

Spatial and temporal domains of scale of grazing cattle

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Abstract. Spatio-temporal patterns of cattle grazing were studied in four annual grassland pastures in California, differing mainly in tree canopy cover. Cows were equipped with global positioning collars that recorded position, temperature and head movements at 5-min intervals during 6 days in each of four seasons repeated during 2 years. The time animals took to traverse areas of varying diameter revealed patches of 6–9-m diameter in the pastures with low, and 18–21-m diameter in the pastures with high tree canopy cover. In agreement with the current model, crookedness of cow paths had two distinct domains. Within distances of 0–40 m, paths were relatively straight and similar, but from 40 to 200 m, they became increasingly tortuous. Correlation of sequential turning angles identified patches of movement with diameters between 40 and 100 m, which correspond to the ‘patch’ level of grazing within grazing sites. Seasonal changes in meal patterns were consistent with changes in temperature and forage quality and interacted with the distribution of shade. Thus, spatial distribution of grazing and temporal distribution of meals were inextricably linked. Low forage quality and high temperatures in summer resulted in highly concentrated grazing around trees. Conversely, winter and early spring forages of very high quality and low availability motivated more widely distributed grazing, with low proportion of areas being re-grazed. Resting sites acted as beginning and end of grazing bouts. We conclude that shade distribution can modulate meal start and duration.

Additional keywords: animal movement, fractals, livestock behaviour.

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Introduction

How can we describe and summarise the interaction of grazing animals with their foraging environment in space and time to promote more learning and better management? Are current abstractions sufficiently specific for management but flexible enough to adapt to new discoveries? These are questions that motivated the present work, in general. Specifically, we ask whether cattle foraging exhibits domains of scale in space and time; do spatial and temporal scales interact, and if so, can we incorporate the information into a conceptual framework that is useful for grazing management and resource conservation? For example, does timing of meals affect the distance between resting sites; or conversely, does distance between desirable resting sites affect meal duration?

The current paradigm, developed by Senft *et al.* (1987), views livestock movement as a series of hierarchical spatial levels going from bites to home ranges. The original work confused scale with hierarchical levels of organisation, but this was later corrected in the more specific and functional scheme posed by Bailey *et al.* (1996). The grazing process is viewed as a series of hierarchically organised levels ranging from biting to migration and dispersal, and associated specific temporal and spatial grains or resolution. Yet, there is little empirical information about

how salient or distinct those levels are, particularly levels that are not evident on casual observation, such as food patches and feeding sites (for exceptions, see Wallace *et al.* 1995; Harvey and Fortin 2013).

The study of animal movement patterns provides a basis for understanding their foraging decisions, space use and distribution (Crist *et al.* 1992). Animal movement can be divided into scale segments. Wiens (1989) called such scale segments ‘domains’ and called the boundaries between these segments ‘transitions’. Nams (2005) suggested that to understand how animals perceive and react to landscape structure, we need to measure these domains of scale, and then study how animals react to their landscape within each domain. He divided animal movement into two domains, namely, the small scale when the animal forages and the larger scale when the animal travels.

The study of scales of foraging is necessary to provide a formal basis for grazing management decisions that routinely involve changes of scale such as the calculation of herbage allowance or number of animals and grazing periods for certain paddocks (Laca 2009). Managers and scientists use information obtained at a certain scale and apply it at a different one. The problem is that non-linear scaling is typical in natural systems (Habeeb *et al.* 2005). Yet, to our knowledge and with the exception of

the occasional use of Kleiber's law, non-linear scaling has never been incorporated quantitatively into grazing management. It is generally assumed that grazing capacity (mass of forage available for grazing per unit area per unit time) is a property of the land that does not change with pasture size, and number of animals to graze is calculated simply as grazing capacity × pasture area/individual forage demand. At best, pasture size is only considered intuitively and informally to decide on stocking rate; larger pastures probably have a lower grazing capacity than do smaller ones, at the very least because smaller pastures allow more detailed control of spatio-temporal distribution of animals in relation to forage availability and other factors that control both forage productivity and efficiency of utilisation.

Thus, our goal was to determine whether spatial scales or 'levels' such as those described by Bailey and Provenza (2008) are identifiable in the spatial and temporal patterns of movement and grazing of cattle and whether the spatial and temporal characteristics of meal and movement change over pasture and seasons. Rather than using a traditional hypothesis-testing approach, we sought to accomplish our goal by identifying and quantifying the scales at which cattle movement and meal patterns exhibit patchiness and changes in degree of tortuosity, length or frequency, using methods for analysing animal paths (Calenge 2006). Patch sizes, temporal and spatial scales detected were then qualitatively compared with the values presented by Bailey *et al.* (1996) to determine whether our findings fit the existing model.

Materials and methods

Pastures

The study used two pairs of pastures at the Sierra Foothill Research & Extension Center (SFREC), which is located in the Foothills of the Sierra Nevada 27 km north-east of Marysville, California. The climate at the SFREC is Mediterranean, characterised by hot, dry summers and mild, rainy winters. Slopes in all pastures ranged from 0% to more than 60%. The dominant herbaceous vegetation was composed of exotic annual grasses and forbs. Main grasses were soft chess (*Bromus hordeaceus* L. ssp. *hordeaceus*), ripgut brome (*Bromus diandrus* Roth), annual ryegrass (*Lolium multiflorum* Lam.), wild oats (*Avena fatua* L.), annual fescue (*Vulpia myuros*

(L.) K.C. Gmel.), foxtail barley (*Hordeum murinum* L. ssp. *leporinum*) and medusa head (*Taeniatherum caput-medusae* Nevskii). Dominant forbs included red stem filaree (*Erodium cicutarium* L.), rose clover (*Trifolium hirtum* All.) and subterranean clover (*T. subterraneum* L.).

One pair of pastures (Haworth7 and Porter21) was open woodland and the other pair (Forbes1 and Forbes2) had been cleared and was mostly devoid of trees, except in a riparian corridor. The two 20-cow herds grazed one pair of pastures one week and the other pair the following week during April 2001 (flowering), August 2001 (dry season), January 2002 (early vegetative), March 2002 (vegetative), April–May 2002 (flowering), August 2002 (dry season), January 2003 (early vegetative) and March 2003 (vegetative) (Table 1).

Permanent north–south transects were established every 30 m in each of the pastures. Botanical composition (forbs, palatable grasses, unpalatable grasses and medusahead), percentage grazed, percentage litter and percentage bare ground were visually estimated in a 0.09-m² quadrat placed every 30 m on each transect, thus creating a square grid of measured points that were marked throughout the experiment. Stubble height was averaged using five height measurements in each quadrat.

Area accessible to grazing in each pasture was estimated as the area within 2.5 m of the union of paths of all animals in all seasons. Area grazed each season was also estimated in the same manner and analysed as a function of pasture and season. Pre-grazing standing crop was estimated using the comparative yield method. George *et al.* (2007) found that the comparable yield method can be used with confidence throughout the year to estimate herbage standing crop. Means were separated using Tukey's method.

Animals

Forty cows (*Bos taurus*) were randomly selected from the cattle herd and split into two groups. Within each group, six cows were equipped with GPS collars (Lotek™ 2200 LR and 3300 LR Series, Lotek Engineering, Newmarket, Ontario, Canada). The same cows were collared for each grazing season except for two replacement cows during the last year of the study. Animals ranged from 3 to 7 years of age and were Hereford, Angus or Hereford–Angus crosses. Cows were bred to calve in the fall. All cows had calves during the experimental periods, except during

Table 1. Mean (kg DM/ha) and standard errors (0.89 kg^{0.5}/ha^{0.5}) of herbage mass available in each pasture immediately before (b) and after (a) each grazing period

Numbers without common letters are significantly different with a probability of error type 1 equal to 5%. Comparisons are valid only within a or within b. Numbers in parenthesis are standard errors in transformed units of 0.89 kg^{0.5}/ha^{0.5}

Pasture (n)	2001			2002			2003	
	Late spring	Summer	Winter	Early spring	Late spring	Summer	Winter	Early spring
Forbes1 (259)	b 3416b (0.46)	2183d (0.46)	842ij (0.46)	607kl (0.46)	1554fg (0.46)	1900e (0.46)	609kl (0.46)	1494g (0.46)
	a 3301b (0.47)		558L (0.47)	705k (0.47)	2636c (0.47)		957ij (0.48)	1740f (0.47)
Forbes2 (247)	b 3809a (0.47)	2292d (0.47)	642kl (0.47)	518L (0.47)	1364g (0.47)	1770ef (0.51)	530L (0.47)	1133h (0.47)
	a 3646a (0.48)		309° (0.48)	427mn (0.48)	2161d (0.48)		902j (0.50)	1354g (0.48)
Haworth7 (225)	b 3251b (0.50)	2188d (0.49)	611kl (0.49)	524L (0.50)	2310d (0.50)	1560fg (0.50)	324m (0.49)	881ij (0.49)
	a 3248b (0.51)		358no (0.50)	545Lm (0.50)	1789ef (0.51)		545Lm (0.51)	1119hi (0.50)
Porter21 (187)	b 3436b (0.54)	2188d (0.54)	609kl (0.54)	545L (0.54)	2607c (0.54)	1733ef (0.54)	744jk (0.54)	965hi (0.54)
	a 3156b (0.55)		340no (0.55)	602kl (0.55)	2001de (0.55)		621kl (0.56)	1173gh (0.55)

the summer (July–August). All animals had previously grazed the four pastures.

The Lotek™ GPS collars were programmed to record a position every 5 min for each 1-week grazing period. Collars recorded longitude, latitude, date, time, elevation, temperature, forward–backward collar movement, left–right collar movement and satellite ephemeris information. Data were downloaded from the collars following each grazing period and differentially corrected by removing the positional error recoded by a stationary ‘base’ unit whose true coordinates were known. Agouridis *et al.* (2004) reported that differentially corrected coordinates obtained with similar collars were within 4 or 12 m of the true locations with 95% confidence when tested in open fields or under tree canopy cover.

Analyses

Our main goal was to determine whether spatial scales or ‘levels’ were identifiable in the movement of cows. For this, we used a series of methods that were designed to quantify characteristics of movement paths such as crookedness and total time spent within areas of varying diameter as a function of the scale of analysis. Spatial levels were identified by significant changes in crookedness, time necessary to cross past an area or other metrics described below.

In total, 266 325 valid animal positions were obtained, most of which had valid values for temperature and activity switches. Each pair of sequential records for each animal in each pasture and during each season was a segment representing a movement vector. Each pair of contiguous segments defined a relative turning angle. For each segment, we calculated speed (v , m/min) and cosine of turning angle ($\cos a$). Net 4-segment speed (v_4) was calculated as the distance from each location to the average of the previous three locations divided by segment time. We standardised counts from activity switches by subtracting the mean and dividing by the standard deviation for each of the 160 cow–pasture–season combinations. Activity during each segment (grazing, resting or traveling) was inferred from speed, cosine of turning angle and other variables following a procedure based on the studies by Ungar *et al.* (2005) and Putfarken *et al.* (2008). First, A1 was defined as ‘resting’ if turning angle was very acute and movement was ($\cos a < -0.1$ and $v < 1.2$), ‘traveling’ if $v > 20$, ‘grazing’ if speed was 1.2–20 and $\cos a > -0.1$, and undetermined otherwise. Then, A1 was analysed with a logistic model including $\cos a$, v , v_4 , animal, and standardised activity switch counts as predictors. The final activity imputed to each record was obtained by applying the prediction equation resulting from the logistic model (not shown). The purpose of this analysis was the classification of all GPS locations and path segments into behaviours, particularly grazing and resting. Grazing represents meals whose duration and temporal and spatial distribution were foci of this study.

For the analysis of behavioural sequences, we removed 2958 of the 266 325 valid records because they were brief (<7.5 h) sequences of valid records interspersed with long periods without information due to GPS malfunction. The resulting file with 263 190 records, including identification columns, coordinates in Universal Transverse Mercator (UTM), date-time, activity

type and temperature, was read into R (R Core Team 2014) and transformed into a trajectory list of 196 paths or ‘bursts’, using the package ‘adehabitatLT’ (Calenge 2006). The trajectory or movement path of an animal is the continuous curve created by the animal as it moves. The sampling of the trajectory implies a step of discretisation, i.e. the division of this continuous curve into several discrete steps connecting successive relocations of the animal (Turchin 1998). Paths were split whenever a gap greater than 123 min between successive coordinates was found, which resulted in 196 different paths for the 160 sets of conditions (4–6 cows \times 4 pastures \times 8 seasons). Trajectories were re-discretised into uniform 5-min steps using the *redisltraj* function and each location in the re-discretised trajectories was associated with the activity recorded that was closest in time and after the location. Locations that were more than 30 min from the closest recorded activity were assigned a missing value for activity. The purpose of these analyses was to obtain paths without gaps and that were formatted as needed for further analyses.

Paths were first analysed with Fractal 5.0 (Nams 1996). Sequential cow locations formed vectors of movement that were analysed to determine the fractal dimension by the V-fractal method (Dvf) and the correlation of cosines of turning angles. The V-fractal is based on the divider method (Sugihara and May 1990) and Dvf can be used to assess the tortuosity or crookedness of a path without the need to suggest or imply that paths have true self-similarity (i.e. that the whole path is roughly similar to a part of itself). Nams (1996) concluded that VFractal adequately estimated Fractal D at different spatial scales. Fractal dimension of a path can vary between its Euclidean dimension of 1 and 2, the dimension of an object that has area, but not volume. Values of Dvf close to 1.0 mean that paths tend to be straight at the measured scale; values >1.0 mean greater sinuosity, and a maximum value of 2.0 represents a path that tends to cover the whole area. Abrupt changes in Dfv can reflect the scale of boundaries between domains of scale, for example, a transition from the scale of feeding within patches to the scale of travel between patches. The purpose of these analyses was to determine whether the crookedness of the paths differed between scales or exhibited patches. Correlation of cosine of turning angles (Cc) is another measure that allows detection of patchiness in animal paths at multiple scales (Nams 2005). Patches and their typical size are detected when the correlation of cosine changes from positive to negative as scale of calculation increases. Correlation of cosine and Dfv only consider spatial characteristics of paths.

Variance of first-passage time along paths (Vfpt) was calculated using the *varlogfpt* function of *adehabitatLT* as a third metric of spatio-temporal scales in cow movements. First passage time is the time that it takes a moving animal to get through a circle of Diameter d , and it is calculated for a range of values of d (Fauchald and Tveraa 2003; Pinaud 2008). Tortuous and slow movement increases first passage time. For example, as animals encounter a patch with more abundant palatable forage, they can respond by getting through the patch more slowly in a straight path or by turning frequently to remain in the patch. Whereas Dfv and Cc can detect only the latter, first passage time can detect any combination of both mechanisms.

As d increases, V_{fpt} peaks at the scale of patches of tortuous, slower versus faster or simpler, more directional movement. Thus, V_{fpt} considers both spatial and temporal characteristics of paths. The aim of this analysis was to determine whether cows exhibited patchy behaviour whereby they spent more time in certain areas by reducing movement speed and/or turning more frequently and sharply.

Grazing of 'virgin' (not previously grazed by an individual animal within the same season) areas was described by the proportion of total area grazed each hour represented by virgin areas (p_v) at two scales, 2 and 20 m. Proportion of virgin area grazed (p_v) was calculated separately for each animal by calculating the difference between the number of unique 1-m pixels that were within 1 or 10 m of the animal's path at the beginning and end of each hourly path segment, and then dividing by the product of segment length and path width (2 or 20 m). When animals grazed areas not previously visited within the current season and pasture, $p_v = 1$. At the other extreme, when all area within 2 or 20 m (depending on the scale of analysis) of the path was previously grazed, $p_v = 0$. Thus, p_v is a measure of spatio-temporal distribution of grazing. The meaning of this analysis was to determine the tendency of cows to repeatedly graze certain areas and how that tendency changed over seasons and pastures. Frequently repeated grazing is generally not desired for proper pasture management.

We visually inspected the 320 graphs of p_v versus time grazing, grouped by years, pasture and seasons, to determine how to further summarise the data. The goal was not to determine whether there were significant differences associated with potential explanatory factors, but to look for global patterns while accounting for obvious differences among pastures of seasons. It was determined that a classification according to seasons was sufficient to summarise the main patterns. The median values of p_v were analysed as a function of time in the pasture with splines and third-degree polynomials.

The proportion of grazed area represented by previously ungrazed locations was a useful dynamic metric of the spatial pattern of grazing. If animals grazed systematically over space with a resolution r , calculated p_v would be equal to 1.0 for scales equal to or smaller than r . If each grazing point were independent of the past locations (an obviously unrealistic case), p_v should tend to be equal to the proportion of pasture area still ungrazed. Thus, p_v represents the tendency of animals to revisit areas previously grazed, which can be viewed at multiple scales; and the difference between proportion of pasture ungrazed and p_v represents the tendency of individual cows to prefer or avoid areas they previously grazed. The present p_v metric does not consider the interaction between animals and areas previously grazed by others, but it will be expanded in the future to describe the behaviour of groups of any size, thus extending the analysis to the herd size dimension.

Results

Herbage mass (Table 1) and sward height (Fig. 1) exhibited a typical pattern of the California annual grassland (George *et al.* 1985). Herbage mass is low and its digestibility and water content are high during winter and early spring. In late spring,

herbage is abundant and of high quality, whereas in summer it is dry and of low digestibility. Sward height distributions indicated that pastures were very heterogeneous in late spring and summer, particularly during the first late spring and summer, when statistical distributions of heights were more uniform.

Porter21 and Haworth7 were ~20% smaller in area and had a greater tree canopy cover than did Forbes1 and Forbes2 (Table 2). Over the eight seasons of the experiment, animals were recorded grazing within 2.5 m of all points in the pastures, except for Porter21, where animals reached 95% of the area. Total proportion grazed (i.e. area reached within 2.5 m by any cow while grazing) was different over pastures and seasons. Haworth7, the pasture with the most canopy cover, had the greatest grazing coverage, which was significantly greater than for Forbes1 and 2. Proportion of area grazed declined with the progression of seasons, particularly after early spring, and it was significantly lower during the dry, hot season when forage quality was lowest and availability was highest (Table 2).

Spatial pattern and scales of movement

The crookedness of movement paths, as represented by D_vf , increased with increasing scale of measurement in all pastures and seasons. However, crookedness increased slowly at small scales, from 1.12 (s.e. = 0.0024) at 10 m to 1.25 (s.e. = 0.0027) at 50 m, and fast at large scales, from 1.21 at 50 m to 1.46 (s.e. = 0.0016) at 90 m. The increase was smaller for Haworth7 and Porter21 than for the pastures with a lower tree canopy cover, particularly in the summer, when crookedness remained almost constant in Haworth7 and Porter21. These changes in rate of change of crookedness with increasing scale may reflect two different domains of scale in movement behaviour corresponding to the patch- and feeding-site levels.

Analysis of correlation of cosine of turning angles (C_c) clearly identified segments of movement paths (hereafter termed 'movement patches') that were more crooked than other segments, by changing from $C_c > 0$ at scales smaller than the segments to $C_c < 0$ at the scale of the segments (Nams 2005). The size of these movement patches may correspond to patches in landscape characteristics such as herbage type and abundance. The correlation of cosine method detected movement patches in most combinations of pasture and season (Fig. 2). However, the size of movement patches identified differed among pastures and seasons, with Haworth7 and Porter21 exhibiting clearer patches than Forbes 1 and 2, with diameters ranging from 45 to 70 m. Patches of similar diameter were detected in the Forbes pastures.

Variance of the time it took animals to cross circles of increasing diameter peaked at different diameters for different seasons and pastures. The highest values for patch diameters ranged from 6 to 9 m in Forbes1 and Forbes2, and from 12 to 21 m in Haworth7 and Porter21 (Fig. 3). No other salient scales were identified by this method of analysis.

Temporal scales and pattern of grazing bouts

Total grazing time per day declined quadratically with increasing herbage mass ($Y = 14.0 - 2.40x + 0.44x^2$, $R^2 = 0.81$, RMSE = 0.74,

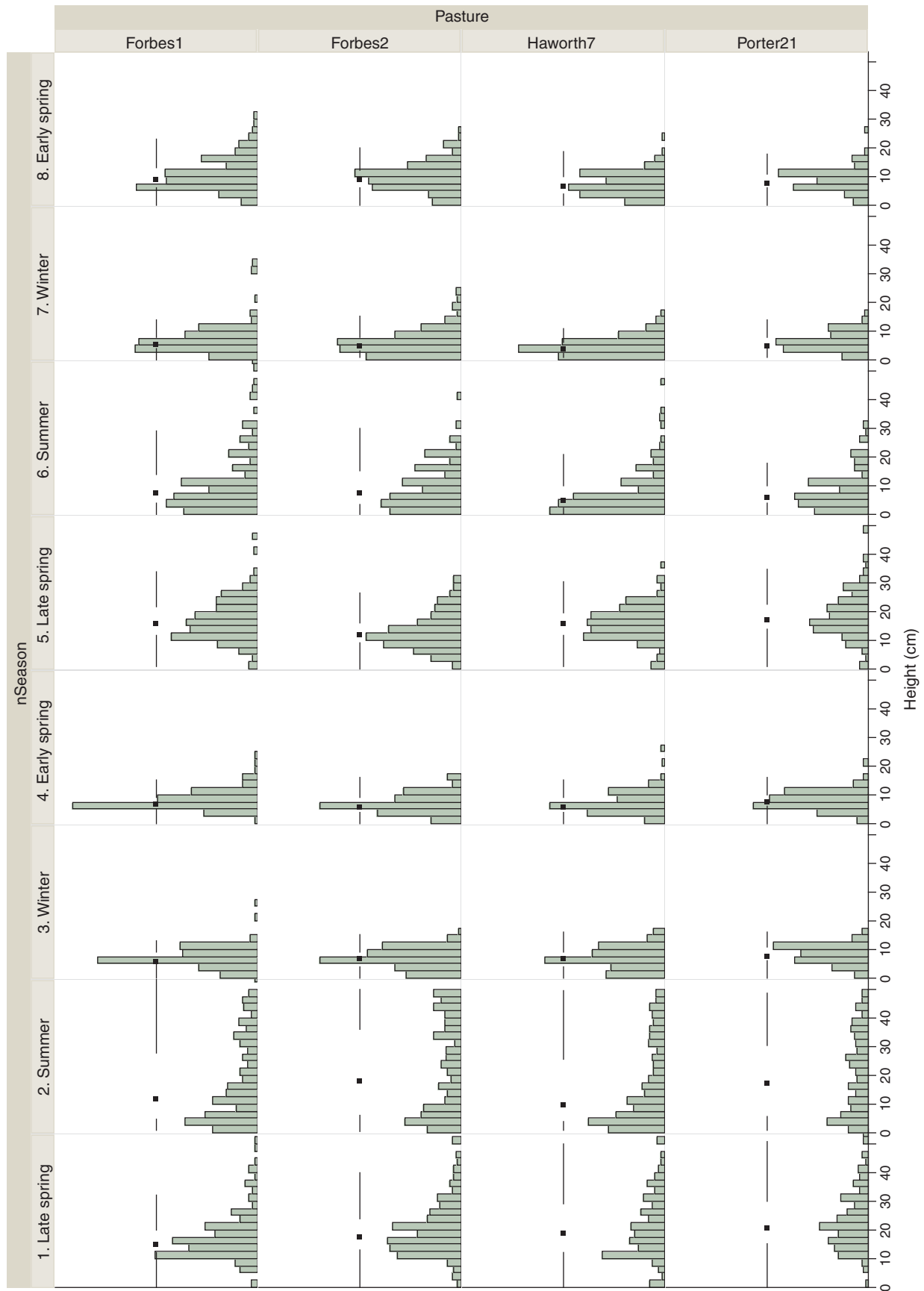


Fig. 1. Distribution of herbage height immediately before grazing periods in each pasture and each season. Horizontal lines are the quartiles of the distribution about the median represented by the dots.

Table 2. Pasture characteristics and the extent of grazing in each season

Means followed by at least one common letter are not significantly different. Standard errors of %grazed for season and pasture means were 2.89% and 5.78%

Pasture	Area (ha)	%Canopy	%Grazeable	%Grazed				Mean
				Winter	Early spring	Late spring	Summer	
Forbes1	25.1	4.1	100	68.2	63.9	60.4	40.8	58.3b
Forbes2	25.1	2.6	100	76.2	63.6	51.4	46.2	59.4b
Haworth7	21.5	22.6	100	82.7	85.0	78.7	61.0	76.8a
Porter21	19.0	12.8	95	76.0	73.5	61.3	60.2	67.8ab
Mean (s.e.)				75.8a	71.5ab	62.9bc	52.1c	

where x is in t/ha) and was 2.4 h greater ($P < 0.001$) for Haworth7 and Porter21 than for the Forbes pastures after correcting for herbage mass.

As previously reported (Low *et al.* 1981; Gregorini 2012), cows had two main grazing periods during the day, one in the early morning and one in the evening, in a pattern that differed among seasons (Fig. 4). In summer, the morning bout started between 0600 hours and 0700, peaked at 0800 hours, and lasted 2–3 h. There was intermittent grazing between late morning and 1700 hours when probability of grazing increased again. The evening grazing bout peaked between 1900 hours and 2100 hours, after which grazing probability remained low for the rest of the day until the following morning, except in winter and early spring. Remarkably, between 2200 hours and 2300 hours, winter and early spring exhibited a third peak with grazing probabilities between 0.5 and 0.6. Late spring pattern of grazing was similar to summer, but it was about 1 h earlier, with high peaks at 0700 hours and 1900 hours. Winter and early spring grazing patterns had shorter times between the morning and evening peaks, and the probability of grazing between these peaks was greater than for late spring and summer.

Average and median grazing-bout length differed among seasons in a manner consistent with the probability of grazing. In general, low probability of grazing was associated with short bout length (Fig. 5), particularly about noon. Seasons with greater noon temperatures exhibited the shortest grazing bouts during that time of day. Overall, the relationship between the probability of grazing and bout length showed that most cows grazed in long bouts during early morning and evening, whereas they took short bouts with low probability during midday, particularly in late spring and summer.

Spatio-temporal pattern of grazing

Most of the variation of the median of hourly proportion of areas grazed represented by virgin areas (pv) was explained by season and time since animals entered each pasture (Fig. 6, Table 3). Proportion of virgin area grazed declined with increasing time while having clear periodic deviations that coincided with the temporal distribution of meals. As expected, when calculated at a scale of 20 m, pv was lower and declined faster than when calculated at a scale of 2 m. At both scales and in all seasons, pv declined sharply and became lower than the long-term trend (represented by the polynomial fit) between late afternoon and early morning, and then increased

sharply during the main meal of the morning. Between late morning and mid-afternoon, pv exhibited a dip that was followed by the late afternoon decline. This spatio-temporal pattern differed among seasons, particularly between summer and the rest of the seasons.

In summer, pv at 2-m scale exhibited daily cycles of much wider amplitude than in the other seasons. Moreover, whereas in winter, early spring and late spring pv remained high between late morning and early afternoon, in summer there was a deep reduction in pv during this period, particularly after animals had been in the pasture a couple of days. In fact, the widest amplitude of pv variation was during the midday period in summer, whereas for the other seasons, it occurred at night.

Discussion

The main questions we posed were as follows: does cow foraging exhibit domains of scale in space and time; do spatial and temporal scales interact, and if so, can we incorporate the information into a conceptual framework that is useful for grazing management and resource conservation? Analyses revealed at least two domains of scale that were consistent with the commonly accepted scales described in Senft *et al.* (1987) and Bailey *et al.* (1996), food patches and feeding sites. Domains of scale were highly plastic and varied significantly due to the integration of daily meal patterns, spatial distribution and abundance of shade, and seasonal changes in temperature, forage availability and forage quality. These results are of practical importance because spatio-temporal patterns of grazing and movement in livestock determine not only welfare and nutrition (Gregorini 2012), but also affect the impact of grazing ruminants on methane emissions (Ricci *et al.* 2014). Temporal meal patterns were determined by a balance between the drive to eat and the effects of grazing on fill or thermal comfort, depending on the season. Our results can be used in the design of pastures and grazing methods, or at least the generate hypotheses about the use of shade and pasture size to obtain specific spatial distributions of grazing. For example, we hypothesise that when forage is of low quality and abundant, animals will fill up faster and tend to travel shorter distances while grazing, thus imposing greater heterogeneity of forage utilisation.

Although the use of fractal dimensions to describe spatio-temporal patterns has been debated, our results are not affected by the debate. Turchin (1996) indicated that fractal analysis is valid to extrapolate over scales only if there are at least scales

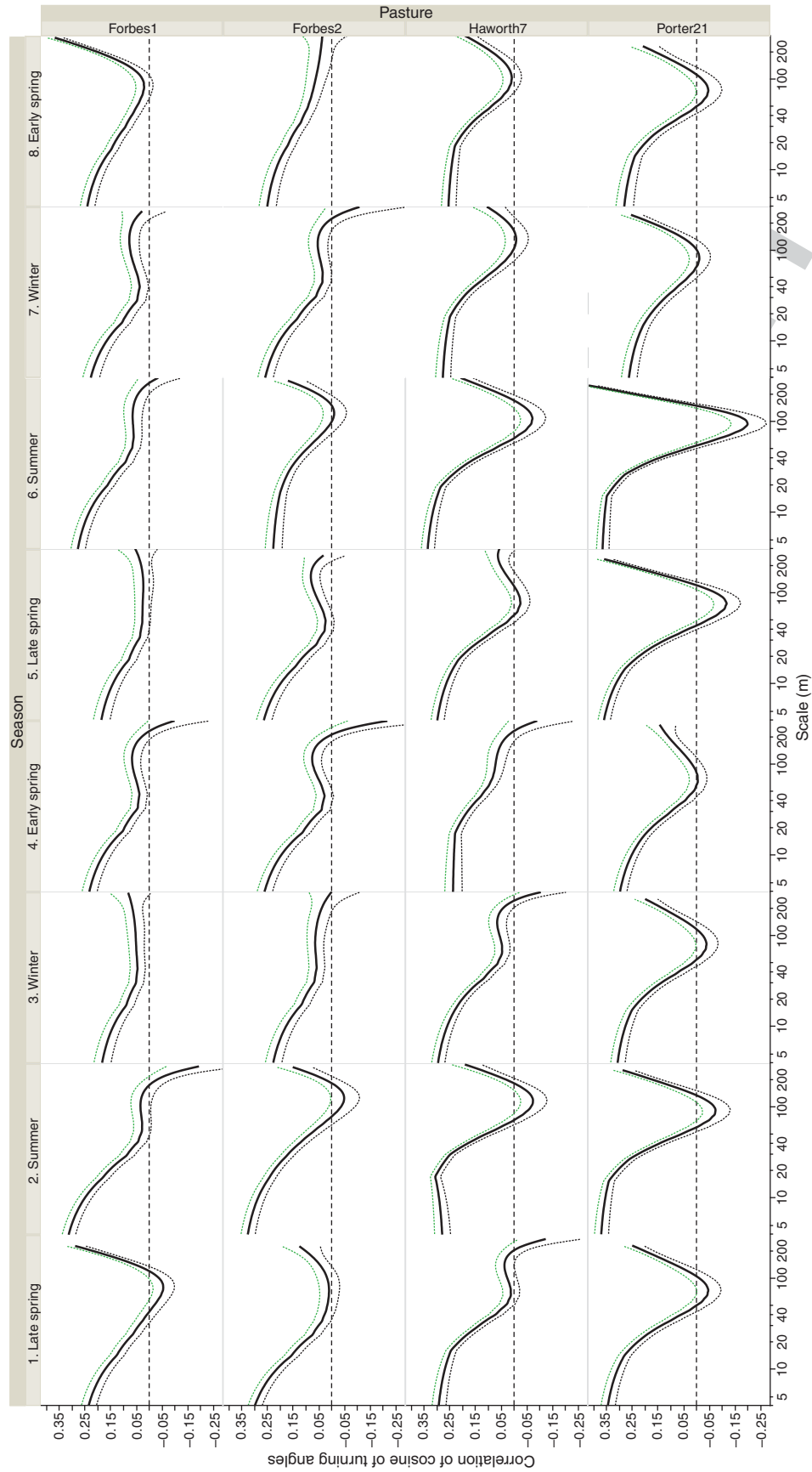


Fig. 2. Fractal dimension of cow paths calculated by the 'correlation of cosine' method as a function of scale, pasture and season. Thick lines are the averages of 4–6 cows moving during 4–6 days. Thin lines represent 95% confidence regions.

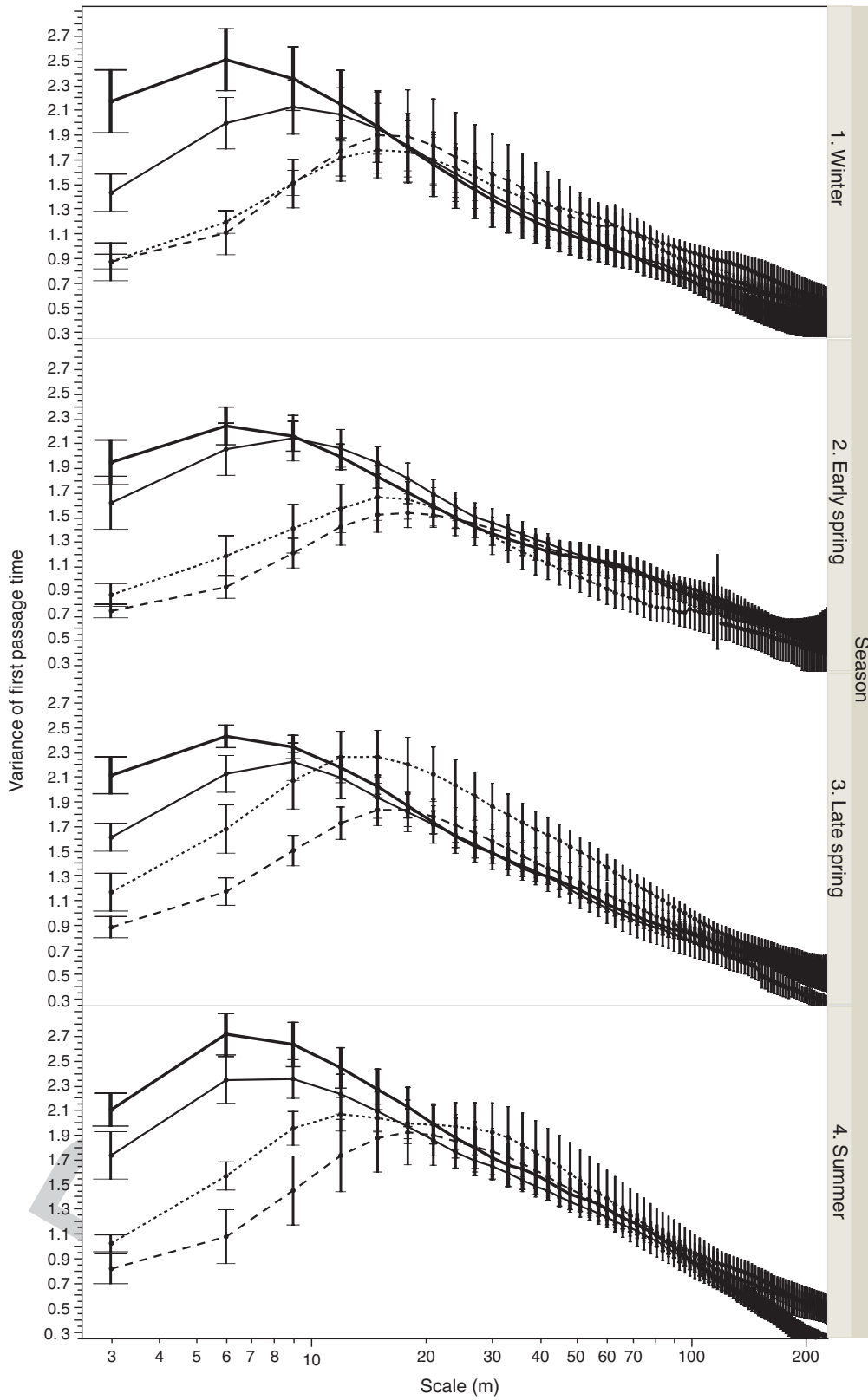


Fig. 3. Variance of first passage time as a function of scale, pasture and season. Thick lines are the averages of 4–6 cows moving during 4–6 days in 2 years. Vertical bars represent 95% confidence intervals calculated separately for each pasture and season.

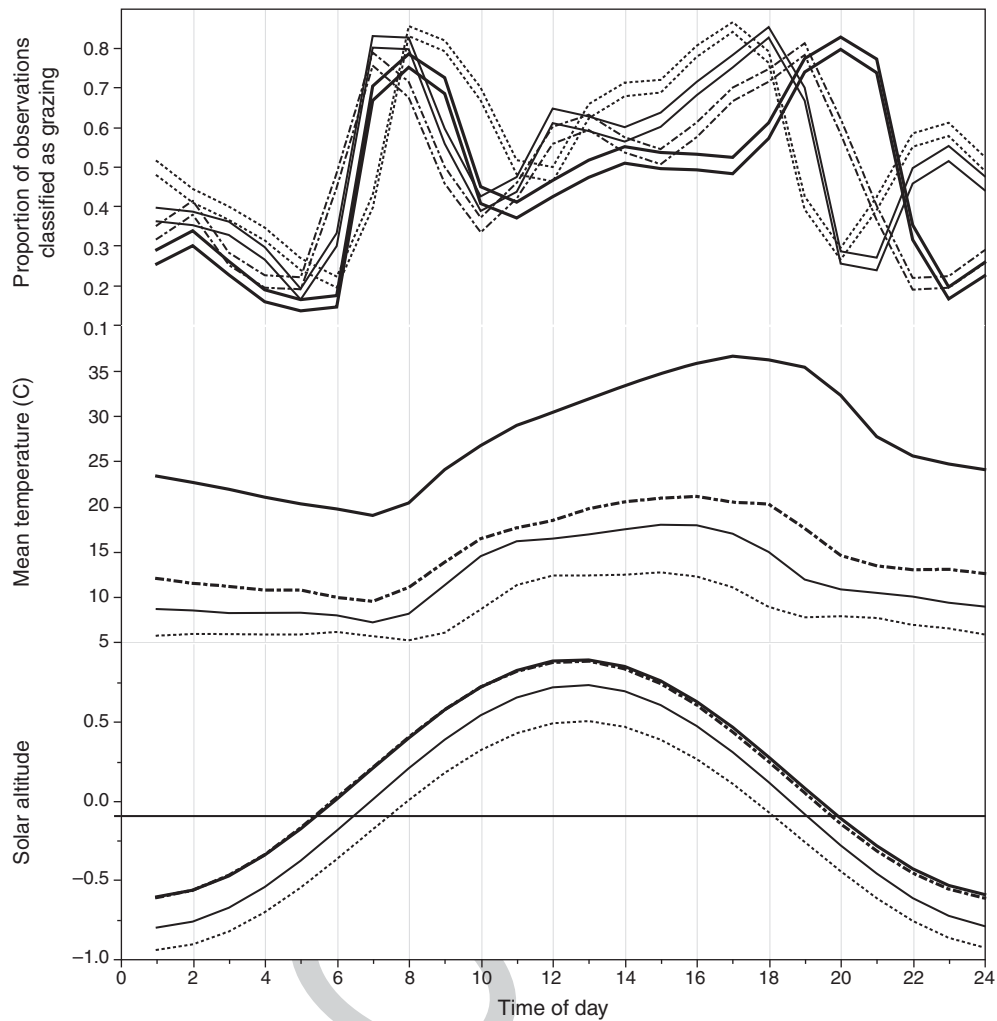


Fig. 4. Timing of grazing in the different seasons in relation to daylength and temperature. Ninety-five per cent confidence intervals for the proportion of activity records classified as 'grazing' during each hour of the day (top). Mean air temperature recorded by GPS collars (middle). Solar altitude (bottom). Horizontal line indicates dawn and dusk. Continuous thick line indicates summer; thick dot-dash line indicates late spring; continuous thin line indicates early spring; dotted line indicates winter.

over which the fractal dimension is constant. We do not use fractal dimension to extrapolate, but just as a quantitative measure of path crookedness that can change with scale. We do not assume that paths have the self-similarity property of fractals, neither are we interested in testing whether paths are fractals. Thus, we believe that Benhamou's (2004) recommendation against the use of fractal dimension is not applicable here. Analysis of fractal dimension is considered a conservative tool for detecting transitions between domains or ranges of scale (Nams 2005).

In a strict sense, the present results and discussion apply only to individual behaviour. Spatial behaviour, in particular the spatio-temporal distribution of grazing of virgin areas and re-grazing, needs to be aggregated over individuals to assess herd behaviour, because social interactions introduce additional mechanisms such as herd cohesiveness (Dumont and Boissy 2000) and individual repellency (Shiyomi and Tsuiki 1999) that most likely generate further spatial

domains of scale at the herd level. Our inability to detect domains of scale beyond ~100 m may be related both to the limited size of the pasture and to the fact that we did not analyse the aggregated spatial distribution of groups of animals.

Domains of spatial scales

One method (Vfpt) detected patches of 6–9 m diameter in the pastures with low canopy cover, and 18–21 m diameter in the pastures with high canopy cover. The V-fractal method defined two distinct domains of scale, 0–50 m with tortuosity ~1.2, and 50–90+ meters, with steeply increasing tortuosity of cow movement paths. According to Sugihara and May (1990), a sudden change in the fractal dimension at a certain spatial scale suggests a change in the way the animal views the landscape, and it indicates that the animal's pattern of movement has been influenced by the landscape. The third method (Cc) identified patches of movement with diameters

5
10
15

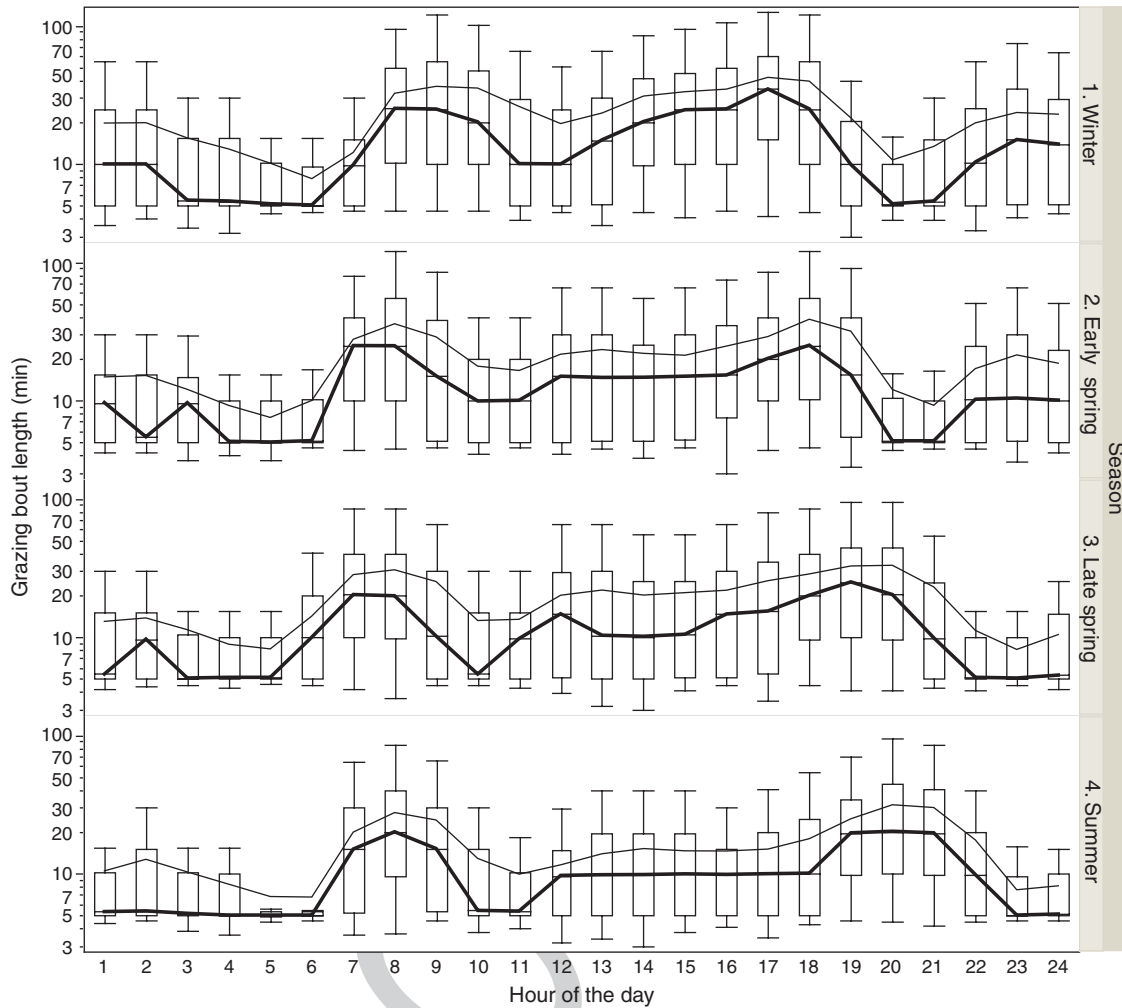


Fig. 5. Effects of time of day and season on grazing bout length. Thick line represents the median of observations pooled over replicate seasons, pastures, individual animals and hour of the day. Thin line is the corresponding mean bout length. Boxes and bars represent the 5, 25, 50, 75 and 95 percentiles. Note that the vertical scale is graphed in log scale.

between 30 and 90 m (average = 52 ± 2.9). These spatial scales loosely match the food-patch and feeding-site scales defined by Bailey *et al.* (1996), who suggested that feeding bouts were associated with small-scale processes related to feeding stations and patches, and larger scales related to feeding sites and camps. As a comparison, the crookedness of cow paths (as quantified by the V-fractal methods) for the domain below 50 m was very similar to the minimum fractal dimension of sheep grazing paths at 5-m scale (Garcia *et al.* 2005), which may be a result of an allometric relationship.

The small patch sizes detected by the Vfpt method might have been related to forage characteristics, but those scales are too close to the resolution of the GPS and should be interpreted with caution. Because cattle can use visual cues to identify desirable forage, they probably do not need to use area-restricted search involving acute and frequent turning angles such as used by bison searching for forage under the snow (Fortin 2003). Most of the movements during long foraging bouts had few and slight turns, which is in agreement with the observations of Garcia *et al.* (2005) for sheep. According to Bell

(1991), animal paths tend to become more tortuous in profitable patches and more linear in unprofitable patches. However, according to Murray (1991), the cost of movement for large animals is high so their movement path is usually linear. Because it incorporates time, the Vfpt method was able to detect small patchiness related to speed of movement in spite of the linearity of paths. Patchiness in forage utilisation is not necessarily revealed by spatial analyses but requires a spatio-temporal approach to the analysis of grazing behaviour.

Temporal scales

We found that the typical daily pattern of grazing bouts for cattle and sheep (Low *et al.* 1981; Gregorini 2012) was with two main bouts and several shorter bouts. Also, as expected, the timing and duration of the bouts changed with forage and temperature conditions over seasons (Fig. 4). Two contrasting temporal patterns of behaviour were identified and attributed to contrasting levels of environmental restrictions.

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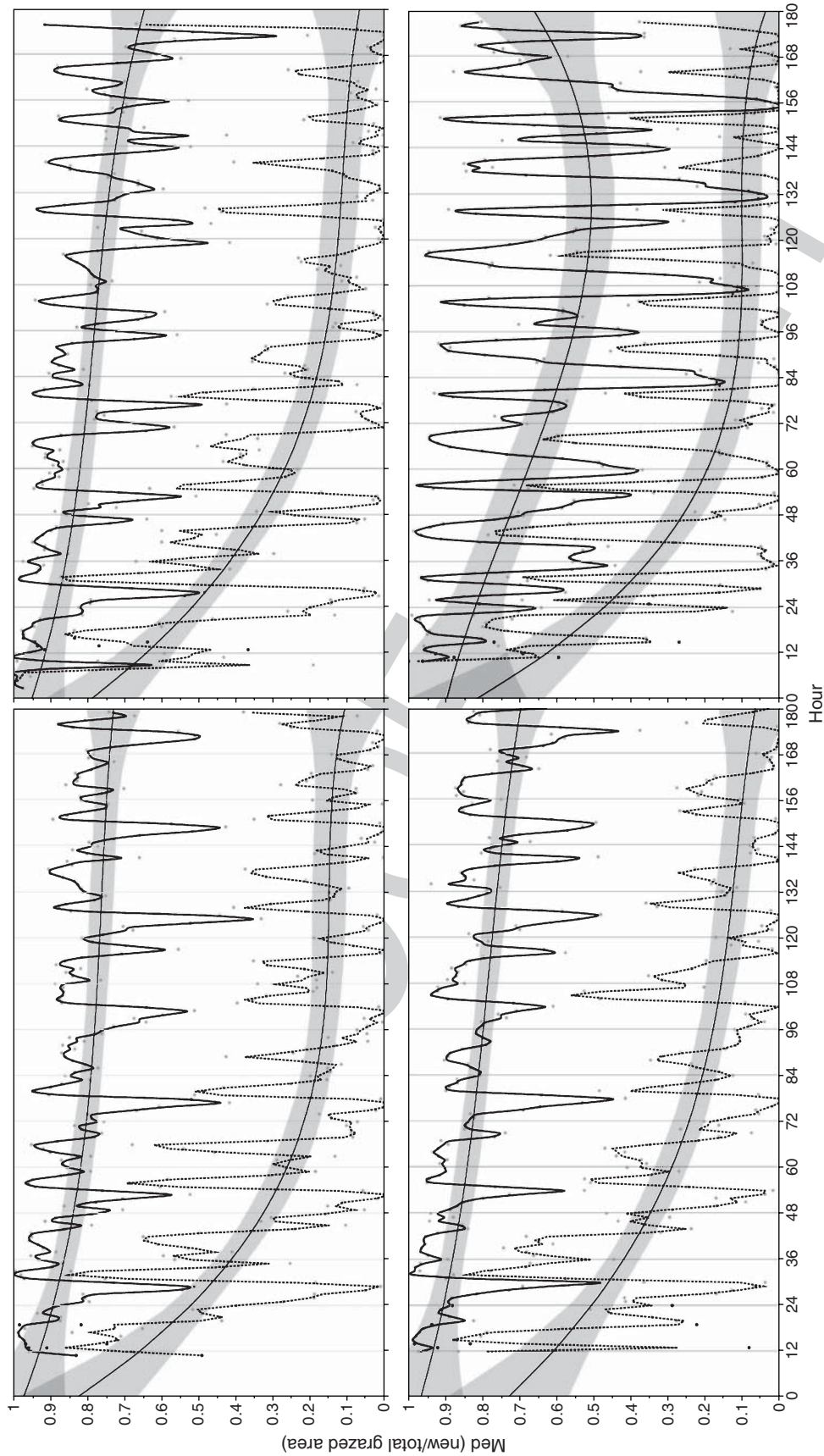


Fig. 6. Ratio of new : total area grazed during each hour (pv) as a function of time in a pasture. Clockwise from the bottom left, figures are for the winter, early spring, late spring and summer. Thick full lines are splines for 2-m-wide paths; thick dotted lines represent 20-m-wide paths. Thin full lines are cubic polynomials, and the shaded areas are 95% confidence intervals. Statistics for these data are presented in Table 2. A pv ratio equal to 0.5 means that half of the additional area grazed had not been grazed by the same animal within the same season.

Table 3. Statistics for curves and models shown in Fig. 6

Scale		Season							
		Winter		Early spring		Late spring		Summer	
		R^2	RMSE	R^2	RMSE	R^2	RMSE	R^2	RMSE
2 m	Spline	0.97	0.021	0.98	0.018	0.96	0.029	0.99	0.028
	Polynomial	0.22	0.117	0.16	0.119	0.23	0.130	0.18	0.240
20 m	Spline	0.98	0.031	0.98	0.028	0.98	0.03	0.99	0.03
	Polynomial	0.44	0.166	0.42	0.169	0.50	0.181	0.36	0.202

Conditions in summer, particularly in the pastures with poor distribution of shade trees, were most stressful. Thus, cattle exhibited shorter grazing bouts and longer separation between the two main meals of the day in summer than in the other seasons. Cattle grazing California annual grasslands in summer are under stress due to both high temperature and low forage quality (George *et al.* 2001). This was particularly severe in pastures Forbes 1 and Forbes 2 where shade availability was restricted to the riparian corridor and very few isolated trees away from the riparian area. Summer conditions were different not only because of temperature and forage, but also because cows were without calves. The total number of animals was smaller, and cows were not restricted by the presence of calves. We believe that the shorter grazing bouts and longer time between main bouts in summer were due to the overriding effects of forage and temperature, because the absence of calves would tend to allow cows to move more freely.

In winter and early spring, forage was of high quality and limited availability, whereas temperatures were mild. This resulted in both the opportunity and the ability for longer grazing bouts. At this stage of growth, the grasses in the California annual grassland have a large proportion of moisture and protein, which results in excessively fast passage rates. Forage bouts are longer and there is a third large forage bout in the night, presumably motivated by the emptying of the rumen and the mild temperature. Longer bouts and limited forage availability give the animals the need and opportunity to graze areas previously ungrazed, providing evidence of the interaction between temporal and spatial processes in meal patterns.

Interaction between spatial scale of grazing and temporal scale of meals

Daily grazing pattern was consistent with two driving factors, namely, forage characteristics and temperature. High midday and afternoon temperatures in summer limited grazing between the two main bouts, with the evening bout taking place later than in the other seasons. We surmise that the late grazing bout combined with the high abundance (Fig. 1) and low quality of dry forage pre-empted any more grazing during the night. While the same effects of forage availability were present in late spring (flowering forage stage, about peak standing crop) as in summer, much lower midday temperatures and better forage quality motivated more grazing between 1000 hours and 1800 hours than in summer. Patterns of grazing during winter and early spring did not seem to be limited by temperatures lower than necessary for thermal comfort (George *et al.* 2007), but the main morning bout was later and the main evening bout was earlier than in

other seasons. The significant peak of grazing present between 2200 hours and 2300 hours in both winter and early spring can be attributed to the very high forage quality and limited availability, as indicated above.

Spatial distribution of grazing and resting, and temporal distribution of meals were inextricably linked. Daily pattern of high temperatures imposed immediate restrictions on meal start and end. Potential low-temperature restrictions on meal initiation at night were overridden when animals became very hungry, which was a state predictable on the basis of forage availability and quality, and timing and duration of previous meals. Restrictions on meal end interacted with spatial distribution of thermal protection represented by tree canopy cover. The interaction between spatial and temporal patterns seemed to differ from the traditional conceptual model in which grazing has a hierarchical organisation of spatio-temporal levels. The pattern observed included a network of resting sites that were selected 'haphazardly', depending on where animals were when conditions pressed for the main meals to end. Between main meals, temporally variable, short grazing bouts were taken within the neighbourhood of the resting site, ending at the original resting site.

We discovered highly structured spatio-temporal patterns of grazing and re-grazing of pasture areas that differed among seasons but not among pastures (Fig. 6). Such patterns were a result of the interaction among spatial arrangement of potential resting (shade) sites, forage characteristics and temperature. Cows exhibited marked grazing bouts, the timing of which depended on the season. In seasons when temperatures were not extreme, cows grazed starting from nightly resting sites. During the morning, they first grazed away from the initial grazing site and then either continued to an alternate site or returned to the original one. Between late morning and afternoon, animals tended to take irregular and short 'round trip' grazing bouts around the resting site. In summer, temperatures during the day were extremely high and forced cows to graze mostly in short round trip about set resting sites. This pattern resulted in a much lower proportion of the pasture being grazed at all during summer than during the other seasons (Table 2). The importance of tree canopy cover was also shown by the fact that pastures with more cover exhibited significantly greater proportions of their areas grazed.

Practical application of spatio-temporal patterns

The study of livestock movement as an ecological process has assumed a conceptual model in which use of space takes a hierarchical structure with nested 'scales' or 'domains' of scale. For example, Senft *et al.* (1987) defined a series of levels of plant-animal interactions to organise observations. Bailey *et al.* (1996) and Bailey and Provenza (2008) extended this paradigm and discussed mechanisms that generate the structure of foraging scales as well as management opportunities to modify the patterns naturally exhibited by livestock. Certainly, knowledge and understanding of spatio-temporal patterns of grazing are helpful, at the very least because they offer a conceptual framework on which to base general management approaches. Such a framework is also

useful to communicate some essential characteristics of the grazing process to students and practitioners.

The differences in spatio-temporal patterns of 'virgin-grazing' and 'repeat-grazing' among seasons was unexpected and novel. We surmise that the frequency of defoliation, a widely accepted determinant of effects of grazing (Vallentine 1990), is directly related to the frequency with which animals revisit the same areas during grazing. Cows exhibited a circadian pattern, grazing new areas in the main morning-grazing bout, with moderate re-grazing during the intermittent grazing bouts of midday except in summer, when the midday bouts exhibited large proportion of areas re-grazed. These patterns were a consequence of the geometry of mostly linear grazing movements to and from resting sites. During the main grazing bouts, movements were long round trips or one-way trips from one to another resting area, whereas during shorter bouts, movements were mainly short round trips, most likely motivated by herd cohesion, combined with a degree of asynchrony in the motivation to eat of different individuals. On average, for winter, early spring and late spring, percentage of re-grazing increased ~4.8% per day of grazing in the same pasture (Fig. 6, 2-m scale), whereas in summer, the increase was 6.7% per day. With a simple model, these percentages could be used to make detailed predictions of timing and frequency of defoliation and repeat defoliation of plants, and thus, they could constitute a quantitative basis for models and decisions about spatio-temporal distribution of grazing as controlled by fencing or herding. For example, a grazing method could be based on moving animals to a new pasture when the average probability of re-grazing reaches a threshold value.

The second interesting finding is related to the effect of scale on the proportion of 'virgin' grazing. The difference in p_v between 2- and 20-m scales stabilises after ~3 days (72 h). This means that it took animals about 3 days to establish the 'large-scale' feeding alleys, and after that they mostly grazed within 20 m of those alleys. It may be that for the specific type of topography and pastures studied, 3 days was a salient temporal scale beyond which animals grazed within 20 m of areas visited in the previous 3 days. The magnitude of the temporal scale might be a characteristic of the combination of landscape characteristics and pasture size. The relationship between landscape characteristics and the time it takes animals to start re-grazing areas deserves further research because it could reveal a temporal scale to move animals from one to another pasture to avoid excessively frequent defoliation and resource degradation.

A third practical result is the importance of shade in determining spatial patterns of grazing in summer. Distance to shade has been recognised as a factor determining grazing distribution (Bailey and Provenza 2008). Animals in heat stress seek shade, and the intensity of shade-seeking behaviour is more pronounced in *Bos taurus* than *Bos indicus* breeds (Bennett *et al.* 1985). Provision of shade allows animals to better regulate their body temperature and may increase productivity (Kendall *et al.* 2006) while promoting more even utilisation of forage resources. On the basis of the finding that temporal and spatial distribution of meals are highly integrated, a good choice of distance between shade structures or trees

would be commensurate with the straight-line distance typically travelled during one of the main grazing bouts.

Fourth, our work demonstrated novel methods to analyse spatio-temporal grazing behaviour. It is necessary to use multiple methods to reveal patchiness of grazing because animals can exhibit grazing patches that are detectable only by changes in speed of movement while grazing.

Conclusions

Several salient spatial and temporal scales were detected in the grazing behaviour of cattle. Detected scales were generally consistent with domains of scale present in the current paradigm, but they seem to be flexible and to vary widely with environmental conditions. Differences in temporal meal patterns over seasons were associated with coherent differences in spatial behaviour, suggesting that animals simultaneously adjust both in concert. This opens the possibility of affecting the temporal schedule of meals by establishing a designed spatial pattern of sites that offer thermal cover or other attractants. The quantification of spatio-temporal behaviour provided information on proportion of area regrazed, which can be used to design grazing methods and to decide when to move animals to new pastures.

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