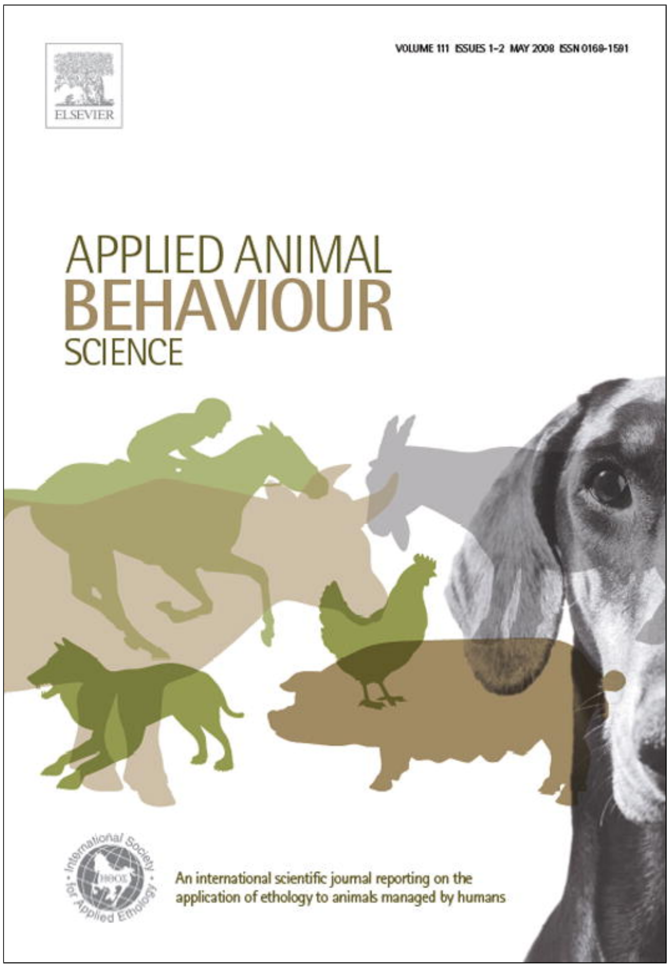
VOLUME 111 ISSUES 1–2 MAY 2008 ISSN 0168-1591
ELSEVIER
APPLIED ANIMAL
BEHAVIOUR
SCIENCE
An international scientific journal reporting on the application of ethology to animals managed by humans

Available online at www.sciencedirect.com
ScienceDirect
ELSEVIER
Applied Animal Behaviour Science 111 (2008) 108–119
APPLIED ANIMAL BEHAVIOUR SCIENCE
www.elsevier.com/locate/applanim

Effect of breed, season and pasture moisture gradient on foraging behaviour in cattle on semi-natural grasslands

Anna Hessle[a,*], Mark Rutter[b,1], Karin Wallin[a]

[a] *Department of Animal Environment and Health, The Swedish University of Agricultural Sciences, Box 234, 532 23 SE-Skara, Sweden*

[b] *Institute of Grassland and Environmental Research, North Wyke, Okehampton EX20 2SB, United Kingdom*

Accepted 21 May 2007
Available online 26 June 2007

Abstract

The objectives of this study were to determine the effects of breed, season and pasture moisture gradient on the extent and location of grazing and ruminating behaviour in cattle kept on heterogeneous semi-natural grasslands. Two groups of heifers, 12 of the traditional Swedish breed Väneko and 12 of the commercial Continental breed Charolais, were allocated into three enclosures per breed. Each enclosure consisted of heterogeneous semi-natural grasslands dominated by *Deschampsia cespitosa* (tufted hairgrass) and each contained dry, mesic and wet areas. In spring, summer and autumn, behaviour was recorded using automatic behaviour recorders, and positioning and activity were recorded using GPS receivers for 24 h for every heifer. The Väneko heifers had a higher activity than the Charolais heifers ($P = 0.006$), which supports the theories of resource allocation and contrafreeloading, but there were no differences between breeds in location of grazing, ruminating or idling. The heifers spent more time grazing in autumn (42.5% of the day) than in spring (38.5%; $P = 0.006$) and summer (38.9%; $P = 0.014$) and the efficiency of grazing (*i.e.* proportion of eating during grazing bouts) increased over the grazing period ($P < 0.001$). The results indicate the heifers avoided grazing in darkness which is consistent with the theory that predation risk affects foraging. Herbage in wet areas had a lower concentration of crude protein ($P = 0.036$) and a higher concentration of neutral detergent fibre ($P = 0.011$) than herbage in dry areas. At the same time, on average over seasons, 28% of the herbage mass was found in the wet areas, whereas only 8% of the grazing occurred there. Furthermore, the proportion of eating during grazing bouts was lower (73.9%; $P < 0.001$) in wet areas than in dry (80.1%) and mesic (79.6%) areas. The results indicate the heifers avoided grazing in wet areas

* Corresponding author. Tel.: +46 511 67143; fax: +46 511 67204.
E-mail address: Anna.Hessle@hmh.slu.se (A. Hessle).
[1] Present address: Harper Adams University College, Newport, Shropshire TF10 8NB, United Kingdom.

0168-1591/$ – see front matter
doi:10.1016/j.applanim.2007.05.017

where forage had a low nutritional value, supporting the theory of optimal foraging. In conclusion, both breed and season affects foraging behaviour of cattle on semi-natural grasslands, as the heifers of the traditional breed had a higher activity than the commercial breed and the grazing time was longer and more effective in late than in early grazing period. The cattle avoided foraging in wet areas, which may impact on the management of these areas.

Keywords: Breed; Season; Pasture; Grazing behaviour; Cattle

1. Introduction

Foraging livestock influence their pasture, partly through selecting or rejecting where to graze, partly by their activity through trampling and also by defecation and urination (Jaramillo and Detling, 1992; Gallet et al., 2004; Pakeman, 2004). Historically in Europe, foraging generally occurred in forests and marginal grasslands with nutrient-poor vegetation (Myrdal, 1998). Therefore, it is plausible that certain adaptive foraging traits in livestock would differ between old, traditional breeds selected in this environment and modern, commercial breeds selected in more intensive production systems. This statement is supported by the theory of resource allocation, which predicts that behaviours of high energetic cost, such as extensive foraging, are more frequent in less domesticated (traditional) breeds, allowing animals of more domesticated (commercial) breeds to allocate a greater proportion of resources to other traits, such as growth (Schütz et al., 2001; Schütz and Jensen, 2001). Furthermore, less domesticated breeds are more inclined to show contrafreeloading, which means that they are more willing to forage not only to maximize nutrient intake, but also to explore their environment (Lindqvist et al., 2002; Väisanen et al., 2005). The theories of resource allocation and contrafreeloading predict traditional cattle breeds to have a less selective grazing behaviour and a higher activity than commercial breeds, which may result in foraging behaviour that is better suited to their use in nature conservation when grazing on semi-natural grasslands. The lesser selectivity can be explained by the reduced metabolic rates and low maintenance requirements in these genotypes (Webster, 1985).

Season is potentially an important variable in the complex dynamic interactions between macro-herbivores, their foraging behaviour and the plants they graze. Season might even be a more important tool to direct the animals' foraging than intensity of grazing (Krueger, 1996). Previous studies have demonstrated that foraging is more selective in the beginning of the grazing period, whereas areas with less preferred species such as sedges, rushes and woody plants are foraged to a higher extent later in the grazing period (Roath and Krueger, 1982; Ganskopp et al., 1999; Evans et al., 2004; Pelster et al., 2004). However, these findings may sometimes be due to a varying relative herbage mass during the grazing period (Evans et al., 2004; Pelster et al., 2004). Season is connected with length of daylight, which impacts on foraging behaviour as anti-predator theory predicts macro-herbivores will avoid foraging during the hours of darkness due to a perceived risk of predation (Rutter, 2006).

The optimal foraging theory predicts animals will maximize their nutrient intakes (Wallis de Vries, 1994). Therefore, in heterogeneous semi-natural grasslands with abundant herbage, cattle seek herbage which gives a nutritional benefit, whereas herbage resulting in malaise or continued hunger is avoided (Launchbaugh and Howery, 2005). Wet semi-natural grasslands in northern Europe often are dominated by Cyperaceae (sedges and rushes) and tufty grasses such as *Deschampsia cespitosa* (tufted hairgrass), all plant species with low digestibility (Garmo, 1986;

Andersson, 1999; Lifvendahl, 2004). Therefore, wet areas of semi-natural grasslands might be avoided by foraging cattle when dryer areas are available. From a nature conservation point of view the opposite would be desirable, as a higher grazing pressure is required in wetter than in dryer areas to obtain optimal viability of at least some rare plant species (Lennartsson, 2000).

The objectives of the experiment reported here were to determine the effects of breed and season on foraging behaviour and location in cattle grazing heterogeneous semi-natural grasslands as well as identify preferred and avoided foraging areas, and thereby contribute to the development of improved grazing management strategies for semi-natural grasslands.

2. Materials and methods

2.1. Experimental design

Grazing behaviour and location were compared in 12 heifers of a traditional breed and 12 heifers of a commercial breed, allocated into three enclosures per breed, on heterogeneous semi-natural grasslands during spring, summer and autumn.

2.2. Animals

Spring-born weaned heifer calves, 14 of the Swedish traditional dual-purpose breed Väneko (Hallander, 1993) and 14 of the Continental commercial beef breed Charolais, were brought from eight commercial suckler herds in November 2003 to the Götala Research Station, Swedish University of Agricultural Sciences. During the previous grazing period, the calves had been kept on semi-natural grasslands together with their dams. They were 8 months old at arrival and the average liveweights were 193 (S.D. 30) kg for the Väneko heifers and 321 (S.D. 44) kg for the Charolais heifers. During the pre-experimental indoor period, the heifers were kept in groups of seven animals per pen. All heifers were fed wilted grass-clover silage containing 90–95% grass (*Lolium perenne* L., *Festuca pratensis* L. and *Phleum pratense* L.) and 5–10% clover (*Trifolium repens* L. and *Trifolium pratense* L.) *ad libitum*. The Väneko heifers had low initial liveweights so they were also fed 1.5 kg oats and 0.2 kg soybean meal per heifer per day during the first 2 months of the indoor period to obtain recommended minimum nutritional concentrations.

The heifers were trained to wear experimental equipment before turn-out to pasture. One week before turn-out, heifers were rearranged according to their liveweights to obtain similar stocking rates, in terms of kg liveweight per hectare (ha^{-1}), in the enclosures at pasture. At turn-out the average liveweights were 309 (S.D. 43) kg for the Väneko heifers and 431 (S.D. 51) kg for the Charolais heifers. Twelve heifers of each breed were included in the experiment, with four Väneko heifers in each of three enclosures and four Charolais heifers in each of three enclosures. The remaining two heifers of each breed were used as ‘‘put-and-take’’ animals to maintain similar sward heights among the six enclosures. They were kept in the enclosures in intervals outside the recording periods and in the same enclosures every time.

2.3. Study site

The experiment was conducted in 18 ha of semi-natural grasslands with a diverse topography and moisture gradient at the Götala Research Station, Skara, in southwestern Sweden (longitude 13°21′E, latitude 58°42′N, elevation 150 m) during the grazing period 4 May to 18 October 2004. Dry, mesic and wet areas in the grasslands were visually determined by two persons according to the physical nature of the ground, plant composition and experience from previous years. Areas were mapped and their acreages estimated by a global positioning system (GPS) receiver with a precision of 1 m (Trimble Pro XR, Trimble®, Sunnyvale, CA, USA). The grassland was divided into six enclosures (2.2–4.1 ha), all of which consisted of dry (10–26% of each paddock), mesic (55–71%) and wet (12–24%) areas. Water, salt and minerals were supplemented to the animals in the mesic areas. A description and an inventory of plant species of the pasture was conducted before the experiment was initiated. The grass-dominated pasture was mainly open, but included small areas of mixed deciduous trees. The dominating plant species in the dry areas were *Festuca ovina* (sheep's fescue), *Deschampsia flexuosa* (wavy hairgrass), *Nardus stricta* (matgrass) and several herb species. *Festuca rubra* (red fescue) and *D. cespitosa* (tufted hairgrass) and herbs dominated in mesic areas, whereas *D. cespitosa* and Cyperaceae (sedges/rushes) were dominent in wet areas.

To ensure an equal herbage supply in all the enclosures, sward heights in each enclosure were measured every second week throughout the grazing period. A route for sward height measurements was established by mapping out a path to be followed that passed through all parts of the enclosures. The path followed the shape of a W in each enclosure, as recommended by Frame (1993). Sward height measurements were performed with a rising plate meter (0.3 m $\times$ 0.3 m with a weight of 430 g) with 25–40 recordings in each enclosure.

At the end of the grazing period, visual assessments of the grazing intensity status of the enclosures were made. Inspections were conducted according to a national protocol developed to accommodate management status (satisfactory, moderate, or weak) for obtaining agri-environmental supports for pastures (Swedish Board of Agriculture, 2004; Persson, 2005).

2.4. *Chemical analysis*

During the grazing period, herbage was sampled during spring (2–3 June), summer (26–27 July) and autumn (16–17 September) for estimation of quantity and chemical composition. In each of the six enclosures, all herbage in five randomly selected 0.5 m $\times$ 0.5 m was cut at 3 cm level in dry, mesic and wet areas. Herbage quantities were estimated for each area in each enclosure per season, whereas samples for chemical analysis were combined to one sample per area (dry, mesic or wet) for all enclosures per season.

Pasture herbage samples were analysed for concentrations of dry matter (DM), ash, crude protein (CP), neutral detergent fibre (NDF) and *in vitro* organic matter digestibility. The DM concentration was determined at 105 °C for 24 h, whereas ash was determined at 550 °C for 5 h. The CP was determined in a Tecator Kjeltec Auto Sampler 1035 Analyzer (Tecator Inc., Höganäs, Sweden) and NDF was determined according to Goering and Van Soest (1970). Metabolizable energy (ME) concentration was calculated from *in vitro* organic matter digestibility (Lindgren, 1979).

2.5. *Behaviour data*

Behaviour was recorded for 24 h for each heifer in spring (21 May to 1 June), summer (12–26 July) and autumn (6–15 September), respectively. The four heifers within an enclosure were recorded on different days and when all heifers were anoestrus.

Jaw movements were recorded automatically using IGER Behaviour Recorders (Rutter et al., 1997). Eating and ruminating jaw movements were distinguished by their appearances using the Graze software (Rutter, 2000). Eating time was defined as the time spent performing eating jaw movements and grazing time was defined as eating time plus pauses between eating bouts shorter than 7 min. The proportion of grazing time consisting of eating time was calculated and defined as grazing efficiency. Ruminating time was defined as time performing ruminating jaw movements plus pauses between ruminating jaw movements shorter than 20 s. Idling time was defined as time not performing grazing or ruminating behaviour.

Animal position fixes were recorded every 15 s using collars equipped with GPS receivers, resulting in, on average, 5649 (S.D. 153) position fixes per animal on each recording day (GPS Plus 2, Vectronic Aerospace GmbH, Berlin, Germany). The precision of the GPS receiver was >90% of data <2.9 m from the true position. Data for activity measurements was recorded by two orthogonally orientated accelerometer sensors on the collars measuring the acceleration 6–8 times/s. The differences between two measurements were accumulated over 5 min and the average value stored (GPS Plus 2, Vectronic Aerospace GmbH, Berlin, Germany). Data was scaled to numerical values from 0 (no activity) to 255 (maximum activity) in the two directions, resulting in a total activity value on a score 0–361 according to the Pythagorean theorem, which was defined as activity. Average activity score was calculated for 24 h as well as separately for times the animals spent eating, grazing, ruminating and idling. The animal data was downloaded to a computer, where it was merged with pasture area data using the GIS software ArcMap (ESRI, 2002). The travelling distances of each animal were calculated from the GPS data. Differential corrections from base stations were investigated before the start of the experiment as a tool for correcting for atmosphere errors and thereby improving the precision of the coordinates. However, the precision was no more accurate with differential corrections, and consequently differential corrections were not used. Instead, the recorded animal travelling distances were corrected by subtracting contemporary distance records from an immobile GPS receiver at the experimental site.

The proportions of dry, mesic and wet areas varied among the enclosures. Therefore, the proportions of performed behaviour in the areas were corrected to correspond to the overall proportions in the enclosures (18.2% dry, 62.1% mesic, 19.7% wet areas).

2.6. Weather and hours of daylight

Weather data was collected continuously every hour by an automatic station not further than 500 m from the enclosures. During the experimental grazing period, the precipitation was heavier than average, especially in July when it was 180 mm and three-fold more than the average values, but it was heavy also in June and August (90 mm each month). In May, September and October, the precipitation was close to the average (45, 50 and 75 mm, respectively). Average 24 h temperatures were 11, 13, 14, 17, 12 and 7 °C in May, June, July, August, September and October, respectively, which was close to average. The hours of daylight were 17.2 h in the spring, 17.5 h in the summer and 13.4 h in the autumn.

2.7. Statistical analysis

The time spent grazing, idling and ruminating, in total and in dry, mesic and wet areas, as well as activity and distance travelled were investigated using a nested model with one fixed factor (breed) and repeated measurement (season) with the procedure Mixed (SAS, 2001) according to the model:

$$y_{ijkl} = \mu + \alpha_i + \beta_j + \alpha\beta_{ij} + c_{ijk} + e_{ijkl}$$

For grazing efficiency, the area was also included in the model:

$$y_{ijkl} = \mu + \alpha_i + \beta_j + \gamma_k + \alpha\beta_{ij} + \alpha\gamma_{ik} + \beta\gamma_{jk} + \alpha\beta\gamma_{ijk} + c_{ijkl} + e_{ijklm}$$

In the models α_i is the effect of breed, β_j the effect of season, γ_k the effect of area, $\alpha\beta_{ij}$ the interaction between breed and season, $\alpha\gamma_{ik}$ the interaction between breed and area, $\beta\gamma_{jk}$ the interaction between season and area, $\alpha\beta\gamma_{ijk}$ the interaction between breed, season and area, c_{ijk} and c_{ijkl} the effects of enclosure, and e_{ijkl} and e_{ijklm} are the error terms. There were 12 samples per treatment (breed) allocated in three enclosures repeated three times (season).

Analyses of preference or aversion of expressing grazing, ruminating and idling in the dry, mesic and wet areas for all heifers during spring, summer and autumn were conducted using the procedure *t*-test (SAS, 2001) with enclosures as replicates. The proportion of behaviour expressed in the area was compared to the proportion of the herbage mass in the area out of the herbage mass in the entire enclosure. Confidence intervals (CI 95%) were analysed for sward height and herbage mass in the enclosures and for precipitation and average temperature during the behaviour recordings using the *t*-test (SAS, 2001).

Differences among the treatment means were denoted as significant at $P < 0.05$ and as a tendency to significance at $0.05 < P < 0.10$.

3. Results

3.1. Animal liveweight gain, weather and pasture

Daily liveweight gains during the grazing period were similar in heifers of the two breeds, on average 0.57 (S.D. 0.16) kg. Also the 95% CI for precipitation and temperature during the behaviour recording days were similar between the two breeds. Precipitation was similar among seasons, but average temperature differed (95% CI: spring 8–10 °C, summer 14–15 °C, autumn 12–14 °C; $P < 0.001$).

The 95% CI for sward height was similar for the two breeds throughout the grazing period. The sward height was higher in the summer (5.0–5.9 cm) than in the spring (3.3–4.2 cm; $P < 0.001$) and autumn (3.8–4.0 cm; $P < 0.001$), but was similar in the spring and autumn. Herbage mass showed the same pattern with higher values in summer and lower in spring (Table 1). The grazing pressure after the grazing period had, according to the official classification (Persson, 2005), been satisfactory high in dry and mesic areas, whereas it had been weak in wet areas (Elin Isaksson, personal communication).

The CP and ME concentrations of the pasture herbage were higher and the NDF concentration was lower in the spring than later in the grazing period (Table 1). Likewise, the CP concentration was higher and the ME concentration tended to be higher, whereas the NDF concentration was lower in dry areas compared to mesic or wet areas (Table 1).

3.2. Behaviour

In the spring, the heifers spent a higher proportion of their time in the mesic and wet areas than later in the grazing period, when instead, they spent a higher proportion of their time in dry areas (Table 2). The heifers spent more time grazing and ruminating in the autumn than in the spring and summer (Table 2). Also their eating time, as a proportion of the day, was higher in the autumn than in the summer (36.2% *versus* 31.6%; $P < 0.001$), which was higher than in the spring (26.6%; $P < 0.001$).

No main effect of breed on time budget or location of behaviour was found but there were two interactions between breed and season. The Charolais heifers spent a higher proportion of their ruminating and idling time in the wet areas in spring (10.2% for ruminating and 11.2% for idling) than the Väneko heifers (2.1%, $P = 0.016$ for ruminating; 2.0%, $P = 0.004$ for idling).

Table 1
Herbage mass (HM), dry matter (DM) content, concentrations (kg DM^{-1}) of metabolizable energy (ME), crude protein (CP) and neutral detergent fibre (NDF) in dry, mesic and wet areas of semi-natural grassland in spring, summer and autumn; *P* is the effect of area and season, respectively

	Area				Season			
	Dry	Mesic	Wet	*P*	Spring	Summer	Autumn	*P*
HM (tonnes DM ha^{-1})	0.8^{c}	1.1^{b}	1.6^{a}	<0.001	0.9^{c}	1.4^{a}	1.1^{b}	<0.001
DM content (g kg^{-1})	270	272	265	NS	312^{a}	229^{c}	265^{b}	<0.001
ME (MJ)	9.9	9.4	9.0	0.085	11.5^{a}	8.5^{b}	8.4^{b}	<0.001
CP (g)	140^{a}	124^{b}	122^{b}	0.036	152^{a}	114^{b}	121^{b}	0.003
NDF (g)	553^{b}	600^{a}	608^{a}	0.011	480^{b}	654^{a}	627^{a}	<0.001

Means in a row with different letters (a, b, c) differ significantly ($P < 0.05$) according to $LSD_{0.05}$-test. Level of significance for effect of area or season: NS = non-significance; $P > 0.10$.

Table 2
Proportion of eating time during grazing and proportion of grazing, ruminating and idling expressed in dry, mesic and wet areas (18.2, 62.1 and 19.7% of total area, respectively) in 24 heifers of two breeds on semi-natural grasslands in spring, summer and autumn; S.E.M. is standard error of the mean

	Spring	Summer	Autumn	S.E.M.	*P*
Grazing					
Eating (% of grazing time)	69.3^{c}	81.6^{b}	85.0^{a}	1.2	<0.001
Total (% of day)	38.5^{b}	38.9^{b}	42.5^{a}	1.4	0.011
Dry area (% of total)	16.7^{b}	27.3^{a}	24.5^{a}	4.4	<0.001
Mesic area (% of total)	74.1^{a}	67.7^{b}	67.7^{b}	4.5	0.011
Wet area (% of total)	9.4^{a}	5.2^{b}	7.7^{ab}	1.7	0.021
Ruminating					
Total (% of day)	25.1^{c}	29.6^{b}	32.7^{a}	0.7	<0.001
Dry area (% of total)	12.9^{b}	43.6^{a}	48.0^{a}	7.6	<0.001
Mesic area (% of total)	80.7^{a}	54.2^{b}	50.7^{b}	7.5	<0.001
Wet area (% of total)	6.5^{a}	2.0^{ab}	1.4^{b}	1.5	0.044
Idling					
Total (% of day)	36.4^{a}	31.5^{b}	24.9^{c}	1.4	<0.001
Dry area (% of total)	15.1^{c}	37.4^{b}	50.0^{a}	8.3	<0.001
Mesic area (% of total)	77.0^{a}	60.4^{b}	48.7^{b}	8.0	<0.001
Wet area (% of total)	7.6^{a}	2.3^{b}	1.2^{b}	1.5	0.010

Means in a row with different letters (a, b, c) differ significantly ($P < 0.05$) according to $LSD_{0.05}$-test.

Furthermore, Charolais heifers spent more of their ruminating and idling time in the wet areas in spring than they did in the summer (0.7%, $P = 0.002$ for ruminating; 1.3%, $P < 0.001$ for idling) and autumn (0.9%, $P = 0.002$ for ruminating; 0.8%, $P < 0.001$ for idling).

3.3. Activity and travelling distance

The Väneko heifers had a 40% higher level of total activity, a 34% higher level of activity during grazing and a 60% higher level of activity during ruminating than the Charolais heifers (Table 3). Also, during specific eating bouts, Väneko heifers had a higher activity than the Charolais heifers (score 146 *versus* 109; $P = 0.005$). In the autumn, the heifers were 12, 46, and

Table 3
Level of activity (score from 0, minimum, to 361, maximum) during grazing, ruminating, idling and in total, as well as distance travelled per day in heifers of Väneko ($n = 12$) and Charolais ($n = 12$) breed on semi-natural grasslands in spring, summer and autumn; S.E.M. is standard error of the mean

	Breed		Season			S.E.M.	*P*	
	Väneko	Charolais	Spring	Summer	Autumn		Breed	Season
Activity								
Grazing	142	106	123^{ab}	132^{a}	116^{b}	4	0.005	0.008
Ruminating	24	15	22^{a}	24^{a}	13^{b}	1	<0.001	<0.001
Idling	31	18	26^{a}	33^{a}	15^{b}	4	0.089	0.002
Total	73	52	63^{ab}	68^{a}	58^{b}	3	0.006	0.028
Distance (km)	10.9	9.6	11.0^{a}	10.2^{ab}	9.5^{b}	1	NS	0.034

Means for season in a row with different letters (a, b) differ significantly ($P < 0.05$) according to $LSD_{0.05}$-test. NS = non-significance ($P > 0.10$).

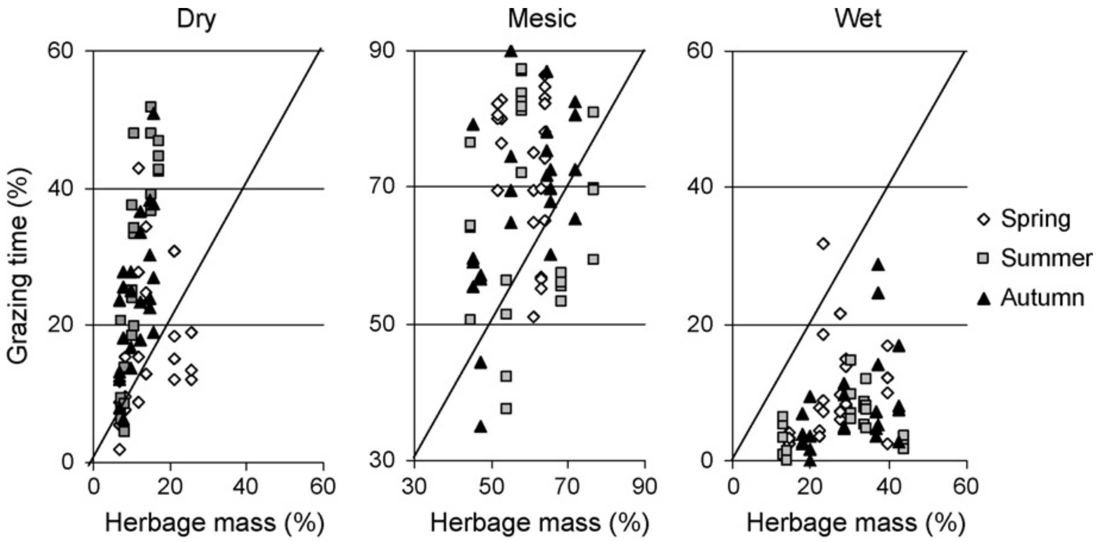

Fig. 1. Proportion of grazing time for 24 heifers in relation to available herbage mass in dry, mesic and wet areas of heterogeneous semi-natural grasslands in spring, summer and autumn.

54% less active during grazing, ruminating and idling, respectively, than in the summer (Table 3). Also, during specific eating bouts, the activity was lower in the autumn than in the summer (score 120 *versus* 135, $P = 0.005$). The heifers travelled 16% further in the spring than in the autumn. No interaction between breed and season in activity or distance travelled were found.

3.4. Preference and aversion of areas

When comparing the proportion of grazing time with the proportion of available herbage mass in dry, mesic and wet areas, the heifers preferred to graze in the dry areas in the summer ($P = 0.014$) and autumn ($P < 0.001$), and they preferred to graze in the mesic areas in spring ($P = 0.041$) and autumn ($P = 0.048$; Fig. 1). Consequently, the heifers avoided grazing in the wet areas throughout the grazing period ($P < 0.001$; Fig. 1). During grazing bouts, the proportion of eating time was lower in the wet areas than in the mesic and dry areas (73.9% in wet areas, 79.6% in mesic areas, and 80.1% in dry areas, $P < 0.001$).

When comparing the proportion of ruminating time and idling time with the proportion of dry, mesic and wet areas out of total enclosure area, the heifers preferred to conduct their ruminating and idling behaviour on the mesic areas in the spring ($P = 0.012$ for ruminating and $P = 0.049$ for idling), and on the dry areas in the summer ($P = 0.024$ for ruminating and $P = 0.045$ for idling) and autumn ($P = 0.028$ for ruminating and $P = 0.022$ for idling). Heifers avoided ruminating and idling in the wet areas throughout the grazing period ($P = 0.006$, <0.001 and <0.001 for ruminating in the spring, summer and autumn, respectively, and $P = 0.008$, <0.001 and <0.001 for idling in the spring, summer and autumn, respectively).

4. Discussion

Owners of traditional cattle breeds consider their breeds to be better adapted to grazing semi-natural grasslands than commercial breeds (Sæther and Vangen, 2001; Rook et al., 2006). In this study, the Väneko heifers were more active than the Charolais heifers (Table 3). The results may indicate the Väneko heifers roamed around more and grazed over a greater proportion of their surroundings. The result supports the theories of resource allocation and contrafreeloading and is in agreement with earlier studies where less specialized production breeds of livestock were more active and more inclined to explored their environment during foraging than livestock of production breeds (Gustafsson et al., 1999; Schütz et al., 2001; Schütz and Jensen, 2001; Väisanen et al., 2005; Sæther et al., 2006a). However, the breed difference in activity might not entirely be due to the degree of domestication but could also be an effect of the varying liveweights of the breeds studied (Rook et al., 2004). Nevertheless, the higher activity and consequent trampling of the Väneko heifers may be of significance for seed germination of annual plants. However, there was no breed difference in distance travelled, indicating the activity was higher on a small scale only.

No breed effects on foraging areas were found. In studies where breed effects on foraging area have been shown, traditional breeds of ruminants foraged in areas with higher proportions of plants with low nutrient concentrations than commercial breeds (Winder et al., 1996; Osoro et al., 1999; Sæther et al., 2006b). Breed differences in preference of foraging areas interact with herbage mass where the differences are more obvious in harsh environments with sparse herbage mass than in situations with abundant herbage, as in our study (Osoro et al., 1999).

Over the grazing period, the heifers increased their grazing time and ruminating time but decreased their distance travelled and their level of activity (Tables 2 and 3). Their efficiency in grazing increased over the grazing period, *i.e.* they had less pauses between single eating jaw movements in the late than in the early grazing period (Table 2). One reason for the lower efficiency of grazing in spring might be due to the performance of explorative behaviour in the novel environment. However, at the time of the recording in spring the heifers had already been on the pasture for 3 weeks and studies have shown that naive grazers make their decisions on what plant species to forage within a few days after turn-out to pasture (Ganskopp and Cruz, 1999). The increased nutrient requirements in the growing heifers over the grazing period were most likely compensated by increased bite weights (Cazcarra et al., 1995). The increased grazing time and ruminating time along the grazing period might instead have been caused by the 27% lower ME concentration and 31% higher NDF concentration in the herbage in the autumn compared to the herbage in spring (Table 1; Tjardes et al., 2002).

However, the decreased nutrient concentrations in herbage does not explain the increased efficiency in grazing in the autumn (Table 2). The anti-predator theory predicts large herbivores will avoid foraging during the hours of darkness due to a perceived risk of predation (Rutter, 2006). In this study, the proportion of the day with daylight (from sunrise to sunset) was more than 70% in the spring and summer, whereas the proportion of daylight time was 56% in the autumn. The proportion of grazing out of daylight time was 53 and 55% in the spring and summer, respectively, whereas the proportion was as high as 76% in the autumn, indicating the extent of daylight hours were limiting the grazing time and may explain why the grazing was more effective in autumn than earlier in the grazing period. The shorter distance travelled and lower activity in the animals in the autumn also support the anti-predator theory by indicating immobility during the longer nights (Table 3).

The heifers avoided grazing the wet areas as, on average over seasons, 28% of the herbage mass was found in the wet areas, whereas only 8% of the grazing occurred there (Fig. 1). Consequently, at the end of the grazing period a majority of the wet areas were assessed as having had too little grazing pressure to be optimal for maintaining the biodiversity (Elin Isaksson, personal communication). Furthermore, the 7% lower proportion of the heifer's eating time (and thereby the longer pauses) during grazing bouts in the wet areas compared to grazing bouts in the dry and mesic areas, may indicate the heifers foraging the wet areas were searching for more preferred plots to forage. According to the theory of optimal foraging, grazing cattle optimize their nutrient intakes (Wallis de Vries, 1994). Wet areas were dominated by *D. cespitosa*, *Juncus* spp. and *Carex* spp., tufty species with low digestibility (Garmo, 1986; Andersson, 1999; Lifvendahl, 2004). Consequently, herbage in the wet areas had a higher NDF concentration and a lower CP concentration than herbage in the dry areas (Table 1). Also Humphrey and Patterson (2000) showed cattle avoided foraging in wet *Juncus*-dominated areas when the alternative was to graze dryer areas, but the authors thought the primary reason for this was the lower herbage mass in the *Juncus* area. In contrast, cattle studied by Huber et al. (1995) preferred to graze riparian meadows instead of dryer uplands, whereas cattle studied by Asamoah et al. (2003) foraged riparian meadows and dryer uplands to the same extent. If livestock avoid foraging in wet semi-natural grasslands dominated by *D. cespitosa* and Cyperaceae, our options to conserve biodiversity in these areas may be negatively impacted. Splitting up heterogeneous grasslands with fences to direct the animals to these areas may be necessary to obtain a satisfactory management of wet areas of semi-natural grasslands.

5. Conclusion

Behaviour was more affected by season than breed, but the Väneko heifers had a higher level of activity than the Charolais heifers. Furthermore, the heifers foraged more effectively in the autumn than earlier in the grazing period and they avoided grazing in wet areas dominated by *D. cespitosa* and Cyperaceae throughout the grazing period. Splitting up semi-natural grasslands with fences to direct livestock to wet areas may be necessary to obtain the satisfactory management of these areas.

Acknowledgements

The study was financed by MISTRA, The Foundation of Skaraborg Savings Bank and The Swedish University of Agricultural Sciences. From The Swedish University of Agricultural Sciences, the authors thank Eva Spörndly, Lena Lidfors and Elisabet Nadeau for suggestions on the experimental design, Johanna Wetterlind, Holger Dettki and Mats Söderström for advice regarding GPS equipment and mapping, Jonas Dahl and David Johansson for taking good care of the heifers, and Jan-Eric Englund for statistical consultation. We also thank Elin Isaksson at the County Administration Board of Västra Götaland for assessing the grazing management status and Margaret Knipe for linguistic scrutiny.

References

Andersson, A., 1999. Chemical composition in grasses from semi-natural grasslands. Master Thesis No. 112. Dept. Animal Nutrition and Management, Swedish University of Agricultural Sciences, Uppsala, p. 32 (in Swedish, with English summary).

Asamoah, S.A., Bork, E.W., Irving, B.D., Price, M.A., Hudson, R.J., 2003. Cattle herbage utilization patterns under high-density rotational grazing in the Aspen Parkland. Can. J. Anim. Sci. 83 (3), 541–550.

Cazcarra, R.F., Petit, M., D'hour, P., 1995. The effect of sward height on grazing behaviour and herbage intake of three sizes of Charolais cattle grazing cocksfoot (*Dactylis glomerata*) swards. Anim. Sci. 61, 511–518.

ESRI, 2002. ArcMap™ 8.3. ESRI®, Redlands, CA.

Evans, S.G., Pelster, A.J., Leininger, W.C., Trlica, M.J., 2004. Seasonal diet selection of cattle grazing a montane riparian community. J. Range Manage. 57 (5), 539–545.

Frame, J., 1993. Herbage mass. In: Davis, A., Baker, R.D., Grant, S.A., Laidlaw, A.S. (Eds.), Sward Measurement Handbook. Br. Grassl. Soc., Reading, England, pp. 39–67.

Gallet, S., Lemauviel, S., Roze, F., 2004. Responses of three heathland shrubs to single or repeated experimental trampling. Environ. Manage. 33 (6), 821–829.

Ganskopp, D., Cruz, R., 1999. Selective differences between naive and experienced cattle foraging among eight grasses. Appl. Anim. Behav. Sci. 62, 293–303.

Ganskopp, D., Svejcar, T., Taylor, F., Farstvedt, J., Paintner, K., 1999. Seasonal cattle management in 3 to 5 year old bitterbrush stands. J. Range Manage. 52 (2), 166–173.

Garmo, T., 1986. Chemical composition and *in vitro* dry matter digestibility of indigenous mountain pasture plants in different plant groups. Rangifer 6, 14–22 (in Norwegian, with English summary).

Goering, H.K., Van Soest, P.J., 1907. Forage fiber analysis (apparatus, reagents, procedures and some applications). Agric. Handbk. No. 379. Agric. Res. Serv., USDA Department, Washington, DC, 20 pp.

Gustafsson, M., Jensen, P., de Jonge, F.H., Schuurman, T., 1999. Domestication effects on foraging strategies in pigs (*Sus scrofa*). Appl. Anim. Behav. Sci. 62 (4), 305–317.

Hallander, H., 1993. Lantraser-93, Bokförlaget Blå Ankan AB. Ljungbergs Tryckeri, Höganäs, pp. 32–37 (in Swedish).

Huber, S.A., Judkins, M.B., Krysl, L.J., Svejcar, T.J., Hess, B.W., Holcombe, D.W., 1995. Cattle grazing a riparian mountain meadow: effects of low and moderate stocking density on nutrition, behavior, diet selection, and plant growth response. J. Anim. Sci. 73 (12), 3752–3765.

Humphrey, J.W., Patterson, G.S., 2000. Effects of late summer cattle grazing on the diversity of riparian pasture vegetation in an upland conifer forest. J. Appl. Ecol. 37 (6), 986–996.

Jaramillo, V.J., Detling, J.K., 1992. Small-scale heterogeneity in a semiarid North American grassland. 2. Cattle grazing of simulated urine patches. J. Appl. Ecol. 29 (1), 9–13.

Krueger, W.C., 1996. Developing an effective grazing strategy for riparian vegetation. Livestock Management in Grazed Watersheds—A Review of Practices that Protect Water Quality. Publ. 3381. Univ. Calif. Davis, Calif. Agr. Issues Center, pp. 15–23.

Launchbaugh, K.L., Howery, L.D., 2005. Understanding landscape use patterns of livestock as a consequence of foraging behavior. Rangeland Ecol. Manage. 58 (2), 99–108.

Lennartsson, T., 2000. Management and population viability of the pasture plant *Gentianella campestris*. The role of interaction between habitat factors. Ecol. Bull. 48, 111–121.

Lifvendahl, Z., 2004. Fodder value in wet semi-natural grasslands – analysis of five species. Master Thesis. Dept. of Conserv. Biol., the Swedish University of Agricultural Sciences, Uppsala, 41 pp. (in Swedish, with English summary).

Lindgren, E., 1979. The nutritional value of roughages determined *in vivo* and by laboratory methods. Report No. 45. Dept. Anim. Nutr., Swedish University of Agricultural Sciences, Uppsala (in Swedish).

Lindqvist, C., Schütz, K.E., Jensen, P., 2002. Red jungle fowl have more contrafreeloading than White Leghorn layers: effect of food deprivation and consequences for information gain. Behaviour 139, 1195–1209.

Myrdal, J., 1998. Jordbruket under feodalismen. Natur och Kultur/LTs förlag, Borås, p. 300 (in Swedish).

Osoro, K., Olivan, M., Celaya, R., Martinez, A., 1999. Effects of genotype on the performance and intake characteristics of sheep grazing contrasting hill vegetation communities. Anim. Sci. 69, 419–426.

Pakeman, R.J., 2004. Consistency of plant species and trait responses to grazing along a productivity gradient: a multi-site analysis. J. Ecol. 92 (5), 893–905.

Pelster, A.J., Evans, S., Leininger, W.C., Trlica, M.J., Clary, W.P., 2004. Steer diets in a montane riparian community. J. Range Manage. 57 (5), 546–552.

Persson, K., 2005. Ängs-och betesmarksinventeringen—inventeringsmetod. Rep. No. 2005:2. Swedish Board of Agriculture, Jönköping, pp. 16–40 (in Swedish).

Roath, L.R., Krueger, W.C., 1982. Cattle grazing influence on a mountain riparian zone. J. Range Manage. 35 (1), 100–104.

Rook, A.J., Dumont, B., Isselstein, J., Osoro, K., Wallis de Vries, M.F., Parente, G., Mills, J., 2004. Matching type of livestock to desired biodiversity outcomes in pastures—a review. Biol. Conserv. 119, 137–150.

Rook, A.J., Dumont, B., Isselstein, J., Mills, J., Osoro, K., Scimone, M., Wallis de Vries, M.F., 2006. Effects of livestock breed and grazing intensity on biodiversity and production in sustainable grazing systems. In: Lloveras, J., Gonzáles-Rodríguez, A., Vázquez-Yañez, O., Piñeiro, J., Santamaría, O., Olea, L., Poblaciones, M.J. (Eds.), Sustainable Grassland Productivity, Proc. 11th Gen. Meet. Euro. Grassl. Fed., Badajoz, Spain, April 3–6, pp. 646–648.

Rutter, S.M., 2000. Graze: a program to analyze recordings of the jaw movements of ruminants. Behav. Res. Methods Instrum. Comput. 32 (1), 86–92.

Rutter, S.M., 2006. Diet preference for grass and legumes in free-ranging domestic sheep and cattle: current theory and future application. Appl. Anim. Behav. Sci. 97 (1), 17–35.

Rutter, S.M., Champion, R.A., Penning, P.D., 1997. An automatic system to record foraging behaviour in free-ranging ruminants. Appl. Anim. Behav. Sci. 54, 185–195.

Sæther, N.H., Vangen, O., 2001. Motives for utilizing the Blacksided Trønder and Nordland: a native cattle breed in Norway. Anim. Genet. Resourc. Inform. 31, 15–26.

Sæther, N.H., Bøe, K., Vangen, O., 2006a. Differences in grazing behaviour between a high and a moderate yielding Norwegian dairy cattle breed grazing semi-natural mountain grasslands. Acta Scand. Sect. A: Anim. Sci. 56, 91–98.

Sæther, N.H., Sickel, H., Norderhaug, A., Sickel, M., Vangen, O., 2006b. Plant and vegetation preferences for one old native and one modern Norwegian dairy cattle breed when grazing on shared semi-natural mountain pasture. Anim. Res. 55, 367–387.

SAS, 2001. User's Guide. Release 8.02. SAS Institute Inc., Cary, NC, USA.

Schütz, K., Forkman, B.E., Jensen, P., 2001. Domestication effects on foraging strategy, social behaviour and different fear responses: a comparison between the red junglefowl (*Gallus gallus*) and a modern layer strain. Appl. Anim. Behav. Sci. 74 (1), 1–14.

Schütz, K.E., Jensen, P., 2001. Effects of resource allocation on behavioural strategies: a comparison of red junglefowl (*Gallus gallus*) and two domesticated breeds of poultry. Ethology 107 (8), 753–765.

Swedish Board of Agriculture, 2004. Stöd för miljövänligt jordbruk 2004. EU-information från Jordbruksverket. Tabergs Tryckeri AB, Jönköping, pp. 12–15 (in Swedish).

Tjardes, K.E., Buskirk, D.D., Allen, M.S., Templeman, R.J., Bourquin, L.D., Rust, S.R., 2002. Neutral detergent fibre concentration in corn silage influences dry matter intake, diet digestibility and performance of Angus and Holstein steers. J. Anim. Sci. 80, 841–846.

Väisanen, J., Lindqvist, C., Jensen, P., 2005. Co-segregation of behaviour and production related traits in an F3 intercross between red junglefowl and White Leghorn laying hens. Livest. Prod. Sci. 94 (3), 149–158.

Wallis de Vries, M.F., 1994. Foraging in a landscape mosaic: diet selection and performance of free-ranging cattle in heathland and riverine grassland. Doctoral Thesis 1777. Wageningen Agricultural University, Wageningen, p. 161.

Webster, A.J.F., 1985. Differences in the energetic efficiency of animal growth. J. Anim. Sci. 61 (Suppl. 2), 92–103.

Winder, J.A., Walker, D.A., Bailey, C.C., 1996. Effect of breed on botanical composition of cattle diets on Chihuahuan desert range. J. Range Ecol. 49 (3), 209–214.