



REVIEW: Behavior and Daily Grazing Patterns of Cattle

P. GREGORINI,*† PAS, S. TAMMINGA,‡ and S. A. GUNTER,*¹ PAS

*Southwest Research and Extension Center, Division of Agriculture, University of Arkansas, Hope 71801; †Facultad de Ciencias Agrarias y Forestales, Universidad Nacional de La Plata, La Plata, CP1900, Buenos Aires, Argentina; ‡Wageningen Institute of Animal Science, Wageningen University and Research Centre, 6700 AH Wageningen, The Netherlands

Abstract

Grazing ruminants consume their food in discrete grazing events. The frequency and distribution of these events depend on the current physiological state of the animal and its environment. Within a small spatio-temporal scale, foraging decisions such as when to begin, which frequency, and how to distribute the grazing events may determine how cattle allocate time to meet their nutritional needs. The longest and most intense grazing events occur normally at dusk; this intake pattern serves to maximize daily energy intake, provide a steady release of nutrients, and maintain satiety over the night. Although ruminants may have a high motivation to seek food at dawn, this grazing event normally is of lesser intensity and duration than the dusk grazing event. Because of the timing of these grazing events, ruminants seem to be crepuscular animals, and light provides an environmental cue as to when to seek food. Certainly, the preference for twilight grazing plays a role in shaping the daily grazing pattern, yet it remains to be explained if this preference also reflects temporal variation in the underlying physiology. On the other hand, modern husbandry could not have eliminated any evolved anti-predator strategy legated

by their ancestors. Voluntary feed intake ultimately abuts on animal psychology. Clearly, there are major gaps in our knowledge because there are virtually no published data relating the last question to domestic ruminants.

Key words: behavior, grazing, pattern, cattle

Introduction

Herbage, the resource under exploitation by grazing ruminants, is rarely presented in discrete packages (Bergman et al., 2000). What we call ruminant nutrition at pasture is therefore an exciting area of research that links the nutritional and behavioral sciences. Regardless of the way forage is offered, ruminants consume their food in discrete meals that alternate with periods of rumination and idling (Forbes, 1995). The choice of which behavioral activity is performed depends on the current state of the animal, its environment, and possibly past and anticipated states (Mangel and Clark, 1986). Under temperate grazing conditions, cattle seem to discriminate between temporal states of pasture and graze selectively when confronted with heterogeneous swards. That is, foraging strategies are dynamic in response to changing sward conditions, and selection arises as one of the main mechanisms en-

abling animals to control herbage intake and diet quality (WalliesDeVries and Delabout, 1994). This selectivity appears to be strongly affected by landscape, and seems to differ greatly among patch types (WalliesDeVries and Delabout, 1994). In addition, WalliesDeVries and Laca (1999) have shown that size of patches affects selection. An intriguing question thus arises with regard to how to describe grazing behavior and what happens at the paddock level. Could daily grazing pattern be changed? The objectives of this review are to discuss an outline about how to describe the grazing patterns of cattle at the paddock level, to identify gaps in our knowledge of grazing behavior, and to propose approaches to address these gaps.

Review and Discussion

Spatio-Temporal Scales. Scale is an essential concept in ecological and social sciences that refers primarily to temporal and spatial dimensions at which phenomena are observed (van Gardingen et al., 1997; Paterson and Parker, 1998). Integration of area and time is referred to as spatio-temporal extent (Rietkerk et al., 2002), and its resolution as grain (Wu, 1999). Scale gives us a fundamental framework in which an ecological phenomena can be studied and understood (Wu and

¹To whom correspondence should be addressed: sgunter@uaex.edu

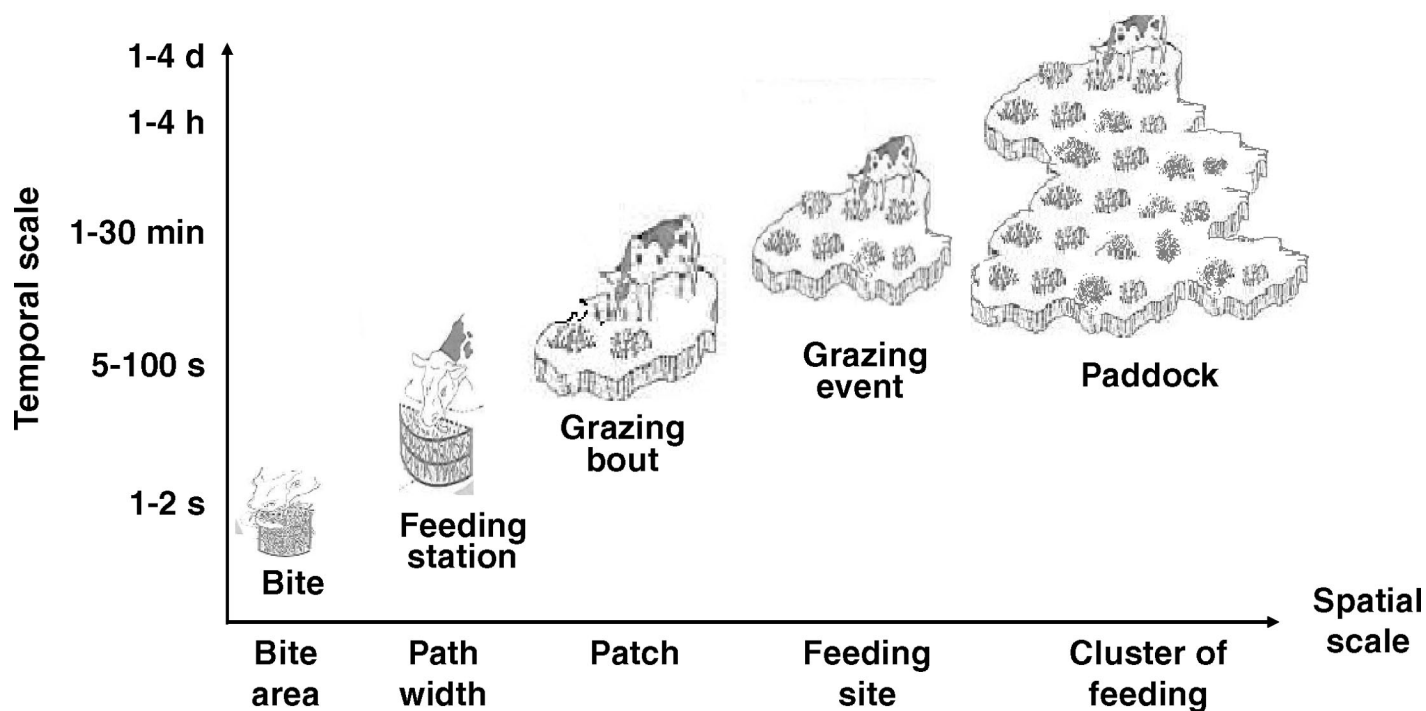


Figure 1. Attributes of different extents of scale in the foraging of a large herbivores [Adapted from Bailey et al. (1996) and drawing adapted from Galli (1994)].

Qi, 2000; Pereira, 2002). Moreover, patterns and processes observed in plants and animals depend on scales, as well as the functional responses. In ecology, this response is defined as the relationship between animal voluntary intake and the food offered (Holling, 1959), or the relationship between predation rate and prey density [Solomon (1949), cited by Jeschke et al. (2002)].

Giving attention to scales is important (Wiens, 1989), and that of nutritional ecology of grazing ruminants is not the exception (Fryxell et al., 2001). If there is an imbalance of scales, then scaling-up or down leads to errors in interpretation (Brown and Allen, 1989; Wiens, 1989; Marriot and Carrere, 1998). Integrating functional responses from small to larger scales (Figure 1), as in the calculation of daily herbage intake, is one such example. Such scaling-up has been made through daily grazing time: herbage intake = (bites/unit time) \times (intake/bite) \times (grazing time). This type of scaling-up should be restricted to homogeneous grazing environ-

ments where sward variables that determine intake rate remain constant (WalliesDeVries et al., 1998). However, cattle normally graze heterogeneous pastures (Schwinning and Parson, 2001). Heterogeneous environments are characterized by spatial and temporal changes in their descriptors. Hence, mean values of biomass, height, or chemical composition would be poor predictors of any functional response (Laca et al., 1992; Bergman et al., 2000, 2001). This fact was clearly demonstrated by Champion et al. (1994), Orr et al. (1997), and Gibb et al. (1998) (Figures 2 and 3) as well as Barret et al. (2001), who found different parameter values of the grazing process during the day. The latter clearly demonstrated the negative impact of the progressive sward depletion on bite mass: 0.74 vs. 0.62 g DM at 0700 h and 1800 h, respectively.

From a practical point of view, a sum of feeding sites (Figure 1) could be considered a paddock, which could be seen as homogeneous; but heterogeneity increases during graz-

ing, both spatially and temporally. Moreover, heterogeneity may be measured, even before grazing starts, since bulk density (Barthram et al., 2000) and chemical composition (Delagarde et al., 2000; Taweel, 2004) vary from the top to the bottom of the canopy, and through the day. Hence, when interpreting the response of grazing ruminants, heterogeneity must be considered (Parsons and Dumont, 2003). Given that heterogeneity is scale-dependent (Kolasa and Rollo, 1991), one could argue that the study of plant-animal relationships is also dependent on scale (Rietkerk et al., 2002) and scales should be considered if the objective is to gain better understanding of concepts and mechanisms controlling cattle-pasture relationships. Hence, functional heterogeneity, defined as the relationship between an organism and its environment, (Kotliar and Wiens, 1990), is relevant in these types of studies. For this reason, perceptions of the cattle rather than the investigators must be considered [Wiens (1976), cited by Ardit and Dacorogna

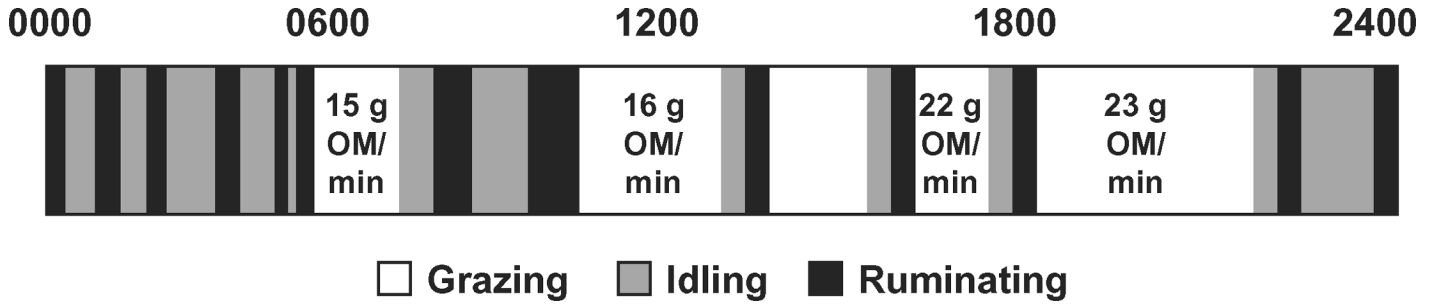


Figure 2. Typical grazing pattern and organic matter intake rate of dairy cows under continuous stocking (M. J. Gibb, Inst. of Grassland and Environ. Res., Okehampton, North Wyke, UK, personal communication).

(1988)]. It is thus a challenge to recognize how our perceptual scales condition the way we describe the scales of animals (Allen and Hoekstra, 1992; Levin, 1992; Ritchie, 1998), how patterns change across them, and how phenomena at different scales influence each other.

Ecosystems, landscapes, communities, and populations are usefully described as hierarchies of nested components (Allen and Hoekstra, 1992). Within these hierarchies the nested components are distinguished by the appropriate spatio-temporal scales. Bailey et al. (1996) identified 6 scales for large herbivores in the foraging hierarchy: bite, feeding station, patch, feeding site, camp, and home range. If the extent of our work is an arrangement (cluster) of feeding sites (Figure 1), then it is useful to look at the paddock to understand the con-

text and the next levels down to understand the mechanisms (Allen and Hoekstra, 1992).

Grazing Events. Foraging decisions made at broader scales (home range, at dispersal, or during migration) answer where to start grazing at the beginning of a grazing event (Bailey et al., 1996). However, that decision probably is irrelevant for animals in small paddocks because the entire area is readily accessible (Bailey et al., 1996). Metz (1975) suggested the concept of a meal (grazing event in this case) as a cluster of grazing bouts, and Gibb (1998) pointed out that all grazing events are cumulative and therefore sum to daily grazing time. Because grazing time encompasses a cluster of discrete grazing events, foraging decisions such as when to begin, at which frequency, and how to spread the grazing events through

time might be more important within a smaller scale (i.e., paddock). Such decisions determine how cattle invest their time in feeding to meet metabolic requirements for nutrients.

Frequency and distribution. The relevant period of time where meals occur differs distinctly among animal types (Collier and Johnson, 1990; 2004). In grazing ruminants, this period lasts 24 h because their meal pattern is circadian. In temperate climates, ruminants have 3 to 4 major grazing events per day (Figure 2; Gibb et al., 1998). However, this frequency is not inflexible and is affected by external environment or behavioral adaptations. During short days, grazing events could merge as a consequence of increased grazing bout length and a decreased number. Preference to graze during daylight hours may reflect greater difficulty of food selec-

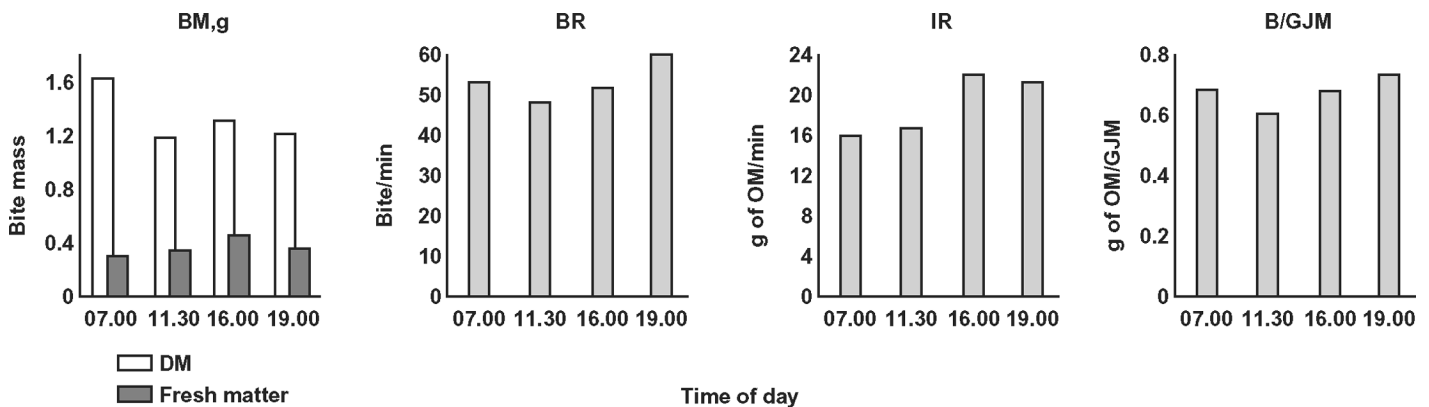


Figure 3. Effect of time of day on grazing behavior of lactating dairy cows, under continuous grazing (J. M. Gibb, Institute of Grassland and Environ. Res., Okehampton, North Wyke, UK, personal communication). BM = bite mass; BR = bite rate; IR = intake rate; B/GJM = bite per grazing jaw movement.

tion in the dark (Linnane et al., 2001). As a result of this change in grazing pattern, daily grazing time can be maximized. Cattle have become adapted to modern husbandry methods, which can be used to stimulate the motivation to graze (Toates, 2002). As such, the precise time of the grazing events can be modified, depending for instance upon events such as removal for milking (M. J. Gibb, Inst. Grassland Environ. Res., Okehampton, North Wyke, UK, personal communication) or time of herbage allocations (Gregorini et al., 2004, 2005a,b). Regardless of frequency, the major grazing events occur near sunrise and sunset (Figures 2 and 3), with the latter having greater intensity and longer duration (Gibb et al., 1998; Taweel, 2004). Shorter and less intense grazing events occur at night. These events represent a small percentage of daily grazing time and contribute minimally to daily herbage intake (O'Connell et al., 1989; Krysl and Hess, 1993).

Discriminatory grazing activity.

Preference is the discrimination that an animal displays in choosing between swards or sward components when grazing (Hodgson, 1979). Hodgson (1979) suggested use of this term until we are better able to assess the relative importance of factors involved in the grazing process.

Daily patterns in dietary preference have been demonstrated by Newman et al. (1994) and Parsons et al. (1994). Recently, more detailed examination of grazing behavior recordings has shown the existence of both of the 2 major grazing events mentioned above (Taweel, 2004), and differences in the functional response among all grazing events (Figure 3). These findings provide definitive evidence that the grazing patterns throughout the day are discriminatory.

Several studies have shown diurnal variation in herbage chemical composition (Fulkerson et al., 1994; Orr et al., 2001b; Mayland et al., 2003; Burns et al., 2005). Furthermore, diurnal variation has been noted in grazed horizons (Barthram et al.,

2000; Taweel, 2004; Griggs et al., 2005; P. Gregorini, unpublished data). Dry matter and soluble carbohydrate concentrations of the sward increase through the day with the accumulation of photosynthates (Orr et al., 2001b; Griggs et al., 2005), primarily in the upper layers of the sward (Delegarde et al., 2000). Increased non-structural carbohydrate concentrations support greater digestibility (Civarella et al. 2000; Linnane et al., 2001) and palatability (Provenza et al., 1998). Thus, diurnal changes in herbage quality may play a role in driving the preference for an intense, extended grazing event at dusk. From an evolutionary viewpoint, it seems reasonable for cattle to graze at dusk as this makes more efficient use of plant phenology (Linnane et al., 2001). But the question remains, why? Provenza et al. (1998) suggested that grazing behavior may also be related to diurnal changes in food quality; animals may prefer foods that are more digestible or greater in macronutrients (Provenza, 1996). Furthermore, animals may use short-term intake rate or post-ingestive outcomes to integrate information obtained through diet selection (Provenza, 1995; WalliesDeVries et al., 1998). Thus, consequences at lesser hierarchical levels such as grazing bout or event might be used to develop expectations at greater levels of the feeding process such as grazing event, daily intake, or even grazing pattern (Figure 1; Bailey et al., 1996; WalliesDeVries et al., 1998). However, research evidence for this is lacking. Most foraging behavior studies have examined functional responses that occur within one or just a few grazing bouts and are not able to fully capture the dynamics of the grazing process (Newman et al., 1994). Momentary maximization is a mechanism that explains diet selection and animal movement along the grazing pathway, which assumes that animals select the best available alternative at any given time (Staddon, 1983). Thus, additional questions arise regarding whether this phenomenon takes place and if this concept

can be applied to a longer time interval, such as a day. If it cannot be applied, it would appear that cattle either apply an optimal foraging strategy by trying to maximize the long-term (daily) intake rate of energy (Stephens and Krebs, 1986), or they just look for the most comfortable situation. From a daily and longer perspective, the maximization of energy intake rates through a longer and more intensive grazing event at dusk makes sense for the animals, because fitness (Newman et al., 1995) and performance can be improved. This premise is supported by results of Orr et al. (2001a), Eirin et al. (2005a,b), and Gregorini et al. (2004; 2005a,b).

The longer, more intense grazing event at dusk could also serve to maintain a steady release of nutrients, maintaining a comfortable state through the night. Satiety is defined as the effect of a food or a meal on appetite after eating has ended (Kral and Rolls, 2004). It is also the state from the end of one meal to the occurrence of the next during which an animal does not eat and is not motivated to eat [Le Mangen, (1986), cited by Lindstrm (2000)]. Satiety comes from an integrated, complex set of signals from many parts of the body (Forbes, 1999, 2000), even from oral levels (Lindstrm, 2000; Toates, 2002). A short-term supply of excess nutrients or an imbalanced diet such as found in herbage at morning (Rearte and Santini, 1989; Poppi et al., 1999; Elizalde and Santini, 1992) can result in satiety that may also be described as a state of metabolic discomfort. As such, the ratio of nutrients being absorbed from the gastro-intestinal tract would induce a metabolic imbalance (Forbes, 2000). The importance of nutrient imbalance in the control of intake has been addressed (Poppi and McLennan, 1995; Illius and Jessop, 1996; Simpson et al., 2004) and might be relative to this question. Conversely, under-eating (relative to demands) generates hunger (Forbes and Provenza, 2000). The degree of hunger would be dependent on previous nutrition, both short- and long-

term (Forbes and Provenza, 2000). However, the process of satiation is also directed within the context of achieving the most comfortable situation. While comfort is a function of appropriate nutrient supply, it is also affected by other factors such as fear of predators (Forbes, 2000). Animals can perform only one behavior at a time, even if the stimuli appropriate for more than one behavior are present (Lindström, 2000; Toates, 2002). This means that there must be a decision-making process to determine which activity the animal performs at any given time. Natural evacuation of digesta from the gastro-intestinal tract leads to the smallest ruminal pool size early in the morning. This would generate hunger and could be one of the reasons explaining the high motivation to graze at sunrise when herbage has the most constraining features for consumption, from a nutritive and harvesting view point. Therefore, the internal state (Mangel and Clark, 1986; Newman et al., 1995) and external incentives (sight, delivery of fresh food, food presentation, and a cue that food will soon be available) might stimulate the motivation of animals to graze at dawn. Here, questions emerge: How big and measurable is the stimulus of natural digesta in the rumen, with ruminal fill as one main determinant of the internal state on the animal (Newman et al., 1995)? How does this stimulus affect not only short-term intake rate, but also grazing dynamics? Can grazing dynamics be managed through manipulated ruminal fills?

Despite that strong motivation, the first grazing event is both of lesser intensity (intake rate) and shorter duration with longer intra-meal intervals (Rook et al., 1994; Rook and Huckle, 1997). This grazing pattern may be a function of an imbalanced diet or an unbalanced ratio of post-ingestive compounds such as volatile fatty acids (Chilibroste, 1999). However, plant physical characteristics and environmental conditions may also contribute to this grazing pattern. Short-term intake rate is dependent upon

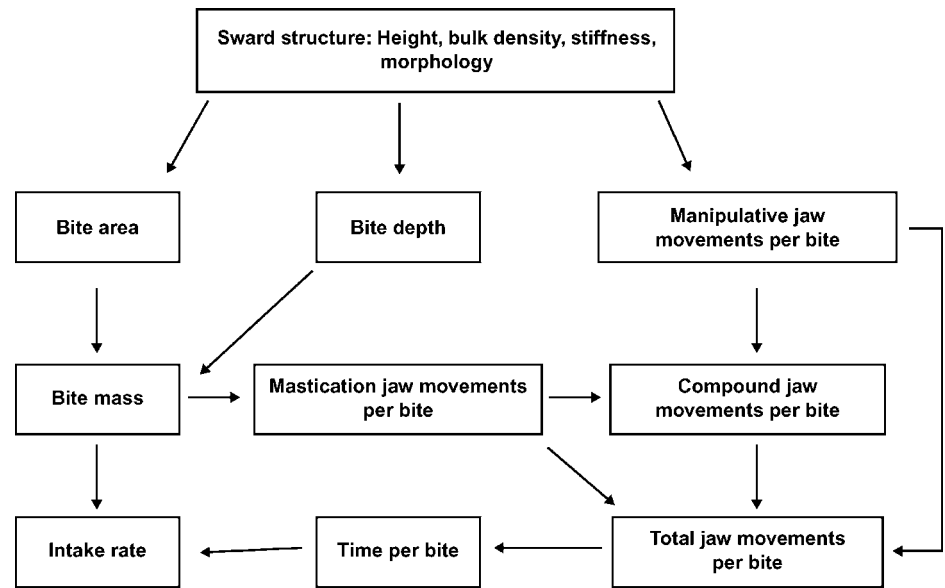


Figure 4. The components of ingestive behavior, which mediate between sward structure and short-term intake rate.

bite mass in cattle and in other ruminants (Hudson and Frank, 1986; Illius and Gordon, 1987; Shipley and Spalinger, 1992), and bite mass is controlled by the way that plant physical characteristics (Burlison et al., 1991; Laca et al., 1992; Ungar, 1996) interact with the mouth morphology (Figure 4; Illius and Gordon, 1987; Shipley et al., 1994; Rook et al., 2004). Surface moisture also plays a part in this interaction. Surface moisture, prevalent on grasses in the morning (Tallowin et al., 1991), may also explain the lower bite mass at this time of the day (Gibb et al., 1998), as lubricity of the leaf laminae may increase slippage between the incisors and dental pad.

Photo-effect: A Stimulus. Photoperiod has been hypothesized as one factor controlling grazing activity (Hogan et al., 1987; Linnane et al., 2001). Due to the occurrence of dawn and dusk grazing events, ruminants can be described as crepuscular animals (Phillips, 1993). Strong evidence for this kind of pattern has been found in the African buffalo (Sinclair, 1977), bison (Hudson and Frank, 1986), and grazing sheep (Champion et al., 1994; Orr et al., 1997), as well as in dairy cows (Gibb et al., 1998; Orr et

al., 2001b) and beef heifers (Gregorini et al., 2004, Gregorini et al., 2005b). This pattern follows a circadian rhythm, and its association with sunrise and sunset implies that it is sensitive to a photo-effect. This is supported by the timing of dusk GE, which changes with day length during the year. Moreover, duration of the grazing event remains constant regardless of the actual time of sunset (Rutter et al., 2002). When the sun is near to horizon (sunrise and sunset) the ratio of shorter and longer wavelengths is different compared to that at mid-day. The concurrence of these different wavelengths with the most intense GE led Linnane et al. (2001) to suggest that these light characteristics have a stimulatory effect on appetite. In addition, Phillips and Schofield (1989) found cows had increased numbers of feeding bouts when extra light was provided during short days, while Rutter et al. (2002) reported a disruption of grazing patterns of dairy cows during a total solar eclipse. Although light should not be regarded as the dominant environmental cue, it influences cattle decisions about when to seek food, and thus plays a role in shaping daily grazing patterns. Notwithstanding, it remains to be

seen if these temporal variations in the grazing process reflect similar variation in the underlying physiology and whether or not light acts synergistically to initiate or intensify grazing events. It should also be noted that seasonal photoperiod variations affect herbage intake (Rhind et al., 2002), but such larger scale variation is beyond the scope of this discussion. On the other hand, it is possible that some other factors associated with light intensity participate in the temporal arrangement of grazing events.

Is It a Psychological Question? Recently, studies have begun to investigate the importance of greater levels of trade-off other than energetic benefits vs. time requirements. One such trade-off is between foraging benefits (net energy intake) and the cost of predation risk (Houtman and Dill, 1998). Ruminants evolved primarily as grazing animals, with a unique, anti-predator digestion-enhancing foraging strategy (Phillips, 1993). This strategy involves consuming herbage as rapidly as possible, followed by mastication later, when hidden in relative safety. Mastication occurs mostly at night (Newman et al., 1995; Prins, 1996; Houtman and Dill, 1998) because grazing diminishes alertness and increases the risk of predation (Charnov et al., 1976). Emmons and Kiryazakis (1995) have described the evolutionary advantages of optimized food intake by farm animals. However, psychological effects are rarely considered, and intake is often viewed in isolation from other adaptive characteristics, such as synchrony of certain behaviors.

It appears that cattle attempt to maximize their intake rate at dusk (Gibb et al., 1998). Even though intake rate increases with the level of feeding motivation in both animals and humans (Nielsen, 1999), it remains unclear why they should be motivated. An answer could be the predation hazard, but it might possibly be related to biochemical or physiological processes or the retention of an evolutionary anti-predator strategy.

In reviewing over 50 studies of mammals and birds, Elgar (1989) reported a negative correlation between group size and vigilant behavior, and most of the studies concluded that the relationship partly explained why individuals foraged as groups. Although wild ruminants presumably are vigilant for predators (Jarman, 1974; Underwood, 1982; Fortin et al., 2004a,b; Frair et al., 2005), there is great debate about whether domestic ruminants are under any serious threat of predation (Newman et al., 1995). However, sheep graze longer when they are in groups [Penning et al. (1993); Dumont and Boissy (2001), cited by Parsons and Dumont (2003)], and the same tendency has been observed in dairy cows (Rind and Phillips, 1999). Rook and Huckle (1997) suggest that the preference to graze and to be active in the light may be a vestigial defense mechanism that may reflect an increased need for alertness.

Several studies (Samuelsson et al., 1996; Johansson et al., 1999; Lindström, 2000) make reference to cortisol and oxytocin as motivational hormones for feeding behavior. Recently, serotonin has been considered as a key neuro-hormone agent in intake regulation (W. Pittroff, University of California, Davis, and P. Soca, Universidad de la Republica, Paysandu, Uruguay; personal communication). For our purposes, we consider serotonin and melatonin. Serotonin is synthesized from the amino acid tryptophan, and melatonin is derived from serotonin in a 2-step enzymatic reaction. Serotonin levels are high in the pineal gland during the light hours, but diminish during the darkness as the hormone is converted to melatonin (Nelson, 1995). Serotonin depletion as a deficiency syndrome may lead to symptoms of lethargy, anxiety, and carbohydrate craving (Wurtman and Wurtman, 1989), and as such serotonin is necessary to maintain alertness and vigilance. Tryptophan circulates in the blood at low levels and is converted to serotonin in the brain (Cooper et al., 1986,

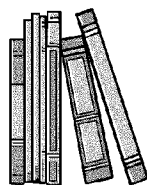
cited by Nelson, 1995). Diet affects this conversion process because carbohydrates stimulate pancreatic β -cells to secrete insulin, which in turn facilitates the uptake of sugars and non-tryptophan amino acids into peripheral cells (Nelson, 1995). This results in a relatively high ratio of tryptophan to other amino acids in the blood. Because tryptophan competes with the other amino acids for access to the central nervous system tissue, carbohydrate ingestion results in more tryptophan crossing the blood-brain barrier and thus higher production of serotonin. Solving carbohydrate cravings might stop the effect of serotonin depletion in human beings (Wurtman and Wurtman, 1989; Hoebel et al., 1992). The question remains whether this phenomenon could be related to the behavioral tendency of greater carbohydrate intake found in the dusk grazing event.

Livestock were domesticated 10,000 to 11,000 yr ago in the Neolithic period (Campbell and Lasley, 1969; Pearse, 1971). However, this time period is insignificant compared with their longer period of evolution. Moreover, modern husbandry could not have eliminated any evolved anti-predator strategy legated by their ancestors. Clearly, there are major gaps in our knowledge because virtually no data bear directly on the questions of whether cattle suffer anxiety, have fear of darkness, or need to be alert to predation hazard. Voluntary feed intake ultimately abuts on animal psychology (Ungar, 1996; Illius et al., 2000). Therefore, elucidation of how signal integration is affected by the cognitive, physiological, and mental state of the animal remains an important challenge (Illius et al., 2000).

Implications

Because grazing is the product of trade-offs, even at paddock level, its behavior should be analyzed integrating spatio-temporal scales. This is essential for a better understanding of grazing process because functional heterogeneity implies that foraging

strategies may not be constant but vary through time. Daily grazing pattern is the product of complex decisions made by cattle responding to multiple variables. Cattle seem to maximize energy intake, preferring to graze more intensively at dusk, when the herbage has the greater quality. Thus, linking plant and animal processes to management strategies emerges as an option to manipulate temporal distribution, duration and intensity of grazing events, and thereby nutrient supply. Finally, grazing behavior is beginning to reveal how ruminants have evolved to exploit forage plants and survive in hostile environments. Consequently, we are able to go further in the knowledge of the main causes of the feeding patterns of domestic ruminants on pasture.



Literature Cited

- Allen, T. F. H., and T. W. Hoekstra. 1992. *Toward a Unified Ecology*. Columbia Univ. Press, New York, NY.
- Arditi R., and B. Docarogna. 1988. Optimal foraging on arbitrary food distributions and the definition of habitat patches. *Am. Nat.* 131:837.
- Bailey, D. W., J. E. Gross, E. A. Laca, L. R. Rittenhouse, M. B. Coughenour, D. M. Swift, and P. L. Sims. 1996. Mechanism that result in large herbivore grazing distribution patterns. *J. Range. Manage.* 49:386.
- Barret, P. D., A. S. Laidlaw, C. S. Mayne, and H. Chistie. 2001. Pattern of herbage intake rate and bite dimensions of rotationally grazed cows as sward height declines. *Grass Forage Sci.* 56:362.
- Barthram, G. T., D. A. Elsto, and G. R. Bolton. 2000. A comparison of three methods for measuring the vertical distribution of herbage mass in grassland. *Grass Forage Sci.* 55:193.
- Bergman, C. M., J. M. Fryxell, G. C. Cormack, and D. Fortin. 2001. Ungulate foraging strategies: energy maximizing or time minimizing? *J. Anim. Ecol.* 70:289.
- Bergman, C. M., J. M. Fryxell, and C. C. Gates. 2000. The effect of tissue complexity and sward height on the functional response of Wood Bison. *Funct. Ecol.* 14:61.
- Brown, B. J., and T. F. H. Allen. 1989. The importance of scale in evaluating herbivore impacts. *Oikos* 54:189.
- Burlison, A., J. Hodgson, and A. W. Illius. 1991. Sward canopy structure and the bite dimensions and bite weight of grazing sheep. *Grass Forage Sci.* 46:29.
- Burns, J. C., H. F. Mayland, and D. S. Fisher. 2005. Dry matter intake and digestion of alfalfa harvested at sunset and sunrise. *J. Anim. Sci.* 83:262.
- Campbell, J. R., and J. F. Lasley. 1969. *The Science of Animal that Serve Mankind*. McGraw-Hill, Inc., New York, NY.
- Champion, R. S., S. M. Rutter, P. D. Penning, and A. J. Rook. 1994. Temporal variation in grazing behavior of sheep and the reliability of sampling periods. *Appl. Anim. Behav. Sci.* 42:99.
- Charnov, E. L., H. O. Gordon, and K. Hyatt. 1976. Ecological implications of resource depression. *Am. Nat.* 110:247.
- Chilibroste, P., 1999. Grazing time: The missing link? A study on the plant-animal interface by integration of experimental and modeling approaches. Ph.D. Diss., Wageningen University, Wageningen, The Netherlands.
- Ciavarella, T. A., H. Dove, B. J. Leary, and R. J. Simpson. 2000. Diet selection by sheep grazing *Phalaris aquatica* L. pastures of differing water-soluble carbohydrate content. *Aust. J. Agric.* 51:757. [Au: this reference is not cited in text. Either add to text or delete here]
- Collier, G., and D. F. Johnson. 1990. The time window of feeding. *Physiol. Behav.* 48:771.
- Collier, G., and D. F. Johnson. 2004. The paradox of satiation. *Physiol. Behav.* 82:149.
- Cooper, J. R., F. E. Bloom, and R. H. Roth. 1986. *The Biochemical Basis of Neuropharmacology*. 5th ed. Oxford Univ. Press, New York, NY.
- Delagarde, R., J. L. Peyraud, L. Delaby, and P. Faverdin. 2000. Vertical distribution of biomass, chemical composition and pepsin-cellulase digestibility in a perennial ryegrass sward: Interaction with month and year, re-growth age and time of day. *Anim. Feed Sci. Technol.* 84:49.
- Dumont, B., and A. Boissy. 2001. Grazing behavior of sheep in situation of conflict between feeding and social motivations. *Behav. Processes* 49:131.
- Eirin, M., Gregorini, P., M. L. Agnelli, R. Refi, M. Ursino, and O. Ansin. 2005a. Respuesta productiva de vaquillonas en recre ante dos momentos de asignacin diaria de forraje fresco. 29th Congr. Argentino de Produccion Animal. Bahia Blanca, Buenos Aires. *Rev. Argent. Prod. Anim. Argent. Prod. Anim.* VII.
- Eirin, M., P. Gregorini, R. Refi, M. Ursino, and O. Ansin. 2005b. Timing of herbage allocation 2. Effect on beef heifers weights gain, body condition score and daily herbage intake. *J. Anim. Sci.* 83(Suppl. 2):202. (Abstr.)
- Elgar, M. A. 1989. Predator vigilance and group size in mammals and birds: A critical review of the empirical evidence. *Biol. Rev. Camb. Philos. Soc.* 64:13.
- Elizalde, J. C., and F. J. Santini. 1992. Factores nutricionales que limitan las ganancias de peso en bovinos en el período otoño-invierno. *Bol. Téc. Estacion-Exp.-Agropecuaria,-Balcarce* 104:54.
- Emmans, G. C., and I. Kyriazakis. 1995. The idea of optimization in animals: Uses and dangers. *Livest. Prod. Sci.* 44:189.
- Forbes, J. M. 1995. *Voluntary Feed Intake and Diet Selection in Farm Animals*. CAB Int., Wallingford, UK.
- Forbes, J. M. 1999. Minimal and total discomfort as a concept for the control of food intake and selection. *Appetite* 33:371.
- Forbes, J. M. 2000. Consequences of feeding for future feeding. *Comp. Biochem. Physiol. A* 128:461.
- Forbes, J. M., and F. D. Provenza. 2000. Integration of learning and metabolic signals into a theory of dietary choice and food intake. In *Ruminant Physiology, Digestion, Metabolism, Growth and Reproduction*. P. Cronje, ed. CAB Int., Wallingford, UK.
- Fortin, D., M. S. Boyce, and E. H. Merrill. 2004a. Multi-tasking by mammalian herbivores: Overlapping processes during foraging. *Ecology* 85:2312.
- Fortin, D., M. S. Boyce, E. H. Merrill, and J. M. Fryxell. 2004b. Foraging costs of vigilance in large mammalian herbivores. *Oikos* 107:172.
- Frair, J. L., E. H. Merrill, D. R. Visscher, D. Fortin, H. L. Beyer, and J. M. Morales. 2005. Scales of movement by elk (*Cervus elaphus*) in response to heterogeneity in forage resources and predation risk. *Landsc. Ecol.* 20:273.
- Fryxell, J. M., C. B. D. Fortin, and J. Wilmshurst. 2001. On the scale dependence of foraging in terrestrial herbivores. *Proc. of the XIXth Int. Grassland Congr.* pp. 271-275. Sao Pablo, Brazil.
- Fulkerson, W. J., K. Slack, and K. F. Lowe. 1994. Variation in the response of *Lolium* genotypes to defoliation. *Aust. J. Agric. Res.* 45:1309.
- Galli, J. 1994. *CONPAST*. Thesis. Universidad Nacional de Mar del Plata, Argentina.
- Gibb, M. J. 1998. Animal grazing/intake terminology and definitions. In *Pasture Ecology and Animal Intake*. Proc. Workshop, Dublin. Concerned Action. AIR3-CT93-0947. Occasional Publ. No. 3.
- Gibb, M. J., C. A. Huckle, and R. Nuthall. 1998. Effect of time of day on grazing behavior by lactating dairy cows. *Grass Forage Sci.* 53:41.
- Gregorini, P., M. Eirin, Agnelli, M. L., R. Refi, M. Ursino, and O. Ansin. 2005a. Efecto del momento de asignacin diaria de forraje fresco en el patrón diario de pastoreo de vaquillonas aberdeen angus. 29° Congreso Argentino de Producción animal. Bahia Blanca, Buenos Aires. *Rev. Argent. Prod. Anim. Argent. Prod. Anim.* VII.
- Gregorini, P., M. Eirin, R. Refi, M. Ursino, and O. Ansin. 2004. Efecto de dos momentos de

- asignación del forraje fresco sobre el tiempo de pastoreo y su distribución durante el día. II Reunión Binacional de Ecología, XXI Reunión Argentina de Ecol., XI Reunión de la Sociedad de Ecología de Chile.
- Gregorini, P., M. Eirin, R. Refi, M. Ursino, and O. Ansin. 2005b. Timing of herbage allocation 1. Effect on beef heifers daily grazing pattern. *J. Anim. Sci.* 83(Suppl 2):202.
- Griggs T. C., J. W. MacAdam, H. F. Mayland, and J. C. Burns. 2005. Nonstructural carbohydrate and digestibility patterns in orchardgrass swards during daily defoliation sequences initiated in evening and morning. *Crop Sci.* 45:295.
- Hodgson, J. 1979. Nomenclature and definitions in grazing studies. *Grass Forage Sci.* 34:11.
- Hoebel, B. G., S. F. Leibowitz, and L. Hernandez. 1992. Neurochemistry of anorexia and bulimia. In *The Biology of Feast and Famine*. G. H. Anderson and S. H. Kennedy, ed. p 21. Acad. Press, San Diego, CA.
- Hogan, J. P., P. A. Kenny, and R. H. Weston. 1987. Factor affecting the intake of feed by grazing animals. In *Temperate Pastures: Their Production and Management*. J. L. Wheeler, C. J. Pearson, and G. E. Robards, ed. Australian Wool Corporation/CSIRO, Australia.
- Holling, S. C. 1959. Some characteristics of simple types of predation and parasitism. *Can. Entomol.* 91:385.
- Houtman, R., and L. M. Dill. 1998. The influence of predation risk on diet selectivity: A theoretical analysis. *Evol. Ecol.* 12: 251.
- Hudson, R., and S. Frank, 1986. Foraging ecology of bison in aspen boreal habits. *J. Range Manage.* 40:71
- Illius, A. W., and I. J. Gordon. 1987. The allometry of food intake in grazing ruminants. *J. Anim. Ecol.* 56:989.
- Illius, A. W., and N. S. Jessop. 1996. Metabolic constraints on voluntary Intake in ruminants. *J. Anim. Sci.* 74:3052.
- Illius, A. W., N. S. Jessop, and M. Gill. 2000. Mathematical models of food Intake and metabolism in ruminants. In *Ruminant Physiology: Digestion, Metabolism, Growth and Reproduction*. P. B. Cronje, ed. CAB Int., Wallingford, UK.
- Jarman, P. J. 1974. The social organization of antelope in relation to their ecology. *Behaviour* 48:215.
- Jeschke, J. M., M. Kopp, and R. Tollrian. 2002. Predator functional responses: discrimination between handling and digesting prey. *Ecol. Monogr.* 72:95.
- Johansson, B., I. Redbo, and Svennersten-Sjaunja, K. 1999. Effect of feeding before, during and after milking on dairy cow behaviour and the hormone cortisol. *Anim. Sci.* 68: 597.
- Kolasa, J. and C. D. Rollo. 1991. The heterogeneity of heterogeneity: A glossary. In *Ecological Heterogeneity*. J. Kolasa and S. T. A. Pickett, ed. p 1. Springer-Verlag, New York, NY.
- Kotliar, N. B., and J. A. Wiens. 1990. Multiple sales of patchiness and patch structure: A hierarchical framework for the study of heterogeneity. *Oikos* 59:253.
- Kral, T. J. E., and B. Rolls. 2004. Energy density and portion size: Their independent and combined effects on energy intake. *Physiol. Behav.* 82:131.
- Krysl, L. J., and B. W. Hess. 1993. Influence of supplementation on behavior of grazing cattle. *J. Anim. Sci.* 71:2546.
- Laca, E. A., E. D. Ungar, N. Seligman, and M. W. Demment. 1992. Effect of sward height and sward density on bite dimensions of cattle grazing homogeneous swards. *Grass Forage Sci.* 47:102.
- Le Magnen, J. 1986. Hunger. Cambridge Univ. Press, Cambridge, New York, NY.
- Levin, S. A. 1992. The problem of patterns and scale in ecology. *Ecology* 73:1943.
- Lindström, T. 2000. Feeding behaviour in dairy cows, motivational aspects. Ph.D. Diss., Swedish Univ. Agric. Sci., Uppsala, Sweden.
- Linnane, M. I., A. J. Brereton, and P. S. Giller. 2001. Seasonal changes in circadian grazing patterns of Kerry cows (*Bos taurus*) in semi-feral conditions in Killarney National Park, Co. Kerry, Ireland. *Appl. Anim. Behav. Sci.* 71:277.
- Mangel, M., and C. W. Clark. 1986. Towards a unifiend foraging theory. *Ecology* 67:1127.
- Marriott, C., and P. Carrere. 1998. Structure and dynamics of grazed vegetation. *Ann. Zoolotech.* 47:359.
- Mayland, H. F., J. W. MacAdam, G. E. Shewmaker, and N. J. Chatterton. 2003. The diurnal cycling of sugars in grasses impact strip-graze management plans. In *Proc. 2nd Natl. Conf. Grazing Lands*, pp. 466-468. Nashville, TN. CD-ROM.
- Metz, J.H.M. 1975. Time Patterns of Feeding and Rumination in Domestic Cattle. Mededelingen Landbouwhogeschool, Wageningen, The Netherlands.
- Nelson, R. J. 1995. Biological Rhythms and Behavior. In *An Introduction to Behavioral Endocrinology*. R. J. Nelson, ed. Sinauer Associates, Inc. Sunderland, MA.
- Newman, J. A., A. J. Parsons, and P. D. Penning. 1994. A note on the behavioural strategies used by grazing animals to alter their intake rates. *Grass Forage Sci.* 49:502.
- Newman, J. A., A. J. Parsons, J. H. M. Thornley, P. D. Penning, and J. R. Krebs. 1995. Optimal diet selection by a generalist grazing herbivore. *Funct. Ecol.* 9:255.
- Nielsen, B. L. 1999. On the interpretation of feeding behavior measures and the use of feeding rates as an indicator of social constraint. *Appl. Anim. Behav. Sci.* 79:79.
- O'Connell, J., P. S. Giller, and W. Meaney. 1989. A comparison of dairy cattle behavioral pattern at pasture and during confinement. *Ir. J. Agric. Res.* 28:65.
- Orr, R. J., P. D. Penning, A. Harvey, and R. A. Champion. 1997. Diurnal patterns of intake rate by sheep grazing monocultures of rye grass or white clover. *Appl. Anim. Behav. Sci.* 53:65.
- Orr, R. J., P. D. Penning, S. M. Rutter, R. A. Champion, A. Harvey, and A. J. Rook. 2001a. Intake rate during meals and duration for sheep in different hunger states, grazing grass or white clover swards. *Appl. Anim. Behav. Sci.* 75:33.
- Orr, R. J., S. M. Rutter, P. D. Penning, and A. J. Rook. 2001b. Matching grass supply to grazing patterns for dairy cows. *Grass Forage Sci.* 56:352.
- Parsons, A. J., and B. Dumont. 2003. Spatial heterogeneity and grazing process. *Anim. Res.* 52:161.
- Parsons, A. J., J. A. Newman, P. D. Penning, and A. Harvey. 1994. Diet preference of sheep: Effect of recent diet, physiological state and species abundance. *J. Anim. Ecol.* 63:465.
- Paterson, D. L., and V. T. Parker. 1998. Ecological Scale: Theory and Applications. p 615. Columbia Univ. Press, New York, NY.
- Pearse, C. K. 1971. Grazing in the Middle East: Past, present and future. *J. Range Manage.* 24:13.
- Penning, P. D., A. J. Parsons, J. A. Newman, R. J. Orr, and A. Harvey. 1993. The effect of group size on grazing time in sheep. *Appl. Anim. Behav. Sci.* 37:101.
- Pereira, G. M. 2002. A typology of spatial and temporal scale relations. *Geogr. Anal.* 34:21.
- Phillips, C. J. C. 1993. Nutritional Behavior. In *Cattle Behavior*. C. J. C. Phillips, ed. p 233. Farming Press, Ipswich, UK.
- Phillips, C. J. C., and S. A. Schofield. 1989. The effect of supplementary light on the production and behavior of dairy cows. *Anim. Prod.* 48:293.
- Poppi, D. P., J. France, and, S. R. McLennan. 1999. Intake, passage and digestibility. In *Feeding Systems and Feed Evaluation Models*. M. K. Theodorou and J. France, ed. p 481. CAB Int., Wallingford, UK.
- Poppi, D. P., and S. R. McLennan. 1995. Protein and energy utilization by ruminants at pasture. *J. Anim. Sci.* 73:278.
- Prins, H. T. 1996. Ecology and Behaviour of African Buffalo: Social Inequality and Decision Making. Chapman & Hall, London, UK.
- Provenza, F. D. 1996. Acquired aversions as the basis for varied diets of ruminants foraging on rangelands. *J. Anim. Sci.* 74:2010.
- Provenza, F. D. 1995. Postingestive feedback as an elementary determinant of food selection and intake in ruminant. *J. Range Manage.* 48:2.
- Provenza, F. D., J. J. Villalba, C. D. Cheney, and S. J. Werner. 1998. Self-organization of foraging behaviour: From simplicity to complexity without goals. *Nutr. Res. Rev.* 11:199.

- Rearte, D. H., and F. J. Santini. 1989. Digestion ruminal y produccion en animales en pastoreo. *Revista Argentina de Prod. Anim.* 9:93.
- Rhind, S. M., Z. A. Archer, and C. L. Adam. 2002. Seasonality of food intake in ruminants: Recent developments in understanding. *Nutr. Res. Rev.* 15:4.
- Rietkerk, M., J. van de Koppel, L. Kumar, F. van Langevelde, and H. H. T. Prins. 2002. The ecology of the scale. *Ecol. Model.* 149:1.
- Rind, M. I., and C. C. Phillips. 1999. The effects of group size on the ingestive and social behavior of grazing dairy cows. *Anim. Sci.* 68:589.
- Ritchie, M. E. 1998. Scale-dependent foraging and patch choice in fractal environments. *Evol. Ecol.* 12:309.
- Rook, A. J., A. Harvey, A. J. Parsons, S. M. Orr, and S. M. Rutter. 2004. Bite dimensions and grazing movements by the sheep and cattle grazing homogeneous perennial ryegrass swards. *Appl. Anim. Behav. Sci.* 88:227.
- Rook, A. J., and C. A. Huckle. 1997. Activity bout criteria for grazing dairy cows. *Appl. Anim. Behav. Sci.* 54:89.
- Rook, A. J., C. A. Huckle, and P. D. Penning. 1994. Effect of sward height and concentrate supplementation on the ingestive behavior of spring calving dairy cows grazing grass clover swards. *Appl. Anim. Behav. Sci.* 40:101.
- Rutter, S. M., V. Tainton, R. A. Chamion, and P. le Grice. 2002. The effect of a total solar eclipse on grazing behavior of dairy cattle. *Appl. Anim. Behav. Sci.* 58:1.
- Samuelsson, B., K. Uvnas-Moberg, R. C. Gorewit, and K. Svennersten-Sjaunja. 1996. Profiles of the hormones somatostatin, gastrin, CCK, prolactin, growth hormone and cortisol. I. In dairy cows that are milked and fed separately or milked and fed simultaneously. *Livest. Prod. Sci.* 46:49.
- Schwinning, S., and A. J. Parson. 2001. The stability of grazing systems revisited: Spatial models and the role of heterogeneity. *Funct. Ecol.* 13: 737.
- Shipley, L. A., J. E. Gross, D. E. Spalinger, N. T. Hobbs, and B. A. Wunder. 1994. The scaling of intake rate on mammalian herbivores. *Am. Nat.* 143:1055.
- Shipley, L. A., and D. E. Spalinger. 1992. Mechanics of browsing in dense food patches: Influence of plant animal morphology on intake rate. *Can. J. Zool.* 70:1743.
- Simpson, S. J., R. M. Sibly, P. M. Lee, S. T. Behmer, and D. Raubenheimer, 2004. Optimal foraging when regulating intake of multiple nutrients. *Anim. Behav.* 68:1299.
- Sinclair, A. E. 1977. *The African buffalo: A Study of Resource Limitation of Populations.* Univ. Chicago Press, Chicago, IL.
- Solomon, M. E. 1949. The natural control of animal populations. *J. Anim. Ecol.* 18:1-35.
- Staddon, J. R. 1983. *Adaptive Behavior and Learning.* Cambridge Univ. Press, Cambridge, UK.
- Stephens, D. W., and J. R. Krebs. 1986. *Foraging Theory.* Princeton Univ. Press, Princeton, NJ.
- Tallowin, J. B., C. M. Tyson, and S. E. Brookman. 1991. Differences in lamina wetability in some permanent pasture grass species and two *Lolium perenne* cultivars. *Grass Forage Sci.* 46:265.
- Taweel H. 2004. *Perennial ryegrass for dairy cows, grazing behavior, intake, rumen function and performance.* Ph.D. Diss., Wageningen Univ., Wageningen, The Netherlands.
- Toates, F. 2002. Physiology, motivation and the organization of behavior. In *The Ethology of Domestic Animals: An Introductory Text.* P. Jensen, ed. CAB Int., Wallingford, UK.
- Underwood, R. 1982. Vigilance behaviour in grazing African antelopes. *Behav.* 79:81.
- Ungar, E. D. 1996. Ingestive behavior. In *The Ecology and Management of Grassland Systems.* J. Hodgson and A. W. Illius, ed. p 185. CAB Int., Wallingford, UK.
- van Gardingen, P. R., G. M. Foody, and P. J. Curran 1997. *Scaling-Up. From Cell to Landscape.* Cambridge Univ. Press, Cambridge, UK.
- WalliesDeVries, M. F., and C. Delabout. 1994. Foraging strategy of cattle in patchy grassland. *Oecologia* 100:98.
- WalliesDeVries, M. F., and E. Laca. 1999. The importance of scale of patchiness for selectivity in grazing herbivores. *Oecologia* 121:355.
- WalliesDeVries, M. F., E. Laca, and M. W. Demment. 1998. From feeding station to patch: Scaling up food intake measurements in grazing cattle. *Appl. Anim. Behav. Sci.* 60:301.
- Wiens, J. A. 1976. Population responses to patchy environments. *Annu. Rev. Ecol. Syst.* 7:81.
- Wiens, J. A. 1989. Spatial scaling in ecology. *Funct. Ecol.* 3:385.
- Wu, J. 1999. Hierarchy and scaling: Extrapolating information along a scaling ladder. *Can. J. Remote Sensing* 25:367.
- Wu, J., and Y. Qi. 2000. Dealing with landscape analysis: An overview. *Geogr. Inform. Sci.* 6:1.
- Wurtman, R. J., and J. J. Wurtman. 1989. Carbohydrates and depression. *Sci. Am.* 262:68.