

# Grazing management: setting the table, designing the menu and influencing the diner

Pablo Gregorini<sup>A,D,E</sup>, Juan J. Villalba<sup>B</sup>, Pablo Chilibroste<sup>C</sup> and Frederick D. Provenza<sup>B</sup>

<sup>A</sup>Feed and Farm Systems Group, DairyNZ<sup>1</sup>, Private Bag 3221, Hamilton 3240, New Zealand.

<sup>B</sup>Department of Wildland Resources, S.J. and Jessie E. Quinney College of Natural Resources, Utah State University, Logan, UT 84322-5230, USA.

<sup>C</sup>Department of Animal Science, Faculty of Agronomy – EEMAC, University of the Republic, Ruta 3 km 363, Paysandú, CP 60000 Uruguay.

<sup>D</sup>Present address: Department of Agricultural Sciences, Lincoln University, Lincoln 7647, Christchurch, New Zealand.

<sup>E</sup>Corresponding author. Email: Pablo.Gregorini@lincoln.ac.nz

**Abstract.** Pastoral livestock-production systems are under increasing environmental, social and consumer pressures to reduce environmental impacts and to enhance biodiversity and animal welfare. At the same time, farmers face the challenge of managing grazing, which is intimately linked with profitability. Recent advances in understanding grazing patterns and nutritional ecology may help alleviate such pressures. For instance, by managing grazing to (1) manipulate links between ingestive–digestive decisions and temporal patterns of nutrient excretion, (2) provide phytochemically diverse diets at appropriate temporal (the menu) and spatial (the table) scales and (3) influence the behaviour of animals (the diners) on the basis of their specific ‘personalities’ and needs, to overcome or enhance animal differences, thereby enhancing their and farm productivity and welfare, as well as our health. Under pastoral systems, synergies between animals’ and farmers’ grazing decisions have the potential to offer greater benefits to the animal, the environment and the farm than does simple and parsimonious grazing management based on a single component of the system. In the present review, we look at grazing and its management through an alternate lens, drawing ideas and hypotheses to stimulate thinking, dialogue and discussions that we anticipate will evolve into innovative research programs and grazing strategies. To do so, we combined experimental and observational studies from a wide range of disciplines with simulation-modelling exercises. We envisage a more holistic approach to manage grazing based on recent advances in the understanding of the nutritional ecology of grazing animals, and propose management practices that may enable pastoral livestock-production systems to evolve continually as complex creative systems.

**Additional keywords:** agriculture, diets, foraging, health, ruminants.

Received 23 September 2016, accepted 3 February 2017, published online dd mmm yyyy

## Introduction

By providing food and wealth, livestock fulfil essential roles in agriculture, economies and societies. Nonetheless, pastoral livestock-production systems are under increasing pressure to reduce their environmental impacts (Foote *et al.* 2015; Gerber *et al.* 2015) and production costs (Doole and Kingwell 2015), and enhance biodiversity (Rook *et al.* 2004; Reid *et al.* 2009; Sabatier *et al.* 2015), animal welfare (Webster *et al.* 2015), product quality (Makkar 2016) and soil health (Doran *et al.* 2002; Sangha *et al.* 2005; de Faccio Carvalho *et al.* 2010). At the same time, farmers face another key challenge, namely, managing grazing to increase production and profitability. These pressures have led to substantial research, in the first

instance, to focus systematically on single parts of the systems and to respond rapidly (i.e. problem-solving approach) with new technologies of inputs (Voss *et al.* 2006; Beukes *et al.* 2010), but with less emphasis on developing systemic practices that link ecological processes such as grazing with the health of ecosystems (Schiere *et al.* 2012; Provenza *et al.* 2013).

For decades, grazing has been viewed as a succession of feeding events structured around other animal activities (e.g. ruminating, idling), with those events as building blocks of daily herbage intake (Gibb 1996, 2007). Viewed as a process, grazing is not so simple. Grazing is an arrangement of decisions leading to ingestive actions nested in spatio-temporal domains

<sup>1</sup>The views expressed in this publication are those of the authors and do not necessarily reflect the views or policies of DairyNZ.

(Senft *et al.* 1987). These decisions include trade-offs affecting short-term behavioural and physiological (ingestive and digestive) tactics (from a bite to a meal) and mid-term strategies (meal arrangements) as the means by which animals acquire energy and meet needs for nutrients, medicines and comfort (Gregorini 2011; Gregorini *et al.* 2015a). The spatio-temporal domain delimits the dimension at which these decisions are observed and can be managed (Laca 2009; Larson-Praplan *et al.* 2015). Farmers' grazing-management decisions set the context (i.e. the table and menus), and thereby modulate the animal's grazing, production and well being. Under pastoral livestock-production systems, some synergies between animals' grazing and farmers' grazing-management decisions have the potential to offer greater benefits to the animal, the farm and the environment than do simple and parsimonious grazing-management approaches based on managing a single component of the system, including factors such as the sward, or cow or soil.

Within this conceptual framework, recent advances in understanding grazing patterns and nutritional ecology of ruminants may help alleviate some of the societal pressures pastoral livestock-production systems are experiencing. For instance, by managing grazing to (1) manipulate links between ingestive–digestive decisions and temporal patterns of nutrient excretion (e.g. urine nitrogen (N; Betteridge *et al.* 2013; Clark *et al.* 2010b), (2) provide chemically diverse diets at meaningful temporal and spatial scales to improve animal welfare, health and production (Villalba *et al.* 2009, 2015b), (3) influence behaviour of animals based on their specific personalities and emotions to overcome or use those animal differences productively (Sih and Bell 2008; Searle *et al.* 2010; Koolhaas and Van Reenen 2016), (4) alter animal reward systems, metabolic homeostasis and decisions (Ginane *et al.* 2015) and (5) use transgenerational links between livestock and foodscapes (Provenza *et al.* 2015a, 2015b). All these interventions suggest new concepts and possible ways to design feeding circuits (tables) and diets (menus) that will motivate cows' (diners) feeding and dietary diversity (Meuret and Provenza 2015a).

'Grazing', as a descriptive noun, locates 'cows' within a particular part of the landscape, namely, the grasslands and pastures where they graze or are grazed (Gregorini 2015). Our objective is to deal with the active and passive voices of the verb graze, since managing grazing allows us to think about how to set the table by creating functional foodscapes, design goal-oriented 'menus', and thus influence the 'diner's' decisions to enable natural processes to enhance farms and the landscape we all inhabit. In the present review, we view grazing and its management through an alternate lens, drawing ideas and hypotheses to stimulate thinking, dialogue and discussions that we anticipate will evolve into innovative research programs and grazing practices. To do so, we have compiled and combined experimental and observational studies from a wide range of disciplines with simulation-modelling exercises. We envisage a more holistic approach to manage grazing on the basis of recent advances in the understanding of the nutritional ecology of grazing animals, and propose management practices that may enable pastoral livestock-production systems to continually evolve as complex creative systems (Provenza *et al.* 2013).

### **Ingestive–digestive and excretion decisions: the missing link?**

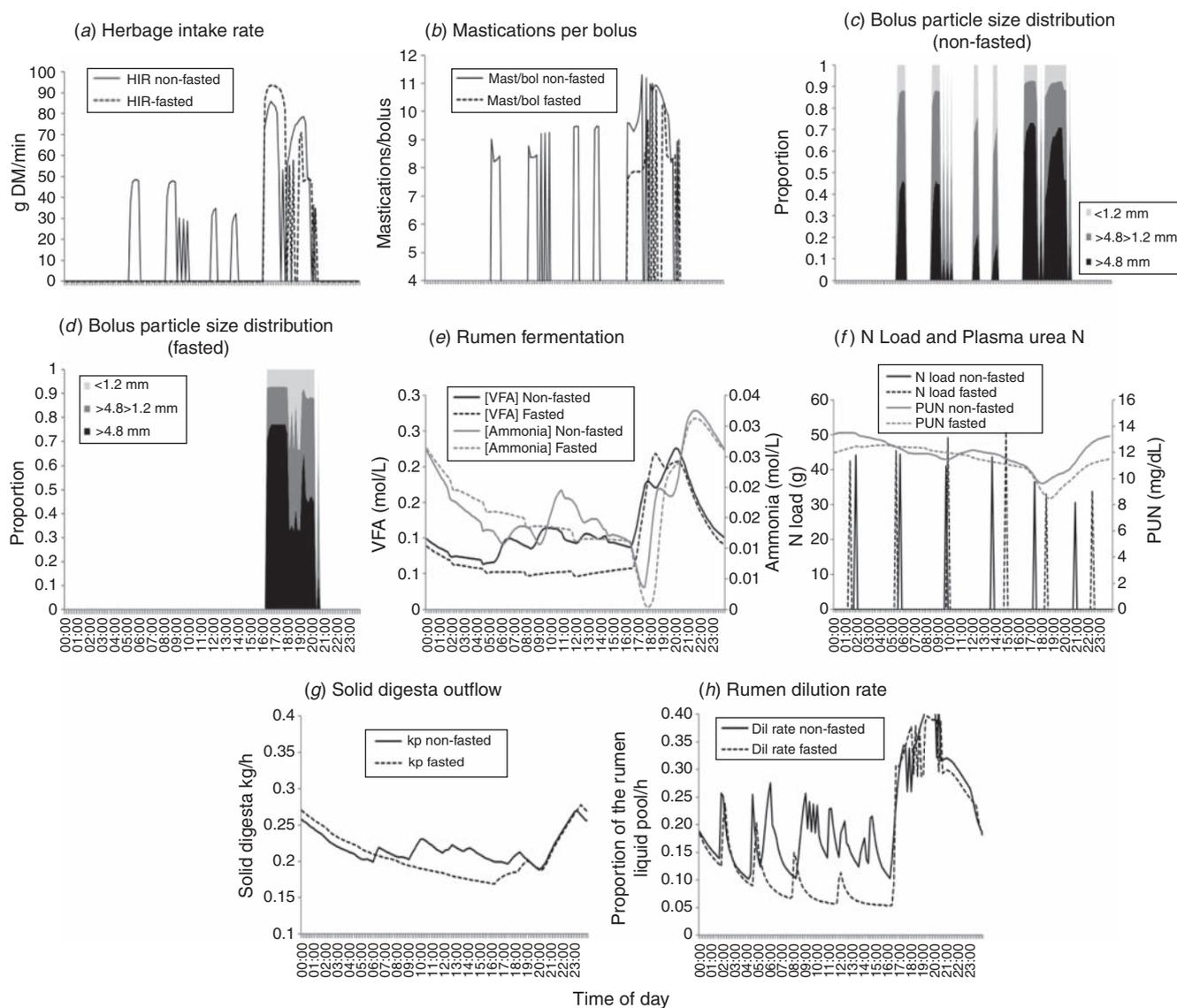
In a review of behavioural adaptations of dairy cows to changes in grazing management, Chilibroste *et al.* (2015) concluded that most of the available information focusing on short-term ingestive responses (i.e. herbage intake rate) lacked essential links with post-ingestive behaviours such as rumen function and excretion. In this section, we focus on some of these gaps and pose some hypotheses.

#### *Mastication, a critical link between ingestion and digestion*

Mastication of ingesta determines the physical characteristics of the bolus to be swallowed, most importantly the particle-size distribution (Bailey and Balch 1961; Prinz and Lucas 1997). That, in turn, influences the rate of digestion kinetics and nutrient availability in the rumen, as well as rumen fill (Chilibroste *et al.* 1998; Poppi *et al.* 2000), both being important post-ingestive signals in the control of food selection and intake. Mastication initiates the release of soluble cell contents, with a wide range (25–70%) of release values reported in the literature (Hogan *et al.* 1985; McLeod and Minson 1988; Waghorn *et al.* 1989). This variability relates to plant species, animal features and intake rate, as oral processing and mastication both influence short-term intake rate (Wilson and Kennedy 1996). Particle size in the bolus increases with intake rate, which varies within and between meals (Bailey and Balch 1961). The latter is illustrated in Fig. 1. The effect of mastication on availability of nutrients for rumen microbes, and ultimately for the host animal, has been described in two mechanistic and dynamic models of grazing dairy cattle, CTR Dairy and MINDY (Chilibroste *et al.* 2008; Gregorini *et al.* 2013a). However, these masticatory effects have yet to be seriously considered in more empirical approaches as a lever for grazing management (see Boudon and Peyraud 2001; and Boudon *et al.* 2006).

#### *Mastication and holding capacity of the rumen influence meal grazing dynamics*

Under certain conditions, such as, strip-grazing on swards with high herbage availability and accessibility, grazing cattle with high nutrient demand or hunger can ingest large volumes of herbage quickly, but they seem unable to pack it properly in the rumen (Chilibroste *et al.* 2005). This limited capacity to pack big volumes of rapidly ingested and poorly masticated ingesta creates a filling sensation even at low rumen DM digesta contents (Thiago 1988; Gregorini *et al.* 2009b). This, in turn, helps explain premature cessation of intensive grazing bouts, and within-meal changes in ingestive behaviour including bite features, mastication rates and foraging velocities (Gregorini *et al.* 2007). Poorly masticated ingesta leads, in turn, to longer pseudo-rumination events and delays proper rumination of digesta, which accounts for delays in particle-size reduction in the rumen (Spalinger *et al.* 1986). Collectively, these factors conspire to make it more difficult for a cow to begin ruminating recently ingested lush herbage. 'She' is less able to regurgitate a bolus from a rumen mat without stratification, with a low density of big, slightly



**Fig. 1.** MINDY (see definition below) outputs on the effect of pasture restriction on fasted (20 h) versus non-fasted grazing patterns, herbage-intake rate, bolus particle-size distribution, rumen function, plasma urea nitrogen (N) and N load onto pasture. MINDY is a mechanistic and dynamic model of a dairy cow representing diurnal patterns of ingestion, digestion and metabolism, excretion and production based on explicit relationships among direct and indirect controls of motivation to feed (Gregorini *et al.* 2013a, 2015b). For this simulation, MINDY was initialised as a 500 kg Holstein–Friesian cow (150 days in milk) grazing a ryegrass-based sward. Non-fasted versus fasted respectively: milk yield (kg/day), 22.2, 19; herbage DM intake (kg/day), 15, 11.1; grazing time (min), 403, 201; urinary N excretion (g/day), 254, 242; mean urinary N, (g/L), 9.1, 7.8; urine volume (L), 28, 31; methane (CH<sub>4</sub>) emissions (g/day), 330, 250; CH<sub>4</sub> yield (g/kg DM intake), 22, 22.6; foraging energy expenditure (MJ/day) 16, 9.4. Note: Fajardo *et al.* (2015) reported that fasted (13 h) dairy cows had no difference in milk production and composition, despite a reduced herbage DM intake, arguing that fasted cows had less energy expenditure than did non-fasted cows, which walked 3.4 km less than the fasted ones. Nowadays, large grazing herds (800–1000 cow) are common in Australasia and South America, with walking requirements more than 4–6 km/day. At this level, minimal reductions of walking distances while grazing may have a beneficial impact on production.

broken, tough and pliable particles in a rumen with high water content (Deswysen and Ehrlein 1979). Ultimately, poor mastication and improper packing of ingesta lead to longer retention times of digesta in the rumen and, thereby, non-glucogenic and methanogenic rumen fermentation patterns, and reduce energy utilisation for productive purposes and increase environmental impact.

#### Hunger management for short and intensive meals

The length of inter-meal intervals determines hunger level, which influences the diner's feeding motivation and expectations of the next meal (Forbes and Gregorini 2015). The latter modulates the dynamics of ingestive tactics such as mastication and then, intake rate, and, consequently, digestive

patterns within and between meals (Greenwood and Demment 1988; Chilibruste *et al.* 2007; Gregorini 2011). Longer inter-meal intervals increase herbage-intake rate, which reduces DM, organic matter and neutral detergent fibre rumen pools and the ratio between solid and liquid fractions, as well as the major volatile fatty acid pool sizes. Collectively, these factors can delay the availability of rapidly fermentable substrate (Chilibruste *et al.* 1997, 1998).

If sward conditions allow (see Chilibruste *et al.* 2007), hungry cattle can eat the majority of their DM intake (DMI) quickly. Fasted dairy cows grazing on swards with high herbage availability and accessibility can consume over 85% of their daily herbage DMI in less than 4 h, only using ~40% or less of the grazing time spent by their non-fasted counterparts, (Chilibruste *et al.* 2007; Gregorini *et al.* 2009a; Mattiauda *et al.* 2013). Compared with non-fasted cows, fasted cows have greater bite and intake rates, and a longer stride length; they walk and eat faster and explore smaller areas while grazing (Gregorini *et al.* 2011), all of which increase grazing efficiency and reduce grazing energy expenditure (Fig. 1). Similar grazing patterns have been observed in fasted beef cattle (Gregorini *et al.* 2007, 2008a). These findings led Chilibruste *et al.* (2007, 2015) to propose hunger management through the length of the inter-meal intervals as a way to design effective grazing strategies to increase and/or alter nutrient supply to and production from lactating dairy cattle.

Interest in this type of management is also reflected in the increasing use of stand-off periods that restrict time at pasture. Restricting time at pasture diminishes environmental impacts by reducing urinary N loaded onto pastures and, as a consequence, N leaching (Clark *et al.* 2010a; Shepherd *et al.* 2016). Nitrogen utilisation by dairy cows grazing on temperate swards rarely exceeds 30% (Castillo *et al.* 2001), meaning that at least 70% of the N ingested is excreted, mainly (over 60%) in urine (Kebreab *et al.* 2001; Gregorini *et al.* 2010). In grazing systems, ~82% of the urinary N is discharged onto pastures (Oudshoorn *et al.* 2008; Clark *et al.* 2010a) and ~30% is leached and 2% transformed to nitrous oxide (IPCC 2006). These leachate and gas emissions confirm the need to respond to this pressure. Restricting the access to pasture to only 8 h per day between morning and afternoon milking reduced urine volume deposited onto it by 56% (Clark *et al.* 2010a), and restricting access to pasture between milkings reduced urinary N loaded onto pastures by 36.5% (Shepherd *et al.* 2016).

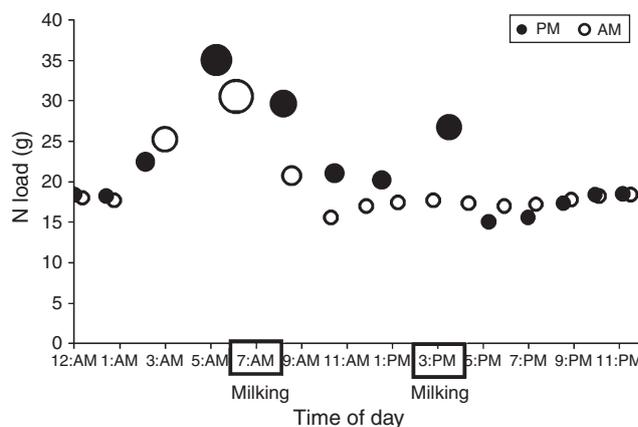
Hungry cattle swallow boli with larger particles and retain the digesta in the rumen longer (Greenwood and Demment 1988). Longer retention of digesta in the rumen favours methanogenesis (Janssen 2010b). At similar daily herbage intakes, fasted beef heifers had a slower ruminal dilution and particle passage rate, and a longer liquid and solid turnover than did their non-fasted counterparts (Gregorini *et al.* 2008a). Unfortunately, there is little quantitative information on the effect of adaptive (hunger influenced) mastication dynamics on rumen digesta outflow in grazing dairy cows. Figure 1 presents some model outputs to illustrate this case in the context of grazing dairy cows. So, are stand-off and fasting periods a bad practice?

Conversely, a longer rumen retention time increases rumen organic matter and fibre digestion, (Poppi *et al.* 2000). Cellulose and hemicellulose are the cheapest nutrient sources in pastoral

systems. Moreover, as reported by Gregorini *et al.* (2008a), fasted cattle have a lower average concentration of ammonia in the rumen than do non-fasted cattle. Rumen ammonia is intimately related to plasma urea and urinary N concentration and excretion (Maltz and Silanikove 1996; Bannink *et al.* 1999). Small increments of methane (CH<sub>4</sub>) yield as a result of carbohydrate fermentation in the rumen can be easily offset by reductions in urinary N and subsequent nitrous oxide emissions (Dijkstra *et al.* 2013). So, how bad are stand-off practices?

Hunger management through manipulation of inter-meal intervals allows managers to set available grazing times, and influence short-term meal ingestive–digestive strategies, such as compensatory reductions of mastication, to increase herbage-intake rate (Chilibruste *et al.* 2007) or increments in retention time of digesta in the rumen (Gregorini *et al.* 2012). Moreover, it allows managers to locate short- and intensive-grazing meals in time and space, thus influencing the diner's expectations about particular foods in subsequent meals, helping with the design of feeding circuits and menus (as discussed below). Chemical and biomechanical characteristics of herbage change throughout the day, with an increase in feeding value from dawn to dusk. Such changes in herbage nutritive characteristics are reflected in rumen function and nutrient supply from different meals within the day (Gregorini *et al.* 2008b; Gregorini 2012). On the basis of this information, it seems logical to influence the linkages between herbage ingestion and rumen digestion to alter the dynamics of nutrient supply to 'the diner' and, thereby, 'manipulate' animal production (Chilibruste *et al.* 2007).

Last, but not least, we hypothesise that influencing ingestion patterns through grazing management (e.g. simple alterations of timing of pasture and fasting-period allocation) may reduce



**Fig. 2.** MINDY (for definition, see Fig. 1; for this simulation MINDY was initialised as a 500 kg Holstein-Friesian cow (200 days in milk) grazing a ryegrass-based sward) outputs on the effect of timing of pasture allocation (AM versus PM, after morning or afternoon milking respectively) on diurnal urination pattern, daily urinary nitrogen (N) excretion and methane (CH<sub>4</sub>) yield and emissions. N load = volume (L) × [N] (g/L) of each urination. The size of the bubble represents the volume of each urination. Daily urinary N excretion (g/day): 292 versus 271 for AM and PM respectively. N loaded (% of total N excreted in urine) on non-pasture surfaces (milking shed and races): 17 versus 22 for AM and PM respectively. CH<sub>4</sub> yield (g/day): 21.5 versus 19.8 for AM and PM respectively. CH<sub>4</sub> emission: 326 versus 290 for AM and PM respectively.

environmental impact by altering urine excretion patterns, as illustrated in the model (MINDY) simulations presented in Figs. 1 and 2, and supported by Clark *et al.* (2010a) and Shepherd *et al.* (2016). Ultimately, this influence would provide the opportunity to influence where, when and what the diner is going to design toilettes and urinate.

### Grazing personalities and manipulating individual diner's emotions

Nobody who has worked with cattle questions the significant variations in how they behave. No two individuals will react in the same way to a challenge, from novel feeds, to changes in management, to foraging at the same pasture. These 'individualities' have driven decades of research regarding their biological significance for behaviour, physiology and animal welfare in the fields of ecology, evolutionary biology and ethology. However, the view of individual variation as a nuisance has led animal-production experimentation (Koolhaas *et al.* 2010; Koolhaas and Van Reenen 2016) to overlook the implications for management. Nonetheless, individual animal differences in wild and domestic ruminants have spurred interest in the implications for range management and landscape protection (Searle *et al.* 2010). Here, we use the functionality of some morpho-physiological mechanisms underlying individual differences, animal personalities and emotional elements to help us think about and design functional grazing-management practices that alleviate some of the current pressures on livestock-production systems.

#### *Different animals: the cow versus the moose*

Individual differences are driven by inherited (morphology (forms), physiology (function), and personalities) and acquired (learned) behavioural mechanisms. The most apparent individual variation relates to morphological and physiological differences in breed, sex, age and 'type of animal', which set animals' different coping capacities to acquire (Searle *et al.* 2010), digest and excrete nutrients. Although less apparent, changes in form, function and behaviour, enabled by epigenetic expression, allow animals to continually evolve as environments change (Provenza *et al.* 2015a, 2015b).

#### *Animal type*

Digestive differences among and within different ruminants have been framed in the concept of *cow* and *moose* type of animal (Clauss and Lechner-Doll 2001; Clauss *et al.* 2010). These differences, natural or created (see Distel and Provenza (1991; Distel *et al.* 1994) lead to distinct retention times of digesta in the rumen, and thereby rumen function (Clauss *et al.* 2010; Janssen 2010a).

*Moose*-type animals present narrower dental arcades and shorter muzzles. *Cow*-type animals have deeper mandibles, shorter molar tooth row and narrower palate. As a result, forage particle sizes swallowed by *cow*-type animals on a similar sward and displaying comparable internal state (i.e. hunger) are smaller (Lentle and Janssen 2008). Moreover, *moose*-type animals have greater intake rates, and smaller rumen capacity and rumen mat than do *cow*-type animals (Clauss *et al.* 2008). The best grazing strategy for *moose*-type

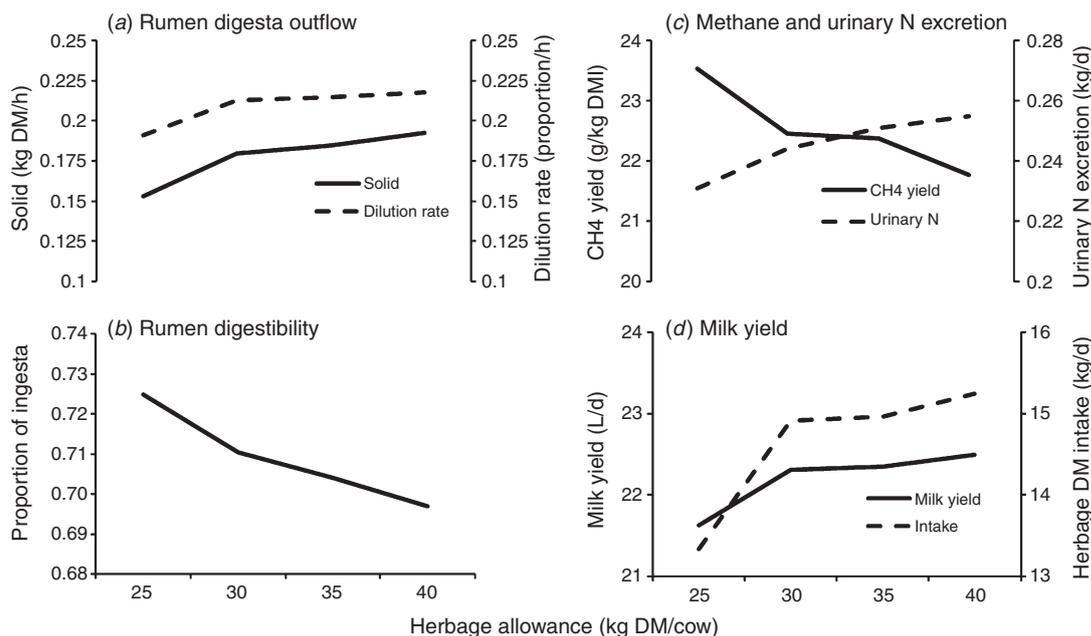
animals to increase nutrient intake and absorption seems then to be achieving a short retention time of digesta in the rumen (van Wieren 1995). This strategy may reduce CH<sub>4</sub> yield (g/kg DMI; Janssen 2010a), as supported by the comparatively lower CH<sub>4</sub> yield for *moose*-type than for *cow*-type animals reported by Johnson and Ward (1996) and Goopy *et al.* (2014), who reported marked differences in rumen form and function of sheep selected for differential CH<sub>4</sub> yield. Sheep with low CH<sub>4</sub> yield had smaller rumen volume, shorter mean retention time of solid and liquid digesta, lower amount of rumen particulate content, more clearly demarcated rumen gas and liquid phases, and an 'absence' of ruminal mat.

From these insights, we can ask the following question: can we characterise and select for *moose*-type animals within our cow herds. If so, how can we manage *cow* grazing to mimic *moose* rumen function to reduce methanogenesis? A tentative and simple grazing alternative would be to increase herbage allowance, since it would increase leaf proportion in the diet and potentially make *cows* emit less CH<sub>4</sub>. But, how good is that? Is there any trade-off? To illustrate tentative answers to these questions, we used MINDY to simulate the effect of herbage allowance on milk production, DMI, rumen function and urinary N excretion (Fig. 3).

In a temperate grass-based sward, increments in herbage allowance would increase leaf proportion in the diet, herbage DM and N intake, and reduce rumen retention time and subsequent CH<sub>4</sub> yield. Therefore, and on the basis of outputs from MINDY (Fig. 3), *cows* grazed with greater herbage allowance would emit less CH<sub>4</sub>. However, urinary N excretion would increase. The trade-off between CH<sub>4</sub> emission and urinary N excretion is always present (Gregorini *et al.* 2016). Increments in herbage allowance, as shown in Fig. 3, reduce rumen digestion efficiency of fibre, the cheapest source of nutrient in pastoral systems. How efficient are we then by selecting for or grazing as *moose*? At high herbage allowance, the key would be to think of grazing-management strategies to reduce herbage-intake rates, and, thereby, rapid inflows of N to the rumen. Reductions of intake rate also stimulate ingestive mastication (see Fig. 1a, b). Increasing mastication during ingestion increases rumen fermentation, but also accelerates digesta outflow from the rumen. Alternatively, or complementarily, supplementation with forages or feeds containing tannins appears to be an option. Also, moderate differential feeding of energy concentrates to particular individuals may reduce and dilute N intake herbage intake rate (Gregorini *et al.* 2015b, 2016) and, potentially, CH<sub>4</sub> yield. Further research is needed to test the last premise.

#### *Age*

Tooth effectiveness, which influences particle-size reduction of ingesta, is related to animal age (i.e. tooth wearing; Pérez-Barbería and Gordon 1998). Tooth effectiveness increases with age until maturity. Increasing the number of mastications per mouthfull is one strategy to maintain masticatory efficiency. However, for a cow, maintaining intake rate is a priority and mastication efficiency decreases with age, leading to ingestion of larger particles. If the goal is to maintain the level of intake, do old animals purposely increase digesta outflow rate, as observed in red deer (Pérez-Barbería and Gordon 1998), or do they opt for a



**Fig. 3.** MINDY (for definition, see Fig. 1; for this simulation MINDY was initialised as a 500 kg Holstein-Friesian cow (150 days in milk) grazing a ryegrass-based sward) outputs on the effect of herbage allowance (kg DM above ground/cow per day) on (a) rumen digesta outflow, (b) rumen digestibility, (c) methane yield and urinary nitrogen excretion and (d) herbage DM intake and milk yield.

longer rumen retention time and more efficient digestion? Both lead to differences in methanogenesis. Fasted dairy cows ruminate for less time per unit of intake (Gregorini 2012), and both the total number of chews and the time spent chewing per rumination bolus increase with cow age (Gregorini *et al.* 2013b; Grandl *et al.* 2016b). Rumination is voluntary, and cows regulate rumination in an attempt to increase or reduce rumen retention time (Wilson and Kennedy 1996). Thus, less but more intensive rumination time seems to be a strategy of ‘the old’ to increase digestion efficiency. Is that enough? It may not be. Methane yields in dairy cows grazing the same sward increases (8%) with age (Grandl *et al.* 2016a). On the same diet, sheep less than 1 year old have a lower (20%) CH<sub>4</sub> yield than do adult sheep (Lassey *et al.* 2001; Ulyatt *et al.* 2005). Age-related changes such as the reduction of mastication efficiency and increase in digesta particle size have been also reported for other ruminants such as reindeer (Veiberg *et al.* 2007), and monogastrics such as humans (Helkimo *et al.* 1978) and rats. Colon methanogenesis and CH<sub>4</sub> concentration in breath both increase with rat age (Stephen *et al.* 1986; Maczulak *et al.* 1989; Fernandes *et al.* 2000).

Young animals forage more selectively than do older ones (Cazcarra and Petit 1995; Rook *et al.* 2004), owing to different metabolic demands (Rook *et al.* 2004). The young eat more leaf than do older peers (Lazo and Sorriquer 1993; Cazcarra and Petit 1995), and they have a greater step rate with fewer bites per step while they are eating (Lazo and Sorriquer 1993). In addition, they have greater masticatory effectiveness (Pérez-Barbería and Gordon 1998). So, if they eat more nutritious and easily comminuted plant parts, their digesta should ferment and flow out faster from the rumen, reducing CH<sub>4</sub> yield, as found with

young sheep (Graham 1980), cattle (Molano *et al.* 2003) and deer (Swainson *et al.* 2007).

Should we get rid of ‘the old’ cow sooner? From the CH<sub>4</sub> viewpoint, replacements are expensive, including two CH<sub>4</sub>-producing and unproductive years (Beukes *et al.* 2010; Grandl *et al.* 2016a). From a farm-level bio-economic efficiency, to cull old cows for only this reason is not likely to be a cost-effective option. Then, how should we graze ‘the old’ to help them produce less CH<sub>4</sub>? Let us look at the pioneering work of Stobbs (1978) on ‘leaders and followers’. Milk from leader cows had a greater percentage of non-fat solids and protein, and a lower ‘butterfat’ percentage, indicating that their rumen fermentation pattern was more glucogenic with greater potential reduction in the digesta retention time; that is, they were less methanogenic. Therefore, one alternative to ‘help the old’ may be to make them ‘lead’ (also, see Fig. 3). The question here is how expensive is the penalty for the ‘young followers of the old’? Could differential supplementation and ‘current herd-segmentation managements’ be an option to mediate the penalty?

#### *Different personalities*

Individual variation of certain processes seems to be clustered in behavioural syndromes (Sih *et al.* 2004; Searle *et al.* 2010). Behavioural syndromes are sets of correlated decisions and ensuing actions consistent across contexts, which give rise to ‘personalities’ (Boissy and Erhard 2014). Some of the most common are exploration, aggressiveness and boldness. Studies of behavioural syndromes have focussed on birds, rodents and humans, mainly in laboratory settings. A few studies with ruminants have shown evidence of animal personalities, such

as, reproductive status, age- or bodyweight-independent temperament in wild sheep (Réale *et al.* 2000). Individual and heritable docility differences exist for beef (Le Neindre *et al.* 1995) and dairy cattle (Gibbons *et al.* 2011). Are there grazing syndromes? There is little information on sets of correlated actions relating to the grazing process, and that information was obtained in extensive systems (Michelena *et al.* 2009; Sibbald *et al.* 2009; Wesley *et al.* 2012). In these works, Sibbald *et al.* (2009) and Michelena *et al.* (2009) studied personality-related spatial distribution of grazing sheep across grassland patches and Wesley *et al.* (2012) evaluated similar traits in rangeland-raised beef cattle. For instance, the mean nearest-neighbour distance and spread of shy sheep were less than that for bold animals, with shy individuals moving towards one another more often (Sibbald *et al.* 2009).

To our knowledge, the work of Gregorini *et al.* (2015c) is, so far, the only study that has explored ‘grazing personalities’ of grazing dairy cows. Using a multivariate approach, Gregorini *et al.* (2015c) identified two groups of cows with considerably different grazing patterns. One of them prioritised grazing and rumination, concentrating on grazing at the time that fresh pasture was allocated. While grazing, cows in this group walked (explored) less and more slowly, masticated less and took more bites per feeding station. Moreover, this group of cows spent ~30% energy while grazing, with the major energy ‘saving’ during the first and main meal of the day (Gregorini *et al.* 2016). On the basis of these results, Gregorini *et al.* (2015c, 2016) postulated that these cows were more efficient grazers. Grazing efficiency relates to trade-offs that define short-term decision making (from a bite to a meal and meal arrangement) as the means by which animals acquire nutrients (Bergman *et al.* 2001; Owen-Smith *et al.* 2010; Emmans and Kyriazakis 2001). Do different grazing personalities exist in those two groups of cows? Do we have ‘efficient’, ‘inefficient’, ‘aggressive’ and ‘laid-back’ grazers? If so, the challenge is to identify how to graze all cows most efficiently, so as to enhance their strengths or reduce their weaknesses. Moreover, can we breed for those personalities? Personalities can be inherited (Boissy and Erhard 2014). Breeding for increments in dairy cow Breeding Worth in New Zealand has selected for ‘aggressive’ grazers (Rossi *et al.* 2005), as supported by recent results showing that, independent of herbage allowance, cows with high Breeding Worth have considerably fewer mastications per bite (P. Gregorini, unpubl. data).

Indoor studies with the same group of cows used by Gregorini *et al.* (2015c, 2016) focussed on rumen physiology (Rius *et al.* 2012). ‘The more efficient grazers’ were cows selected as calves for low residual feed intake. Compared with their ‘inefficient’ counterparts selected for high residual feed intake, the ‘efficient grazers’ had considerably smaller rumen pools and faster rumen fractional dilution, which can lead to lower CH<sub>4</sub> yield (Alford *et al.* 2006; Hegarty *et al.* 2007). On the basis of their grazing pattern, Gregorini *et al.* (2015c) suggested that these cows would have a greater herbage- and leaf-intake rate. Is this evidence suggesting that the ‘efficient’ cows are *moose*-type animals? If so, would they have a rumen with a diminished methanogenic environment? However, a faster intake rate of high-quality leaves (high N content) leads to greater and faster N input to the rumen and momentary excesses. Low residual feed-intake

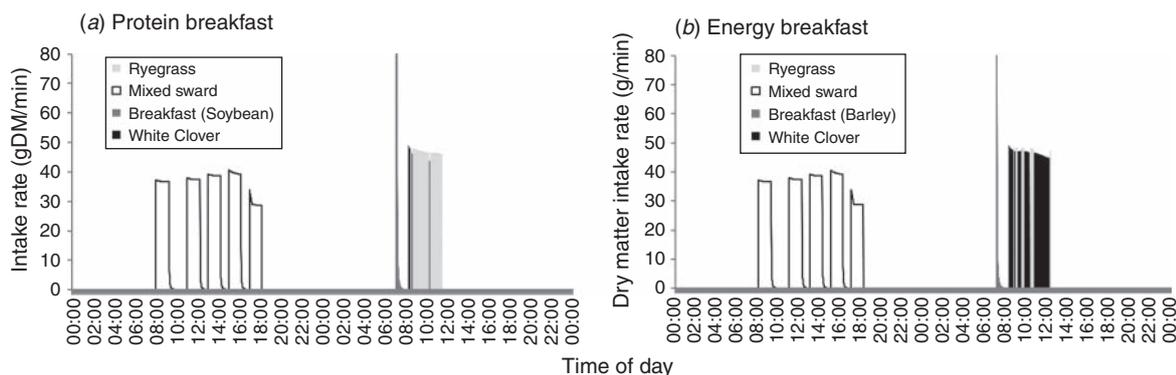
cows (‘the efficient *moose*’) not only had greater (20%) daily mean of rumen ammonia concentration, but also a considerably greater (66%) concentration right after feeding (Rius *et al.* 2012). Rumen ammonia is intrinsically related to urinary N concentration and excretion (Maltz and Silanikove 1996; Bannink *et al.* 1999). These differences support the idea of a differential N-urination pattern according to animal individual differences. What and when the ‘efficient’ grazer *moose* urinates is different from a *cow*. We must still question the ‘efficiency’ of the *moose*...

Grazing pattern is an arrangement of correlated ingestive decisions and actions nested in time and spatial scales (Senft *et al.* 1987). The study of grazing patterns, then, may show hidden personalities and transgenerational links. In a study of behavioural syndromes with two groups of range-beef cattle, Wesley *et al.* (2012) identified that one of these groups had a greater intake rate, covered larger range areas per day, exhibited a less winding foraging trajectory, and had greater serum cortisol concentrations than did their counterparts. Increments in cortisol concentrations have been associated with temperamental, stress- and anxiety-related behaviour in cattle (Bristow and Holmes 2007). Behavioural syndromes, i.e. personalities, emerge as a multitude of correlated traits. They cannot be studied by looking at each decision in isolation. It is tempting to hypothesise that grazing personalities come with different ‘baggage’. The challenge is managing the diners’ personalities by influencing their decisions about how, when and where to graze. Can we provide soothing menus and tables (see next section)? Can we customise ‘menus’ (what is available) by the courses we bring to the pasture context, i.e. ‘table’?

#### *Influencing diner’s emotions*

The concept of personality incorporates elements of behaviour, cognition and emotion (Boissy and Erhard 2014). Emotions (affective state) result from how an individual evaluates a situation (e.g. feeding environment), followed by its response (decision making to deal with) to that situation (Lazarus 1991). Assessments are based on characteristics such as familiarity, pleasantness, expectations, coping potential, internal state and comfort of the individual (Mangel and Clark 1986; Boissy and Erhard 2014). The results of this evaluation determine emotional experiences, whether negative or positive. These experiences can, according to the intensity of the experience, temporarily or persistently influence decision making (e.g. ‘wanting’ to eat it; Ginane *et al.* 2015) when appraising the reward from similar or new situations.

A key element of emotional experiences is the feeling of comfort (Boissy and Erhard 2014). In the context of foraging, neurally mediated interactions between the chemical senses, cells and organ systems throughout the body (Furness *et al.* 2013), and the microbiome (Alcock *et al.* 2014), enable ruminants to ‘sense’ the post-ingestive consequences (positive or negative) of food ingestion and modify food selection accordingly in search of comfort (Provenza 1995; Forbes and Provenza 2000). Several studies on dairy cattle have supported this idea (Emmick 2007; Pinheiro Machado Filho *et al.* 2014). Combinations of foods that meet nutritional needs lead to satiety and a feeling of well-being, whereas post-ingestive excesses and deficits can lead to nausea and malaise, and feelings



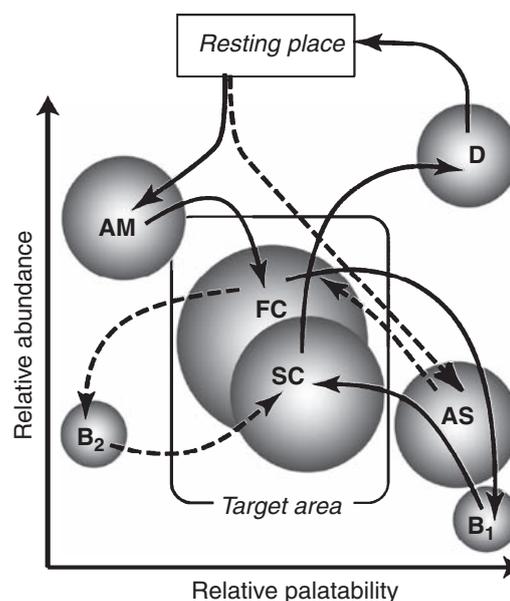
**Fig. 4.** Meal and preference patterns of MINDY (for definition, see Fig. 1; for this simulation MINDY was initialised as a 500 kg Holstein-Friesian cow (150 days in milk) grazing a ryegrass-based sward) when fed herbage from a mixed sward plus overnight fasting, a load ('breakfast') of either soybean meal or barley grain immediately before the feed test of either a monoculture of perennial ryegrass or white clover.

of discomfort. On the basis of the post-ingestive feedback theory, sensations and animal requirements, Forbes and Provenza (2000) developed an integrative theory and model of 'minimal total discomfort'. This model was incorporated into MINDY (Gregorini *et al.* 2015b), which helps illustrate how diurnal and within-meal patterns of preference and, thus, selection can be manipulated as a result of changes in minimal total discomfort (Fig. 4). Managing comfort from a nutritional standpoint, therefore, emerges as a way to influence the individual diner's emotions, expectations, preferences, aversions and, thereby, grazing in time and space within foodscapes, so providing a rich variety of phytochemicals as nutrition centres and pharmacies to enable animals to meet their needs (Provenza *et al.* 2015a). It is tempting to hypothesise that modulating individuals' comfort may then help manage grazing personalities, such as, those of the 'efficient moose'.

Under intensive rotational-grazing management (a competitive grazing context with high grazing pressures), dairy cows face a trade-off between selective behaviour and herbage-intake rate (Chapman *et al.* 2007; Soder *et al.* 2007). When grazing mixed swards, such a context conditions and reduces animal's possibilities to express temporal and spatial selectivity, reducing potential benefits of spatio-temporal arrangements of the diet. As presented in Fig. 4, and supported by the empirical work with dairy cows (Emmick 2007; Pinheiro Machado Filho *et al.* 2014), managing diner's comfort through strategic feeding emerges as a way to overcome the constraints presented by such a competitive grazing context. These emotional influences allow to manage and create or enhance temporarily any preferences (i.e. 'liking') of individuals or the herd, timing the consumption of particular plant species, even when aiming at high 'pasture utilisations'. Temporal managements of 'liking and wanting' of particular plant species would also allow farmers to use a single mix sward (single sector) as first and second course, with different plant/s being consumed (mainly) in each course (see the previous section of the text, and Fig. 5).

### Diversity and diverse diets

Benefits for herbivores from grazing biochemically diverse plant species are possible because of the inherent ability of



**Fig. 5.** MENU model that French herders use to design daily feeding circuits to stimulate feeding motivation in target areas, forages or swards and dietary diversity. Herders use forage relative abundance and palatability to sequence meals in time and space (taken and adapted from Meuret and Provenza 2015a). AM, appetite moderator; AS, appetite stimulator, FC, first course on a target area; SC, second course on a target area; Bi, appetite boosters/moderator; and D, dessert. The size of the bubble represents the relative size of the course. Resting place in a dairy farm can be seen as the milking shed or a feed/stand-off pad. Sectors (e.g. within a dairy farm) can change within a season or years, and can contain different forages within a season and years and result from variations in the abundance or relative palatability of the particular forage (at the time) of the sector. Variations of these two parameters can also come from herders' MENU design and forage depletion as well as plant growth and phenology.

any animal to build its own diet (Provenza 1995; Provenza and Villalba 2006). Herbivores learn to select nutritious diets on the basis of the association between sensorial characteristics of food and its post-ingestive effects (Provenza 1995). Flavours, textures and sights are all cues that animals use to distinguish

specific foods. Post-ingestive feedback calibrates palatability of foods with homeostatic utility (Ginane *et al.* 2015). This is why herbivores, such as cattle, form preferences for foods that provide the most required nutrients and medicines, and aversions to those that supply excesses of nutrients and toxins (Villalba and Provenza 2007).

Food diversity plays a key role in the nutrition and welfare of livestock. They benefit from diverse diets due to synergies among different forages, and the primary and secondary compounds (Provenza *et al.* 2003; Villalba *et al.* 2010). Some arrays of plant secondary compounds also improve animal health (Min and Hart 2003), quality of animal products (Vasta *et al.* 2008; Priolo *et al.* 2009), reduce methanogenesis (MacAdam and Villalba 2015), increase efficiency of N use by ruminants (Waghorn *et al.* 1987; Waghorn and McNabb 2003; Waghorn 2008), and may reduce negative associative effects often observed under concentrate-supplementation regimens. Moreover, synergies among chemicals have the potential to offer benefits beyond the sum of the actions of the individual plant components (Tilman 1982). However, the concepts of food diversity and synergy have been ignored ‘parsimoniously’, focusing research on single nutrients, ‘toxins’ or food benefits (Duke *et al.* 2006), as opposed to whole foods with multiple combinations of compounds (Jacobs and Tapsell 2007). In this and the next section, we attempt to reinforce the case to consider the importance for productivity and health of herbivores and humans, and the profitability of farmers, from allowing cattle to graze on diverse rather than monotonous dietary menus.

#### *Diversity and nutrients*

Foods are complementary when the benefit of consuming two or more foods together exceeds the averaged benefit of consuming the foods in isolation (Tilman 1982). The complementary-nutrient hypothesis assumes that different foods contain different ratios of required nutrients. No single forage has the perfect balance of nutrients found in a variety of forages (Westoby 1978). Thus, through diversity, grazing animals can obtain a more beneficial and balanced mix of nutrients. In contrast, animals grazing on a single and unbalanced forage may stop eating as they satisfy their requirements for the nutrient in highest concentration, before satisfying requirements for nutrients occurring in lower concentrations, a phenomenon known as incidental restriction (Raubenheimer 1992). Alternatively, animals such as dairy cows continue grazing to satisfy their requirements, a compensation that inevitably leads to overconsuming the nutrient occurring in highest concentration, a phenomenon known as incidental augmentation (Raubenheimer 1992; Bartness and Demas 2004; Chapman *et al.* 2007; Rutter 2010). This response incurs extra grazing costs, results in nutrient excesses (e.g. N) and promotes inefficient nutrient utilisation, with the concomitant decreases in animal welfare, productivity and incremental impact on the environment (Castillo *et al.* 2000; Beukes *et al.* 2014; Edwards *et al.* 2015; Gregorini *et al.* 2016), all of which can create food aversions that diminish food intake (Provenza 1996). Despite the logical benefits of dietary diversity, as discussed by Rutter (2010) and Pembleton *et al.* (2015) for dairy cattle, information on the value of dietary diversity on milk production of grazing dairy cows is ambiguous and scarce

(Soder *et al.* 2007; Vibart *et al.* 2016). Moreover, much of the research on diet diversity of grazing dairy cows has been conducted comparing simple associations to homogeneously mixed complex swards. The latter constrains spatial and then temporal selective behaviour and its concomitant benefit (see next sections, Chapman *et al.* 2007 and Edwards *et al.* 2008). More research is needed to assess interactions among multiple arrangements in time and space of plants, containing mixtures of primary and secondary compounds, at the same or varying resource (e.g. herbage) allocations, and their effect on incidental restriction and augmentation.

#### *Diversity and the sensorial attributes of food*

As an animal eats a specific food, its chemical sensory systems (i.e. smell and taste) generate oro-sensorial experiences that eventually trigger satiety (Blundell *et al.* 1994; Blundell and Bellisle 2013). That happens through a decline in wanting (appetite; see next sections) and liking (hedonics) for the food. This process, known as sensory-specific satiety (Rolls *et al.* 1982), plays a key role in regulating feed intake (Sørensen *et al.* 2003). Sensory-, nutrient- and secondary compound-specific satieties all interact to influence food selection and intake (Provenza 1996; Provenza *et al.* 2015b). Individuals can better meet their needs for nutrients and increase intake when offered a diverse diet than when constrained to a single food (set of nutrients), even if the food is nutritionally ‘balanced’. Diversity is key, since a single ‘set of nutrients or balanced feeds’ can cause premature satiety. Intake-related sensorial neurons stop responding to a particular food eaten to satiety, yet they continue to respond to ‘other foods (~set of nutrients)’. If other foods are not available or offered, animals stop responding and intake decreases. In contrast, diverse oro-sensorial stimuli may restore the motivation to eat (Epstein *et al.* 2009).

Lambs fed a choice of different flavours in the same ration consumed more feed and tended to grow faster than animals fed rations with single flavours (Villalba *et al.* 2011). In addition, exposure to diverse flavours induced a more even consumption of feed across time, by reducing peaks and nadirs of intake, compared with when animals were exposed to monotonous rations. Flavour diversity also led to changes in the hormonal profiles involved in feed-intake regulation (e.g. CCK, GLP-1; Villalba *et al.* 2011), which was likely to be a consequence of changes in the animals’ feeding patterns. Flavour diversity also enhanced subsequent acceptability and preference for novel feeds by lambs (Villalba *et al.* 2011, 2012; Catanese *et al.* 2012). Moreover, Catanese *et al.* (2013) reported that dietary diversity *per se*, as opposite to monotonous diets, increased intake rate and attenuated stress-related responses (cortisol concentrations and neutrophil to lymphocyte ratio) in lambs. The following two questions arise: do cattle respond to dietary diversity in the same way as do the lambs in these examples; and, if so, could we use flavours to influence our diners to better adapt to our grazing managements, goal-oriented menus or feeding circuits (see next section)?

#### *Diversity and plant secondary compounds*

At high doses, plant secondary compounds constrain intake and negatively affect animal cells, tissues, metabolic processes

and productivity, even to the point of toxicity (Cheeke and Shull 1985). Consequently, one of the objectives for forage improvement has been to reduce concentrations of these compounds. This approach makes sense when plants grow in monocultures. However, ancestors of livestock did not eat single foods. Rather, they selected diets from a diverse array of plants in time and space, as do wild herbivores and livestock foraging on rangelands today (Provenza *et al.* 2003, 2007).

Plant secondary compounds offer advantages for plants and livestock. Plant secondary compounds are vital for attracting pollinators and seed dispersers, helping plants recover from injury, protecting plants from ultraviolet radiation and defending plants against pathogens and herbivores (Rosenthal and Berenbaum 2012). Moreover, the lack of plant secondary compounds may negatively affect plant persistence and adaptability (Asay *et al.* 2001; Thom *et al.* 2013). Secondary compounds are also increasingly recognised as important in the health, welfare and nutrition of animals, including humans (Engel 2003; Crozier *et al.* 2008; Waghorn 2008; Steiner 2010). Under natural conditions where diverse mixtures of plants is the rule, not the exception, eating a variety of foods is how animals cope with, and likely benefit from, the health benefits of secondary compounds in their diets.

A sward or a purposely designed menu with a diverse array of plant secondary compounds allows animals to harvest greater amounts of nutrients while maintaining intake of plant secondary compounds below toxic levels. This is because different compounds are less toxic when ingested as a dilute mixture than when ingested in a larger dose (Freeland and Janzen 1974). For instance, sheep eat more when offered choices of foods, with various plant secondary compounds affecting different detoxification mechanisms (Villalba *et al.* 2004; Lyman *et al.* 2008). In addition to complementary detoxification pathways, complexation among different compounds in diverse diets may enhance tolerance of the mix. As an example, condensed tannins and saponins bind in the gastrointestinal tract, nullifying the effects of both compounds (Freeland *et al.* 1985). Goats increase intake when shrubs contain a combination of condensed tannins and saponins, relative to when animals are offered single shrubs (Rogosic *et al.* 2006), and sheep offered a choice between saponin- and tannin-containing rations eat more than when they are offered only tannins or saponins in single rations (Copani *et al.* 2013). Sheep eat more of combinations of tannin- and saponin-containing legumes than do animals offered the same legumes in single diets (Lagrange and Villalba 2016).

Stable complexes between alkaloids and condensed tannins make alkaloids less available in the gastrointestinal tract, thus reducing their toxic effects (Catanese *et al.* 2014). The tannin-containing legume birdsfoot trefoil ingested before eating endophyte-infected tall fescue or reed canarygrass, both alkaloid-containing forage grasses, enabled lambs and calves to consume more fescue or reed canarygrass than did lambs and calves fed the same grasses without the legumes (Lyman *et al.* 2012; Jensen *et al.* 2013). Likewise, lambs offered tannin-containing supplements ingested more alkaloid-containing rations than did lambs offered just the alkaloid-containing rations (Lyman *et al.* 2008; Owens *et al.* 2012). This information is consistent with the notion of complexation and

inactivation of combinations of plant secondary compounds. Radial diffusion assays demonstrated that ergotamine, an alkaloid from an endophyte-infected grass such as tall fescue, binds to condensed tannins extracted from sainfoin, a complexation which leads to greater intake of fescue by sheep supplemented with sainfoin than by sheep that did not receive this legume (Villalba *et al.* 2016a).

The strategic incorporation and benefits of plants with specific secondary compounds in the menu of grazing ruminants is evident and promising. However, more research is needed in the agronomic adaptation and persistency of these type of plants to different grazing regimes and environments.

### *Spatial and temporal diversity*

#### *Spatial dimension*

Foraging animals continually make choices about where and what they graze, even in a homogeneous sward (Senft *et al.* 1987). Heterogeneity is a key variable regarding the spatial distribution of feed resources in a diverse plant community (Laca 2008). How an animal perceives heterogeneity is scale-dependent and, thus, a function of body size (Laca *et al.* 2010). At one end of the spectrum, selectivity is constrained when patches become smaller than the size that the herbivore can bite. For instance, sheep can select a higher-quality diet than the average quality present in a mixed sward, but a cow with a mouth and bite area several times the size of the distance between clusters of forages may not. Thus, as the spatial scale becomes smaller, heterogeneity declines to a point of not being functional (Wallis de Vries and Schippers 1994; Drescher *et al.* 2008). At the other end of the spectrum, too great a spatial separation of food resources eventually makes it impossible for animals to get a mixed diet within a meal (Prins and Van Langevelde 2008). Spatial heterogeneity can be manipulated as a function of the grazer in ways that optimise animal health, welfare and productivity, all with important managerial implications.

Searching for and handling preferred forages in a diverse plant community takes time, which, in turn, can reduce harvest efficiency (Chapman *et al.* 2007). Studies offering animals the choice of alternative forage species such as ryegrass and white clover growing side-by-side, rather than sown as a conventional intermingled mixture, provide evidence that animal performance improves with choices (Nuthall *et al.* 2000; Cosgrove *et al.* 2001; Edwards *et al.* 2008). When grass and clover were planted in strips, as opposed to homogeneous mixtures, intake of forage by sheep increased by 25% and milk production by dairy cows increased by 11% (Cosgrove *et al.* 2001). Separation of plant species minimises the time needed to select and handle desired amounts of differentially preferred (at the time) forages. In addition, planting forages in strips mimics what happens naturally as different plant species aggregate in response to environmental conditions (Chapman *et al.* 2007). However, a constraint for grazing systems involves animals preferably selecting one species over another. The question is: will livestock that learn about complementarities among forages, mix those forages more efficiently, incorporating a higher proportion of less palatable feeds into their diets? Cattle allowed a free choice between strips of tall fescue- and sainfoin or tall fescue- and lucerne, mixed legumes with tall fescue in their

diets, even when legumes were available *ad libitum* (Maughan *et al.* 2014; Villalba *et al.* 2015a). Cattle could have selected just the highest-quality food resource (legumes) without additional costs during these grazing trials, but they mixed their diet instead. It becomes apparent that sensorial attributes of foods, balancing of nutritional needs, complexation of plant secondary compounds, and learning about grass–legume complementarities help explain these patterns of food selection. In addition to animals voluntarily mixing their diet, grazing and feeding management can be used to influence the diner's diet mixing in space and time (see Fig. 4).

### *Temporal dimension*

When and where animals graze different combinations of plant species has strong managerial implications, which is described in the next section 'Learning from French chefs'. The temporal sequence in which foods are ingested affects food intake. For instance, when offered foods high in terpenes and tannins, sheep eat more food with terpenes when they first eat food with tannins (Mote *et al.* 2008). A supplement of either lucerne (containing saponins) or birdsfoot trefoil (containing tannins) before eating tall fescue (containing alkaloids) caused lambs to ingest more than do lambs fed only tall fescue (Owens *et al.* 2012). Heifers that grazed in a sequence of lucerne to tall fescue spent considerably more time grazing on fescue than did heifers that grazed in the reverse sequence (Lyman *et al.* 2012). Thus, availability of legumes improved the use of tall fescue, and the sequence of forage use was important to achieve the benefit. Animals that graze free-choice adjacent monocultures of ryegrass and clover prefer clover (70%) and achieve higher daily intakes to those that graze pure clover, even though choice animals are including 30% grass in their diet, which offers considerably lower intake rates than does clover (Chapman *et al.* 2007). Intake increases when grass is included in the diet, presumably because grass allows animals to overcome some discomfort constraint to eating pure clover (Cosgrove *et al.* 2001; Champion *et al.* 2004; Gregorini *et al.* 2015b). Such discomfort involves the rate of ammonia production in the rumen and subsequent uptake in the blood. By timely mixing of grass with clover, animals can control the rate of accumulation of ammonia in rumen fluid (Hill *et al.* 2009).

Interactions among secondary compounds reduce the negative post-ingestive effects of a single compound, e.g. stable complexes form between alkaloids and tannins (Villalba *et al.* 2016a). Saponins in lucerne may also neutralise alkaloids in fescue (Lyman *et al.* 2012; Jensen *et al.* 2013). Thus, legumes containing diverse plant secondary compounds can reduce toxicity induced by alkaloids in grasses.

Finally, plant secondary compounds in herbage may improve the efficiency of nutrient use in ruminants. Condensed tannins increase rumen undegradable protein, providing high-quality protein to be digested in the small intestine (Barry *et al.* 2001; Ramírez-Restrepo and Barry 2005). Moreover, at low doses, tannins may even improve the efficiency of ruminal fermentation (Frutos *et al.* 2008). Saponins and tannins ingested before consuming high-protein foods also alleviate malaise by inhibiting fast rates of ammonia production in the rumen (Salem *et al.* 2005; Waghorn 2008).

Collectively, spatial and temporal dietary diversity represents a sustainable alternative to improve animal production, reduce environmental impact and enhance health, welfare and nutrition in pasture-based livestock-production systems, including dairy. And, as we discuss in the next section, this can improve the health and well-being of livestock and human beings.

### **Setting the table and designing the menu for them, and us**

Temperate pasture-based dairy systems in New Zealand, Australia, England, the Netherlands, Ireland and parts of South and North America have been built on the production of low-cost feed, herbage, from monoculture swards or relatively simple two-way associations such as perennial ryegrass and white clover. Since the legendary research of McMeekan (1961), Australasian intensive pastoral dairies have evolved and revolved around the use of such swards, which has led to highly productive and specialised, but monotonous systems. However, environmental conditions and social pressures are slowly changing the face of these systems. Farmers are being advised to use diverse swards, forage crops and herbs, and strategically use supplements to reduce N ingestion and excretion (e.g. Forages for Reducing Nitrogen Leaching, MBIE Program, New Zealand). These changes are increasing biodiversity and, inadvertently and inevitably, creating opportunities to include non-traditional forages such as trees, shrubs and herbs into pasture systems, with many of these plants with prophylactic and therapeutic properties (i.e. medicinal plants). Given the taxonomic, chemical and spatio-temporal complexity of this diverse foodscape, the main challenge ahead for evolving future farms will be to identify potential food courses and design the sequences of meals in time and space that better fit the individual animal, so as to reduce societal pressures on pastoral farming while maintaining or even enhancing profitability.

### *Learning from French chefs*

Skilled herders in France design grazing circuits at a meal scale to continuously motivate feeding and diet diversity, avoid grazing weariness, and increase intake of abundant but less palatable forages by sheep and goats. They aim to create synergies among meals and meal phases (Meuret and Provenza 2015a, 2015b). To do so, they 'set the table' by partitioning foodscapes into grazing sectors that are carefully sequenced within daily circuits. Meals are based on complementary blends of terrain and plant communities within and among sectors, not on individual plants. Herders identify and ration various sectors into phases of a meal, namely, appetite stimulator or moderator, first course, booster, second course and dessert sectors (Fig. 5).

According to herders, animals develop a 'temporary palatability scoring' as they judge, in a comparative way, whether the foods are satisfactory. Herders can successfully modulate 'palatability scoring' by organising access to sectors that enable minor foraging transitions over several days. They prevent the herd from having a much better foraging 'experience' on one day than on others, so the animals will not spend most days searching for, or expecting, favoured forages and failing to use other forages. Conversely, offering the same

foods (or sequence of sectors) repeatedly (monotony in time) leads livestock to satiate on both the forages and the locations, and thereby creating 'grazing weariness' (Meuret and Provenza 2015a, 2015b). As suggested by Boissy and Erhard (2014) and Rutter (2010), and supported in the previous section on diversity and diverse diets, 'grazing weariness' has welfare implications since dietary monotony induces stress. Given the same territory, breed of livestock, herd size and stock density, no two herders or herds will achieve the same performance. Herd and foodscape performance depend on herder's ability to set the 'table' and design and execute 'menus' into feeding circuits and distinctive feeding habits of herds and individuals, including appreciation of different animal personalities. The synergies herders enable can be understood as a consequence of interactions between the foodscape and the animal's reward system (diner's emotions) and the regulation of metabolic homeostasis.

#### *Designing the menu by understanding 'wanting', 'liking' and 'learning'*

'Wanting,' 'liking' and 'learning' are complementary aspects of meals and feeding (Ginane *et al.* 2015) and are the science concept behind the 'French chefs'. Initially, the decision to consume food is made on the basis of the expected rather than actual rewards, on the basis of past experiences with the combinations of forages on offer, which then influences 'wanting' and 'liking' for a food. In the appetitive phase of a meal, animals receive information about the food on the basis of sensory perceptions of sight, smell and taste. These pre-ingestive stimuli reinforce motivation to eat or avoid a food. 'Wanting' is the incentive to eat a food, which is linked with the rewards for eating a food (Berridge 1996). If positive enough, the reward reinforces eating a particular food. If the reward is negative enough, the motivation to eat from that feed diminishes (Provenza 1995), consequently affecting 'liking' and 'wanting' (Ginane *et al.* 2015). Dopamine pathways calibrate the degree to which expectation and reward match and enable animals to recalibrate expectations on the basis of consequences within and among meals. It is obvious that previous and, thereby, subsequent expected 'affective' experiences with a food are crucial in the initiation phase of a meal and the design of the daily menu.

'Liking' is the sensory (hedonic) property of eating (the pleasure of eating that food), mainly influenced centrally by opioid, cannabinoid and gamma-aminobutyric acid (GABA) systems. 'Wanting' and 'liking' act in concert to modulate feeding behaviour. If a liked food is also wanted, the preference for it over time is reinforced and learning is facilitated (Ginane *et al.* 2015). Foods with needed phytochemicals are highly preferred, while foods that are excessive or deficient have low hedonic value and are avoided (Provenza 1996). As suggested by Ginane *et al.* (2015), the interplay of 'liking' and 'wanting' help explain some of the observed inconsistencies in animal behaviour within and among animals consuming the same food. These inconsistencies, in turn, emerge as one of the 'chef's tools' to design menus and to influence diners.

'Learning' links environmental cues, such as sight, odour and taste, with homeostatic utility, all being closely linked with

'wanting' and 'liking'. Learning links 'wanting' with 'liking' by calibrating the preferences of foods according to the post-ingestive consequences of eating a food or combination of foods. 'Learning' is, therefore, an influential way to 'teach' grazing. In other words, we can 'teach them' to eat and 'enjoy' what we want 'them' to eat. Examples of cattle, sheep and goats trained to eat 'weeds' support this premise (Walker *et al.* 1992).

#### *A conceptual framework for considering the design of feeding circuits and menus for dairy cows*

Let us imagine a diverse pasture-based system for dairy cows containing, at a particular time, a base of two or three mixed swards (simple associations and complex mixes) plus one or two monoculture swards (e.g. winter or summer annuals grasses (depending of the time of year), herbs (e.g. chicory, plantain), legumes (e.g. lucerne, lotus, sainfoin), a grazeable crop (e.g. brassicas, beets) and access to two different types of supplement (e.g. energy and protein concentrates), as well as feed additives. Let us assume that farmers allocate pasture twice or even three times a day, cows are milked twice a day, and a cow can receive supplements in the milking shed and on a feed pad (before or after milking, or both) and there is a stand-off pad in the farm where supplements can be fed and urine captured, 'the designed *toilette*'. Last, but not least, let us assume that some paddocks and races contain medicinal trees and shrubs that some cows can browse and self-medicate with. The goal of the feeding circuit should not necessarily be only to increase DMI. A more holistic approach, which might actually decrease DMI while improving animal performance, would aim at optimising nutrient intake (primary and secondary plant compounds) for the animal (cells, organ systems and rumen microbes), thus improving animal welfare while reducing environmental impacts such as carbon and N footprints. Within such a diverse system, animal type, personalities and emotions should play a key role in the design of the menu and strategic setting of the table, feeding circuits, as French chefs strive to do.

On the basis of Fig. 5, pastoral dairy farmers can think of the base swards as 'target areas', and motivate cows for a predetermined herbage utilisation (e.g. residual). The farmer should also assess, identify and use complementarities among 'target areas', other forages and grazing sectors, and supplemental foods, as well as additives (e.g. flavours, anti- and probiotics). Initially, the farmer should prepare the 'menu' and 'set the table' (size, location and amount of food to grow) to balance productivity with enhanced animal welfare and reduced environmental impacts. The assessment criteria of available or potentially available foods in the menu should be performed according to functionality. Functionality, in this case, is related to the goal of grazing management, as well as the order in which components of the menu are presented in time and space. All of this is flexible and should change as conditions change in time and space. Biodiversity creates opportunities to manage ever-changing environments.

As food for thought, we suggest the following merely as one example. At the beginning of a feeding circuit, let us say before morning milking, when the cows are most hungry

(Gregorini 2012), farmers could feed (supplements) or graze (grazeable crops) highly palatable (appetite-stimulating), but not necessarily abundant, or less palatable but abundant (appetite moderating) foods or sectors. The duration of this phase of the meal would be determined by the forage to be used next. The decision of what to feed and when depends on the chemical composition and abundance of the first course (target area), and the rate at which the first course is fed or grazed. For example, a 30-min appetiser phase of birdsfoot trefoil markedly increases the intake of endophyte-infected tall fescue (Lyman *et al.* 2011, 2012). As another example, if the first course is high in N, farmers may want to reduce N intake to avoid high rates of ammonia formation in the rumen, by decreasing the amount of time cows graze (or intake rate and mastication, as discussed in the first section) during that course of the menu. Or, a farmer could feed part of the herd (e.g. the ‘efficient-moose’, ‘the youngsters’) an appetite moderator, or have cows consume a forage (appetite stimulator) with plant bioactives such as condensed tannins that help reduce rumen ammonia formation, increase supply of amino acids to the duodenum (Waghorn *et al.* 1987) and shift N from urine to faeces (Salem *et al.* 2005; Gardiner *et al.* 2016). It needs to be born in mind that the appetite-stimulator or appetite-moderator features are related to the interplay of ‘wanting–liking–learning’. As in any menu, the role of the appetite stimulator or appetite moderator is primarily in relation to the main course of the menu.

As discussed in the first section, and observed in sheep (Meuret and Provenza 2015a) and cattle (Gregorini *et al.* 2009a), the DMI rate of the first course slows as animals satiate. Therefore, if the purpose is to keep the animal motivated to eat by reducing sensory-, nutrient- and secondary compound-specific satieties, that can be achieved by allowing access to a complementary booster feed or sward (Fig. 5). In a dairy context, the booster course can come late in the morning or afternoon before milking. The booster course can be highly palatable or not. Highly palatable booster feeds can be used to encourage cows to move to stand-off pad, allowing capture of the urine generated by consuming the first course and, together, to create positive consequences (such as, e.g. ‘pleasant snack’, shade, fresh water) and emotions. Short browsing sessions on shrubs and trees may add different sensorial dimensions and post-ingestive effects (e.g. provision of bioactives) with medicinal (e.g. anthelmintic, antibacterial) or health-enhancing (e.g. antioxidant) effects (Villalba *et al.* 2016a, 2016b) and may also be used as boosters. This sequence can also add unpredictability (i.e. nice surprise) to the system or ‘teach’ the herd (or individual cows) the potential benefits of this booster phase to a meal (Meuret and Provenza 2015a). A booster course can also be used to influence grazing behaviour on the second course by modulation of cows’ minimal total discomfort (see Fig. 4).

The second course can be similar to the first course, for example, a sward or a summer- or winter-annual monoculture. The second course could also be of a more abundant forage. As cows have been provided with incentives to keep eating, the second course should occur in late afternoon or early evening (after the afternoon milking), when animals have extra motivation to eat and the feeding value of grazed forage

is the greatest (Gregorini 2012). Afternoon milking can also be an occasion to feed cows an additive to increase fibre digestion. Ruminants prefer forages such as grasses with greater content of fibre at this time of day (Rutter 2006), which may be related to slower but more steady supply of energy and nutrient from the rumen overnight when they generally fear predation do not graze (Gregorini 2012; Tyler *et al.* 2016).

The dessert course can stimulate the last bit of cows’ motivation to feed (Fig. 5). Who can say no to a tempting dessert? The key for an effective dessert is irregularity and unpredictability of the provision of a highly palatable and easy to consume food such as sainfoin (Villalba *et al.* 2015a). Dessert (e.g. a sweet supplement) can also be served on overnight ‘stand-offs’. Night and dawn urinations have the greatest volumes and concentrations of N (Betteridge *et al.* 2013). When cows wake up, they get up and urinate (see Fig. 2). We want them to do it in the ‘toilette’, where the urinary N can be captured.

### *Their menu, their product, our taste and health*

We hypothesise that feeding circuits (tables) that use diverse and customised diets (menus) enhance not only animal, but human health as well. Studies that have compared the effects on health of specific compounds, combinations of compounds, individual foods and combinations of foods have shown that biochemically rich mixtures of foods are etiologic in health of humans (Jacobs and Tapsell 2007) and herbivores (Provenza *et al.* 2015b). Phytochemically rich foods for herbivores and humans include ‘primary compounds’ that cells require to thrive (energy, protein, minerals and vitamins), as well as a plethora of ‘plant secondary compounds’ (Provenza *et al.* 2015b). Our hypothesis is supported by the fact that certain secondary compounds reduce inflammation, improve brain and vascular functions, inhibit growth of cancer, boost immune function and provide protection as antioxidant and anthelmintic (Craig 1999; Crozier *et al.* 2008; Villalba *et al.* 2014, 2016b). The lack of research on how phytochemical richness of livestock diets affects the flavour or quality of meat or dairy for human consumption reflects the fact that researchers, livestock producers and consumers are just beginning to appreciate the value of phytochemical richness in the diet and health of herbivores and humans (Provenza *et al.* 2015b).

The menu (plant diversity and chemistry) and how it is designed and ‘served’ (e.g. sequence of meal courses) affects the nutrient composition of meat and milk (Wrage *et al.* 2011). Grazing on phytochemically rich alpine swards increases milk solids (Farruggia *et al.* 2008), along with polyunsaturated fatty acid diversity and concentrations (Moloney *et al.* 2008). The richness of secondary compounds in alpine swards can change rumen microbial populations and function and help explain the greater concentration of omega-3 fatty acids in the milk of cattle grazed on those swards (Leiber *et al.* 2005). Eating meat of kangaroo grazing on native plants caused markedly lower postprandial inflammatory responses than eating meat of wagyu cattle finished on a monotonous diet of grain (Arya *et al.* 2010). Despite the confounded effect (diet and animal) of that study, the findings of Arya *et al.* (2010) lended support to our hypothesis. Low-grade systemic inflammation, characterised by an increase in plasma concentrations of pro-inflammatory

markers such as TNF- $\alpha$ , IL-6 and C-reactive protein, is strongly implicated as a cause of cancer and heart disease in humans (Hotamisligil 2006; O'Keefe and Bell 2007). Future studies should investigate how phytochemical diversity of meat and milk products affects inflammatory responses in humans.

Although much remains to be learned, some studies have suggested that dietary diversity and phytochemical richness confer flavourful aroma-active compounds to meat and dairy products (Vasta *et al.* 2008; Schatzker 2010; Manca 2013). The flavour and phytochemical richness of cheese are enhanced when dairy cows can select a diet from botanically diverse swards as opposed to standardised and simple total-mixed ration (Carpino *et al.* 2004a, 2004b). Compared with some studies of grass-fed beef (Van Elswyk and McNeill 2014), consumers preferred meat from cattle finished on grass accompanied by sainfoin (Maughan *et al.* 2011, 2014). Tannins in plants, such as sainfoin, reduce rumen bacteria that produce skatole and indole from protein fermentation, which produce 'off-flavours' in meat and milk (Schreurs *et al.* 2003; Priolo *et al.* 2009). Yields of skatole in milkfat cows grazing perennial ryegrass swards are twice as high in afternoon than

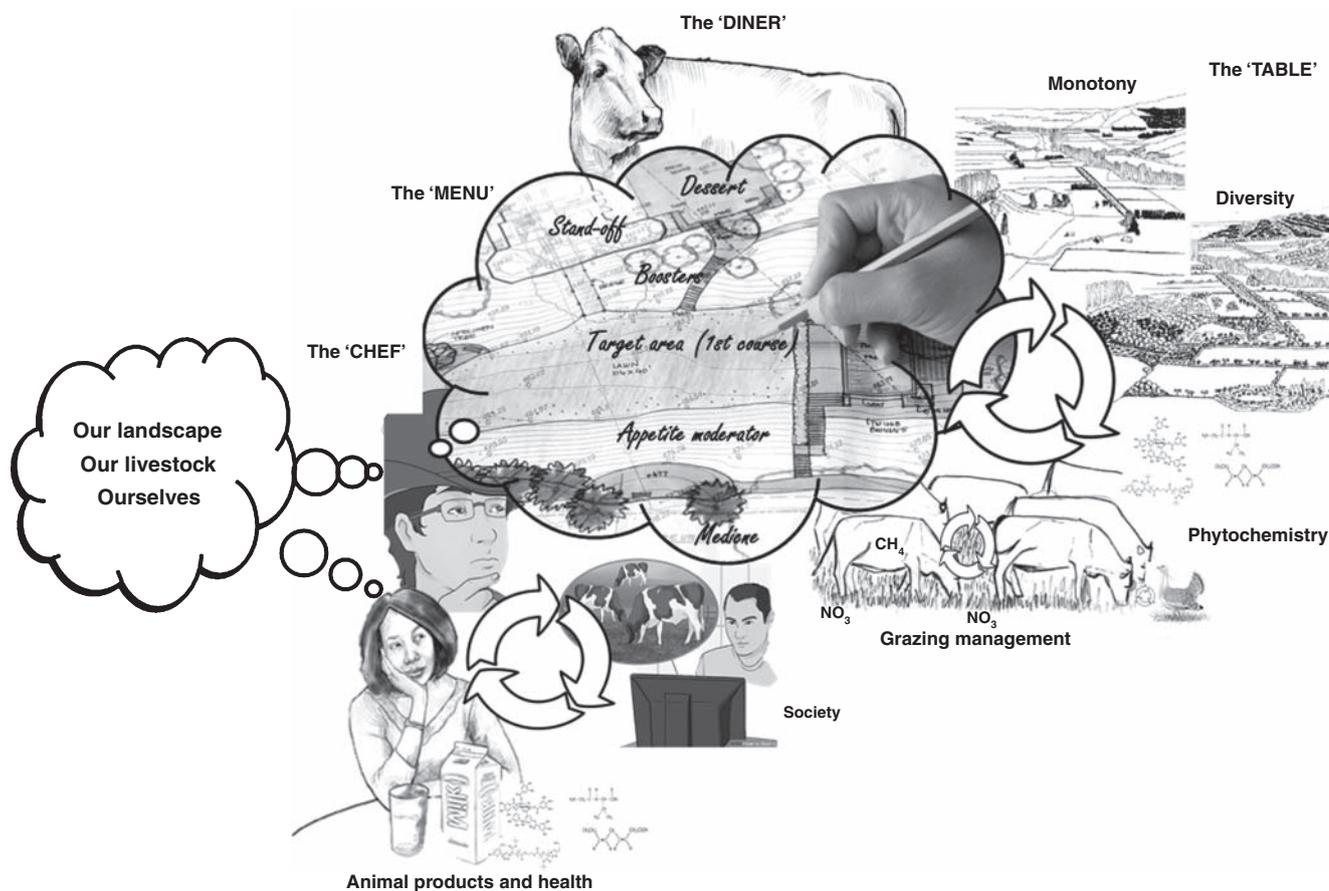
morning milk, and have been related to the concentration of sugar in the herbage and its effect on N utilisation in the rumen (Tavendale *et al.* 2006). This suggests that rumen responses to diurnal fluctuation of sugar concentration of herbage and morning feeding appear to influence the flavour of milk. Like other animals, cattle have a 'sweet tooth' (Plice 1952), preferring herbage and forage harvested in the afternoon, when the sugar concentrations are the greatest (Fisher *et al.* 2002; Burritt *et al.* 2005; Mayland *et al.* 2005). It is tempting to hypothesise that incorporating 'their sweet tooth' into phytochemically rich design menus, would produce tastier milk and meat.

Ultimately we are what we eat *eats!*

## Conclusions

We envisage a more holistic view of grazing, with management practices that may enable pastoral livestock-production systems to continually evolve as complex creative systems (Fig. 6).

Ultimately, dairy and meat products reflect the history of landscapes, foodscapes and agricultural systems, manifested



**Fig. 6.** Setting the TABLE, designing the MENU and influencing the DINER. We envisage farms as taxonomically, chemically and spatially diverse foodscapes that provide multiple environmental benefits to soil, plants, herbivores, human beings and all life on landscapes. The challenging opportunity for the farmer (the CHEF) is to create foodscapes (set the TABLE) and design sequences of feeding events in time and space (design the MENU) that consider individual differences and personalities among his or her cows (the DINERS), with the aim of achieving the maximum number of complementarities and synergies to promote resilience, animal welfare and improved quality of animal products to society.

through soil and plant chemistry, and, thereby, grazing management. By managing grazing, we can manipulate links between ingestive–digestive and excretory processes and the diner’s foraging decisions in time and space. By providing chemically diverse diets in temporal (the menu) and spatial (the table) scales, we can increase resilience, improve the nutrition and welfare of animals, and potentially reduce environmental impacts. Knowing diners’ morpho-physiological characteristics and ‘personalities’ allows us to design grazing management to influence their grazing, overcoming or strategically enhancing their differences. One size does not fit all! In summary, under pastoral systems, synergies between animals’ and farmers’ grazing decisions have the potential to offer more greater benefits to our livestock, our landscape and ourselves. . .

## Acknowledgements

We gratefully acknowledge Mark Neal and Taisekwa Chikazhe (DairyNZ, New Zealand) for reviewing the original version of this manuscript, as well as Dr Eric Kolver (DairyNZ, New Zealand) and Professor Eric Hillerton for their valuable comments, suggestions and constructive criticism. We also thank Pierre Beukes and Alvaro Romera (DairyNZ, New Zealand) for their patience at the time to listen and ‘digest’ our ideas.

This work is dedicated to all whose heart beats faster when watching ruminants graze. Among them Mindy, Eva, Sofia and Manolo.

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