.007.

Hadley, G.L., C.A. Wolf, and S.B. Harsh. 2006. Dairy cattle culling patterns, explanations, and implications. J. Dairy Sci. 89:2286–2296. doi:10.3168/JDS.S0022-0302(06)72300-1.

Haskell, M.J., G. Simm, and S.P. Turner. 2014. Genetic selection for temperament traits in dairy and beef cattle.. Front. Genet. 5:368. doi:10.3389/fgene.2014.00368.

Hedlund, L., and H. Løvlie. 2015. Personality and production: Nervous cows produce less milk. J. Dairy Sci. 98:5819–5828. doi:10.3168/jds.2014-8667.

Heinrichs, A.J., and B.S. Heinrichs. 2011. A prospective study of calf factors affecting first-lactation and lifetime milk production and age of cows when removed from the herd. J. Dairy Sci. 94:336–341. doi:10.3168/JDS.2010-3170.

Hessing, M.J., A.M. Hagelsø, W.G. Schouten, P.R. Wiepkema, and J.A. Van Beek. 1994. Individual behavioral and physiological strategies in pigs. Physiol. Behav. 55:39–46. doi:10.1016/0031-9384(94)90007-8.

Hessle, A.K. 2009. Effects of social learning on foraging behaviour and live weight gain in first-season grazing calves. Appl. Anim. Behav. Sci. 116:150–155. doi:10.1016/j.applanim.2008.08.004.

Hewitson, L. 2002. The foraging behaviour of sheep in response to environmental uncertainty. University of Edinburgh,.

Hewitson, L., I.J. Gordon, and B. Dumont. 2007. Social context affects patch-leaving decisions of sheep in a variable environment. Anim. Behav. 74:239–246. doi:10.1016/j.anbehav.2006.07.020.

Hosseinkhani, A., T.J. DeVries, K.L. Proudfoot, R. Valizadeh, D.M. Veira, and M.A.G. von Keyserlingk. 2008. The effects of feed bunk competition on the feed sorting behavior of close-up dry cows. J. Dairy Sci. 91:1115–1121. doi:10.3168/jds.2007-0679.

Hötzel, M.J., C. Longo, L.F. Balcão, C.S. Cardoso, and J.H.C. Costa. 2014. A survey of management practices that influence performance and welfare of dairy calves reared in Southern Brazil. PLoS One 9:e114995. doi:10.1371/journal.pone.0114995.

Hulbert, L.E., J.A. Carroll, N.C. Burdick, R.D. Randel, M.S. Brown, and M.A. Ballou. 2011. Innate immune responses of temperamental and calm cattle after transportation. Vet. Immunol. Immunopathol. 143:66–74. doi:10.1016/j.vetimm.2011.06.025.

Huzzey, J.M., T.J. DeVries, P. Valois, and M.A.G. von Keyserlingk. 2006. Stocking density and feed barrier design affect the feeding and social behavior of dairy cattle. J. Dairy Sci. 89:126–133. doi:10.3168/jds.S0022-0302(06)72075-6.

Huzzey, J.M., J.A. Fregonesi, M.A.G. von Keyserlingk, and D.M. Weary. 2013. Sampling behavior of dairy cattle: Effects of variation in dietary energy density on behavior at the feed bunk. J. Dairy Sci. 96:247–256. doi:10.3168/jds.2012-5796.

Jensen, M.B. 2004. Computer-controlled milk feeding of dairy calves: The effects of number of calves per feeder and number of milk portions on use of feeder and social behavior. J. Dairy Sci. 87:3428–3438. doi:10.3168/jds.S0022-0302(04)73478-5.

Jensen, M.B., and L. Holm. 2003. The effect of milk flow rate and milk allowance on feeding related behaviour in dairy calves fed by computer controlled milk feeders. Appl. Anim. Behav. Sci. 82:87–100. doi:10.1016/S0168-1591(03)00054-6.

Jones, K.A., and J.-G.J. Godin. 2010. Are fast explorers slow reactors? Linking personality type and anti-predator behaviour. Proc. R. Soc. B Biol. Sci. 277:625–632. doi:10.1098/rspb.2009.1607.

Jørgensen, G.H.M., I.L. Andersen, and K.E. Bøe. 2007. Feed intake and social interactions in dairy goats-The effects of feeding space and type of roughage. Appl. Anim. Behav. Sci. 107:239–251. doi:10.1016/j.applanim.2006.10.007.

Keil, N.M., M. Pommereau, A. Patt, B. Wechsler, and L. Gygax. 2017. Determining suitable dimensions for dairy goat feeding places by evaluating body posture and feeding reach. J. Dairy Sci. 100:1353–1362. doi:10.3168/jds.2016-10980.

von Keyserlingk, M., and D. Weary. 2010. Review: Feeding behaviour of dairy cattle: Measures and applications. Can. J. Anim. Sci. 90:303–309. doi:10.4141/CJAS09127.

Khan, M.A., A. Bach, D.M. Weary, and M.A.G. von Keyserlingk. 2016. Invited review: Transitioning from milk to solid feed in dairy heifers. J. Dairy Sci. 99:885–902. doi:10.3168/jds.2015-9975.

Khan, M.A., H.J. Lee, W.S. Lee, H.S. Kim, S.B. Kim, K.S. Ki, J.K. Ha, H.G. Lee, and Y.J. Choi. 2007. Pre- and postweaning performance of Holstein female calves fed milk through step-down and conventional methods. J. Dairy Sci. 90:876–885. doi:10.3168/JDS.S0022-0302(07)71571-0.

Kirkden, R.D., and E.A. Pajor. 2006. Using preference, motivation and aversion tests to ask scientific questions about animals' feelings. Appl. Anim. Behav. Sci. 100:29–47. doi:10.1016/J.APPLANIM.2006.04.009.

Koolhaas, J.M., S.F. De Boer, B. Buwalda, and K. Van Reenen. 2007. Individual variation in coping with stress: A multidimensional approach of ultimate and proximate mechanisms. Brain. Behav. Evol. 70:218–226. doi:10.1159/000105485.

Koolhaas, J.M., S.M. Korte, S.F. De Boer, B.J. Van Der Vegt, C.G. Van Reenen, H. Hopster, I.C. De Jong, M.A.W. Ruis, and H.J. Blokhuis. 1999. Coping styles in animals: current status in behavior and stress-physiology. Neurosci. Biobehav. Rev. 23:925–935. doi:10.1016/S0149-7634(99)00026-3.

Koolhaas, J.M., and C.G. Van Reenen. 2016. Animal behavior and well-being symposium: Interaction between coping style/personality, stress, and welfare: Relevance for domestic farm animals. J. Anim. Sci. 94:2284–2296. doi:10.2527/jas2015-0125.

Krohn, C.C., and S.P. Konggaard. 1979. Effects of isolating first-lactation cows from older cows. Livest. Prod. Sci. 6:137–146. doi:10.1016/0301-6226(79)90015-0.

Kurvers, R.H.J.M., S. Hamblin, and L.A. Giraldeau. 2012. The effect of exploration on the use of producer-scrounger tactics. PLoS One 7:e49400. doi:10.1371/journal.pone.0049400.

Kyriazakis, I., B.J. Tolkamp, and G. Emmans. 1999. Diet selection and animal state: an

integrative framework. Proc. Nutr. Soc. 58:765–772. doi:10.1017/S0029665199001044.
Laland, K.N. 2004. Social learning strategies. Anim. Learn. Behav. 32:4–14. doi:10.3758/BF03196002.
Lauber, M.C.Y., P.H. Hemsworth, and J.L. Barnett. 2006. The effects of age and experience on behavioural development in dairy calves. Appl. Anim. Behav. Sci. 99:41–52. doi:10.1016/j.applanim.2005.10.009.
Launchbaugh, K.L., and L.D. Howery. 2005. Understanding landscape use patterns of livestock as a consequence of foraging behavior. Rangel. Ecol. Manag. 58:99–108. doi:10.2111/03-146.1.
Launchbaugh, K.L., F.D. Provenza, and M.J. Werkmeister. 1997. Overcoming food neophobia in domestic ruminants through addition of a familiar flavor and repeated exposure to novel foods. Appl. Anim. Behav. Sci. 54:327–334. doi:10.1016/S0168-1591(96)01194-X.
Lecorps, B., D.M. Weary, and M.A.G. von Keyserlingk. 2018. Pessimism and fearfulness in dairy calves. Sci. Rep. 8:1421. doi:10.1038/s41598-017-17214-3.
Lee, C., L.M. Cafe, S.L. Robinson, R.E. Doyle, J.M. Lea, A.H. Small, and I.G. Colditz. 2017. Anxiety influences attention bias but not flight speed and crush score in beef cattle. Appl. Anim. Behav. Sci. 0–1. doi:10.1016/j.applanim.2017.11.003.
Lee, C., E. Verbeek, R. Doyle, and M. Bateson. 2016. Attention bias to threat indicates anxiety differences in sheep.. Biol. Lett. 12:20150977. doi:10.1098/rsbl.2015.0977.
Lensink, B., C. van Reenen, B. Engel, T. Rodenburg, and I. Veissier. 2003. Repeatability and reliability of an approach test to determine calves' responsiveness to humans: "a brief report". Appl. Anim. Behav. Sci. 83:325–330. doi:10.1016/S0168-1591(03)00138-2.
Lensink, B.J., X. Fernandez, X. Boivin, P. Pradel, P. Le Neindre, and I. Veissier. 2000. The impact of gentle contacts on ease of handling, welfare, and growth of calves and on quality of veal meat. J. Anim. Sci. 78:1219–1226.
Leonardi, C., and L.E. Armentano. 2003. Effect of quantity, quality, and length of alfalfa hay on selective consumption by dairy cows. J. Dairy Sci. 86:557–564. doi:10.3168/jds.S0022-0302(03)73634-0.
Llonch, P., M. Somarriba, C.-A. Duthie, M.J. Haskell, J.A. Rooke, S. Troy, R. Roehe, and S.P. Turner. 2016. Association of temperament and acute stress responsiveness with productivity, feed efficiency, and methane emissions in beef cattle: An observational study. Front. Vet. Sci. 3:1–9. doi:10.3389/fvets.2016.00043.
Lockwood, S.A., H.G. Kattesh, P.D. Krawczel, F.D. Kirkpatrick, A.M. Saxton, J.D. Rhinehart, and J.B. Wilkerson. 2015. Relationships among temperament, behavior, and growth during performance testing of bulls. J. Anim. Sci. 93:5856. doi:10.2527/jas.2015-9302.
Loerch, S.C., and F.L. Fluharty. 1999. Physiological changes and digestive capabilities of newly received feedlot cattle. J. Anim. Sci. 77.
Loretz, C., B. Wechsler, R. Hauser, and P. Rüsch. 2004. A comparison of space requirements of horned and hornless goats at the feed barrier and in the lying area. Appl. Anim. Behav. Sci. 87:275–283. doi:10.1016/j.applanim.2004.01.005.
Løvendahl, P., and L. Munksgaard. 2016. An investigation into genetic and phenotypic variation in time budgets and yield of dairy cows. J. Dairy Sci. 99:408–417. doi:10.3168/jds.2015-9838.
Lu, C.D. 1988. Grazing behavior and diet selection of goats. Small Rumin. Res. 1:205–216. doi:10.1016/0921-4488(88)90049-1.

Lynch, J.J., G.N. Hinch, and D.B. Adams. 1992. The Behaviour of Sheep : Biological Principles and Implications for Production. C.A.B. International.
Mainardes, G.., and T.J. DeVries. 2016. Effect of social feeding environment on the feeding behaviour of dairy cows and their willingness to consume a novel feed. Appl. Anim. Behav. Sci. 185:23–29. doi:10.1016/j.applanim.2016.10.002.
Marchetti, C., and P.J. Drent. 2000. Individual differences in the use of social information in foraging by captive great tits. Anim. Behav. 60:131–140. doi:10.1006/anbe.2000.1443.
McCowan, L.S.C., and S.C. Griffith. 2015. Active but asocial: exploration and activity is linked to social behaviour in a colonially breeding finch. Behaviour 152:1145–1167. doi:10.1163/1568539X-00003272.
Meagher, R.K., D.M. Weary, and M.A.G. von Keyserlingk. 2017. Some like it varied: Individual differences in preference for feed variety in dairy heifers. Appl. Anim. Behav. Sci. 195:8–14. doi:10.1016/j.applanim.2017.06.006.
Meale, S.J., F. Chaucheyras-Durand, H. Berends, L.L. Guan, and M.A. Steele. 2017. From pre- to postweaning: Transformation of the young calf's gastrointestinal tract. J. Dairy Sci. 100:5984–5995. doi:10.3168/JDS.2016-12474.
Medrano-Galarza, C., S.J. LeBlanc, T.J. DeVries, A. Jones-Bitton, J. Rushen, A. Marie de Passillé, M.I. Endres, and D.B. Haley. 2018. Effect of age of introduction to an automated milk feeder on calf learning and performance and labor requirements. J. Dairy Sci. 101:9371–9384. doi:10.3168/JDS.2018-14390.
Melin, M., H. Wiktorsson, and L. Norell. 2005. Analysis of feeding and drinking patterns of dairy cows in two cow traffic situations in automatic milking systems.. J. Dairy Sci. 88:71–85. doi:10.3168/jds.S0022-0302(05)72664-3.
Mellado, M., L. Olivares, W. Pittroff, H. Díaz, R. López, and J.A. Villarreal. 2007. Oral morphology and dietary choices of goats on rangeland. Small Rumin. Res. 71:194–199. doi:10.1016/j.smallrumres.2006.06.005.
Mellado, M., A. Rodriguez, J.A. Villarreal, and A. Olvera. 2005. The effect of pregnancy and lactation on diet composition and dietary preference of goats in a desert rangeland. Small Rumin. Res. 58:79–85. doi:10.1016/j.smallrumres.2004.07.014.
Melotti, L., M. Oostindjer, J.E. Bolhuis, S. Held, and M. Mendl. 2011. Coping personality type and environmental enrichment affect aggression at weaning in pigs. Appl. Anim. Behav. Sci. 133:144–153. doi:10.1016/J.APPLANIM.2011.05.018.
Michelena, P., A.M. Sibbald, H.W. Erhard, and J.E. McLeod. 2009. Effects of group size and personality on social foraging: The distribution of sheep across patches. Behav. Ecol. 20:145–152. doi:10.1093/beheco/arn126.
Miller-Cushon, E., and T. DeVries. 2016. Effect of social housing on the development of feeding behavior and social feeding preferences of dairy calves. J. Dairy Sci. 99:1406–1417. doi:10.3168/jds.2015-9869.
Miller-Cushon, E.K., and T.J. DeVries. 2011. Effect of early feed type exposure on diet-selection behavior of dairy calves. J. Dairy Sci. 94:342–350. doi:10.3168/jds.2010-3382.
Miller-Cushon, E.K., and T.J. DeVries. 2015. Invited review: Development and expression of dairy calf feeding behaviour. Can. J. Anim. Sci. 95:341–350. doi:10.4141/cjas-2014-163.
Miller, K., and D.G.M. Wood-Gush. 1991. Some effects of housing on the social behaviour of dairy cows. Anim. Prod. 53:271–278. doi:10.1017/S0003356100020262.
Miranda-de la Lama, G.C., and S. Mattiello. 2010. The importance of social behaviour for goat

welfare in livestock farming. Small Rumin. Res. 90:1–10. doi:10.1016/j.smallrumres.2010.01.006.
Miranda-de la Lama, G.C., W.S. Sepúlveda, H.H. Montaldo, G.A. María, and F. Galindo. 2011. Social strategies associated with identity profiles in dairy goats. Appl. Anim. Behav. Sci. 134:48–55. doi:10.1016/j.applanim.2011.06.004.
Montoro, C., I. Ipharraguerre, and A. Bach. 2011. Effect of flavoring a starter in a same manner as a milk replacer on intake and performance of calves. Anim. Feed Sci. Technol. 164:130–134. doi:10.1016/J.ANIFEEDSCI.2010.11.023.
MPI. 2018. NZ Code of Welfare: Goats51.
Müller, R., and M.A.G. von Keyserlingk. 2006. Consistency of flight speed and its correlation to productivity and to personality in Bos taurus beef cattle. Appl. Anim. Behav. Sci. 99:193–204. doi:10.1016/j.applanim.2005.05.012.
Muri, K., S.M. Stubsjøen, and P.S. Valle. 2013. Development and testing of an on-farm welfare assessment protocol for dairy goats. Anim. Welf. 22:385–400. doi:10.7120/09627286.22.3.385.
Murray, C.F. 2014. Characteristics, risk factors and management programs for vitality of newborn dairy calves. PhD Thesis. University of Guelph, Ontario, Canada,.
Murray, C.F., and K.E. Leslie. 2013. Newborn calf vitality: Risk factors, characteristics, assessment, resulting outcomes and strategies for improvement. Vet. J. 198:322–328. doi:10.1016/J.TVJL.2013.06.007.
Murray, C.F., D.M. Veira, A.L. Nadalin, D.M. Haines, M.L. Jackson, D.L. Pearl, and K.E. Leslie. 2015. The effect of dystocia on physiological and behavioral characteristics related to vitality and passive transfer of immunoglobulins in newborn Holstein calves.. Can. J. Vet. Res. 79:109–19.
Natarajan, D., H. de Vries, D.-J. Saaltink, S.F. de Boer, and J.M. Koolhaas. 2009. Delineation of violence from functional aggression in mice: An ethological approach. Behav. Genet. 39:73–90. doi:10.1007/s10519-008-9230-3.
Nawroth, C., E. von Borell, and J. Langbein. 2015. 'Goats that stare at men': dwarf goats alter their behaviour in response to human head orientation, but do not spontaneously use head direction as a cue in a food-related context. Anim. Cogn. 18:65–73. doi:10.1007/s10071-014-0777-5.
Nawroth, C., P.M. Prentice, and A.G. McElligott. 2017. Individual personality differences in goats predict their performance in visual learning and non-associative cognitive tasks. Behav. Processes 134:43–53. doi:10.1016/J.BEPROC.2016.08.001.
Neave, H.W., J.H.C. Costa, D.M. Weary, and M.A.G. von Keyserlingk. 2018a. Personality is associated with feeding behavior and performance in dairy calves. J. Dairy Sci. 101:7437–7449. doi:10.3168/JDS.2017-14248.
Neave, H.W., M.A.G. von Keyserlingk, D.M. Weary, and G. Zobel. 2018b. Feed intake and behavior of dairy goats when offered an elevated feed bunk. J. Dairy Sci. 101:3303–3310. doi:10.3168/JDS.2017-13934.
Neave, H.W., D.M. Weary, and M.A.G. von Keyserlingk. 2018c. Review: Individual variability in feeding behaviour of domesticated ruminants. animal 12:s419–s430. doi:10.1017/S1751731118001325.
Neisen, G., B. Wechsler, and L. Gygax. 2009. Effects of the introduction of single heifers or pairs of heifers into dairy-cow herds on the temporal and spatial associations of heifers and

cows. Appl. Anim. Behav. Sci. 119:127–136. doi:10.1016/j.applanim.2009.04.006.
Neja, W., A. Sawa, M. Jankowska, M. Bogucki, and S. Kr˛ E˙ Zel-Czopek. 2015. Effect of the temperament of dairy cows on lifetime production efficiency. Arch. Anim. Breed 58:193–197. doi:10.5194/aab-58-193-2015.
Ngwa, A.T., D.K. Pone, and J.M. Mafeni. 2000. Feed selection and dietary preferences of forage by small ruminants grazing natural pastures in the Sahelian zone of Cameroon 88:253–266. doi:10.1016/S0377-8401(00)00215-7.
Nicol, A.M., and M.A. Sharafeldin. 1975. Observations on the behaviour of single-suckled calves from birth to 120 days. Proc N Z Soc Anim Prod 35:221–230.
Nicol, C.J. 1995. The social transmission of information and behaviour. Appl. Anim. Behav. Sci. 44:79–98. doi:10.1016/0168-1591(95)00607-t.
Nielsen, B.L. 1999. On the interpretation of feeding behaviour measures and the use of feeding rate as an indicator of social constraint. Appl. Anim. Behav. Sci. 63:79–91. doi:10.1016/S0168-1591(99)00003-9.
Nielsen, P.P., M.B. Jensen, and L. Lidfors. 2008. Milk allowance and weaning method affect the use of a computer controlled milk feeder and the development of cross-sucking in dairy calves. Appl. Anim. Behav. Sci. 109:223–237. doi:10.1016/J.APPLANIM.2007.01.015.
Nkrumah, J.D., D.H. Crews, J.A. Basarab, M.A. Price, E.K. Okine, Z. Wang, C. Li, and S.S. Moore. 2007. Genetic and phenotypic relationships of feeding behavior and temperament with performance, feed efficiency, ultrasound, and carcass merit of beef cattle. J. Anim. Sci. 85:2382. doi:10.2527/jas.2006-657.
Nomakuchi, S., P.J. Park, and M.A. Bell. 2009. Correlation between exploration activity and use of social information in three-spined sticklebacks. Behav. Ecol. 20:340–345. doi:10.1093/beheco/arp001.
Nordmann, E., K. Barth, A. Futschik, R. Palme, and S. Waiblinger. 2015. Head partitions at the feed barrier affect behaviour of goats. Appl. Anim. Behav. Sci. 167:9–19. doi:10.1016/j.applanim.2015.03.011.
Nordmann, E., N.M. Keil, C. Schmied-Wagner, C. Graml, J. Langbein, J. Aschwanden, J. von Hof, K. Maschat, R. Palme, and S. Waiblinger. 2011. Feed barrier design affects behaviour and physiology in goats. Appl. Anim. Behav. Sci. 133:40–53. doi:10.1016/J.APPLANIM.2011.04.016.
NRC (National Research Council). 2007. Nutrient Requirements of Small Ruminants: Sheep, Goats, Cervids, and New World Camelids. National Academies Press, Washington, D.C.
Olofsson, J. 1999. Competition for total mixed diets fed for ad libitum intake using one or four cows per feeding station. J. Dairy Sci. 82:69–79. doi:10.3168/jds.S0022-0302(99)75210-0.
Pascual-Alonso, M., G.A. María, W.S. Sepúlveda, M. Villarroel, L. Aguayo-Ulloa, F. Galindo, and G.C. Miranda-De La Lama. 2013. Identity profiles based on social strategies, morphology, physiology, and cognitive abilities in goats. J. Vet. Behav. Clin. Appl. Res. 8:458–465. doi:10.1016/j.jveb.2013.05.003.
Patison, K.P., D.L. Swain, G.J. Bishop-Hurley, P. Pattison, and G. Robins. 2010. Social companionship versus food: The effect of the presence of familiar and unfamiliar conspecifics on the distance steers travel. Appl. Anim. Behav. Sci. 122:13–20. doi:10.1016/j.applanim.2009.11.001.
Penner, G.B., J.R. Aschenbach, G. Gäbel, and M. Oba. 2009. Technical note: Evaluation of a continuous ruminal pH measurement system for use in noncannulated small ruminants. J.

Anim. Sci. 87:2363–2366. doi:10.2527/jas.2008-1665.
Perals, D., A.S. Griffin, I. Bartomeus, and D. Sol. 2017. Revisiting the open-field test: what does it really tell us about animal personality?. Anim. Behav. 123:69–79. doi:10.1016/j.anbehav.2016.10.006.
Pérez-Barbería, F.J., and I.J. Gordon. 1999. The functional relationship between feeding type and jaw and cranial morphology in ungulates. Oecologia 118:157–165. doi:10.2307/4222224.
Petherick, J.C., R.G. Holroyd, V.J. Doogan, and B.K. Venus. 2002. Productivity, carcass and meat quality of lot-fed Bos indicus cross steers grouped according to temperament. Aust. J. Exp. Agric. 42:389. doi:10.1071/EA01084.
Pfister, J.A., J.C. Malechek, and D.F. Balph. 1988. Foraging behaviour of goats and sheep in the Caatinga of Brazil. J. Appl. Ecol. 25:379. doi:10.2307/2403830.
Pinedo, P.J., A. De Vries, and D.W. Webb. 2010. Dynamics of culling risk with disposal codes reported by Dairy Herd Improvement dairy herds. J. Dairy Sci. 93:2250–2261. doi:10.3168/JDS.2009-2572.
Place, N.T., A.J. Heinrichs, and H.N. Erb. 1998. The effects of disease, management, and nutrition on average daily gain of dairy heifers from birth to four months.
Prins, H. 1996. Ecology and Behaviour of the African Buffalo: Social Inequality and Decision Making. Chapman & Hall, London.
Proudfoot, K., and G. Habing. 2015. Social stress as a cause of diseases in farm animals: Current knowledge and future directions. Vet. J. 206:15–21. doi:10.1016/j.tvjl.2015.05.024.
Proudfoot, K.L., D.M. Weary, S.J. LeBlanc, L.K. Mamedova, and M.A.G. von Keyserlingk. 2018. Exposure to an unpredictable and competitive social environment affects behavior and health of transition dairy cows. J. Dairy Sci. 101:9309–9320. doi:10.3168/JDS.2017-14115.
Provenza, F.D. 1995. Postingestive feedback as an elementary determinant of food preference and intake in ruminants. J. Range Manag. 48:2–17.
Provenza, F.D., and D.F. Balph. 1987. Diet learning by domestic ruminants: Theory, evidence and practical implications. Appl. Anim. Behav. Sci. 18:211–232. doi:10.1016/0168-1591(87)90218-8.
Provenza, F.D., and E.A. Burritt. 1991. Socially induced diet preference ameliorates conditioned food aversion in lambs. Appl. Anim. Behav. Sci. 31:229–236. doi:10.1016/0168-1591(91)90007-K.
Provenza, F.D., J.J. Villalba, L.E. Dziba, S.B. Atwood, and R.E. Banner. 2003. Linking herbivore experience, varied diets, and plant biochemical diversity. Small Rumin. Res. 49:257–274. doi:10.1016/S0921-4488(03)00143-3.
Raeth-Knight, M., H. Chester-Jones, S. Hayes, J. Linn, R. Larson, D. Ziegler, B. Ziegler, and N. Broadwater. 2009. Impact of conventional or intensive milk replacer programs on Holstein heifer performance through six months of age and during first lactation. J. Dairy Sci. 92:799–809. doi:10.3168/JDS.2008-1470.
Raju, P.S. 1980. Optimum stimulation level: Its relationship to personality, demographics, and exploratory behavior. J. Consum. Res. 7:272. doi:10.1086/208815.
Ralphs, M.H., D. Graham, and L.F. James. 1994. Social facilitation influences cattle to graze Locoweed. J. Range Manag. 47:123–126. doi:10.2307/4002819.
Ramseyer, A., A. Boissy, B. Thierry, and B. Dumont. 2009. Individual and social determinants of spontaneous group movements in cattle and sheep. animal 3:1319–1326.

doi:10.1017/S1751731109004790.
Rault, J.-L., D.C. Lay, and J.N. Marchant-Forde. 2011. Castration induced pain in pigs and other livestock. Appl. Anim. Behav. Sci. 135:214–225. doi:10.1016/j.applanim.2011.10.017.
Raussi, S., S. Niskanen, J. Siivonen, L. Hã, H. Hepola, L. Jauhiainen, and I. Veissier. 2010. The formation of preferential relationships at early age in cattle. Behav. Processes 84:726–731. doi:10.1016/j.beproc.2010.05.005.
Réale, D., S.M. Reader, D. Sol, P.T. McDougall, and N.J. Dingemanse. 2007. Integrating animal temperament within ecology and evolution. Biol. Rev. 82:291–318. doi:10.1111/j.1469-185X.2007.00010.x.
Reinhardt, C.D., W.D. Busby, and L.R. Corah. 2009. Relationship of various incoming cattle traits with feedlot performance and carcass traits. J. Anim. Sci. 87:3030–3042. doi:10.2527/jas.2008-1293.
Reinhardt, V., and A. Reinhardt. 1981. Natural sucking performance and age of weaning in zebu cattle (Bos indicus). J. Agric. Sci. 96:309–312. doi:10.1186/1751-0147-53-28.
Rey, M., F. Enjalbert, and V. Monteils. 2012. Establishment of ruminal enzyme activities and fermentation capacity in dairy calves from birth through weaning. J. Dairy Sci. 95:1500–1512. doi:10.3168/JDS.2011-4902.
Rice, M., E.C. Jongman, S. Borg, K.L. Butler, and P.H. Hemsworth. 2016a. Characterisation of shy-feeding and feeding lambs in the first week in a feedlot. Appl. Anim. Behav. Sci. 179:39–45. doi:10.1016/j.applanim.2016.03.011.
Rice, M., E.C. Jongman, K.L. Butler, and P.H. Hemsworth. 2016b. Relationships between temperament, feeding behaviour, social interactions, and stress in lambs adapting to a feedlot environment. Appl. Anim. Behav. Sci. 183:42–50. doi:10.1016/j.applanim.2016.07.006.
Rioja-Lang, F.C., D.J. Roberts, S.D. Healy, A.B. Lawrence, and M.J. Haskell. 2009. Dairy cows trade-off feed quality with proximity to a dominant individual in Y-maze choice tests. Appl. Anim. Behav. Sci. 117:159–164. doi:10.1016/j.applanim.2008.12.003.
Rohrer, G.A., T. Brown-Brandl, L.A. Rempel, J.F. Schneider, and J. Holl. 2013. Genetic analysis of behavior traits in swine production. Livest. Sci. 157:28–37. doi:10.1016/j.livsci.2013.07.002.
Ros-Freixedes, R., L.J. Sadler, S.K. Onteru, R.M. Smith, J.M. Young, A.K. Johnson, S.M. Lonergan, E. Huff-Lonergan, J.C.M. Dekkers, and M.F. Rothschild. 2014. Relationship between gilt behavior and meat quality using principal component analysis. Meat Sci. 96:264–269. doi:10.1016/j.meatsci.2013.07.004.
Rosenberger, K., J.H.C. Costa, H.W. Neave, M.A.G. von Keyserlingk, and D.M. Weary. 2017. The effect of milk allowance on behavior and weight gains in dairy calves. J. Dairy Sci. 100:504–512. doi:10.3168/jds.2016-11195.
Roth, B.A., E. Hillmann, M. Stauffacher, and N.M. Keil. 2008. Improved weaning reduces cross-sucking and may improve weight gain in dairy calves. Appl. Anim. Behav. Sci. 111:251–261. doi:10.1016/J.APPLANIM.2007.06.007.
Roth, B.A., N.M. Keil, L. Gygax, and E. Hillmann. 2009. Influence of weaning method on health status and rumen development in dairy calves. J. Dairy Sci. 92:645–656. doi:10.3168/jds.2008-1153.
Rousing, T., B. Ibsen, and J.T. Sørensen. 2005. A note on: On-farm testing of the behavioural response of group-housed calves towards humans; test–retest and inter-observer reliability

and effect of familiarity of test person. Appl. Anim. Behav. Sci. 94:237–243. doi:10.1016/J.APPLANIM.2005.02.011.
Ruis, M.A., J.H. te Brake, J.A. van de Burgwal, I.C. de Jong, H.J. Blokhuis, and J.M. Koolhaas. 2000. Personalities in female domesticated pigs: behavioural and physiological indications. Appl. Anim. Behav. Sci. 66:31–47. doi:10.1016/S0168-1591(99)00070-2.
Rushen, J., and A.M. de Passillé. 1995. The motivation of non-nutritive sucking in calves, Bos taurus. Anim. Behav. 49:1503–1510. doi:10.1016/0003-3472(95)90071-3.
Rushen, J., A.A. Taylor, and A.M. de Passillé. 1999. Domestic animals' fear of humans and its effect on their welfare. Appl. Anim. Behav. Sci. 65:285–303. doi:10.1016/S0168-1591(99)00089-1.
Rutten, C.J., A.G.J. Velthuis, W. Steeneveld, and H. Hogeveen. 2013. Invited review: Sensors to support health management on dairy farms. J. Dairy Sci. 96:1928–1952. doi:10.3168/jds.2012-6107.
Rutter, S.M. 2006. Diet preference for grass and legumes in free-ranging domestic sheep and cattle: Current theory and future application. Appl. Anim. Behav. Sci. 97:17–35. doi:10.1016/j.applanim.2005.11.016.
Sanon, H.O., C. Kaboré-Zoungrana, and I. Ledin. 2007. Behaviour of goats, sheep and cattle and their selection of browse species on natural pasture in a Sahelian area. Small Rumin. Res. 67:64–74. doi:10.1016/j.smallrumres.2005.09.025.
Sant'Anna, A.C., M.J.R. Paranhos da Costa, F. Baldi, P.M. Rueda, and L.G. Albuquerque. 2012. Genetic associations between flight speed and growth traits in Nellore cattle. J. Anim. Sci. 90:3427–3432. doi:10.2527/jas.2011-5044.
Sárová, R., M. Spinka, J.L. Arias Panamá, and P. Sime Cek. 2010. Graded leadership by dominant animals in a herd of female beef cattle on pasture. Anim. Behav. 79:1037–1045. doi:10.1016/j.anbehav.2010.01.019.
Schwartzkopf-Genswein, K.S., S. Atwood, and T.A. McAllister. 2002. Relationships between bunk attendance, intake and performance of steers and heifers on varying feeding regimes. Appl. Anim. Behav. Sci. 76:179–188. doi:10.1016/S0168-1591(02)00009-6.
Sewalem, A., F. Miglior, and G.J. Kistemaker. 2011. Short communication: Genetic parameters of milking temperament and milking speed in Canadian Holsteins. J. Dairy Sci. 94:512–516. doi:10.3168/jds.2010-3479.
Shivley, C.B., J.E. Lombard, N.J. Urie, C.A. Kopral, M. Santin, T.J. Earleywine, J.D. Olson, and F.B. Garry. 2018. Preweaned heifer management on US dairy operations: Part VI. Factors associated with average daily gain in preweaned dairy heifer calves. J. Dairy Sci. 101:9245–9258. doi:10.3168/jds.2017-14022.
Sibbald, A.M., H.W. Erhard, R.J. Hooper, B. Dumont, and A. Boissy. 2006. A test for measuring individual variation in how far grazing animals will move away from a social group to feed. Appl. Anim. Behav. Sci. 98:89–99. doi:10.1016/j.applanim.2005.08.015.
Sibbald, A.M., H.W. Erhard, J.E. McLeod, and R.J. Hooper. 2009. Individual personality and the spatial distribution of groups of grazing animals: An example with sheep. Behav. Processes 82:319–326. doi:10.1016/j.beproc.2009.07.011.
Sibbald, A.M., and R.J. Hooper. 2003. Trade-offs between social behaviour and foraging by sheep in heterogeneous pastures. Behav. Processes 61:1–12. doi:10.1016/S0376-6357(02)00160-2.
Sibbald, A.M., and R.J. Hooper. 2004. Sociability and the willingness of individual sheep to

move away from their companions in order to graze. Appl. Anim. Behav. Sci. 86:51–62. doi:10.1016/j.applanim.2003.11.010.
Sih, A., and A.M. Bell. 2008. Chapter 5 Insights for Behavioral Ecology from Behavioral Syndromes. Adv. Study Behav. 38:227–281. doi:10.1016/S0065-3454(08)00005-3.
Sloan Wilson, D., A.B. Clark, K. Coleman, and T. Dearstyne. 1994. Shyness and boldness in humans and other animals. Trends Ecol. Evol. 9:442–446. doi:10.1016/0169-5347(94)90134-1.
Soberon, F., E. Raffrenato, R.W. Everett, and M.E. Van Amburgh. 2012. Preweaning milk replacer intake and effects on long-term productivity of dairy calves. J. Dairy Sci. 95:783–793. doi:10.3168/jds.2011-4391.
Solaiman, S.G. 2010. Goat Science and Production. Wiley-Blackwell Publishing, Ames, Iowa.
Squires, V.R., and G.T. Daws. 1975. Leadership and dominance relationships in Merino and Border Leicester sheep. Appl. Anim. Ethol. 1:263–274. doi:10.1016/0304-3762(75)90019-X.
Stamps, J., and T.G.G. Groothuis. 2010. The development of animal personality: Relevance, concepts and perspectives. Biol. Rev. 85:301–325. doi:10.1111/j.1469-185X.2009.00103.x.
Staněk, S., V. Zink, O. Doležal, and L. Štolc. 2014. Survey of preweaning dairy calf-rearing practices in Czech dairy herds. J. Dairy Sci. 97:3973–3981. doi:10.3168/JDS.2013-7325.
Stears, K., G.I.H. Kerley, and A.M. Shrader. 2014. Group-living herbivores weigh up food availability and dominance status when making patch-joining decisions. PLoS One 9:e109011. doi:10.1371/journal.pone.0109011.
Stefanski, V. 1998. Social stress in loser rats: Opposite immunological effects in submissive and subdominant males. Physiol. Behav. 63:605–613. doi:10.1016/S0031-9384(97)00492-7.
Sutherland, M.A., and S.K. Dowling. 2014. The relationship between responsiveness of first-lactation heifers to humans and the behavioral response to milking and milk production measures. J. Vet. Behav. Clin. Appl. Res. 9:30–33. doi:10.1016/j.jveb.2013.09.001.
Swartz, T.H., M.L. McGilliard, and C.S. Petersson-Wolfe. 2016. Technical note: The use of an accelerometer for measuring step activity and lying behaviors in dairy calves. J. Dairy Sci. 99:9109–9113. doi:10.3168/JDS.2016-11297.
Sweeney, B.C., J. Rushen, D.M. Weary, and A.M. de Passillé. 2010. Duration of weaning, starter intake, and weight gain of dairy calves fed large amounts of milk. J. Dairy Sci. 93:148–152. doi:10.3168/jds.2009-2427.
Thouless, C.R. 1990. Feeding competition between grazing red deer hinds. Anim. Behav. 40:105–111. doi:10.1016/S0003-3472(05)80669-4.
Tolkamp, B.J., I. Kyriazakis, J.D. Oldham, M. Lewis, R.J. Dewhurst, and J.R. Newbold. 1998. Diet choice by dairy cows. 2. Selection for metabolizable protein or for ruminally degradable Protein?. J. Dairy Sci. 81:2670–2680. doi:10.3168/JDS.S0022-0302(98)75824-2.
Tölü, C., İ.Y. Yurtman, H. Baytekin, C. Ataşoğlu, and T. Sava. 2012. Foraging strategies of goats in a pasture of wheat and shrubland. Anim. Prod. Sci. 52:1069. doi:10.1071/AN11251.
Torres-Vázquez, J.A., and M.L. Spangler. 2016. Genetic parameters for docility, weaning weight, yearling weight, and intramuscular fat percentage in Hereford cattle. J. Anim. Sci. 94:21. doi:10.2527/jas.2015-9566.
USDA. 2009. Goat 2009: Disease and Mortality on U.S. Goat Operations. Fort Collins, CO.

USDA. 2011. Dairy Heifer Raiser 2011. Fort Collins, CO.
USDA. 2016. Dairy 2014: Dairy Cattle Management Practices in the United States. Fort Collins, CO.
Val-Laillet, D., A.M. de Passillé, J. Rushen, and M.A.G. von Keyserlingk. 2008a. The concept of social dominance and the social distribution of feeding-related displacements between cows. Appl. Anim. Behav. Sci. 111:158–172. doi:10.1016/j.applanim.2007.06.001.
Val-Laillet, D., D.M. Veira, and M.A.G. von Keyserlingk. 2008b. Short communication: dominance in free-stall-housed dairy cattle is dependent upon resource.. J. Dairy Sci. 91:3922–6. doi:10.3168/jds.2008-1332.
Van, D.T.T., N.T. Mui, and I. Ledin. 2005. Tropical foliages: effect of presentation method and species on intake by goats. Anim. Feed Sci. Technol. 118:1–17. doi:10.1016/j.anifeedsci.2004.10.016.
Van De Stroet, D.L., J.A. Calderón Díaz, K.J. Stalder, A.J. Heinrichs, and C.D. Dechow. 2016. Association of calf growth traits with production characteristics in dairy cattle. J. Dairy Sci. 99:8347–8355. doi:10.3168/jds.2015-10738.
Van Oortmerssen, G.A., S. Den Daas, J.M. Koolhaas, and R.F. Benus. 1990. Routine formation and flexibility in social and non-social behaviour of aggressive and non-aggressive male mice. Behaviour 112:176–193. doi:10.1163/156853990X00185.
Van Reenen, C.G., B. Engel, L.F.M. Ruis-Heutinck, J.T.N. Van Der Werf, W.G. Buist, R.B. Jones, and H.J. Blokhuis. 2004. Behavioural reactivity of heifer calves in potentially alarming test situations: A multivariate and correlational analysis. Appl. Anim. Behav. Sci. 85:11–30. doi:10.1016/j.applanim.2003.09.007.
Van Reenen, C.G., N.E. O'Connell, J.T.N. Van Der Werf, S.M. Korte, H. Hopster, R.B. Jones, and H.J. Blokhuis. 2005. Responses of calves to acute stress: Individual consistency and relations between behavioral and physiological measures. Physiol. Behav. 85:557–570. doi:10.1016/j.physbeh.2005.06.015.
Van Reenen, C.G., J.T.N. Van der Werf, R.M. Bruckmaier, H. Hopster, B. Engel, J.P.T.M. Noordhuizen, and H.J. Blokhuis. 2002. Individual differences in behavioral and physiological responsiveness of primiparous dairy cows to machine milking. J. Dairy Sci. 85:2551–2561. doi:10.3168/jds.S0022-0302(02)74338-5.
Vannucchi, C.I., J.A. Rodrigues, L.C.G. Silva, C.F. Lúcio, and G.A.L. Veiga. 2012. A clinical and hemogasometric survey of neonatal lambs. Small Rumin. Res. 108:107–112. doi:10.1016/j.smallrumres.2012.05.013.
Vasseur, E., F. Borderas, R.I. Cue, D. Lefebvre, D. Pellerin, J. Rushen, K.M. Wade, and a M. de Passillé. 2010. A survey of dairy calf management practices in Canada that affect animal welfare. J. Dairy Sci. 93:1307–15. doi:10.3168/jds.2009-2429.
Vasseur, E., J. Rushen, and A.M. de Passille. 2009. Does a calf's motivation to ingest colostrum depend on time since birth, calf vigor, or provision of heat?. J. Dairy Sci. 92:3915–3921. doi:10.3168/jds.2008-1823.
Veissier, I., and I. Stefanova. 1993. Learning to suckle from an artificial teat within groups of lambs: Influence of a knowledgeable partner. Behav. Processes 30:75–82. doi:10.1016/0376-6357(93)90013-H.
Verbeek, E., I. Colditz, D. Blache, and C. Lee. 2019. Chronic stress influences attentional and judgement bias and the activity of the HPA axis in sheep. PLoS One 14:e0211363. doi:10.1371/journal.pone.0211363.

Verbeek, M.E.M., P. Drent, P. De Goede, and P. Wiepkema. 1999. Individual behavioural characteristics and dominance in aviary groups of great tits. Behaviour 136:23–48. doi:10.1163/156853999500659.
Verbeek, M.E.M., P.J. Drent, and P.R. Wiepkema. 1994. Consistent individual differences in early exploratory behaviour of male great tits. Anim. Behav. 48:1113–1121. doi:10.1006/ANBE.1994.1344.
Villalba, J.J., F. Catanese, F.D. Provenza, and R.A. Distel. 2012. Relationships between early experience to dietary diversity, acceptance of novel flavors, and open field behavior in sheep. Physiol. Behav. 105:181–187. doi:10.1016/j.physbeh.2011.08.031.
Villalba, J.J., X. Manteca, and F.D. Provenza. 2009. Relationship between reluctance to eat novel foods and open-field behavior in sheep. Physiol. Behav. 96:276–281. doi:10.1016/j.physbeh.2008.10.010.
von Holst, D. 1986. Psychosocial stress and its pathophysiological effects in tree shrews (Tupaia belangeri). Springer Berlin Heidelberg, Berlin, Heidelberg.
Warmington, B.G., and A.H. Kirton. 1990. Genetic and non-genetic influences on growth and carcass traits of goats. Small Rumin. Res. 3:147–165. doi:10.1016/0921-4488(90)90089-O.
Webb, L.E., B. Engel, H. Berends, C.G. van Reenen, W.J.J. Gerrits, I.J.M. de Boer, and E.A.M. Bokkers. 2014. What do calves choose to eat and how do preferences affect behaviour?. Appl. Anim. Behav. Sci. 161:7–19. doi:10.1016/j.applanim.2014.09.016.
Webb, L.E., C.G. van Reenen, M.B. Jensen, O. Schmitt, and E.A.M. Bokkers. 2015. Does temperament affect learning in calves?. Appl. Anim. Behav. Sci. 165:33–39. doi:10.1016/j.applanim.2015.01.013.
Whalin, L., D.M. Weary, and M.A.G. von Keyserlingk. 2018. Short communication: Pair housing dairy calves in modified calf hutches. J. Dairy Sci.. doi:10.3168/JDS.2017-14361.
Wilson, T.R., S.J. LeBlanc, T.J. DeVries, and D.B. Haley. 2018. Effect of stall design on dairy calf transition to voluntary feeding on an automatic milk feeder after introduction to group housing. doi:10.3168/jds.2017-14011.
Wood-Gush, D.G.M., and K. Vestergaard. 1989. Exploratory behavior and the welfare of intensively kept animals. J. Agric. Ethics 2:161–169. doi:10.1007/BF01826929.
Zentall, T.., and B.. Galef. 1988. Social Learning: Psychological and Biological Perspectives. T.. Zentall and B.. Galef Jr., ed. Psychology Press, New York, NY.
Zobel, G., H.W. Neave, and J. Webster. 2018. Understanding natural behavior to improve dairy goat (Capra hircus) management systems. Transl. Anim. Sci.. doi:10.1093/tas/txy145.
Zobel, G., K.S. Schwartzkopf-Genswein, B.M.A. Genswein, and M.A.G. von Keyserlingk. 2011. Impact of agonistic interactions on feeding behaviours when beef heifers are fed in a competitive feeding environment. Livest. Sci. 137:1–9. doi:10.1016/j.livsci.2010.09.022.