Japanese Society of Grassland Science ISSN1744-6961

ORIGINAL ARTICLE

Effect of herbage mass on the selection and use by cattle of fine-scale locations in a progressively grazed tropical grass pasture

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Keywords
Feeding location; herbage availability; herbage quality; large herbivore; spatial heterogeneity.

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Received: 18 March 2007;
accepted: 19 June 2007

doi: 10.1111/j.1744-697X.2007.00097.x

Abstract

This study quantified herbage mass and feeding behavior by animals at a fine spatial scale, in a 1.1-ha bahiagrass (*Paspalum notatum* Flügge) pasture progressively (4 or 5 days) grazed by a herd of 32–33 beef cows and 8–13 calves in three seasons (spring, summer and autumn). Herbage mass was nondestructively estimated every day, using an electronic capacitance probe, at 91 fixed locations (50 cm × 50 cm; approximating a feeding station scale) along a permanent line transect. At the same time, selection and use of the individual locations by cows were measured every day, in terms of the number of visits, number of bites and residence time. Vegetation of the pasture created a trade-off between availability (herbage mass) and quality (nitrogen concentration, dry matter digestibility) in summer and autumn but not in spring. There were always considerable location-to-location variations in the feeding behavior of animals; that is, some locations were not visited and bitten at all or were visited infrequently (once or twice daily) and grazed only for a short time (<10 s daily) receiving relatively few bites (<10 bites daily), whereas some locations were frequently visited (5–10 times daily) and utilized for a long period (>30 s daily) receiving many bites (>30 bites daily). Although regression analysis showed a tendency for animals to select and use locations with higher herbage mass in spring and those with lower or intermediate herbage mass in autumn as a result of the seasonally different availability–quality relationships, neither herbage mass nor herbage quality was an absolute factor determining the choice and use of locations by animals. The results show that the choice and use of fine-scale locations by animals foraging in actual grasslands are not fully explained by major forage factors such as mass, nitrogen and digestibility.

Introduction

The grazing process by large herbivores can be seen as a series of selections and uses of feeding locations in a hierarchical framework of multiple spatiotemporal scales (Senft *et al.* 1987; Bailey *et al.* 1996). During a day, animals choose feeding sites where they forage during individual feeding bouts. Within a feeding site, they select patches (an area of herbage differing from its surrounding with respect to the nature and appearance, e.g. quantity, quality, botanical composition) where they choose feeding stations (an area of herbage accessible to an animal without moving its forefeet). Finally, they select bites (prehension and severance of herbage) within a feeding station to harvest and ingest food. A better knowledge and understanding of factors determining the choice and use of feeding locations at various spatiotemporal scales are of primary importance in better management of grazing systems aiming at conservation of natural resources (e.g. water, soil, vegetation, wildlife) and/or sustainable agricultural production.

A number of studies have been conducted to identify the criteria for feeding location choice by herbivores (Bailey *et al.*

1996; Laca and Demment 1996; Roguet *et al.* 1998a). However, relatively little information is available on the selection and use of fine-scale locations (e.g. feeding station, bite) by animals foraging in actual grasslands (i.e. under natural grazing conditions) (Roguet *et al.* 1998b; Hirata *et al.* 2002; Ogura *et al.* 2002), because most studies have focused on a coarser spatial scale such as feeding site or patch (Langvatn and Hanley 1993; Dumont *et al.* 1995; Wilmshurst *et al.* 1995; Ganskopp and Bohnert 2006) or investigated choice of fine-scale locations in well-controlled experimental environments (i.e. simplified reality) where animals were offered an artificially created vegetation mosaic with a high degree of contrast (e.g. tall versus short) (Laca *et al.* 1993; Distel *et al.* 1995). Although food quantity and quality are likely to affect selection and use of feeding locations at every level from feeding site to bite under either artificial or natural vegetation conditions (Bailey *et al.* 1996), their effect seems to be less clear at finer spatial scales (Roguet *et al.* 1998a; WallisDeVries *et al.* 1999) and in actual grasslands, because of the increased involvement of nonforage factors such as abiotic environment (topography, distance to water, microclimate, predator risks) and animal characteristics (cognitive abilities and social organization) (Bailey *et al.* 1996; Roguet *et al.* 1998a).

In the present study, we examined the effect of herbage mass on the selection (number of visits) and use (number of bites and residence time) by cattle of fine-scale locations (50 cm × 50 cm; approximating a feeding station scale) in a tropical grass pasture progressively (4 or 5 days) grazed in three seasons (spring, summer and autumn). The results were interpreted taking account of the quality–quantity relationships of herbage in the pasture (Ogura *et al.* 2002) and the nonforage factors involved in the grassland system, in an effort to evaluate the extent to which the choice and use of fine-scale locations by animals grazing an actual grassland can be explained by herbage mass and herbage quality. Although a part of the results from this experiment was already reported as the effects of herbage mass and quality on daily rate of defoliation (Ogura *et al.* 2002), the current study aimed to focus on animals' decisions to graze locations (visit, bite and reside in locations).

Materials and methods

Study site and grazing and pasture management

The study was conducted in a 1.1-ha paddock of a bahiagrass (*Paspalum notatum* Flügge cv. Pensacola) pasture at the Sumiyoshi Livestock Farm (31°59′N, 131°28′E), Faculty of Agriculture, Miyazaki University, southern Kyushu, Japan. This paddock was one of five paddocks rotationally grazed by Japanese Black cows and calves. The vegetation was highly dominated by bahiagrass and virtually monospecific during the measurements. The paddock was adjoined with a resting area (0.4 ha) with water and shade trees to which animals were able to access freely during grazing.

The climate of the study site is warm temperate (close to subtropical) with warm, humid summers and cool, dry winters. The long-term averages (1961–1990) for mean monthly air temperature and monthly rainfall are, respectively, 22.8–27.2°C and 288–377 mm for the summer months (June–August) and 6.8–8.7°C and 50–83 mm for the winter months (December–February). The mean annual air temperature and annual rainfall are 17.0°C and 2435 mm, respectively. Bahiagrass is utilized from May (late spring) to October–November (autumn) because the grass is dormant for the rest of the year. Pastures are rarely irrigated.

During the grazing season (May–November) of 1999, the paddock was grazed by a herd of 30–33 cows (mean liveweight, 457 kg) and 8–13 calves (mean liveweight, 79 kg) for six 4–6-day periods at intervals of 11–38 days; that is, 22–25 May, 21–25 June, 3–7 August, 13–18 September, 22–25 October and 6–11 November (0900–1600 hours each day). The total duration of grazing periods was 30 days. Calves consumed a negligible amount of herbage in the pasture, because they were at a preweaning stage (<4 months old) and separately fed with concentrate and roughage (ryegrass hay or corn silage). The annual fertilization rates in the paddock were 70 kg N (split applications in April and August), 17 kg P (April) and 20 kg K (April) ha^{-1}. The paddock was mowed to a height of 9 cm above ground level on 20 April to remove spring weeds.

Relationships between herbage quality and availability in the pasture

Vegetation of the paddock showed seasonally different relationships between herbage quality and availability (Ogura *et al.* 2002). In mid-May (spring), both N concentration and dry matter digestibility (DMD) of herbage were high (24–26 and 543–605 g $[kg\ DM]^{-1}$, respectively) irrespective of herbage mass, except for one location with the lowest herbage mass (Figure 1). In late July (summer) and mid-October (autumn), N concentration and DMD showed lower values (12–21 and 442–545 g $[kg\ DM]^{-1}$, respectively) than in spring (excluding the location with the lowest herbage mass). In these seasons, locations with higher herbage mass showed lower quality, except that N concentration in summer showed an almost constant tendency across herbage mass. The degree of decrease in herbage quality with increasing herbage mass was larger in autumn than in summer.

Quantifying herbage availability and utilization at fine-scale locations in the pasture

Three grazing periods (i.e. 22–25 May, 3–7 August and 22–25 October) were selected as measurement periods. These

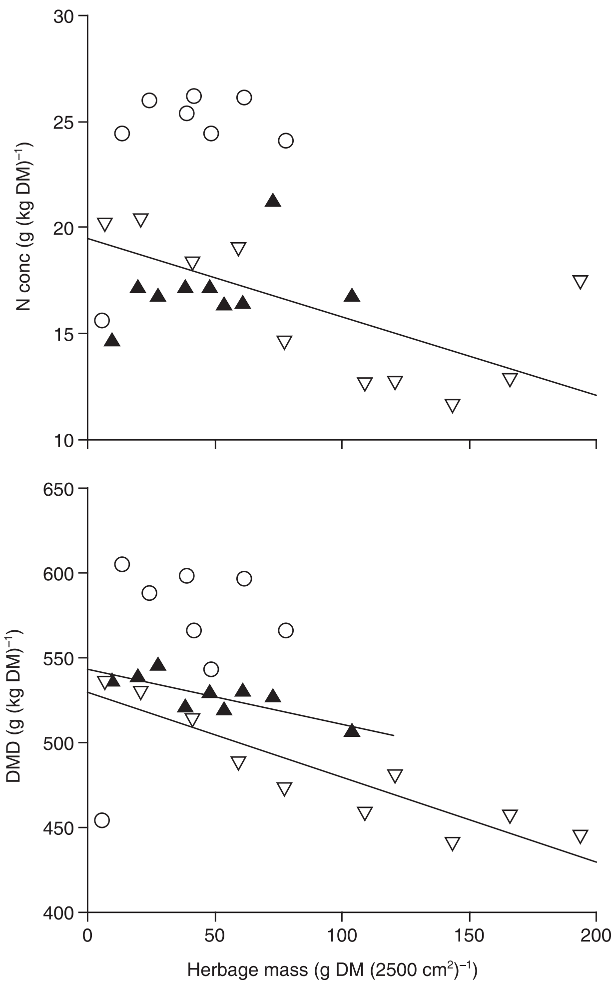

Figure 1 Relationships of nitrogen (N) concentration and dry matter digestibility (DMD) to herbage mass in spring (○), summer (▲) and autumn (▽). Regression equations are: $y = 19.5 - 0.037x$ ($r = -0.682$, $P < 0.05$) for N concentration in autumn; $y = 543 - 0.324x$ ($r = -0.797$, $P < 0.05$) for DMD in summer; $y = 530 - 0.498x$ ($r = -0.920$, $P < 0.001$) for DMD in autumn. Selected data from Ogura *et al*. (2002), with digestibility as predicted *in vivo* DMD.

dates are, respectively, referred to as days 1–4 in spring, days 1–5 in summer and days 1–4 in autumn hereafter. The herd consisted of 33 cows and eight calves in spring, 32 cows and 13 calves in summer, and 32 cows and 10 calves in autumn. Herbage availability and utilization were quantified every day during each measurement period, at 91 fixed locations (50 × 50 cm each) spaced at 1-m intervals along a 90-m permanent line transect crossing the paddock.

Pregrazing herbage mass (>3 cm height) at the individual locations was nondestructively estimated using an electronic capacitance probe (PastureProbe, Mosaic Systems, Palmerston North, New Zealand) (Hirata 2000). For day 1, measurements were conducted immediately before the commencement of grazing (i.e. before 0900 hours). For days 2–4 (spring and autumn) or 2–5 (summer), measurements were conducted immediately after grazing on the previous day (i.e. after 1600 hours on days 1–3 or 1–4) except some overnight postponements (see Results), assuming no detectable changes in herbage mass until the next morning. The ability of a capacitance probe to estimate herbage mass of bahiagrass in this study site is higher than that reported for many grasses in other sites (mainly seasonally dry tropics and subtropics), presumably because of a higher proportion of green material resulting from higher rainfall (Hirata 2000; Ogura *et al.* 2005).

Choice and use of the locations by cows were quantified throughout the daily grazing period (0900–1600 hours) by seven to nine observers equipped with a stopwatch (chronograph). Whenever any of the 91 locations along the transect was visited and grazed (at least one bite) by a cow, the position of the location, the number of bites the cow took from the location, and the time the cow spent feeding at the location were recorded. From these records, the number of visits, number of bites and residence time at each of the 91 locations were obtained as daily values. For measuring the residence time by a cow in a location, the stopwatch was started when the head of the cow entered the location close to the sward surface and was stopped when the head departed the location. Time spent only for grazing (e.g. searching for bite locations, biting, chewing, swallowing) was considered, with time for nongrazing activities (e.g. resting, social interactions; only infrequent) being excluded by suspending the stopwatch. The stopwatch record was discarded when the cow departed the location without a bite. Residence time data with one or two bites was corrected by average time per bite obtained by pooling daily data, to avoid likely errors due to short measurement periods.

A small plastic tag (2 cm × 4 cm) showing a location number (0–90) was fixed on the ground at a 1-m distance from each location, and all observers were trained every day before grazing so that they were able to identify the 50 cm × 50 cm area of each location accurately from the position of the tag. Thus, a minimal distance of 1 m was secured between a cow and an observer during the measurements; and because all cows were tame and accustomed to the presence of observers, this distance was enough for measuring the ingestive behavior variables without disturbing the cows.

Data analysis

Characteristics of pregrazing herbage mass across the locations were evaluated by frequency distributions and some fundamental statistics (minimum, maximum, mean, standard deviation [SD] and coefficient of variation [CV, proportion]). Relationship of the choice (number of visits) and use (number of bites and residence time) of locations by animals to herbage mass was evaluated by fitting a linear ($y = a + bx$) and a quadratic ($y = a + bx + cx^2$) equation to data. A regression equation was considered to be significant when both regression coefficient(s) (b, or b and c) and correlation coefficient (r) were significant at $P < 0.05$. There was no case where both linear and quadratic equations were significant at the same time. Association of behavior on one day with that on the preceding day(s) within each progressive grazing period was evaluated by Spearman's rank correlation coefficient (r_S).

Results

Weather conditions and grazing activity by animals

The weather during the measurement periods was fine (3 days), cloudy (8 days including 4 days with light, occasional rainfall) or rainy (2 days), with a mean daily air temperature of 17.9–22.3°C, 25.7–27.3°C and 16.7–19.0°C in spring, summer and autumn, respectively. Cows always grazed the paddock actively during the grazing period (0900–1600 hours) even on warm and/or rainy days, except for occasional rest, drinking, rumination and nursing (only cows with their calves). Calves did not visit and graze any of the 91 locations along the transect, and therefore did not affect herbage mass and utilization at the locations.

Performance of the electronic capacitance probe

On some occasions, herbage mass was not estimated immediately after grazing (i.e. shortly after 1600 hours), because wet herbage surface due to rainfall disabled the use of an electronic capacitance probe which is sensitive to moisture; however, herbage mass was estimated early the next morning when surface water had disappeared. Coefficient of determination (R^2) and SE of estimation of the calibration equations for estimating herbage mass were, respectively, 0.912–0.977 and 1.4–5.7 g DM (2500 cm^2)$^{-1}$ in spring, 0.938–0.994 and 4.1–10.0 g DM (2500 cm^2)$^{-1}$ in summer, and 0.830–0.943 and 19.8–24.8 g DM (2500 cm^2)$^{-1}$ in autumn.

Herbage availability

In spring, pregrazing herbage mass at the commencement of the progressive grazing period (day 1) was in a relatively low and narrow range between 16.1 and 62.0 g DM (2500 cm^2)$^{-1}$ with a mean of 31.3 g DM (2500 cm^2)$^{-1}$ (Figure 2). As grazing progressed, herbage mass was distributed in lower and narrower ranges, with decreasing minimum, maximum, mean and SD values. The range of pregrazing herbage mass on day 4 was as narrow as 2.1–24.8 g DM (2500 cm^2)$^{-1}$, with a mean of 10.8 g DM (2500 cm^2)$^{-1}$. In summer, pregrazing herbage mass on day 1 was distributed in a higher and wider range (25.3–121.0 g DM [2500 cm^2]$^{-1}$) than in spring, with a higher mean value (69.3 g DM [2500 cm^2]$^{-1}$). With the progress of grazing, herbage mass shifted in lower and narrower ranges, to reach the final range and mean of 12.2–89.2 g DM (2500 cm^2)$^{-1}$ and 38.6 g DM (2500 cm^2)$^{-1}$, respectively, on day 5. In autumn, pregrazing herbage mass on day 1 was in a further higher and wider range (34.6–167.3 g DM [2500 cm^2]$^{-1}$), with a further higher mean (101.6 g DM [2500 cm^2]$^{-1}$). Like spring and summer, minimum and mean herbage mass decreased as grazing progressed. However, contrarily to the preceding two seasons, the range of herbage mass broadened with the progress of grazing, showing constant maximum and increased SD values. On days 3 and 4, pregrazing herbage mass was distributed as widely as 0–161.8 and 0–172.1 g DM (2500 cm^2)$^{-1}$, respectively. Unlike spring and summer, the frequency distribution patterns in autumn always showed no distinct peaks in herbage mass, indicating a tendency toward a random distribution.

Number of visits

The number of visits that individual locations received from animals each day varied considerably across the locations (Figure 3). During grazing, some locations were not selected at all or were visited infrequently (once or twice daily), whereas some locations were frequently visited (5–10 times daily). The daily number of visits was significantly related to pregrazing herbage mass on eight occasions, showing relatively low r-values of 0.219–0.621 (absolute values). In spring, locations with higher pregrazing herbage mass were more frequently visited on days 1–3. In summer, a similar phenomenon occurred on day 2, but locations with intermediate herbage mass (50 or 60 g DM [2500 cm^2]$^{-1}$) were most frequently visited on days 3 and 5. In autumn, locations with lower pregrazing herbage mass were more frequently visited on day 1, and locations with intermediate herbage mass (~90 g DM [2500 cm^2]$^{-1}$) were most frequently visited on day 3.

The total number of visits that individual locations received from animals during the progressive grazing period (cumulated from day 1 to day 4 [spring and autumn] or 5 [summer]) was still uneven across the locations, though the variability became smaller than on a daily basis (Figure 4). Some locations received less than eight visits during the 4 or 5-day grazing period, whereas some locations were visited more than 17 times. The total number of visits was significantly related to initial herbage mass (pregrazing herbage mass on day 1) in spring and autumn with relatively low r-values of 0.558 and 0.363, respectively. Locations with higher initial herbage mass were more frequently visited in spring, and locations with intermediate herbage mass (~90 g DM [2500 cm^2]$^{-1}$) were most frequently visited in autumn.

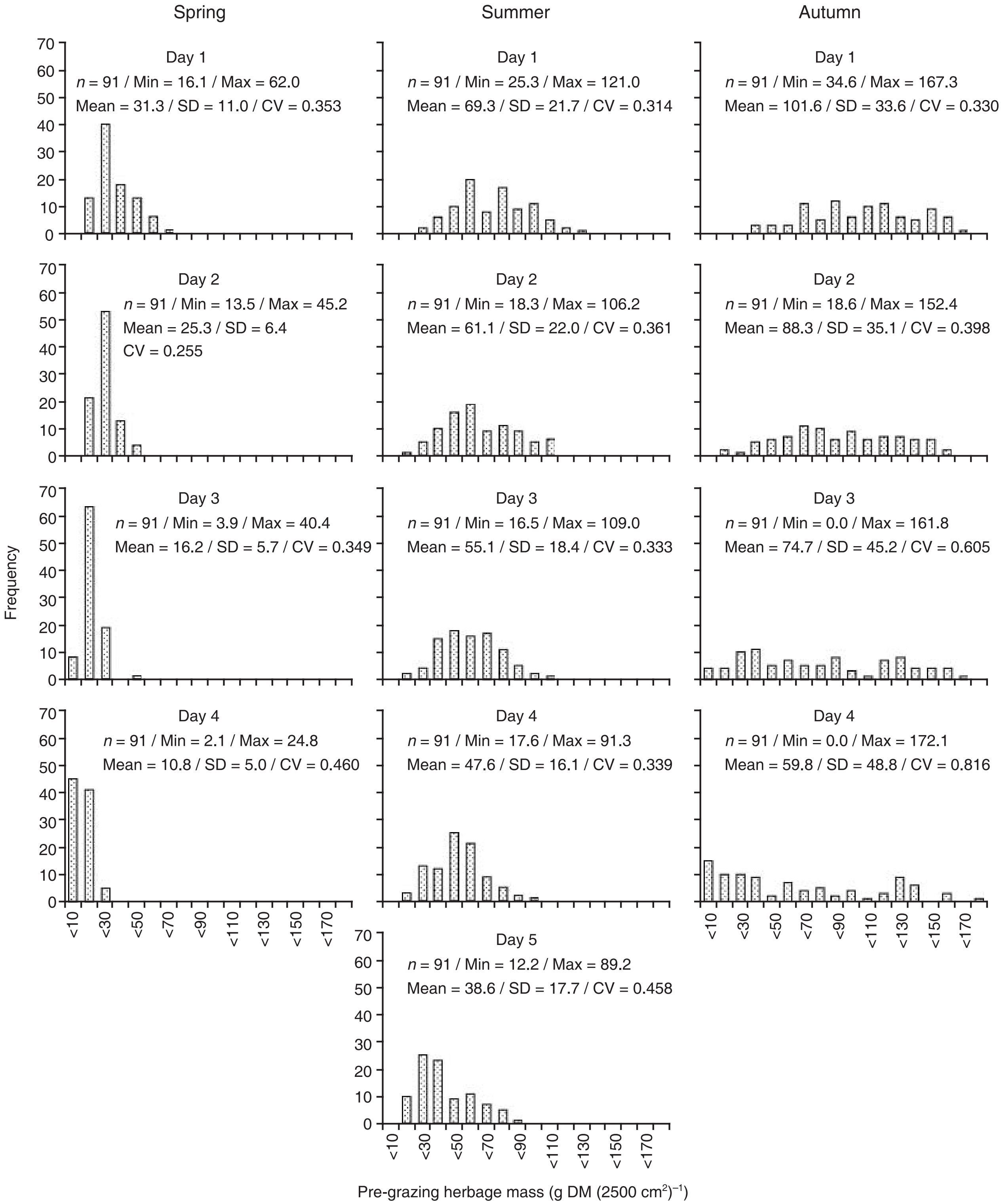

Figure 2 Frequency distributions of pregrazing herbage mass during progressive grazing periods (days 1–4 or 5) in spring, summer and autumn. The statistical parameters are data number (*n*), minimum, maximum, mean, standard deviation (SD) and coefficient of variation (CV, proportion).

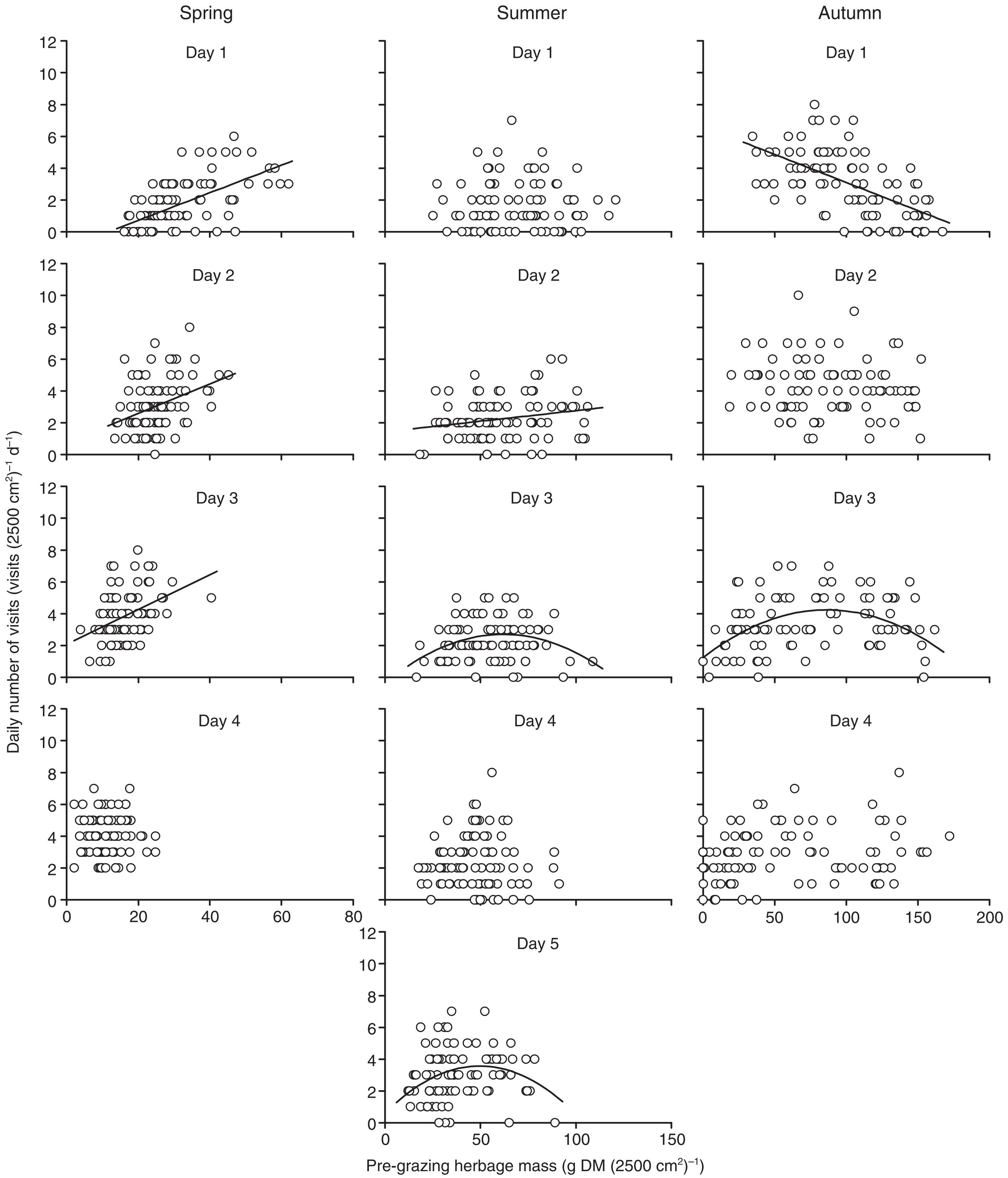

Figure 3 Relationships between daily number of visits and pregrazing herbage mass during progressive grazing periods (days 1–4 or 5) in spring, summer and autumn. Regression equations are: $y = -1.01 + 0.087x$ ($r = 0.621$, $P < 0.001$), $y = 0.73 + 0.093x$ ($r = 0.375$, $P < 0.001$) and $y = 2.08 + 0.11x$ ($r = 0.392$, $P < 0.001$) for days 1–3 in spring, respectively; $y = 1.43 + 0.013x$ ($r = 0.219$, $P < 0.05$), $y = -0.36 + 0.099x - 0.00083x^2$ ($r = 0.294$, $P < 0.01$) and $y = 0.61 + 0.12x - 0.0012x^2$ ($r = 0.291$, $P < 0.01$) for days 2, 3 and 5 in summer, respectively; $y = 6.63 - 0.035x$ ($r = -0.587$, $P < 0.001$) and $y = 1.25 + 0.069x - 0.00039x^2$ ($r = 0.420$, $P < 0.001$) for days 1 and 3 in autumn, respectively.

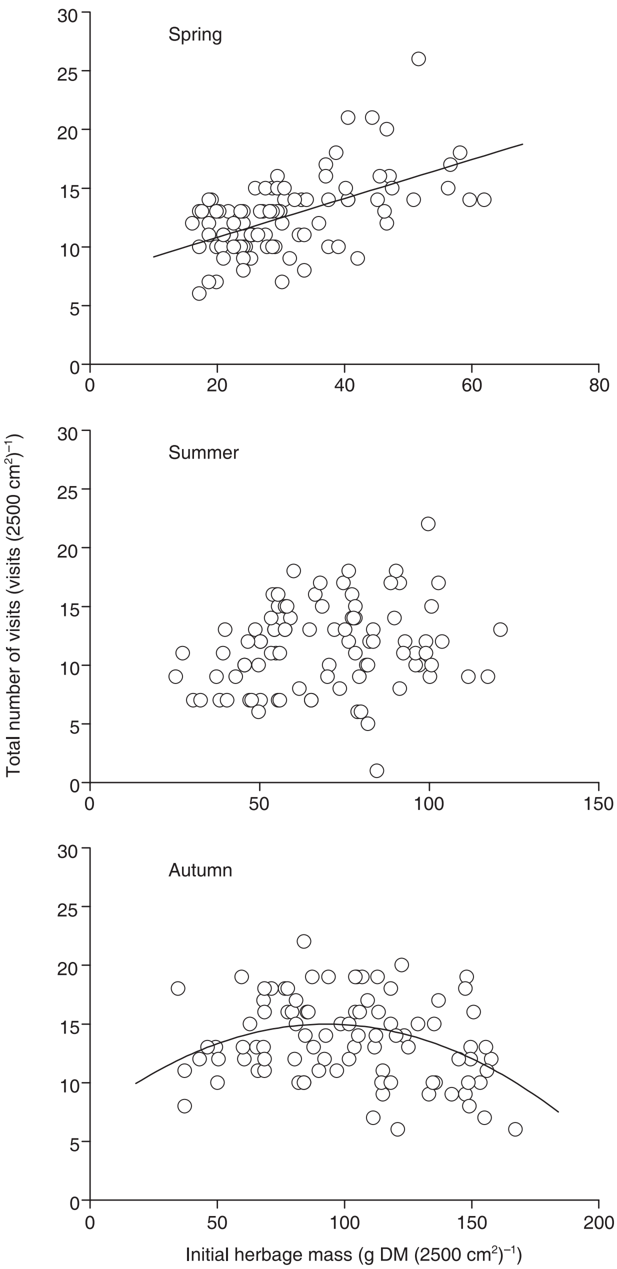

Figure 4 Relationships between total number of visits during progressive grazing period (cumulated from days 1–4 or 5) and initial herbage mass (pregrazing herbage mass on day 1) in spring, summer and autumn. Regression equations are: $y = 7.50 + 0.17x$ ($r = 0.558$, $P < 0.001$) and $y = 7.21 + 0.17x - 0.00093x^2$ ($r = 0.363$, $P < 0.01$) for spring and autumn, respectively.

The daily number of visits on days 2–4 or 5 showed no association or only loose association (two significant cases) with the number of visits on the preceding day(s), as shown by the low r_S values of 0.001–0.253 (absolute values); that is, locations frequently visited during the preceding grazing(s) were visited neither frequently nor infrequently thereafter (Table 1).

Table 1 Association of the number of visits on one day (days 2, 3, 4 or 5) with that on the preceding day(s) (days 1, 1–2, 1–3 or 1–4)† in spring, summer and autumn

Combination of days	Spring	Summer	Autumn
Day 2 versus day 1	0.253*‡	−0.210*	−0.001
Day 3 versus days 1–2	0.041	0.205	−0.031
Day 4 versus days 1–3	−0.123	0.018	0.069
Day 5 versus days 1–4	–	0.203	–

*Denotes significance at $P < 0.05$. †Cumulative numbers for days 1–2, 1–3 and 1–4. ‡Spearman's rank correlation coefficient.

Number of bites

The number of bites that individual locations received from animals each day was highly uneven across the locations (Figure 5). During grazing, some locations were not bitten at all or received relatively few bites (<10 bites daily) whereas some locations received many bites (>30 bites daily). The daily number of bites was significantly related to pregrazing herbage mass on seven occasions, with relatively low *r*-values of 0.228–0.534 (absolute values). In spring, locations with higher pregrazing herbage mass received more bites on days 1–3. In summer, locations with intermediate herbage mass (55 g DM $[2500\ cm^2]^{-1}$) received most bites on day 3. In autumn, locations with lower pregrazing herbage mass received more bites on days 1 and 2, and locations with intermediate herbage mass (~85 g DM $[2500\ cm^2]^{-1}$) received most bites on day 3.

The total number of bites that individual locations received from animals during the progressive grazing period still varied across the locations, though the variability became smaller than on a daily basis (Figure 6). Some locations received less than 55 bites during the 4 or 5 days, whereas some locations received more than 110 bites. The total number of bites was significantly related to initial herbage mass in spring and autumn with relatively low *r*-values of 0.434 and 0.383, respectively. Locations with higher initial herbage mass received more bites in spring, and locations with intermediate herbage mass (~90 g DM $[2500\ cm^2]^{-1}$) received most bites in autumn.

The daily number of bites on days 2–4 or 5 showed no association or only loose association (one significant case) with the number of bites on the preceding day(s), as shown by the low r_S values of 0.015–0.231 (absolute values); that is, locations frequently bitten during the preceding grazing(s) were bitten neither frequently nor infrequently thereafter (Table 2).

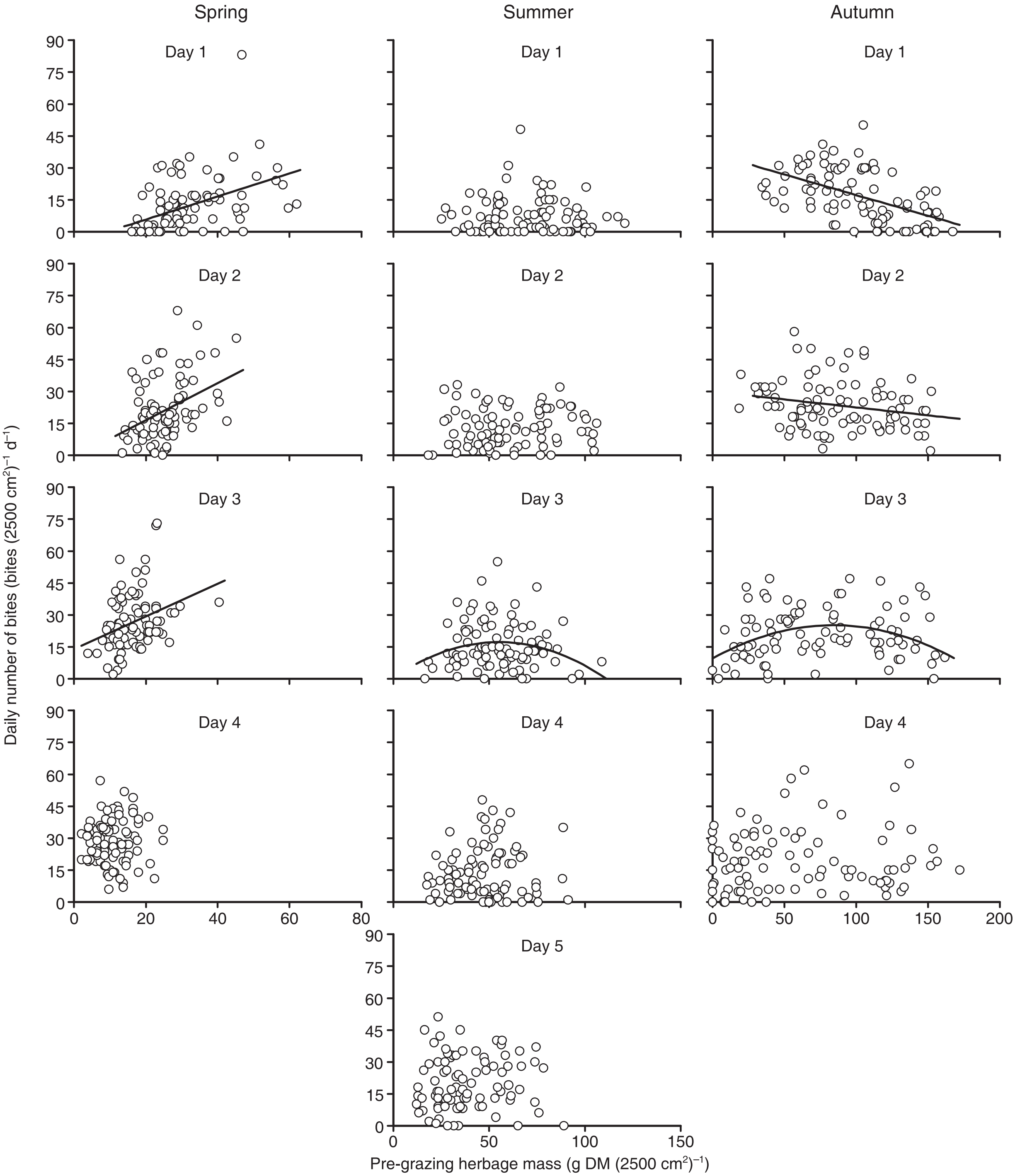

Figure 5 Relationships between daily number of bites and pregrazing herbage mass during progressive grazing periods (days 1–4 or 5) in spring, summer and autumn. Regression equations are: $y = -5.04 + 0.54x$ ($r = 0.459$, $P < 0.001$), $y = -1.03 + 0.88x$ ($r = 0.401$, $P < 0.001$) and $y = 14.0 + 0.77x$ ($r = 0.333$, $P < 0.01$) for days 1–3 in spring, respectively; $y = 0.54 + 0.61x - 0.0055x^2$ ($r = 0.228$, $P < 0.05$) for day 3 in summer; $y = 36.6 - 0.19x$ ($r = -0.534$, $P < 0.001$), $y = 30.0 - 0.075x$ ($r = -0.228$, $P < 0.05$) and $y = 9.64 + 0.37x - 0.0022x^2$ ($r = 0.323$, $P < 0.01$) for days 1–3 in autumn, respectively.

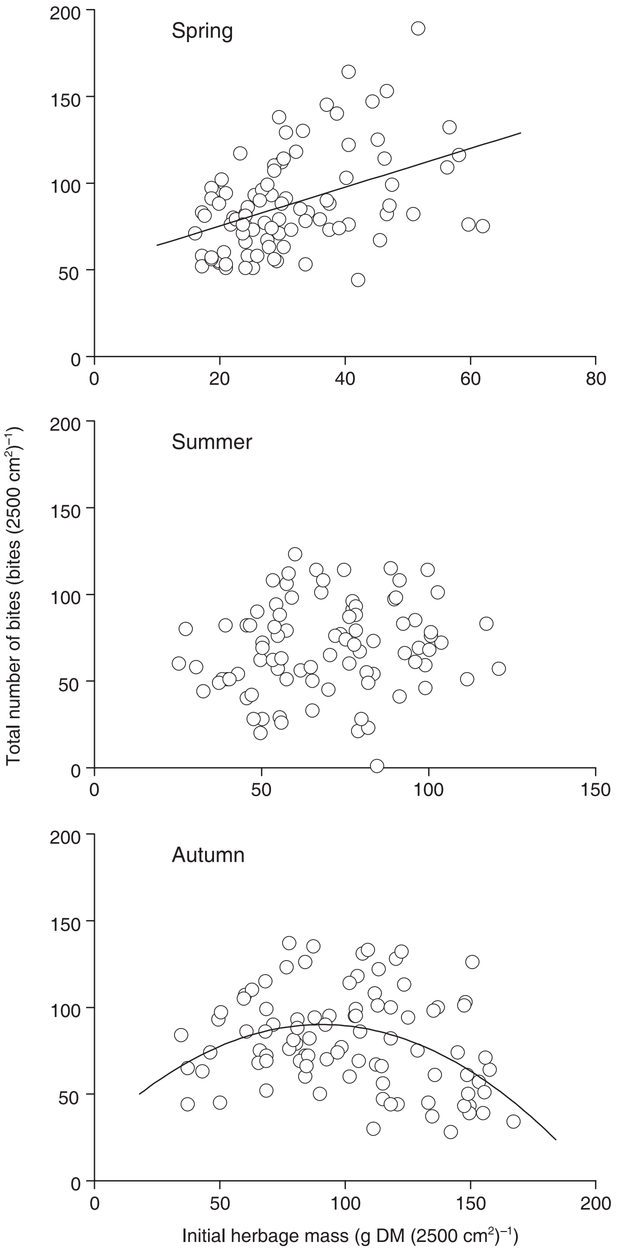

Figure 6 Relationships between total number of bites during progressive grazing period (cumulated from days 1–4 or 5) and initial herbage mass (pregrazing herbage mass on day 1) in spring, summer and autumn. Regression equations are: $y = 52.9 + 1.12x$ ($r = 0.434$, $P < 0.001$) and $y = 27.7 + 1.38x - 0.0076x^2$ ($r = 0.383$, $P < 0.001$) for spring and autumn, respectively.

The mean number of bites that individual locations received from animals during a single visit on each day was also highly uneven across the locations (not shown as a figure). During a visit, some locations received only a few bites (<3 bites visit^{-1}) whereas some locations received many bites (>10 bites visit^{-1}). The mean daily number of bites per visit was not linearly or quadratically related to pregrazing herbage mass on any of the 13 occasions ($P > 0.05$).

Table 2 Association of the number of bites on one day (days 2, 3, 4 or 5) with that on the preceding day(s) (days 1, 1–2, 1–3 or 1–4)† in spring, summer and autumn

Combination of days	Spring	Summer	Autumn
Day 2 versus day 1	0.015‡	−0.231*	0.153
Day 3 versus days 1–2	0.065	0.116	0.044
Day 4 versus days 1–3	0.127	0.054	0.148
Day 5 versus days 1–4	–	0.139	–

* Denotes significance at $P < 0.05$. † Cumulative numbers for days 1–2, 1–3 and 1–4. ‡ Spearman's rank correlation coefficient.

Residence time

The duration for which individual locations were grazed by animals each day varied considerably across the locations (Figure 7). During grazing, some locations were not used at all or were grazed only for a short time (<10 s daily) whereas some locations were used for a long period (>30 s daily). The daily residence time was significantly related to pregrazing herbage mass on five occasions, showing relatively low *r*-values of 0.336–0.519 (absolute values). In spring, locations with higher pregrazing herbage mass were grazed longer on days 1–3. In autumn, the reverse occurred on day 1, and locations with intermediate herbage mass (~85 g DM [2500 cm^2]$^{-1}$) were grazed longest on day 3.

The total duration for which individual locations were grazed by animals during the progressive grazing period was still uneven across the locations, though the variability became smaller than on a daily basis (Figure 8). Some locations were grazed for less than 50 s during the 4 or 5 days, whereas some locations were grazed for more than 110 s. The total residence time was significantly related to initial herbage mass in spring and autumn with relatively low *r*-values of 0.514 and 0.356, respectively. Locations with higher initial herbage mass were grazed longer in spring, and locations with intermediate herbage mass (~90 g DM [2500 cm^2]$^{-1}$) were grazed longest in autumn.

The daily residence time on days 2–4 or 5 showed no association or only loose association (two significant cases) with the residence time on the preceding day(s), as shown by the low r_S values of 0.045–0.261 (absolute values); that is, locations grazed for a long time during the preceding grazing(s) were not used for a long or a short time thereafter (Table 3).

The mean duration for which individual locations were grazed by animals during a single visit on each day was also highly uneven across the locations (not shown as a figure).

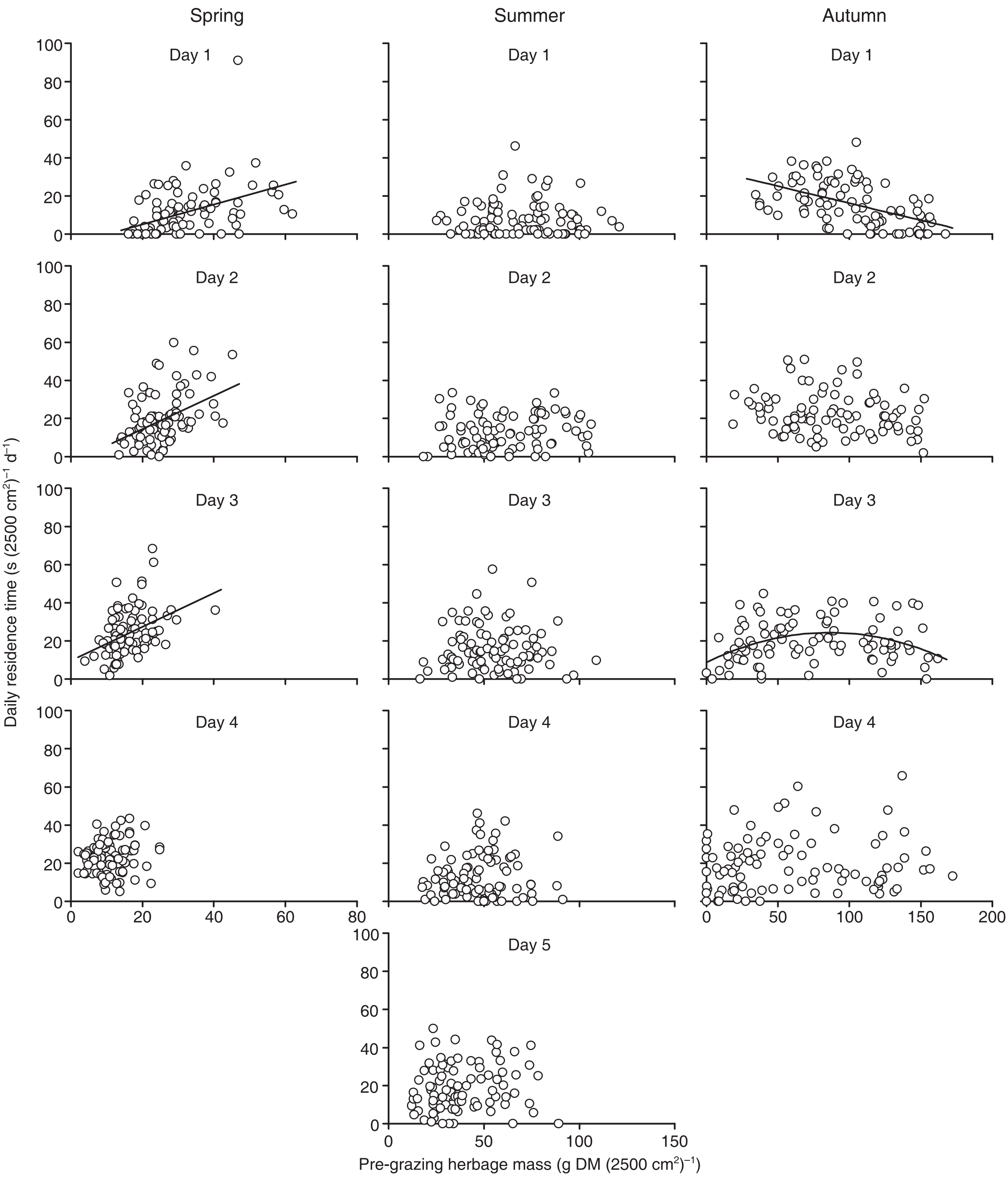

Figure 7 Relationships between daily residence time and pregrazing herbage mass during progressive grazing periods (days 1–4 or 5) in spring, summer and autumn. Regression equations are: $y = -5.31 + 0.52x$ ($r = 0.447$, $P < 0.001$), $y = -2.97 + 0.87x$ ($r = 0.436$, $P < 0.001$) and $y = 9.71 + 0.89x$ ($r = 0.421$, $P < 0.001$) for days 1–3 in spring, respectively; $y = 34.1 - 0.18x$ ($r = -0.519$, $P < 0.001$) and $y = 8.81 + 0.36x - 0.0021x^2$ ($r = 0.336$, $P < 0.01$) for days 1 and 3 in autumn, respectively.

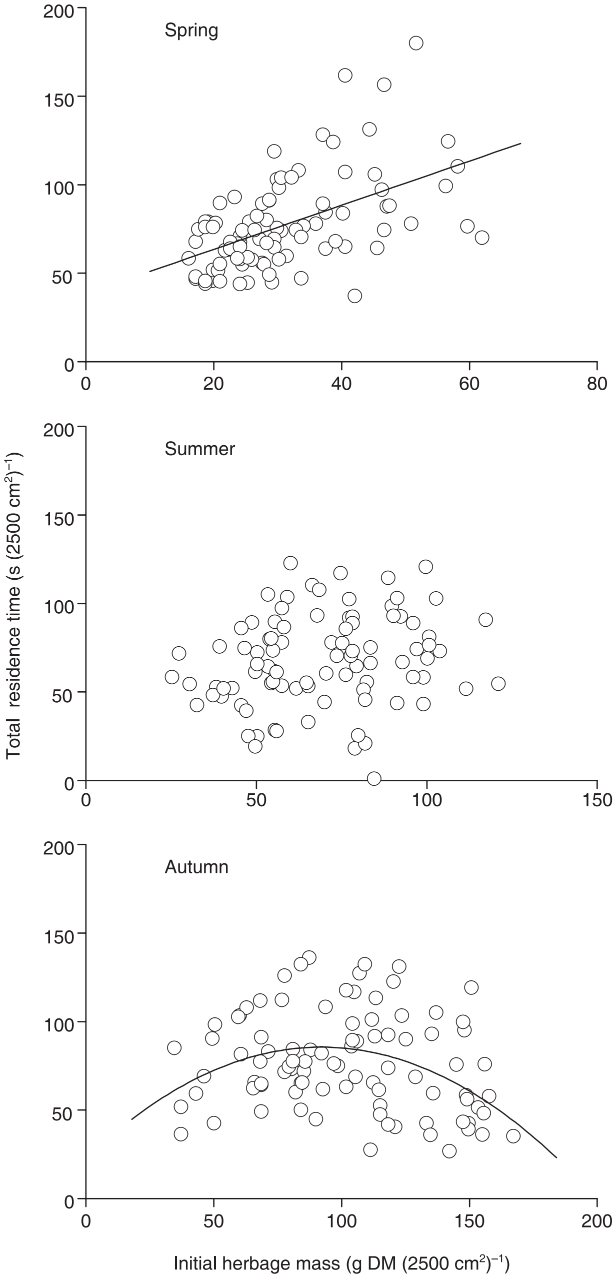

Figure 8 Relationships between total residence time during progressive grazing period (cumulated from days 1–4 or 5) and initial herbage mass (pregrazing herbage mass on day 1) in spring, summer and autumn. Regression equations are: $y = 38.5 + 1.25x$ ($r = 0.514$, $P < 0.001$) and $y = 22.7 + 1.36x - 0.0074x^2$ ($r = 0.356$, $P < 0.01$) for spring and autumn, respectively.

During a visit, some locations were grazed only for a short time (<3 s visit^{-1}) whereas some locations were utilized for a long period (>10 s visit^{-1}). The mean daily residence time per visit was not linearly or quadratically related to pregrazing herbage mass on any occasions ($P > 0.05$).

Table 3 Association of the residence time on one day (days 2, 3, 4 or 5) with that on the preceding day(s) (days 1, 1–2, 1–3 or 1–4)† in spring, summer and autumn

Combination of days	Spring	Summer	Autumn
Day 2 versus day 1	0.082‡	−0.261*	0.195
Day 3 versus days 1–2	0.065	0.140	0.063
Day 4 versus days 1–3	0.133	0.045	0.208*
Day 5 versus days 1–4	–	0.146	–

* Denotes significance at $P < 0.05$. † Cumulative time for days 1–2, 1–3 and 1–4. ‡ Spearman's rank correlation coefficient.

Discussion

Accuracy of herbage mass estimation

The values of R^2 and SE of estimation in calibration equations developed in the present study (0.830–0.994 and 1.4–24.8 g DM [2500 cm^2]$^{-1}$, respectively) are almost comparable to those obtained in previous studies (Hirata 2000; Hirata *et al.* 2002; Ogura *et al.* 2005). This confirms relatively high, stable performance of the electronic capacitance probe in estimating herbage mass of bahiagrass in this study site, which may be attributed to a high proportion of green material in pasture resulting from relatively high rainfall (Ogura *et al.* 2005).

Forage value of locations

Measurements conducted in the pasture in the next year of this study showed close linear relationships between height and herbage mass of locations across the grazing season ($r = 0.833$–0.959, $P < 0.001$) (S Ogura and M Hirata, unpubl. data). Therefore, in the present study, locations with higher herbage mass were generally taller.

It is widely observed in grasslands that herbage quality is higher in shorter patches with lower herbage mass and vice versa (Illius *et al.* 1987; Wilmshurst *et al.* 1995; Cid and Brizuela 1998; Bergman *et al.* 2001). The present study, however, shows that this is not always the case: both N concentration and DMD in spring showed high values across a range of herbage mass except a location with the lowest herbage mass (Figure 1). This phenomenon is explained by the fact that variation in herbage mass across locations in this early grazing season (May) mainly reflected variation in herbage production after the initiation of spring growth (possibly due to spatial variation in soil nutrients and/or moisture), and consequently the majority of herbage was young and of high quality at most locations (Ogura *et al.* 2002). The considerably low herbage quality at the lowest availability location is attributable to the majority of old, poor quality herbage carried over from the previous year in this nonproductive location. By contrast, in agreement with previous studies, N concentration and DMD in autumn were lower at locations with higher herbage masses (Figure 1), because variation in herbage mass across locations in this late grazing season (October) reflected variation in herbage consumption during preceding grazing periods as well as variation in herbage production from spring and therefore locations with higher herbage masses had higher proportions of ungrazed overgrown poor quality materials (e.g. mature, senescent or dead leaves, mature stems or culms). Responses of herbage quality to herbage mass in summer (i.e. decreased DMD but almost constant N concentration; Figure 1) are taken as intermediate between those in spring and autumn. Thus, vegetation created a potential trade-off between herbage availability and quality for grazing animals in autumn, but not in spring (Ogura *et al.* 2002). In summer, a potential trade-off was produced between availability and DMD but not between availability and N concentration.

Furthermore, in summer and autumn, the perceived value of high availability locations for animals is considered to be lower than that expected from their forage value (quantity and quality), because these locations often included fecal pats deposited during preceding grazing periods. It is well known that grazing animals avoid herbage on and near fecal pats (Hirata *et al.* 1987, 1988). On the other hand, in spring, it is considered that there was no such dung-related decrease in the value of high availability locations, because these locations as well as other locations rarely included fecal pats in this first grazing period of the year; that is, most fecal pats deposited in the previous year had almost completely disappeared and therefore all droppings on the pasture were eventually only those deposited in the same grazing period.

Choice and use of locations by animals

In spring, locations with higher herbage mass received more visits, more bites and longer grazing by animals on days 1–3 (Figures 3,5 and 7). Such a positive, linear effect of herbage mass was detected also for the cumulated choice (number of visits) and use (number of bites and residence time) of locations during the progressive grazing period (Figures 4,6 and 8). These phenomena can be explained by the facts that there was no potential trade-off between abundance and quality of herbage (Figure 1) and there was no adverse effect of fecal droppings on the forage value of high availability locations (discussed earlier); that is, animals were able to benefit more from locations with higher availability in both dry matter and quality (N and DMD) of intake. As a result, herbage mass was distributed in lower and narrower ranges as grazing progressed, with the maximum showing greater decreases than the minimum and mean (Figure 2). Two explanations may be possible for the non-significant association of the choice and use of feeding locations with herbage mass on day 4 (Figures 3,5 and 7). First, all or most of the high availability locations on this final day had already lost their quality value due to defoliation on the preceding days, as suggested by the lowering range of herbage mass with the progressive grazing (Figure 2). Second, variation in pregrazing herbage mass was so narrow on day 4 (Figures 2,3,5 and 7) that animals gave up using herbage availability as a criterion for feeding location choice.

In autumn, locations with lower herbage mass received more visits, more bites and longer grazing by animals on day 1 (Figures 3,5 and 7), because these locations were of higher quality (Figure 1) and were not depleted yet on this initial day of the progressive grazing period (Figure 2). Then, on day 3, choice and use by animals shifted to locations with intermediate availability (Figures 3,5 and 7) as a result of depletion of high quality feed at low availability locations. Avoidance of herbage fouled by feces may also be partly responsible for the low selectivity for high availability locations (discussed earlier). Reflecting these, herbage mass was distributed in wider ranges as grazing progressed, with decreased minimum and constant maximum values (Figure 2). The cumulated choice and use of locations during the progressive grazing period peaked at intermediate herbage availability (Figures 4,6 and 8), where short-term (instantaneous) intake rate of digestible nutrient or energy or long-term (daily) intake rate of net energy was maximized (Langvatn and Hanley 1993; Wilmshurst *et al.* 1995; Wilmshurst and Fryxell 1995; Laca and Demment 1996) or daily grazing time was minimized (Bergman *et al.* 2001) due to the trade-off between availability and quality.

However, as a whole, the choice and use of feeding locations by animals were not closely associated with herbage mass (Figures 3,5 and 7). Significant relationships were obtained for only 20 cases out of the 39 (three behavior variables × 13 daily grazing periods). Even when there were significant relationships, they were loose, as shown by the relatively low *r*-values. Furthermore, taking account of the quality–quantity relationships of herbage (Figure 1), the choice and use of feeding locations by animals were also not closely associated with N concentration or DMD. Thus, neither herbage mass nor herbage quality (N and DMD) was an absolute factor determining the choice and use of fine-scale locations by cattle foraging in an actual grassland, which contrasted with more dominant effects of herbage quantity and/or quality at coarser scales such as feeding site and patch (Langvatn and Hanley 1993; Wilmshurst *et al.* 1995; Wilmshurst and Fryxell 1995; Van der Wal *et al.* 2000; Bergman *et al.* 2001; Ganskopp and Bohnert 2006; Hirata *et al.* 2006) or at a feeding station scale in well-controlled experimental environments (Laca *et al.* 1993; Distel *et al.* 1995).

The relative unimportance of forage value (mass, N and digestibility) as a determinant of the choice and use of feeding locations in the current study may indicate involvement of nonforage factors, although possibilities of other physical (e.g. tenderness) and/or chemical (e.g. micronutrients, secondary compounds) attributes of forage (Provenza *et al.* 2007) cannot be completely excluded even in the virtually monospecific grass pasture in this study. The published works suggest that abiotic environment (topography, distance to water, microclimate, predator risks) and animal characteristics (cognitive abilities and social organization) are major nonforage factors (Bailey *et al.* 1996; Roguet *et al.* 1998a). There are thus possibilities that: (i) animals discriminated between similar availability locations based on the abiotic values of the locations such as distance to water and shade and existence (amount and freshness) of fecal pats, although this effect seems minor because the choice and use on one day showed no association or only loose association with the behavior on the preceding day(s) (Tables 1–3); (ii) animals selected locations with low forage values by mistake, for sampling or with motivation to move (Illius *et al.* 1992, 1999; Dumont *et al.* 1995; Wilmshurst *et al.* 1995; Naujeck *et al.* 2005) and/or failed to revisit preferred locations due to limitations in memory at a fine spatial scale, even though they had an ability to assess forage value of vegetation patches (Bailey *et al.* 1996; Gordon and Illius 1997; Roguet *et al.* 1998a) and use spatial memory in locating preferred patches at a larger scale (Bailey *et al.* 1996; Roguet *et al.* 1998a); and (iii) animals chose or avoided locations depending on the cohesive (attractive) and dispersive (repulsive) forces between individuals within the herd (Shiyomi 2004). In addition to these, on occasions when there was a location or were locations receiving no visits by animals during the individual daily grazing period (Figure 3), there is a possibility that animals were not able to encounter all locations in the pasture, because there were so many (~44 000) locations at the scale of 50 cm × 50 cm and herbage allowance was high (75–310 g DM [kg liveweight]$^{-1}$). Any location cannot be chosen and used unless it is encountered by animals, even if its forage and/or nonforage values are high. Future studies thus need to quantify and analyze location-to-location variation in feeding behavior by animals in relation to various forage and nonforage factors, based on a multifactor approach.

Acknowledgments

We thank Maki Nomura, Yuki Nagakura, Tomotsugu Takahashi, Mariko Yamasaki, Ryoko Sekino, Nobue Yuki, Tsuyoshi Nanba, Wempie Pakiding, Satoshi Tanaka, Takuma Nakahara, Yuko Bunya and Rumiko Hirata for assistance in field measurements and Kiichi Fukuyama for pasture and animal management. Dubravko Maćešić thanks the Japanese Ministry of Education, Culture, Sports, Science and Technology for financial support during his fellowship trip to Miyazaki, Japan.

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