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Review: passive immunity in beef-suckler calves

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Colostrum-derived passive immunity is central to the health, performance and welfare of neonatal beef-suckler calves, and economics of beef-farming enterprises. Compared to dairy calves, mainly Holstein-Friesian, there is much less research carried out on passive immunity and associated factors in beef calves. Thus, this review aimed to summarise and interpret published information and highlight areas requiring further research. The transfer of immunoglobulin G1 (IgG1) from blood to mammary secretions is greater for beef × dairy cows compared to most beef breed types. Considerable between-animal variance is evident in first-milking colostrum yield and immunoglobulin concentration of beef-suckler cow breed types. First-milking colostrum immunoglobulin concentrations are similar for within-quarter fractions and for the front and rear quarters of the udder. First-milking colostrum yield is higher for beef × dairy cows than beef × beef and purebred beef breeds, and higher for multiparous than primiparous cows, but generally colostrum immunoglobulin concentration is relatively similar for each of the respective categories. Consequently, colostrum immunoglobulin mass (volume × concentration) production in beef cows seems to be primarily limited by colostrum volume. The effect of maternal nutrition during late gestation on colostrum yield is not well documented; however, most studies provide evidence that colostrum immunoglobulin concentration is not adversely affected by under-nutrition. Factors that impinge upon the duration between birth and first suckling, including dam parity, udder and teat anatomy and especially dystocia, negatively impact on calf passive immunity. Colostrum immunoglobulin mass ingested relative to birth weight post-parturition is the most important variable determining calf passive immunity. Research indicates that feeding the beef calf a colostrum volume equivalent to 5% of birth weight shortly after parturition, with subsequent suckling of the dam (or a second feed) 6 to 8 h later, ensures adequate passive immunity, equivalent to a well-managed suckling situation. Within beef-suckler cow genotypes, calf passive immunity is similar for many common beef breeds, but is generally higher for calves from beef × dairy cows. Compared to older cows, calves from younger cows, especially primiparous animals, have lower serum immunoglobulin concentrations. Most studies have shown no adverse impact of maternal dietary restriction on calf passive immunity. The prevalence of failure of passive transfer (FPT) in beef calves varies considerably across studies depending on the test used, and what cut-off value is assumed or how it is classified. The accuracy and precision of methodologies used to determine immunoglobulin concentrations is concerning; caution is required in interpreting laboratory results regarding defining colostrum 'quality' and calf passive immune 'status'. Further research is warranted on colostrum-related factors limiting passive immunity of beef calves, and on the validation of laboratory test cut-off points for determining FPT, based on their relationships with key health and performance measures.

Keywords: beef calf, beef-suckler cow, colostrum, health, immunoglobulins

Implications

This review shows that the passive immune status of beef-suckler calves on commercial farms may not be superior to dairy calves. The current knowledge deficit pertaining to factors affecting colostrum immunoglobulin mass (colostrum volume × immunoglobulin concentration) production of beef-suckler cows and consumption by their calves, coupled with difficulty in accurate quantification of immunoglobulin concentrations using existing laboratory tests, is a major limiting factor curtailing the provision of recommendations to ensure adequate passive transfer. Consequently, further research is warranted in this area.

Introduction

The importance of colostrum-derived passive immunity, through intestinal absorption of colostral immunoglobulins, to the mortality, morbidity and subsequent growth and

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welfare of a newborn beef calf is recognised internationally (Hickson *et al.*, 2016; Raboisson *et al.*, 2016; Homerosky *et al.*, 2017; Todd *et al.*, 2018). In addition, the negative economic impact that failure of passive transfer (FPT) has on beef farming enterprises has been quantified (Raboisson *et al.*, 2016). However, in comparison to dairy calves, there is much less research carried out on passive immunity and associated factors in beef-suckler calves. Furthermore, the numerous existing reviews in the scientific literature on bovine neonatal immunity almost exclusively relate to dairy calves. Although much of the underlying biology associated with passive immunity applies equally to dairy and beef calves, nevertheless genetic, environmental and management circumstances are usually extremely different, often resulting in them having a very diverse immune status. Therefore, the objective of this paper is to provide a comprehensive review of the scientific literature, including work conducted in our research centre, on factors affecting passive immunity of beef-suckler calves. To put findings in context, appropriate comparison with dairy cows and calves, mainly Holstein-Friesian, is made. The contrast between dairy and beef breeds is also pertinent as in some countries replacement breeding heifers for the beef cow herd are often sourced from the dairy herd, that is, beef × dairy cows.

Analysis of bovine immunoglobulin

Historically, radial immunodiffusion (RID) has been the only method that directly measures and quantifies immunoglobulin G (IgG); however, recent studies have reported IgG concentrations in colostrum, milk and blood measured using ELISA (Gelsinger *et al.*, 2015). Direct tests (e.g. RID and ELISA, for colostrum and blood) quantify the absolute concentration of immunoglobulin, whereas indirect tests for colostrum (e.g. brix refractometry) and blood (e.g. Zinc Sulphate Turbidity) provide an approximation of the immunoglobulin concentration; alternatively, assessment of the blood levels of other components of colostrum, which are similarly absorbed as immunoglobulins (e.g. gamma-glutamyl transferase activity), can be measured to give an indication of the level of passive immunity (Vandeputte *et al.*, 2014; Hogan *et al.*, 2015; Dunn *et al.*, 2018). However, tests for quantification of IgG in bovine colostrum and serum can vary substantially in their accuracy, sensitivity and/or specificity (precision) (Hogan *et al.*, 2015). Recent studies comparing single RID (sRID) and ELISA for quantification of IgG concentrations have found a poor level of agreement between the methods (Gelsinger *et al.*, 2015; Dunn *et al.*, 2018). For example, Dunn *et al.* (2018) using the Bland and Altman method showed a substantial fixed bias, a wide limit of agreement and a poor concordance coefficient between ELISA and sRID for colostrum and serum IgG concentrations. In both studies the absolute concentration of IgG was almost two-fold higher when measured using RID compared to ELISA (×1.9, Gelsinger *et al.*, 2015; ×1.8, Dunn *et al.*, 2018).

Considering these methodological aspects, it is difficult to prescribe discrete industry-wide standards or cut-off points for colostrum 'quality' or successful passive immunity in calf serum or plasma (see later). In addition, it also implies that interpreting published IgG concentrations particularly where different laboratory techniques are used, can be perilous.

Colostrum

Colostrum, the first secretions of the mammary gland after parturition, is rich in nutrients and non-nutrient biologically active components, including carbohydrates, proteins, growth factors, enzymes, enzyme inhibitors, nucleotides and nucleosides, cytokines, fats, minerals and vitamins (Hammon *et al.*, 2013; McGrath *et al.*, 2016). Colostrum is an essential source of dietary nutrients for the neonatal calf; McGee *et al.* (2005 and 2006) reported that beef-suckler cow colostrum had a mean dry matter (DM) concentration of 245 to 285 g/kg, and CP, fat, lactose and ash concentrations (g/kg DM) of 150 to 184, 48 to 70, 26 to 30 and 10 to 13, respectively. In addition, colostral components influence neonatal gastrointestinal microbiome, morphological and functional development, and digestion and absorption, and also have systemic effects on calf metabolism and development (Hammon *et al.*, 2013).

Immunoglobulin antibodies in bovine colostrum are central to the immunological link that occurs when the mother transfers passive immunity to the offspring (Hurley and Theil, 2011). There are three major immunoglobulin isotypes or classes: IgG (subclasses IgG1 and IgG2), IgM and IgA. In beef-suckler cow colostrum, IgG1 predominates (91%), followed by IgM (5%), IgA (2%) and IgG2 (2%) (McGee *et al.*, 2005 and 2006). Most published research pertaining to calf passive immunity only emphasises IgG or IgG1. Although the focus of this paper is passive immunity in relation to immunoglobulins, in terms of immuno-protection, it is recognised that colostrum contains a wide variety of other immune-related factors (Hurley and Theil, 2011; McGrath *et al.*, 2016).

Colostrogenesis

Colostrum is formed during late pregnancy when mammary cells are proliferating and differentiating in preparation for lactation; this process is called colostrogenesis (Baumrucker *et al.*, 2010). Colostral immunoglobulins arise from systemic and local sources (Hurley and Theil, 2011). Bovine IgG1 is specifically transported by a process of transcytosis across the mammary epithelial cells during colostrogenesis by an IgG1-specific receptor, FcRn (Hurley and Theil, 2011). In beef-suckler cows, systemic concentrations of IgG1 and IgG2 in blood are approximately equal (McCutcheon *et al.*, 1991; McGee *et al.*, 2005 and 2006). Concentrations of IgG1 start to decrease about 3 to 4 weeks *prepartum* and cease close to calving, whereas conversely, concentrations of blood IgG2 generally increase *prepartum* (Olson *et al.*, 1981a; McCutcheon *et al.*, 1991; Guy *et al.*, 1994; McGee *et al.*, 2005 and 2006). The appearance of blood IgG2 in bovine colostrum is thought to occur via leaky-tight junctions in the

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blood-milk barrier (Samarütel *et al*., 2016). However, the specific mechanisms of colostrogenesis remain undefined.

The decrease in blood IgG1 concentrations *prepartum* is much greater in dairy (Guy *et al*., 1994) and beef × dairy (McGee *et al*., 2005; Murphy *et al*., 2005; Earley *et al*., 2018) cows compared to beef breed cows, implying that more IgG1 is transferred into colostrum for the dairy and dairy crossbred genotypes. Within several weeks *postpartum*, concentrations of blood IgG1 are equivalent to pre-colostrogenesis (McGee *et al*., 2005 and 2006).

There are inconsistent effects across studies on changes in beef-suckler cow blood IgM concentrations *prepartum* with declines observed in some but not other experiments (Olson *et al*., 1981a; McGee *et al*., 2005 and 2006); concentrations of maternal blood IgA were found to be relatively constant (McGee *et al*., 2005 and 2006). This is not overly surprising as IgM and IgA found in bovine colostrum are produced by plasma cells in mammary tissue (Hurley and Theil, 2011).

Blood IgG1 (Norman *et al*., 1981), and IgG1, IgG2 and IgA (McGee *et al*., 2006) concentrations were reported to be higher in older/multiparous compared to younger/primiparous beef cows, but IgM did not differ in either study.

Colostrum yield

Few published studies have quantified colostrum yield in beef-suckler cows (Figure 1). Considerable between-animal

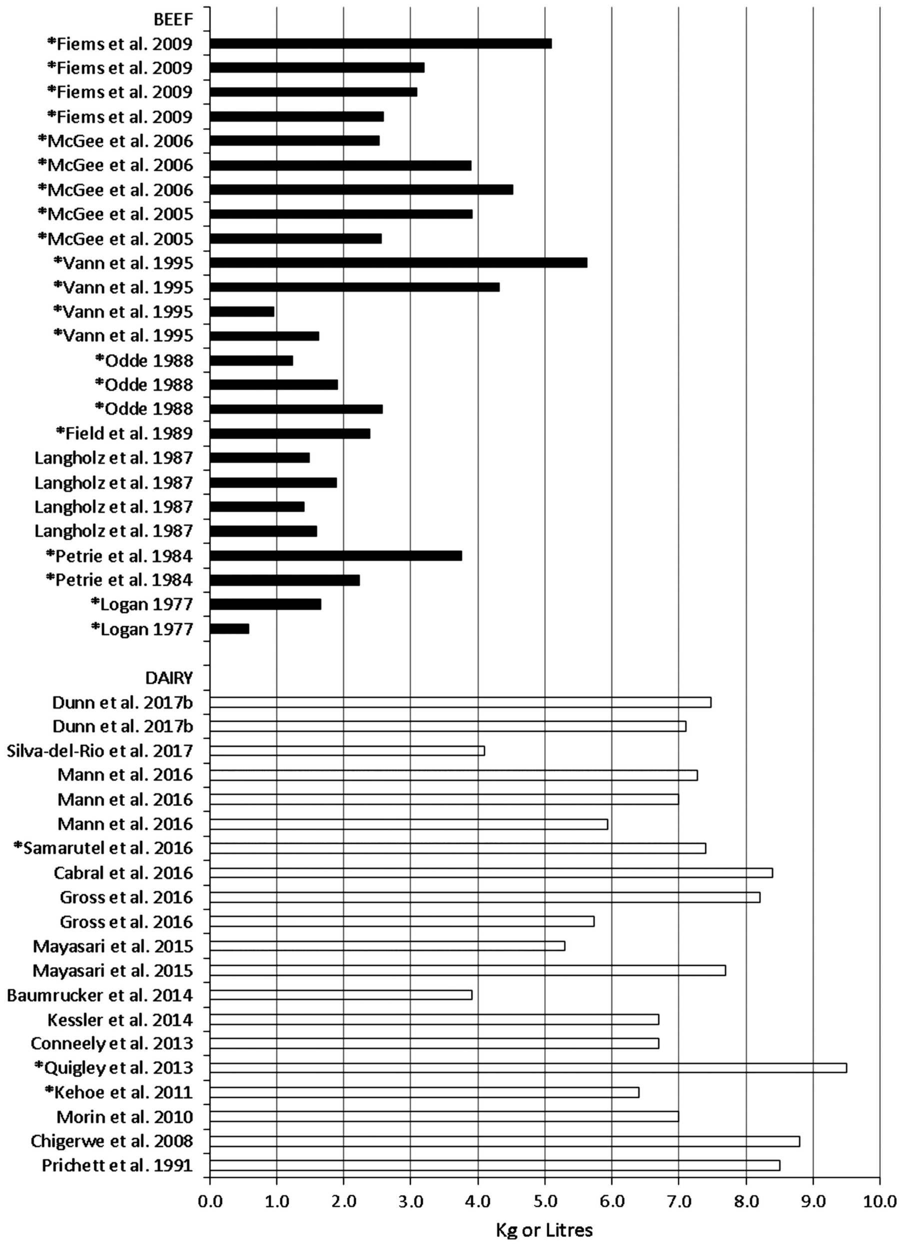

Figure 1 Mean first-milking colostrum yield (kilogram or litres*) in beef ■ and dairy □ cows/heifers. For interpretation of volume *v*. weight values, the density of colostrum is ~1.05 g/ml. References for this figure are provided in the text or Supplementary Material S1.

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variation in first-milking colostrum yield is evident in beef breeds (Logan, 1977; Field *et al*., 1989; McGee *et al*., 2005), dairy breeds (Kehoe *et al*., 2011; Conneely *et al*., 2013; Samarütel *et al*., 2016; Silva-del-Rio *et al*., 2017) and their crosses, that is, beef × dairy (McGee *et al*., 2005 and 2006). For example, in multiparous beef-suckler cows managed similarly, McGee *et al*. (2005) reported that first-milking colostrum yield ranged from 740 to 5490 ml for Charolais and from 1660 to 7230 ml for beef × Friesian animals.

Compared to beef-suckler cows, mean first-milking colostrum yields reported for dairy cows are generally much higher (Figure 1); mean colostrum yield reported for beef-suckler cows is 2.7 (range 0.6 to 5.6) l; corresponding values for dairy cows are 6.7 (3.7 to 9.5). Differences in genotype,

Table 1 *Effect of beef-suckler cow breed type on first-milking colostrum yield and/or immunoglobulin concentrations*

		Colostrum						
		Yield[3]	Immunoglobulin concentration (mg/ml)					
References[1]	Breed type[2]	(l or kg)	IgG	IgG1	IgG2	IgM	IgA	Ig total
Earley *et al.* (2018)	C × L		61					
	L × F		59					
Vandeputte *et al.* (2014)	BB			$X = 95.9$				
	C							
	BA							
	L							
McGee *et al.* (2008)	LF			136				
	S × (L × F)			133				
	L × F			134				
	S × (L × F)			125				
McGee *et al.* (2005)	C	2.56 l^{a}		153.2	2.1^{a}	7.9^{a}	2.5	165.7^{a}
	Beef × F	3.92^{b}		178.1	3.5^{b}	10.9^{b}	3.3	195.7^{b}
Murphy *et al.* (2005)	L × F			79.7				
	L × (L × F)			76.4				
	L			75.7				
	C			95.5				
	S × (L × F)			89.3				
Earley *et al.* (2000)	C			170.1				
	S × (L × F)			168.9				
	L × F			165.6				
Vann *et al.* (1995)	A × A	1.63 l^{a}	50.7^{a}	54.2	3.6	3.9	3.2	115.6^{a}
	B × A	0.97^{a}	100.2^{b}	63.2	4.0	4.0	5.6	177.2^{b}
	A × B	4.33^{b}	94.5^{b}	58.8	2.8	2.7	4.1	162.9^{b}
	B × B	5.63^{b}	64.2^{a}	51.3	2.7	2.2	2.4	122.9^{a}
Petrie *et al.* (1994)	H × AA	1.82 l^{a}						
	H × S	3.87^{b}						
Odde (1988)	A			54.5^{a}		4.6		
	H			60.9^{b}		4.1		
Langholz *et al.* (1987)	F	1.6 kg[4]						
	S	1.4						
	C × F	1.9						
	S × F	1.5						
Norman *et al.* (1981)	H			112.6		7.9^{a}		
	H × A			116.6		10.1^{b}		
Halliday *et al.* (1978)	BG			83.3^{a}	3.1	6.3^{a}		
	H × F			75.6^{b}	3.2	5.4^{b}		
	BG			80.8^{a}	4.3	6.7^{a}		
	H × F			70.3^{b}	3.4	5.1^{b}		

[a,b]Within column and individual experiment, values with different superscripts differ significantly (at least $P < 0.05$).
[1]References for this Table are provided in the text or Supplementary Material S1.
[2]A = Angus; AA = Aberdeen Angus; B = Brahman; BA = Blonde d'Aquitaine; BB = Belgian Blue; BG = Blue Grey; C = Charolais; F = Friesian; H = Hereford; J = Jersey; K = Kiwi; L = Limousin; S = Simmental; and their crosses.
[3]Yield = litres (l) or kilogram.
[4]Suckled (*v.* milked).

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parity and maternal nutrition are likely contributory factors to some of this variance within the beef and dairy categories (see later). Overall, considering that dairy cows are genetically selected for milk production the higher values are expected. Correspondingly, the higher first-milking colostrum yield of beef × dairy cows compared to beef breed cows (Table 1), also reflects their milk yield (Murphy *et al*., 2005).

First-milking colostrum yield was found to be higher in multiparous beef × dairy cows compared to first-parity animals (Table 2). Similarly, Langholz *et al*. (1987) reported that colostrum intake of calves born to multiparous beef-suckler cows was higher, both on an absolute basis (×1.67) and relative to birth weight (×1.44), compared to calves born to heifers. This likely reflects the lower mammary gland

Table 2 *Effect of beef-suckler cow parity/age on first-milking colostrum yield and/or immunoglobulin concentrations*

		Colostrum						
		Yield[3]	Immunoglobulin concentration (mg/ml)					
References[1]	Treatment[2]	(l or kg)	IgG	IgG1	IgG2	IgM	IgA	Ig total
Rocha *et al*. (2014)	1 parity		83.3					
	2		80.7					
	3 + 4		79.7					
	5		87.4					
	6		71.1					
Vandeputte *et al*. (2014)	Parity 1 to 9			$X = 95.9$				
Rocha *et al*. (2012)	PP		78.9				5.8	
	MP		86.6				6.7	
McGee *et al*. (2008)	PP			136				
	MP			134				
	PP			133				
	MP			125				
McGee *et al*. (2006)	PP	2.54 l^{a}		165.4	2.7	11.3	2.6	181.0
	MP	4.52^{b}		190.4	3.2	10.6	3.5	206.4
Earley *et al*. (1998)	PP			188.7				
	MP			159.7				
	PP			154.5				
	MP			170.9				
Odde (1988)	2 years			53.8		4.4		
	3			50.6		4.2		
	4			57.6		4.3		
	5			59.3		4.3		
	6			62.5		5.2		
	7			55.4		4.4		
	8			56.1		4.2		
	9 +			66.0		4.0		
Langholz *et al*. (1987)	PP	1.2 kg^{a}						
	MP	2.0^{b}						
Norman *et al*. (1981)	3 years			93.4^{a}		8.0		
	4			87.3^{a}		6.9		
	5			115.2^{b}		9.5		
	6 to 10			130.5^{b}		9.7		
	11 +			146.5^{b}		10.8		
Delong *et al*. (1979)	2 years		215.8			8.4	15.5^{a}	
	3		177.3			8.8	8.9^{a}	
	4		222.2			11.0	18.6^{a}	
	5		219.7			13.4	17.5^{a}	
	6		164.6			10.4	28.0^{b}	
Dardillat *et al*. (1978)	PP 2 years							109.6[4]
	PP 3 years							124.2
	MP > 3 years							116.3

^{a,b}Within column and individual experiment, values with different superscripts differ significantly (at least $P < 0.05$).
[1]References for this Table are provided in the text or Supplementary Material S1.
[2]PP = primiparous; MP = multiparous.
[3]Yield = litres (l) or kilogram.
[4]γ-Globulin.

Table 3 *Effect of* prepartum *dietary nutrition or body condition score (BCS) on first-milking colostrum yield and/or immunoglobulin concentrations in beef-suckler cows*

References[1]	Dietary treatment	Duration[2] (days)	Colostrum yield[3] (l or kg)	Effect of dietary restriction on colostrum immunoglobulin concentrations[4]
Horn *et al.* (2010)	Control	42	–	= IgG
	1000 IU/day synthetic vitamin E			
	1000 IU/day natural vitamin E			
Fiems *et al.* (2009)	100% energy requirements	140	2.60[a]	= Ig total
	90%		3.10[a]	
	80%		3.20[ab]	
	70%		5.10[b]	
McGee *et al.* (2006)	Grass silage *ad libitum*	15	4.52 l	= IgG1, IgG2, IgM, IgA, Ig total
	Straw *ad libitum*		3.90	
Rytkonen *et al.* (2004)	Grass silage recommended	90	–	= IgG
	Grass silage @ 75% DMD[5]			
Dietz *et al.* (2003)	1.5% fat (control)	47[2]	–	= IgG
	4.0% fat (safflower seed)			
	5.0% fat (whole cottonseed)			
Awadeh *et al.*, (1998)	20 ppm Se (selenite)	190	–	↓ IgG1; = IgM
	60 ppm Se			
	120 ppm Se			
	60 ppm Se (selenomethionine)			
Petrie *et al.* (1984)	Straw + hay	–	2.22	= γ-Globulin
	Straw + silage		3.75	
Shell *et al.* (1995)	75% NRC energy	190	–	↑ IgG1; = IgM
	110%			
Hough *et al.* (1990)	57% NRC energy and CP	90	–	= IgG
	100%			
Odde (1988)	4 BCS	–	1.53	= IgG1, IgM
	5		1.11	
	BCS 3 to 7		–	= IgG1, IgM
Odde (1988)	55% NRC protein	90[2]	1.93 l	↑ IgG1; = IgM
	91%		2.68	
Olson *et al.* (1981a)	33% NRC CP (320 g/day)	156	–	= IgG1, IgG2, IgM
	100% (960 g/day)			
	72% NRC energy (36 MJ/day)			
	100% (51 MJ/day)			
Blecha *et al.* (1981)	520 to 980 g CP/day	100[2]	–	= IgG1, IgG2, IgM
DeLong *et al.* (1979)	370 g CP/day	120	–	= IgG, IgM, IgA
	960 g			
Halliday *et al.* (1978)	75% to 172% energy requirements	84	–	= IgG1, IgG2, IgM
	65% to 125%			
Dardillat *et al.* (1978)	0.544 MJ ME/kg $W^{0.75}$	80	–	= γ-Globulin
	0.669			
Logan (1977)	Out-wintered:	–	0.59 l[a]	= IgG, IgM, IgA
	Housed: silage *ad libitum*		1.66[b]	

NRC = National Research Council; ME = metabolisable energy.
[1]References for this Table are provided in the text or Supplementary Material S1.
[2]These studies used only heifers.
[3]Colostrum yield (litre (l) or kg).
[4] = no statistically significant difference ($P > 0.05$); ↑ statistically significant increase; ↓statistically significant decrease.
[5]Grass silage @75% dry matter digestibility (DMD).

development in heifers. Likewise, a higher colostrum yield in multiparous than primiparous dairy cows was observed in many (e.g. ×1.38, Conneely *et al.*, 2013) but not all (e.g. ×1.03, Kehoe *et al.*, 2011) studies.

Although there is an industry-wide perception that colostrum yield of beef-suckler cows is reduced through under-nutrition *prepartum*, this effect is not clearly evident (Table 3). Ambiguity between studies may be partially attributed to large variance combined with relatively small numbers of experimental animals used, but also to the degree of underfeeding and the cows ability to mobilise body-fat reserves, which negates the effect of nutrient restriction.

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Likewise, recent research with dairy cows has shown no effect of dry-period dietary energy level on first-milking colostrum yield (Mann *et al*., 2016; Dunn *et al*., 2017a).

Colostrum immunoglobulin concentration

Within beef and beef × dairy breeds (McGee *et al*., 2005; Dunn *et al*., 2018) and dairy breeds (Conneely *et al*., 2013; Dunn *et al*., 2017b), there is substantial variation between cows in colostrum IgG (and immunoglobulin subclass) concentration at first milking. Within-quarter fractions of first-milking colostrum have similar concentrations of immunoglobulins in beef × dairy (IgG1, IgG2, IgM and IgA; McGee *et al*., 2006) and dairy (IgG1; Le Cozler *et al*., 2016) cows. In beef-suckler cows immunoglobulin concentrations were found not to differ significantly between the front and rear quarters of the udder (IgG1, IgG2, IgM, Halliday *et al*., 1978; IgG1, Earley *et al*., 2000; IgG1, IgG2, IgM, IgA, McGee *et al*., 2006), although Langholz *et al*. (1987) reported lower concentrations (IgG: −5%, IgM: −16% IgA: −19%) in the front compared to the rear quarters. Similarly, in dairy cows, mean concentrations of immunoglobulin were shown not to differ significantly between the front and rear quarters, although variation between individual quarters was large (IgG, IgG2, Samarütel *et al*., 2016), whereas in contrast, Le Cozler *et al*. (2016) reported that IgG1 concentration was lower (−6%) in front than hind quarters.

In dairy cows, there is normally a negative, but relatively weak, association ($r = -0.16$ to -0.37) between colostrum volume/weight and IgG concentration (Morin *et al*., 2010; Kehoe *et al*., 2011; Conneely *et al*., 2013; Silva-del-Rio *et al*., 2017), although in some studies no statistically significant relationship was found (Baumrucker *et al*., 2010; Samarütel *et al*., 2016). Similarly, Odde (1988) reported a correlation of −0.43 between colostrum volume and IgG1 concentration in beef heifers, whereas conversely, Logan (1977) found no relationship in beef cows, which may be due to the particularly low colostrum yield obtained in that study (Table 1).

In dairy cow studies colostral IgG concentrations are usually negatively associated with interval from calving-to-first-milking, although the rate of decline can vary substantially; 1.1% (Conneely *et al*., 2013) to 3.7% (Morin *et al*., 2010) per hour. In general, a decline in colostral IgG concentration is not readily obvious until after approximately 12 h *postpartum* (Conneely *et al*., 2013; Dunn *et al*., 2017b). Although this occurrence has not been quantified in beef-suckler cows, the aforementioned duration before there is an appreciable decline in colostral immunoglobulin concentration far exceeds time to first-suckling for beef calves in most situations (see later).

Like first-milking colostrum, there is also considerable variance in the immunoglobulin concentration of second- (and subsequent) milking colostrum in beef-suckler (McGee *et al*., 2005 and 2006) and dairy (Silva-del-Rio *et al*., 2017) cows, some of which may partly reflect residual effects of first-milking colostrum. Nevertheless, immunoglobulin (subclass) concentrations in second-milking colostrum are substantially lower (~0.5) than first-milking colostrum in beef (Vann *et al*., 1995; McGee *et al*., 2005), beef × dairy (Logan, 1977; McGee *et al*., 2005 and 2006) and dairy (Silva-del-Rio *et al*., 2017) cows.

It is clear from the few within-study comparisons of dairy and beef cows published that beef cows have greater first-milking colostrum IgG1 concentrations (e.g. 113.4 *v*. 42.7 mg/ml; Guy *et al*., 1994); however, this is not as apparent across studies. The variance in mean colostrum IgG concentrations (determined using only one-of-two recognised quantitative methods, RID and ELISA) across studies for beef and dairy cows (Figure 2), is substantial; mean IgG/IgG1 concentration reported for beef cows is 99 mg/ml (range 31 to 200) and dairy cows is 66 mg/ml (27 to 117). Again, across-study differences in factors such as genotype, parity and maternal nutrition are likely contributory causes to some of the variance within the beef and dairy cow categories (see later) but clearly, there is a large overlap. The upper ends of the range in immunoglobulin concentrations for dairy cows are values more customarily associated with beef-suckler cows. Possible reasons proposed by the authors of those studies for such deviations include, relatively low milk-yielding cow genotypes, short calving-to-colostrum-collection interval, superior nutritional and health-related management of the cow, dissimilarities in sample preparation, and crucially, differences associated with laboratory tests, as discussed earlier. Again, this substantial variance begs the question, how comparable are 'quantitative' values across studies and what concentration of IgG or IgG1 constitutes 'good-quality' colostrum?

Colostrum immunoglobulin concentrations are mainly equivalent between beef × dairy, beef × (beef × dairy), beef × beef and the common (pure) beef breeds (Table 1). This seems counterintuitive as by crossing a beef breed with a dairy breed, the crossbred would be expected to produce colostrum with an immunoglobulin concentration, which is intermediate.

Differences in colostrum immunoglobulin (subclass) concentrations between primiparous and multiparous beef-suckler cows are generally relatively small and do not differ statistically (Table 2). Contrastingly, in dairy breeds, usually older cows have higher colostrum immunoglobulin concentrations than younger cows (Kehoe *et al*., 2011; Le Cozler *et al*., 2016; Dunn *et al*., 2017b; Silva-del-Rio *et al*., 2017), although clear divergence among primiparous and multiparous dairy cows is only evident in some studies (Conneely *et al*., 2013).

Analogous to the situation with colostrum yield, in commercial practice it is perceived that maternal under-nutrition during gestation has an adverse effect on colostrum 'quality'. However, in most published studies dietary energy and/or protein restriction during pregnancy, or reduced body condition score (BCS) at parturition (a proxy for maternal under-nutrition), has no adverse effect on colostrum immunoglobulin concentrations in beef-suckler cows or heifers (Table 3). Similarly, in dairy cows, concentrate

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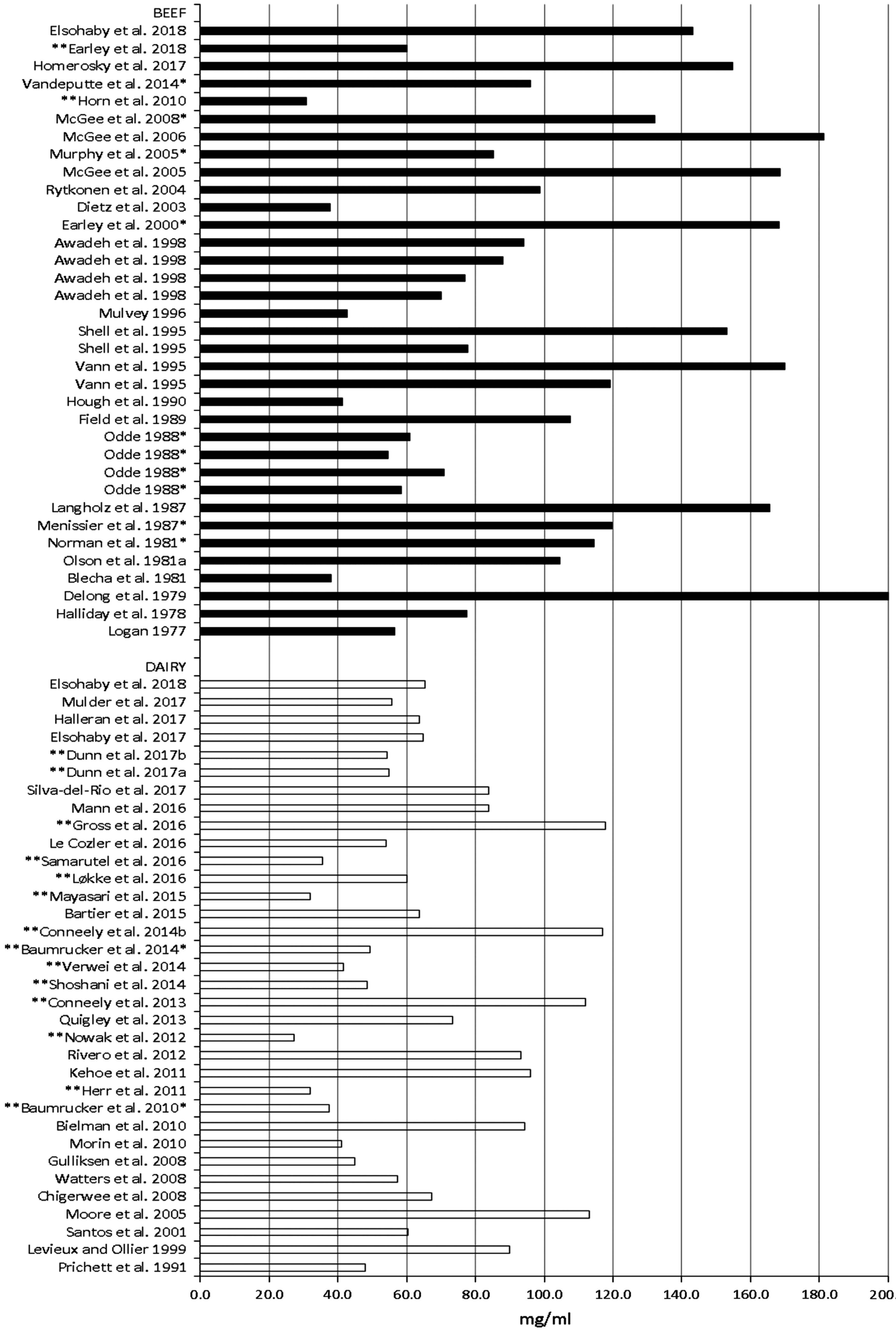

Figure 2 Mean first-milking colostrum IgG (IgG1*) concentrations (mg/ml) in beef ■ and dairy □ cows/heifers determined using single radial immune diffusion or ELISA**. References for this figure are provided in the text or Supplementary Material S1.

supplementation of grass silage during the dry period had no effect on first-milking colostrum IgG concentration (Dunn *et al.*, 2017a). Indeed, Mann *et al.* (2016) reported that feeding dairy cows 150% of energy requirements during the dry period resulted in a lower colostrum IgG concentration compared to those fed to requirements.

Although not as applicable to beef-suckler cows commercially, there is evidence in dairy cows that shortening the dry period from about 8 to 4 weeks has little effect on colostrum IgG concentration (but reduces first-milking colostrum yield), and that omitting the dry period negatively affects both the volume and IgG concentration in colostrum (e.g. Mayasari *et al.*, 2015).

Colostrum immunoglobulin mass

Colostrum immunoglobulin mass is the volume × concentration of immunoglobulin (or subclasses) of that colostrum (McGee *et al.*, 2005). Ultimately, an optimum mass of colostrum IgG needs to be absorbed by the newborn calf within a relatively short time period after birth (see later). In line with the substantial variation in colostrum yield and immunoglobulin concentration discussed earlier, there is also considerable variation in colostrum immunoglobulin mass produced by beef-suckler (McGee *et al.*, 2005 and 2006; Vann *et al.*, 2005;) and dairy (Baumrucker *et al.*, 2010; Morin *et al.*, 2010; Samarütel *et al.*, 2016) cows.

This infers that beef-suckler cows producing higher volumes of colostrum rather than colostrum with greater concentrations of IgG1 will likely have a greater mass of IgG1. In other words, colostrum 'quantity' rather than 'quality' is the likely limiting factor with beef-suckler cows, which is in direct contrast to the dairy cow (Baumrucker *et al.*, 2010). The source of colostrum immunoglobulin mass variation is not well understood.

Although hardly any studies have quantified both colostrum yield and immunoglobulin concentration of beef-suckler cows (Figure 1 and Tables 1 to 3), even fewer have reported colostrum immunoglobulin mass production. Nevertheless, first-milking colostrum immunoglobulin mass was shown to be affected by cow genotype (Vann *et al.*, 1995; McGee *et al.*, 2005), parity and maternal nutrition level in late gestation (McGee *et al.*, 2006). In addition, induction of calving by 2 weeks before expected parturition reduced colostrum IgG mass by 43% in beef cows (Field *et al.*, 1989).

Passive immunity in the neonatal calf

Immunoglobulin absorption

Ingestion of colostrum is essential for providing the neonatal calf with systemic immunologic protection during at least the first 2 to 4 weeks of life until its own active immune system is functional. It is recommended that beef calves should stand and suckle within 2 h of calving; if not, the dam should be restrained and the calf should be assisted. If the calf is unable or unwilling to suckle, the cow should be milked out by hand and the calf fed colostrum with a nipple/teat-bottle or oesophageal/'stomach' tube-feeder (Larson *et al.*, 2004).

Time of colostrum ingestion

It is well established that immunoglobulin absorption by pinocytosis across the intestinal epithelium into the neonatal circulation decreases with time *postpartum*, and ceases after 24 to 48 h; this is known as 'closure'. Consequently, for the newborn calf, the length of time between birth and first suckling is fundamental in the acquisition of passive immunity. For example, Langholz *et al.* (1987) reported that beef-suckler calves which suckled within 3 h *postpartum*, had serum IgG, IgM and IgA concentrations at 36 h *postpartum* that were proportionately 1.68, 1.57 and 1.66, higher, respectively, compared to calves that suckled after 3 h. In terms of colostrum management, one of the obvious primary differences between dairy and beef calves is that the beef-suckler calf usually remains with and suckles its dam, whereas typically, the dairy calf is removed from its dam soon after birth and generally receives colostrum through artificial means.

For the beef calf to ingest sufficient colostrum, it must first stand, walk, find the dam's teat and suckle, while simultaneously the dam must stand, have a good maternal bond with the calf, produce an adequate volume of colostrum with adequate concentrations of immunoglobulins and have teats that can be grasped by the calf (Larson *et al.*, 2004). Circumstances that impinge on these behavioural elements have a negative impact on passive immunity in beef calves.

The mean interval between birth and first standing-up for beef-suckler calves varies from 30 min to almost 2 h; the mean time to first suckling without assistance generally ranges from 60 to 260 min, but it can be much longer for individual animals (Langholz *et al.*, 1987; Odde, 1988; Le Neindre and Vallet, 1992; Hickson *et al.*, 2008). In beef herds with easy calvings, most calves suckle within 4 h (Le Neindre and Vallet, 1992; Homerosky *et al.*, 2017).

Differences in the latency to first suckle is influenced by breed – usually longer for dairy breeds than beef breeds, parity – usually longer for primiparous than multiparous; and, anatomical differences in the udder and teat, which can be related to breed and parity (Langholz *et al.*, 1987; Mayntz and Sender, 2006). For instance, more outward-pointing teats are associated with improved colostrum status of beef calves (Hickson *et al.*, 2016). Dystocia has a large influence on time to first suckling. This can manifest itself as less vigorous calves resulting in a longer interval from calving-to-standing, but also a poorer mothering score, a measure of cow-calf bonding (Odde, 1988; Homerosky *et al.*, 2017). Compared to beef calves that experienced a non-assisted birth, assisted calves took longer to attempt to stand (×2.03), to successfully stand (×1.39) and to suckle (×1.88) (Hickson *et al.*, 2008). Similarly, Homerosky *et al.* (2017) reported that the proportion of beef calves that failed to consume colostrum by 4 h after birth was 0.14, 0.39 and 0.64 for unassisted, easy assist and difficult assist deliveries, respectively. Consequently, factors influencing feto-maternal

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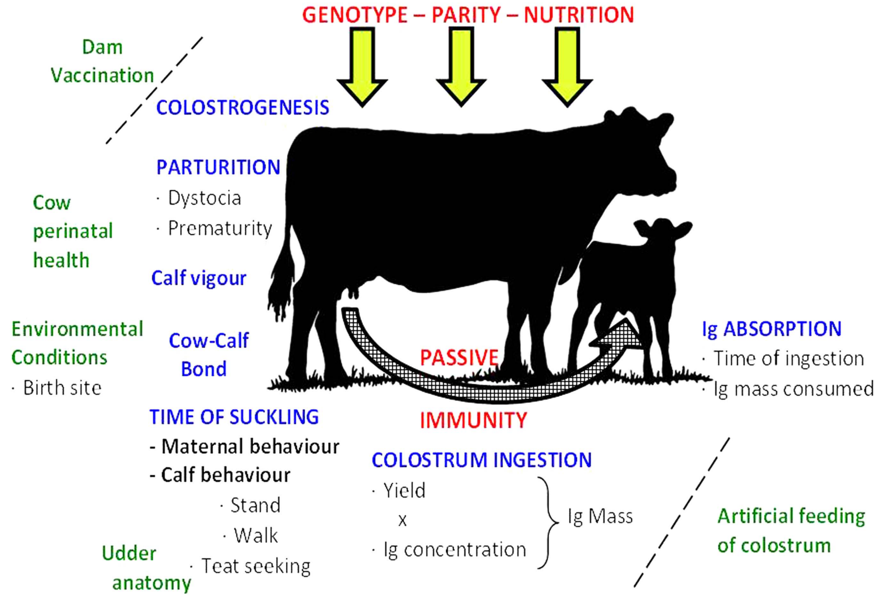

Figure 3 Key factors affecting passive immunity in beef-suckler calves.

disproportion need to be managed in order to reduce calving difficulty and negative effects on calf vigour.

Voluntary colostrum consumption and feeding

Mean duration of first suckling, until full, for newborn beef-suckler calves is between 20 and 26 min (e.g. Langholz *et al.*, 1987). When calves are limited to two sucklings, 4 and 9 h after birth, they can suckle equivalent to 8% of their BW (Le Neindre and Vallet, 1992). Langholz *et al.* (1987) reported that beef-suckler calves voluntarily suckled 1.6 kg of colostrum, equivalent to 4.1% of BW, at birth, and by 12 h *post-partum* had consumed a total of 2.8 kg of colostrum, equivalent to 7.4% of BW. Similarly, earlier reports (pre-1997) in the literature have shown that on average, at first feed, beef and dairy calves will voluntarily drink between 1.9 and 2.7 l from a bucket, suckle between 1.6 and 2.6 l from a teat-bottle, or voluntarily suckle from its dam between 1.5 and 2.5 kg of colostrum (McGee *et al.*, 2006). However, recent studies indicate a higher mean voluntary consumption of colostrum via teat-bottle (3.4 l, 7.3% of birth weight) by dairy calves at their first feed (Bonk *et al.*, 2016).

Compared to suckling the dam, artificial feeding has the benefit that a known volume of colostrum is administered. When properly used, oesophageal feeding has the advantage over a teat-bottle that relatively large volumes of colostrum can be fed, and rapidly, for example, 3 l fed in 5.2 *v.* 17.6 min (Desjardins-Morrissette *et al.*, 2018). It is generally accepted that the oesophageal groove reflex is not triggered when using a tube-feeder resulting in deposition of colostrum in the reticulorumen, compared to directly in the omasum and abomasum when suckling; nevertheless, controlled studies have shown similar IgG concentrations in calves fed relatively high volumes (3.0 to 3.4 l) of colostrum with a stomach-tube compared to a teat-bottle (Bonk *et al.*, 2016; Desjardins-Morrissette *et al.*, 2018). However, Godden *et al.* (2009) found no difference in calf passive immunity between a teat-bottle and tube-feeder when feeding a large volume (3 l) of colostrum 'replacer', but higher immunity and greater apparent efficiency of absorption (AEA) for the teat-bottle when feeding a smaller volume (1.5 l). This indicates that colostrum entering the rumen may have a more demonstrable effect on abomasal emptying rates, and AEA of IgG when relatively small rather than large volumes of colostrum are fed (Desjardins-Morrissette *et al.*, 2018). In this regard, these latter findings may be more applicable to calves from lower-yielding beef cows.

In practice, colostrum feeding of the newborn beef-suckler calf is often based on modified dairy calf guidelines, although in most circumstances this is probably inappropriate. For dairy calves, colostral management recommendations for adequate passive immunity transfer include providing a colostrum IgG mass of at least 150 to 200 g, equivalent to feeding 3 l of colostrum within 2 h after birth by oesophageal-tube (Chigerwe *et al.*, 2008). More recently, Conneely *et al.* (2014) concluded that serum IgG and AEA of IgG was greatest in dairy calves fed 8.5% of birth weight in colostrum, equivalent to 3.2 (range 2.0 to 4.2) l, using a stomach-tube within 2 h *postpartum*. Similarly, Dunn *et al.* (2017a) recommended that dairy calves be fed 10% of birth weight in colostrum imminently after birth.

However, with beef-suckler cows these volume-targets would often not be possible to achieve (Figure 1), especially with lower-yielding genotypes (McGee *et al.*, 2005) and primiparous animals (McGee *et al.*, 2006). Considering the generally higher immunoglobulin concentration in colostrum from beef-suckler cows compared to dairy cows (about 1.5-fold, albeit with large variation; Figure 2), consequently, an equivalent immunoglobulin mass can be achieved with a lower (two-thirds) colostrum volume, for example, 2 rather than 3 l.

From a practical perspective, similarly, our research has shown that feeding the beef-suckler calf 5% of birth weight in colostrum volume using a tube-feeder within 1 h post-calving, with subsequent suckling of the dam (or a second

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feed) 6 to 8 h later, ensures adequate passive immunity, equivalent to a well-managed suckling situation where the calf suckles 'naturally' within 1 h after birth, with unlimited access to the dam subsequently (McGee *et al*., 2006). Correspondingly, Langholz *et al*. (1987) reported that an increase in serum immunoglobulin concentration in beef-suckler calves was only observed up to a consumption of 2 kg of colostrum at first suckling.

In situations where sufficient or suitable colostrum is unavailable, colostrum supplements (provide exogenous IgG from bovine lacteal secretions or bovine serum) or replacers (in addition to exogenous IgG, also provide nutrients – energy, protein, minerals and vitamins) may be used; however, published data concerning their efficacy is inconsistent (Cabral *et al*., 2013).

Efficiency of immunoglobulin absorption

In beef-suckler cows, mass of colostrum IgG1 consumed per kilogram birth weight within 1 h *postpartum* was the most significant variable determining calf passive immune status (McGee and Drennan, 2007). Unlike dairy calf studies, there is little published information on AEA of immunoglobulin

Table 4 *Effect of beef-suckler cow breed type on blood immunoglobulin concentrations in their calves at 24 to 72 h* postpartum

Reference[1]	Breed type[2]	ZST[3] units	Immunoglobulin concentration (mg/ml)					
			IgG	IgG1	IgG2	IgM	IgA	Ig total
Earley *et al.* (2018)	C × L	23.5	18					
	L × F	26.5	20					
Hickson *et al.* (2016)	AA		22.4^{a}					
	A × F		26.4^{b}					
	A × J		25.8^{b}					
	A × K		26.3^{b}					
Walder and Rosengren (2009)[4]	British		29.9					
	Continental		31.0					
	Other		33.5					
McGee *et al.* (2008)	L × F			52				
	S × (L × F)			46				
	L × F			57				
	S × (L × F)			60				
McGee *et al.* (2005)	C	19.9^{a}		48.2^{a}	0.6^{a}	2.8^{a}	0.6	52.2^{a}
	Beef × F	26.7^{b}		62.4^{b}	1.2^{b}	4.3^{b}	0.8	68.5^{b}
	C	17.9^{a}		36.2^{a}	0.5^{a}	2.6^{a}	0.5^{a}	39.8^{a}
	Beef × F	24.5^{b}		54.6^{b}	1.1^{b}	4.0^{b}	0.9^{b}	60.7^{b}
Murphy *et al.* (2005)	L × F	17.9^{a}		27.1^{b}				
	L × (L × F)	14.0^{b}		21.6^{a}				
	L	14.6^{b}		20.6^{a}				
	C	12.6^{b}		18.1^{a}				
	S × (L × F)	14.7^{ab}		24.2^{ab}				
Earley *et al.* (1998)	PP-C	15.1		36.2	0.41	0.93	0.09	37.6
	PP-L × F	15.7		38.6	0.62	1.09	0.11	40.4
	MP-C	11.9^{a}		35.5^{a}	0.54	0.80	0.16	36.9^{a}
	MP-L × F	19.7^{b}		53.6^{b}	0.89	1.30	0.12	55.9^{b}
	MP-S × (L × F)	15.7^{ab}		44.0^{ab}	0.50	0.91	0.08	45.5^{ab}
Odde (1988)	PP-A			8.6		0.75		
	PP-H			10.0		0.83		
	MP-A			14.2		1.27		
	MP-H			12.9		1.10		
Norman *et al.* (1981)	H			44.2^{a}		2.78[5]		
	H × A			50.7^{b}		3.24		
Halliday *et al.* (1978)	BG			26.5^{a}	1.1	2.3^{a}		
	H × F			20.7^{b}	1.1	1.8^{b}		
	BG			27.6^{a}	1.1	1.9^{a}		
	H × F			22.5^{b}	1.0	1.3^{b}		

[a,b]Within column and individual experiment, values with different superscripts differ significantly (at least $P < 0.05$).
[1]References for this Table are provided in the text or Supplementary Material S1.
[2]PP = primiparous; MP = multiparous; A = Angus; AA = Aberdeen Angus; BA = Blonde d'Aquitaine; BB = Belgian Blue; BG = Blue Grey; C = Charolais; F = Friesian; H = Hereford; J = Jersey; K = Kiwi; L = Limousin; S = Simmental; and their crosses.
[3]Zinc Sulphate Turbidity (ZST) test.
[4]Blood sampled between 2 and 8 days *postpartum*.
[5]$P = 0.07$.

(subclasses) in beef-suckler calves, as the quantity of colostrum consumed is much more difficult to assess, and thus rarely determined. Typical mean AEA for dairy calves across studies ranges from 16% to 45%, although this varies widely within study, from 8% to 60% (mean 28%), despite standardised feeding (Halleran *et al.*, 2017). Beef-suckler calves offered approximately 4% to 5% of birth weight in first-milking colostrum within 1 h *postpartum* had mean AEA at 8 h post-feeding of 0.36 to 0.43, 0.34 to 0.46, 0.44 to 0.64, 0.42 to 0.56 and 0.37 to 0.44 for IgG1, IgG2, IgM, IgA and Ig-total, respectively (McGee *et al.*, 2005 and 2006).

It is evident that the passive immune status of suckler-bred calves is superior to dairy-bred calves under controlled research farm conditions, where it is ensured that calves

Table 5 *Effect of beef-suckler cow parity/age on blood immunoglobulin concentrations in their calves at 24 to 72 h* postpartum

			Immunoglobulin concentration (mg/ml)					
References[1]	Treatment[2]	ZST[3] units	IgG	IgG1	IgG2	IgM	IgA	Ig total
Hickson *et al.* (2016)	2 years		22.7[a]					
	3		24.9[ab]					
	4		28.8[c]					
	5		26.2[bc]					
	6		24.7[ab]					
	7		24.1[ab]					
Rocha *et al.* (2012)	PP		25.5				2.7	
	MP		28.2				3.1	
Walder and Rosengren (2009)[4]	PP		26.5[a]					
	MP		31.5[b]					
McGee *et al.* (2008)	PP			52				
	MP			46				
	PP			57				
	MP			60				
McGee *et al.* (2006)	PP	24.4[a]		59.3[a]	1.0	3.9	1.0	65.1[a]
	MP	20.0[b]		45.7[b]	0.7	3.2	0.9	49.9[b]
Earley *et al.* (1998)	PP-C	15.1		36.2	0.41	0.93	0.09	37.6
	MP-C	11.9		35.5	0.54	0.80	0.16	36.9
	PP-L × F	15.7		38.6[a]	0.62	1.09	0.11	40.4[a]
	MP-L × F	19.7		53.6[b]	0.89	1.30	0.12	55.9[b]
Odde (1988)	2 years			8.9[5]		0.71[5]		
	3			15.6		1.47		
	4			14.8		1.49		
	5			13.3		1.04		
	6			10.6		0.93		
	7			16.7		1.37		
	8			15.5		1.34		
	9+			13.0		1.12		
Langholz *et al.* (1987)	PP		21.9[a]			1.71[a]	1.62[a]	
	MP		51.7[b]			4.64[b]	5.65[b]	
Norman *et al.* (1981)	3 years			42.3[6]		3.39		
	4			41.6		2.90		
	5			47.6		3.13		
	6–10			52.1		2.95		
	11+			53.6		2.67		
Delong *et al.* (1979)	2 years		52.0			2.18	3.35[a]	
	3		30.9			1.99	1.91[a]	
	4		48.7			2.97	4.18[a]	
	5		74.6			4.29	5.03[a]	
	6		72.8			4.00	10.23[b]	

[a,b,c]Within column and individual experiment, values with different superscripts differ significantly (at least $P < 0.05$).
[1]References for this Table are provided in the text or Supplementary Material S1.
[2]PP = primiparous; MP = multiparous; C = Charolais; F = Friesian; L = Limousin; and their crosses.
[3]Zinc Sulphate Turbidity (ZST) test.
[4]Blood sampled between 2 and 8 days *postpartum*.
[5]Effect of age, $P < 0.001$.
[6]$P = 0.08$.

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Table 6 *Effect of maternal* prepartum *dietary nutrition or body condition score (BCS) of beef-suckler cows on blood immunoglobulin concentrations in their calves at 24 to 72 h* postpartum

References[1]	Dietary treatment[2]	Duration[3] (days)	Effect of dietary restriction (or reduced BCS) on calf blood immunoglobulin concentrations[4]
McGee and Earley (2013)	Grass silage *ad libitum*	60[3]	= IgG
	Grass silage + straw TMR		
	Grass silage *ad libitum*	60	= IgG
	Grass silage + straw TMR		
Horn *et al.* (2010)	Control		
	1000 IU/day synthetic vitamin E	42	= IgG
	1000 IU/day natural vitamin E		
Walder and Rosengren (2009)[5]	BCS < 5	–	↑ IgG1
	BCS > 5		
Gilles *et al.* (2009)	Control	20 to 35	= IgG
	+ Sodium selenite (400 mg) and calcium iodide (I, 200 mg)		
Lake *et al.* (2006)	BCS 4 *v.* 6	–	= IgG
McGee *et al.* (2006)	Grass silage *ad libitum*	15	↓ IgG1, Ig total, ZST[6] units
	Straw *ad libitum*		= IgG2, IgM, IgA
Rytkonen *et al.* (2004)	Grass silage – recommended	90	↓ IgG
	Grass silage @ 75% DMD[7]		
Dietz *et al.* (2003)	Control	68	= IgG
	Cottonseed supplement		
Awadeh *et al.* (1998)	20 ppm Se (selenite)	190	↓ IgG1, IgM
	60 ppm Se		
	120 ppm Se		
	60 ppm Se (selenomethionine)		
Shell *et al.* (1995)	75% NRC energy	190	= IgG1; = IgM
	110%		
Hough *et al.* (1990)	57% NRC energy and CP	90	= IgG; ~ ↓ IgG[8]
	100%		
Odde (1988)	BCS 3 to 5	–	= IgG1; = IgM
	BCS 3 to 6	–	↓ IgG1; = IgM
	BCS 3 to 7	–	= IgG1; = IgM
Odde (1988)	55% NRC protein	90[3]	↑ IgG1; ~ ↑ IgM
	91%		
DeLong *et al.* (1979)	370 g CP/day	120	= IgG, IgM, IgA
	960 g		
Halliday *et al.* (1978)	75% to 172% energy reqs	84	= IgG1, IgG2, IgM
	65% to 125%		
Fishwick and Clifford (1975)	50% ARC digestible CP	98[3]	= ZST units
	100%		
Calves fed pooled (rather than dams) colostrum after birth			
Blecha *et al.* (1981)	520 to 980 g CP/day	100[3]	↓ IgG1, IgG2; = IgM
Olson *et al.* (1981b)	Control protein	140[3]	= IgG1, IgG2, IgM
	Restricted protein		
	Control energy		
	Restricted energy		

[1]References for this Table are provided in the text or Supplementary Material S1.
[2]TMR = Total Mixed Ration; NRC = National Research Council; ARC = Agricultural Research Council.
[3]These studies used only beef heifers.
[4] = no statistically significant difference (P > 0.05); ↑ statistically significant increase; ↓statistically significant decrease.
[5]Blood sampled between 2 and 8 days *postpartum.*
[6]Zinc Sulphate Turbidity (ZST) test.
[7]Grass silage @ 75% dry matter digestibility (DMD).
[8]No effect of maternal nutrition on calf IgG but calves fed colostrum from restricted cows had less (P < 0.07) circulating IgG.

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suckle the dam and/or are fed sufficient colostrum in a timely manner post-parturition (Earley *et al*., 2000; Dunn *et al*., 2018). However, on commercial farms beef-suckler calves do not necessarily have a superior passive immune status compared to dairy calves (e.g. Todd *et al*., 2018). Reasons for such a discrepancy are likely to be multifaceted, involving a number of the key factors shown in Figure 3.

Within beef-suckler cow genotypes, generally passive immunity of calves from the common beef breeds is similar, but lower than calves from beef × dairy cows (Table 4). As discussed earlier, this effect can largely be attributed to the significantly greater colostrum immunoglobulin mass produced by beef × dairy compared to beef breeds (McGee *et al*., 2005). Similarly, there is evidence that passive immunity is greater in calves from 'dual-purpose' breeds, for example, Simmental (Murphy *et al*., 2005). This highlights the importance of milk production-related 'maternal' traits in the beef dam, and has implications for beef breeding policies. Apparent efficiency of absorption of colostral immunoglobulins does not seem to differ between purebred and crossbred beef calves (Vann *et al*., 1995) or between calves from beef and beef × dairy dams (McGee *et al*., 2005).

Calves from older beef-suckler cows generally have a higher immune status than those from younger and principally, primiparous cows (Table 5). This differential is likely to be due to a lower colostrum immunoglobulin mass produced by primiparous cows primarily attributed to a lower colostrum yield (McGee *et al*., 2006), rather than lower immunoglobulin concentration (Table 2).

Most published research has shown no adverse impact of maternal dietary restriction, or low cow BCS, on passive immunity of beef-suckler calves (Table 6). Similarly, Dunn *et al*. (2017a) found no effect of concentrate supplementation of dairy cows during the dry period on calf serum IgG or AEA at 24 h after birth. A small number of studies have reported negative effects of maternal under-nutrition which are most likely not related to colostrum immunoglobulin concentration (Table 3) but rather a lower colostrum immunoglobulin mass, and also, possibly inhibitory effects on immunoglobulin absorption (Table 3; McGee *et al*., 2006). There is some evidence that trace-mineral supplementation of the beef cow during late pregnancy may be important in relation to calf passive immunity (Table 4). Genetic, environmental and management factors affecting 'length of pregnancy' may have direct and indirect effects on calf passive immunity, although there is little quantifiable research published in this area. Calves from cows induced to calve 2 weeks before expected parturition were shown to have decreased serum IgG concentrations, in the order of 50% (Field *et al*., 1989); this inferior passive immunity may be attributed to a reduction in colostrum IgG mass produced, reduced absorption of IgG by the induced calves, or both. Alternatively, a prolonged gestation, due to differences in factors including dam and sire genotype, cow parity and calf sex may result in relative oversize of the calf and thus have an adverse effect on passive transfer of immunity, as discussed previously.

More 'targeted' passive immunity in beef-suckler calves can be achieved through vaccination of the pregnant cow against particular diseases (Earley *et al*., 2018).

Similar to colostrum immunoglobulin concentration, there is considerable within- and especially across-study variance in beef calf blood immunoglobulin (subclass) concentrations (Tables 4 and 5). Reasons for such variability may be attributed to a combination of the factors discussed previously and illustrated in Figure 3, but also laboratory methodology-related impacts (see earlier). Likewise, large variation in mean calf blood IgG concentration is evident across dairy calf studies, even when a relatively large volume of colostrum is fed soon after birth, for example, 20.7 (Dunn *et al*., 2017) to 39.1 mg/ml (Conneely *et al*., 2014) IgG.

Passive immunity test results are generally categorised for FPT using test-specific cut-off values. For dairy calves cut-off points applied for FPT can vary from 3.5 to 18 mg/ml blood serum/plasma IgG (Raboisson *et al*., 2016), but the most commonly used cut-off is 10 mg/ml IgG (e.g. Hogan *et al*., 2015; Raboisson *et al*., 2016), although the basis of such widespread adoption is not clearly apparent. Moreover, cut-offs for tests that indirectly estimate IgG concentration are most often established by simply identifying the test equivalent to 10 mg/ml serum IgG (Hogan *et al*., 2015). Similarly, multiple IgG cut-off values, ranging between 8 and 24 mg/ml, have been applied to classify FPT in beef calves (Raboisson *et al*., 2016). Clearly, the 'prevalence' of FPT can fluctuate depending on what cut-off value is assumed or how it is classified. Collectively, these observations suggest that more research is needed to validate various test cut-off values for beef calves, based on their relationships with key health and performance outcome measures, such as morbidity, mortality and growth (e.g. Todd *et al*., 2018). Furthermore, cognisance of potential vagaries associated with test methodologies used to measure blood immunoglobulin concentrations must be borne in mind when interpreting results, particularly concerning cut-off points for FPT; absolute values may be an artefact of the test used.

Conclusion

This review has summarised the published research pertaining to the main factors affecting the passive immune status of beef-suckler calves (illustrated in Figure 3). It is clear that compared to the dairy calf, there is much less research and consequently, much less is known about factors affecting the failure of the neonatal beef calf to absorb adequate colostral immunoglobulins. Deficiencies in the literature are highlighted; in particular, published studies evaluating colostrum yield and ultimately colostrum immunoglobulin mass produced by beef-suckler cows, and correspondingly colostrum consumption by their calves are scant. Accurate and precise measurement of immunoglobulin concentrations in colostrum and blood seems to be a challenge; consequently, interpreting absolute values or cut-offs as a means of identifying the 'quality' of colostrum and immune 'status' of

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calves may be hazardous. Evidence is also provided that, commercially at least, the passive immunity of beef calves may not be as high as dairy calves. Further research is needed on colostrum-related factors limiting passive immunity of beef calves, and on the validation of laboratory test cut-off points for determining FPT in beef calves, based on their relationships with key health and performance measures.

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Declaration of interest

None.

Ethics statement

Not applicable.

Software and data repository resources

Not applicable.

Supplementary material

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