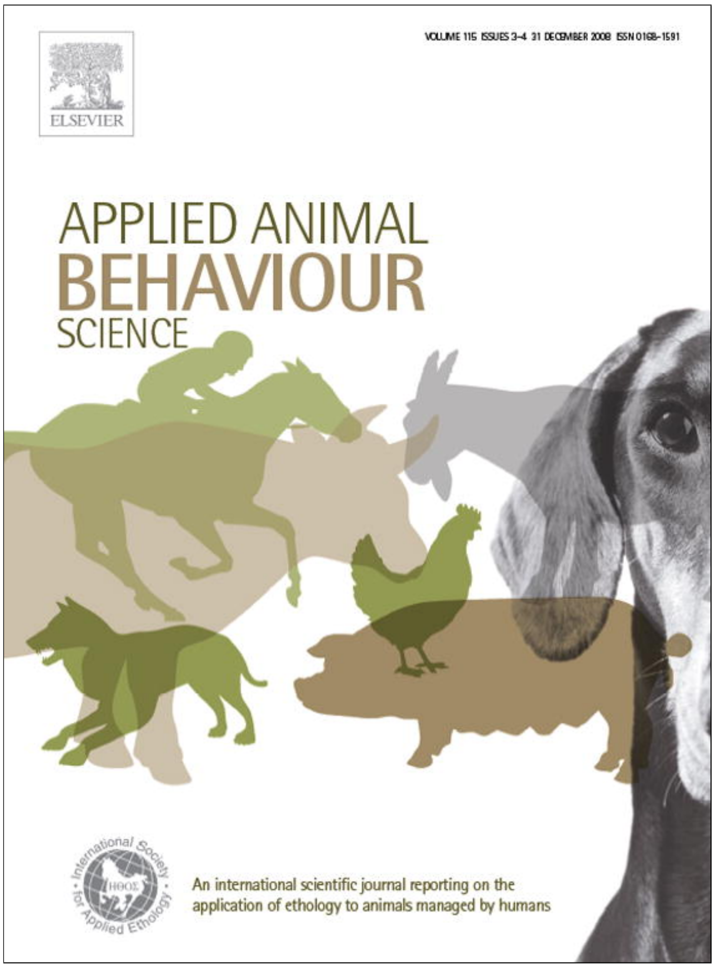
VOLUME 115 ISSUES 3–4 31 DECEMBER 2008 ISSN 0168-1591
ELSEVIER
APPLIED ANIMAL
BEHAVIOUR
SCIENCE
International Society for Applied Ethology
An international scientific journal reporting on the application of ethology to animals managed by humans

Available online at www.sciencedirect.com
ScienceDirect
Applied Animal Behaviour Science 115 (2008) 149–159
APPLIED ANIMAL BEHAVIOUR SCIENCE
www.elsevier.com/locate/applanim

Effects of social behaviour on the spatial distribution of sheep grazing a complex vegetation mosaic

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Accepted 16 June 2008
Available online 21 July 2008

Abstract

In complex environments, the spatial distribution of preferred food types will be a major factor influencing the distribution of foraging animals. However, in highly social animals, such as sheep, social interactions may modify foraging behaviour and hence influence both where animals feed and their impacts on the food resource. This process was investigated in a replicated experiment with six groups of Scottish Blackface sheep ($n = 6$), each grazing a separate 1 ha plot containing a natural vegetation mosaic, consisting of preferred (grass) and less preferred (heather, *Calluna vulgaris*) species. Grass covered 18% of the total area and was distributed across the plots as a complex network of patches, ranging in size from 1 to 690 m^2. In each plot, the sheep showed a preference for grazing on large patches, and were seen together in groups of 4 or more animals more often than would be expected by chance. Irrespective of patch size, mean nearest neighbour (NN) distances for pairs of sheep grazing together on the same patch (4.9 m) were much shorter than those for nearest neighbours grazing different patches (13.4 m) or heather (9.6 m), and similar to values for sheep grazing on larger grass swards. It was concluded that the ability to graze in groups at their preferred spacing was an important factor influencing the preference of sheep for large patches in this mosaic. There were differences in individual mean NN distances, measured over the whole mosaic, which ranged from 6.2 to19.3 m. However, there was no correlation between mean NN distance and the overall percentage of time spent on grass. The results suggest that although social behaviour influenced the choice of grass patches, the scale of heterogeneity in this particular mosaic was such that dietary preferences were not compromised.

Keywords: Grazing; Vegetation patches; Social behaviour; Sheep; Nearest neighbour distances

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0168-1591/$ – see front matter
doi:10.1016/j.applanim.2008.06.007

1. Introduction

The spatial distribution of any group of foraging animals is the result of a complex interaction of factors. According to the ideal free distribution theory (Fretwell and Lucas, 1970), the distribution of organisms between their resources will be the one which maximises individual benefit. In the absence of other constraints, the proportion of animals on a food patch should therefore be equal to the proportion of resources in that patch. However, environmental factors such as weather, topography and the risk of predation may contribute to the benefits of foraging at particular locations. Another layer of complexity is provided by social forces, which can both draw animals together and keep them apart, and the balance between these forces will have a strong influence on the distances between individuals in a group. In this paper we consider the contribution of social behaviour to the distribution of animals foraging in a patchy environment, focusing on sheep as an example of a highly social grazer.

A characteristic feature of the spatial distribution of grazing animals is the preferred distance maintained between nearest neighbours, as a direct result of their social behaviour. In sheep, this distance varies between breeds (Arnold and Dudzinski, 1978; Dwyer and Lawrence, 1999), but it can also be affected by vegetation type (Dudzinski et al., 1982; Dwyer and Lawrence, 1999) and space allowance (Sibbald et al., 2000). In heterogeneous environments, if vegetation patches are far apart, social motivation may conflict with feeding motivation and individual sheep have been shown to opt for staying close to their companions rather than move to a food patch (Dumont and Boissy, 2000; Sibbald and Hooper, 2004). It has also been shown that increased fragmentation of preferred vegetation can increase the overall proportion of time spent feeding on the less-preferred vegetation. This has been demonstrated with groups of sheep grazing mixtures of heather and grass (Clarke et al., 1995) and mixtures of different grass species (Dumont et al., 2000, 2002), and will be partly due to social pressures keeping the group together, even though some individuals may be excluded from the preferred patches (Appleby, 1980).

In natural, heterogeneous environments, patches come in all shapes and sizes and spatial arrangements, and predicting where animals are likely to forage becomes difficult. However, it is probably only through studying animals in these complex environments that we will be able to predict the outcome of the trade-offs that are involved. We tested the hypotheses that social behaviour affects the choice of patches by sheep grazing a complex vegetation mosaic and that time spent on preferred vegetation patches will vary according to individual social motivation, as a result of trade-offs that have to be made.

2. Materials and methods

The experiment was carried out in June 2001, at the Macaulay Institute's Glensaugh Research Station, in north-east Scotland (National Grid reference NO677782).

2.1. Vegetation mosaic

Six hill plots, each 100 m × 100 m, were fenced within an area of building/mature heather-dominated moorland (Gimingham, 1972), on a hillside facing north-northwest. The highly fragmented mosaic, consisting predominantly of heather (*Calluna vulgaris*) with numerous patches of grass (*Agrostis-Festuca* species), was created by many years of grazing (Hester and Baillie, 1998; Nicholson and Robertson, 1958). The plots were fenced in 1990 and had been grazed regularly, during the summer months, over the

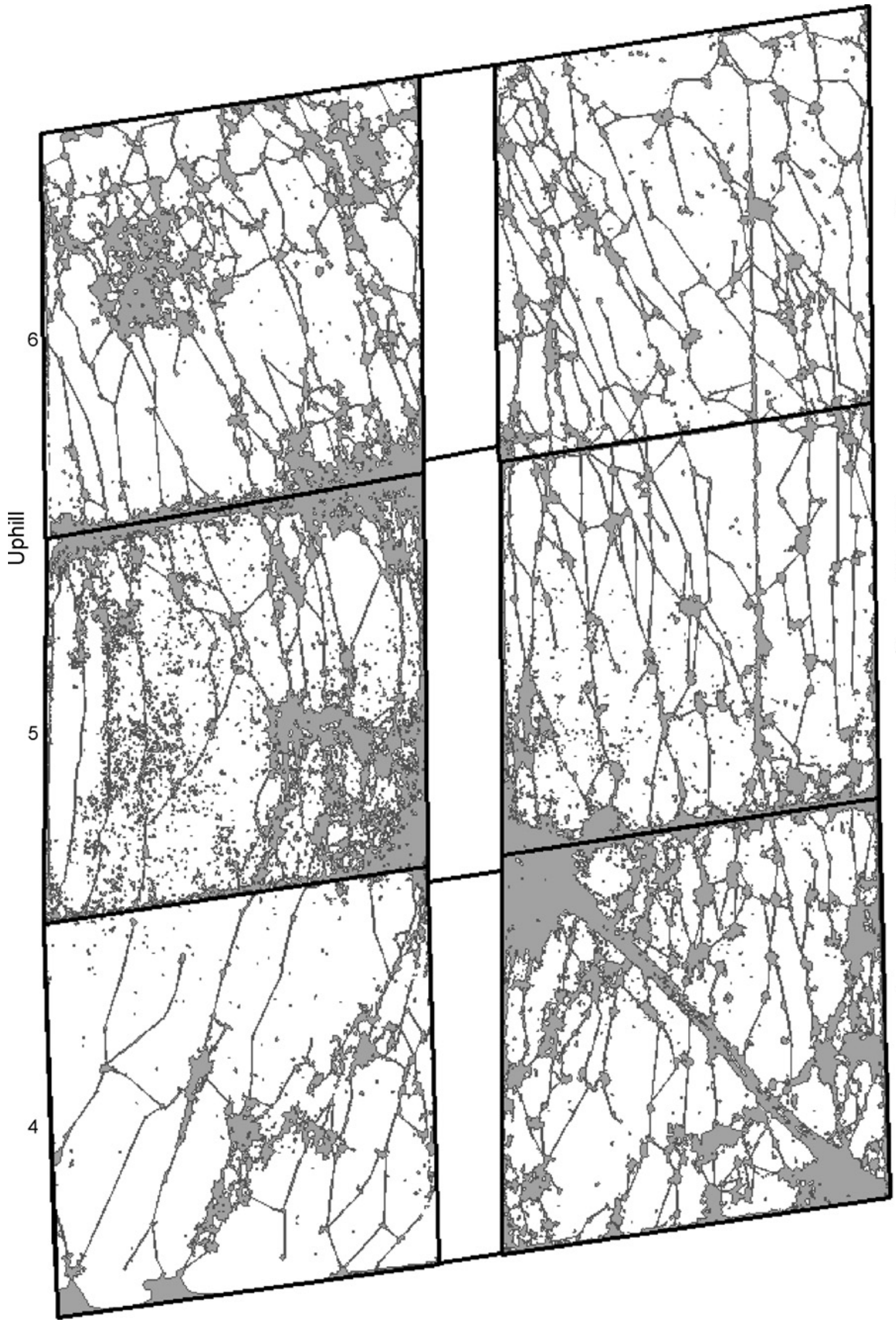

Fig. 1. Map of the six experimental plots, showing heather (white) with grass patches and interconnecting paths (grey).

intervening years. A number of grazing studies using the same plots have been reported (Hester and Baillie, 1998; Hester et al., 1999; Oom, 2003; Oom and Hester, 1999; Oom et al., 2002). Immediately prior to this experiment, the plots were grazed intermittently over winter, with all sheep removed from the plots in April 2001, before any significant grass growth is likely to have taken place.

Vegetation maps of each plot (Fig. 1) were produced using digital aerial photographs taken in October 1998, in which each pixel represented a ground area of 0.05 m × 0.05 m. Since the hillside was on a slope of approximately 17°, the images were ortho-rectified using Erdas Imagine (ERDAS Inc., USA; Version 8.3). The images were classified according to vegetation type using Erdas Imagine and the resulting classes grouped, on the basis of a visual interpretation of the photographs and some supplementary observations in the field, into 'grass' and 'heather'. Paths, indicated by an interruption of the heather canopy, were surveyed in the field and manually digitized. Full details of the mapping process have been described elsewhere by Oom (2003).

According to the above classification process, 79% (S.D. 7.8) of the area of each plot was covered by heather, 18% (S.D. 8.1) was grass, and the remaining 3% (S.D. 1.0) was made up of a network of inter-connecting paths. The grass was divided into an average of 118 (S.D. 26.1) patches per plot, ranging in area from 1 m^2 (which was the lower limit for identification as a discrete patch) to 690 m^2, although the majority (75%) of the patches were less than 10 m^2 in area. Mean grass sward height at the start of the experiment, based on a randomly chosen sample of 114 grass patches, spread across all the plots, was 3.8 (S.D. 0.93) cm and did not show any systematic variation with plot or patch size.

2.2. Animals and experimental design

Thirty-six yearling female Scottish Blackface sheep from a single flock (mean live weight 34.5 (S.D. 2.98) kg) were used for the experiment. The sheep were allocated at random to six groups of six animals, and each animal was marked with a unique pattern on the fleece so that they could be identified from a distance. The groups grazed in separate 30 m × 33 m grass plots for a period of 5 weeks before the start of the experiment. Each group was then allocated to one of the hill plots, where 250 scan samples of the positions and behaviours of individual sheep were carried out during a 2-week observation period. Twenty-five scans were carried out between 07.30 and 21.30 each day for 11 days. Since low-cloud occasionally obscured the plots for a part of the day, observations were carried out over 11 days to ensure that a total of 10 scans were made for each daily time point. Since groups of sheep stayed in the same plots throughout the experiment, effects of plot and group were necessarily confounded.

2.3. Measurements

Scan samples of the behaviour of the sheep in the heather/grass mosaic were carried out, using a telescope, from a site approximately 500 m from the hillside, where the ground surface was viewed at an angle of approximately 73° from the vertical. Plots and sheep within plots were scanned in the same order on each occasion. The locations of the sheep were marked directly onto the vegetation map (Fig. 1) at the time of sampling and behaviour recorded as grazing, lying, standing, walking with head up or drinking.

2.4. Data processing

Sheep locations were transferred to the GIS map of the plots, using ArcView (ESRI, USA; Version 3.2). Using ArcInfo (ESRI, USA; Version 8), each location was identified as being on heather, grass or a path. Data for focal sheep which could not be individually identified, due to the fleece marking being temporarily obscured, were excluded from the analyses, but this only amounted to about 5% of the scans. For the remainder, only data for sheep whose NNs were also grazing were used in the analyses of grazing behaviour and data for sheep whose NNs were also lying were used in the analysis of lying behaviour. For each grazing sheep located on grass, the area of the grass patch being grazed was obtained from the GIS. The GIS was also used to calculate the perpendicular distance to the nearest grass patch edge for all sheep locations on heather, and NN distances for all sheep locations. Percentages of time spent grazing on the different vegetation types and on each of the grass patches were estimated from the percentages of scans in which sheep were observed grazing there. Expected values for the percentages of time that sheep would spend grazing on the different grass patches were based on relative patch areas.

2.5. Statistical analysis

The relationship between percentage of time spent grazing patches and patch area was analysed using a generalised linear mixed model, which compared the number of sheep locations on individual patches with expected values based on the areas of the patches. Assuming a Poisson distribution with a log link and with an offset equal to log area, terms for plot/group and plot/group × log area were fitted. To allow for possible problems due to over-dispersion, patch ID was also included as a random effect in the model, since distinguishing features other than the area of a patch could have contributed to the variation in the data.

The frequencies with which different numbers of sheep (from 0 to 6 animals) were observed on the same patch were compared with the frequencies with which individual animal's visits would be expected to coincide, based on the total number of visits to the patches. A dispersion test was carried out for each plot/group in which the sample variance was compared with the variance for a binomial distribution (Cochran, 1954). The binomial dispersion statistic is given by

$$d = \frac{\sum_{i=1}^{n}(x_i - \bar{x})^2}{N(\bar{x}/N)(1 - (\bar{x}/N))}$$

where $n = 6$ is the number of sheep, $n = 250$ is the number of scans, and x is the number of sheep on the patch in each scan.

Since only six sheep were observed on each occasion, the level of significance was determined by comparing the test statistic with that for simulated data from a binomial distribution, rather than by using a chi-square distribution. Under the null hypothesis of a binomial distribution, the expected number of scans in which there would be 0, 1, 2, 3, 4, 5, and 6 sheep on the patch from Plot 1 in Table 1a would be 38, 84, 77, 38, 10, 2 and 0, respectively. For each patch 10,000 samples were simulated from a binomial distribution with six trials and probability equal to the mean number of sheep on the patch divided by 6. The number of times that the dispersion statistic exceeded the dispersion statistic for the observed data was used to estimate the P-value.

Percentages of time spent grazing and distances between NNs on the various combinations of patch and background vegetation were compared by analysis of variance, using mean values for plots in each case. Where overall mean values and standard deviations (S.D.s) or standard errors (S.E.s) are given, these values were also derived from plot/group means. The relationship between percentage of time sharing patches and mean NN distance when not sharing patches was examined with regression analysis, using individual sheep mean values and fitting plot/group before NN distance. All statistical analyses were carried out using GenStat (Lawes Agricultural Trust, 2002).

3. Results

The sheep spent 95% of their time either grazing (69%) or lying down (26%) and the rest of the time either walking or standing, with drinking accounting for less than 0.1% of scans.

Table 1a
The observed numbers of scans in which different numbers of sheep were seen grazing together on the most preferred patch in each plot, together with the index of dispersion (d), which was significant at $P < 0.001$ for each plot

Plot no.	Patch area (m^2)	Number of sheep							d
		0	1	2	3	4	5	6	
1	690	119	33	23	25	19	13	18	829.0
2	270	136	17	23	17	17	23	17	925.5
3	64	133	28	15	18	26	25	5	824.1
4	56	207	13	6	10	7	6	1	840.5
5	379	166	25	15	20	12	3	9	816.7
6	404	113	28	14	24	20	27	24	920.0

Table 1b
The observed numbers of scans in which different numbers of sheep were seen grazing together on a medium-sized patch in each plot, together with the index of dispersion (d), significant at $^{*}P < 0.01$ or $^{**}P < 0.001$

Plot no.	Patch area (m^2)	Number of sheep							d
		0	1	2	3	4	5	6	
1	71	233	14	3	0	0	0	0	309.1
2	72	226	16	6	2	0	0	0	401.6*
3	49	224	18	7	1	0	0	0	366.4*
4	69	233	12	4	1	0	0	0	385.1
5	71	241	5	1	2	0	0	0	510.6*
6	75	237	5	5	2	1	0	0	574.6**

In each plot, the selected patches were patches (other than the most preferred ones) which had areas closest to 65 m^2.

When sheep were grazing, 69% of the scans showed them to be on grass patches. For each plot and group of sheep there was a positive linear relationship between actual and expected percentages of scans of sheep grazing on patches, as patch area increased, indicating that the sheep spent more time than expected grazing on the larger patches (Fig. 2) and the effect was highly significant over all the plots ($P < 0.001$). Resting behaviour was also seen on the larger patches, but lying and grazing on these patches tended to occur at different times of the day (Fig. 3).

When observations of sheep grazing on the most preferred grass patch in each plot were analysed, there were many more occasions when 4, 5 or 6 sheep grazed there together than would have been expected from the frequency with which the sheep visited those patches (Table 1a). The dispersion test showed that, in each plot, the sample variance was significantly larger than the expected variance for a binomial distribution (Table 1a, $P < 0.001$). A similar exercise was carried out for a medium-sized patch in each plot (mean area 68 m^2, S.E. = 3.9) and this showed that there were significantly more occasions when two or more sheep grazed there together than would have been expected (Table 1b).

Table 2 shows the mean distances between NNs for pairs of sheep distributed across each of the possible combinations of patch and background vegetation. NNs grazing the same

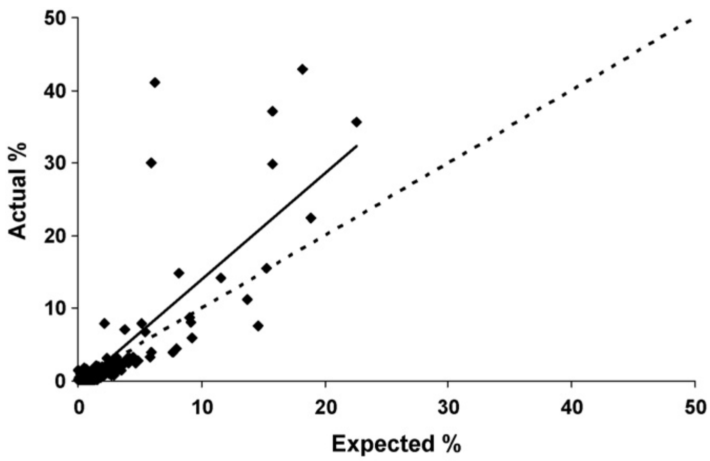

Fig. 2. The relationship between actual and expected percentages of scans of sheep grazing patches, with data for all plots combined and expected values based on relative patch area within plot, showing fitted trend line and 1:1 line (dotted).

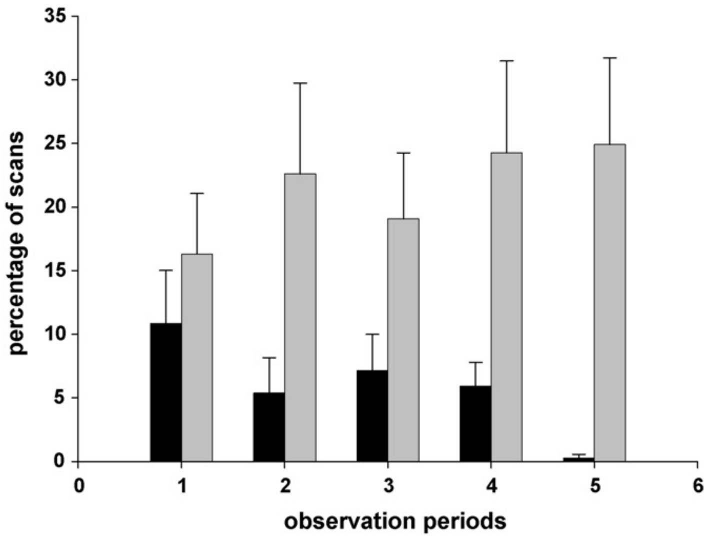

Fig. 3. Percentage of scans of focal sheep grazing on the same large (>100 m^2) patch as their nearest neighbour, when lying (black) and when grazing (grey) during the five 2-h observation periods: (1) 07:30–09:30 h, (2) 10:30–12:30 h, (3) 13:30–15:30 h, (4) 16:30–18:30 h, and (5) 19:30–21:30 h (S.E.s based on variation between plots).

grass patch were significantly closer together than NNs grazing all other combinations of vegetation type. The mean distance between NNs grazing on the same patch increased with patch area up to about 80 m^2, but not thereafter (Fig. 4). Mean NN distances for sheep grazing heather were intermediate between those of NNs on the same patch or grazing different patches. When grazing heather, the mean distance between sheep locations and the nearest grass patch edge was 1.23 m, with sheep grazing significantly closer to grass patches with sheep on them than to empty patches (0.98 m vs. 1.5 m, $F_{1,5} = 11.7$, $P < 0.001$).

There were individual differences in mean NN distance calculated over all vegetation types, with mean values for the 36 sheep ranging from 6.2 to 19.3 m (S.D. = 2.64). There was also a negative linear relationship between the overall proportion of time that individual sheep were seen sharing a patch with their NN and the mean distance to a NN when they were not sharing patches (Fig. 5). This linear relationship was significant when differences between plots were taken into account ($R^2 = 0.81$, $P < 0.001$). There was no relationship between overall individual mean NN distances for individual sheep and the overall percentages of time spent grazing grass.

Table 2
The mean percentage of time spent grazing and the mean distance between a focal sheep and its nearest neighbour (NN) for different combinations of patch and background vegetation

Vegetation types grazed by focal sheep and nearest neighbour	Time spent grazing (%)	Distance to NN (m)
Both sheep on same grass patch	34.3a	4.86a
Sheep on different grass patches	18.6b	13.43b
One sheep on grass and one on heather	30.2ab	11.14bc
Both sheep on heather	11.2b	9.58c
S.E.D.	3.53	0.73

Significance levels based on mean values for each plot ($n = 6$). Values in the same column that do not have the same letters are significantly different at $P < 0.001$.

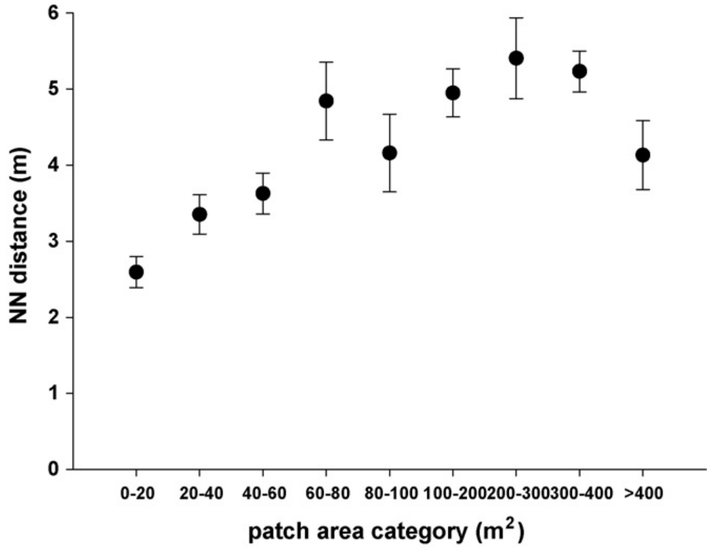

Fig. 4. Mean nearest neighbour distances for sheep grazing the same grass patch, with patches categorized by area (S.E.s based on variation between plots).

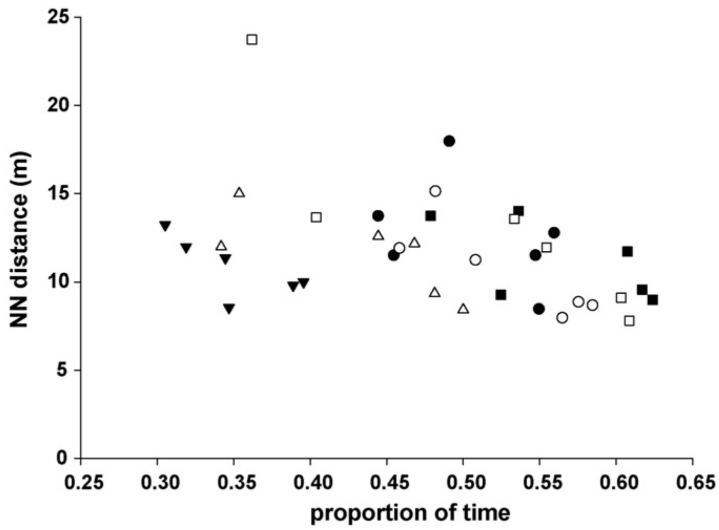

Fig. 5. Relationships between the mean proportion of time spent sharing patches with a NN and the mean distance to a nearest neighbour (NN) when not sharing patches. Data points are values for individual sheep in plot 1 (□), plot 2 (■), plot 3 (○), plot 4 (●), plot 5 (△), and plot 6 (▲).

4. Discussion

The relationship between time spent grazing and patch size suggests that the sheep preferred to graze on some of the largest grass patches in the mosaic. There are various reasons why this may have been the case. The larger patches may have been perceived as superior food resources, although there were no systematic differences in sward height with patch size at the beginning of the experiment. It has also been suggested that foraging costs are lower on large patches (Dumont et al., 2002) and in this mosaic animals may not always have had a clear line-of-sight to the next grass patch, due to the height of the heather plants and the slope of the ground. Another possible reason is that the larger patches tended to be situated in the inner corners of the plots and these positions were associated with the majority of observations of lying behaviour (Oom, 2003). The sheep could, therefore, have been grazing on the patches after moving there in order to rest, although this did not appear to be a strong effect since incidences of sheep grazing and lying on the larger patches tended to occur at quite different times of the day (see Fig. 3).

Our hypothesis was that patch choice would be affected by social behaviour and we suggest that one of the main reasons for the larger grass patches being preferred was because they enabled the sheep to graze in social groups. Obviously the chances of multiple sheep being on a particular patch at the same time will increase as the amount of time each animal spends there increases, so the presence of groups grazing together could simply have been a by-product of the general attraction of the patches. However, the frequencies with which sheep were seen in groups were significantly higher than would have been expected simply from the number of times that individual sheep visited those particular patches, suggesting that the animals made positive choices to graze there together. Although effects of both patch size and social behaviour on grazing distribution have been reported before (e.g. Clarke et al., 1995; Dumont et al., 2002; Sibbald and Hooper, 2003), this is the first time that a causal link between social behaviour and patch choice has been demonstrated in a complex vegetation mosaic.

Further evidence for a social effect is provided by the distances observed between nearest neighbours. Mean NN distances appear to have been constrained by patch size on patches smaller than 80 m^2 (see Fig. 4), but the lack of increase in NN distance thereafter suggests that the sheep were at their preferred spacing at around 5 m. The mean overall NN distance of 4.9 m for sheep sharing patches is also very close to values measured for Scottish Blackface sheep grazing homogeneous grass swards in previous experiments (Sibbald et al., 2000; Sibbald and Hooper, 2003). The opportunity to graze in groups is likely to have contributed to the attraction of the larger patches in this mosaic, and the much greater mean distance seen between nearest neighbours grazing different patches demonstrates that patch sharing was necessary for groups to maintain their preferred spacing while grazing grass.

Although pairs of nearest neighbours could theoretically have been at their preferred social spacing when both animals were on heather, other factors are likely to have come into play. Grazing animals are known to tolerate larger distances between them when the vegetation is of poorer quality (e.g. Dwyer and Lawrence, 1999), as they need to be more selective as they graze. In addition, mature heather plants are relatively difficult to walk through, since they are much taller than grass and have woody stems, and, as in the experiment of Hester and Baillie (1998), the sheep in this experiment tended to stay close to the grass patch edges when they were grazing heather. These physical constraints also reduce the likelihood that sheep will maintain the same spacing as they do on grass swards, when they are grazing heather.

It is well known that sheep show a preference for grazing grass in mixtures of grass and heather species (Armstrong et al., 1997; Osbourne, 1984) and grass was clearly preferred in this mosaic also, even though the relatively low sward heights are likely to have constrained grass intake to some extent (Penning, 1986). Our second hypothesis was that time spent on the preferred vegetation by individual animals would vary with social motivation, as a result of trade-offs that had to be made. There is evidence from previous studies with sheep that some individuals stay consistently closer to their companions than others (Lynch et al., 1985; Sibbald et al., 2005), and in this experiment there were quite large differences between individuals in overall mean NN distance. Sheep that were more likely to share patches were also found to be closer to a NN when grazing on separate patches or on heather. This suggests that there may well have been inherent differences in individual sociability. However, contrary to our hypothesis, these differences were not related to the overall amount of time spent on grass. It is possible that in a heather/grass mosaic with smaller, more widely spaced grass patches, where sheep are likely to spend more time on heather (Clarke et al., 1995) and patch sharing would be less practical, less sociable individuals might have a smaller proportion of grass in their diet.

A preference for the larger patches is not consistent with the results of Hester et al. (1999) obtained on the same vegetation mosaic, when Blackface sheep of the same age appeared to prefer the smaller patches. However, some of the larger patches were not present in the experiment of Hester et al. (1999) and have appeared since then, as a result of grazing and trampling damage by deer (A. Hester, personal communication). It has been shown that social affinity can modify the trade-off between social and foraging behaviour in patchy environments (Boissy and Dumont, 2002), and there were differences in the way the groups of sheep were selected for the two experiments. The groups of sheep used in the current experiment had already been established as social groups for several weeks, whereas in the study of Hester et al. (1999), individuals were randomly selected at the start of each grazing period and it is therefore likely that they had much weaker social bonds between them. This observation further supports our contention that social behaviour was an important factor influencing patch choice in this experiment. However, both experiments used groups of six Scottish Blackface sheep, and further research will be necessary to determine the extent to which the results can be generalised to larger groups, more sociable breeds of sheep and different degrees of environmental heterogeneity.

Acknowledgements

The authors wish to thank the staff at Glensaugh Research Station for provision of animals and the use of experimental facilities, David Elston and Jackie Potts of Biomathematics & Statistics Scotland for statistical help and Alison Hester, Javier Perez-Barbaria and Jim McLeod for helpful comments on earlier versions of the manuscript. The research was funded by the Scottish Executive Environment and Rural Affairs Department.

References

Armstrong, H.M., Gordon, I.J., Grant, S., Hutchings, N.J., Milne, J.A., Sibbald, A.R., 1997. A model of the grazing of hill vegetation by sheep in the UK. II. The prediction of offtake by sheep. J. Appl. Ecol. 34, 186–206.

Arnold, G.W., Dudzinski, M.L., 1978. Ethology of Free-Ranging Domestic Animals. Elsevier, Amsterdam.

Appleby, M.C., 1980. Social rank and food access in red deer stags. Behaviour 74, 294–309.

Boissy, A., Dumont, B., 2002. Interactions between social and feeding motivations on the grazing behaviour of herbivores: sheep more easily split into subgroups with familiar peers. Appl. Anim. Behav. Sci. 79, 233–245.

Clarke, J.L., Welch, D., Gordon, I.J., 1995. The influence of vegetation pattern on the grazing of heather moorland by red deer and sheep. I. The location of animals on grass/heather mosaics. J. Appl. Ecol. 32, 166–176.

Cochran, W.G., 1954. Some methods for strengthening the common chi-square tests. Biometrics 10, 417–451.

Dudzinski, M.L., Muller, W.J., Low, W.A., Shuh, H.J., 1982. Relationship between dispersion behaviour of free ranging cattle and forage conditions. Appl. Anim. Ethol. 8, 225–241.

Dumont, B., Boissy, A., 2000. Grazing behaviour of sheep in a situation of conflict between feeding and social motivations. Behav. Proc. 49, 131–138.

Dumont, B., Maillard, J.F., Petit, M., 2000. The effect of the spatial distribution of plant species within the sward on the searching success of sheep when grazing. Grass For. Sci. 55, 138–145.

Dumont, B., Carrère, P., D'Hour, P., 2002. Foraging in patchy grasslands: diet selection by sheep and cattle is affected by the abundance and spatial distribution of preferred species. Anim. Res. 51, 367–381.

Dwyer, C.M., Lawrence, A.B., 1999. Ewe–ewe and ewe–lamb behaviour in a hill and a lowland breed of sheep: a study using embryo transfer. Appl. Anim. Behav. Sci. 61, 319–334.

Fretwell, S.D., Lucas, J.H.J., 1970. On territorial behavior and other factors influencing habitat distribution in birds. Acta Biotheor. 19, 16–36.

Gimingham, C.H., 1972. Ecology of Heathlands. Chapman and Hall, Oxford.

Hester, A.J., Baillie, G.J., 1998. Spatial and temporal patterns of heather use by sheep and red deer within natural heather/grass mosaics. J. Appl. Ecol. 35, 772–784.

Hester, A.J., Gordon, I.J., Baillie, G.J., Tappin, E., 1999. Foraging behaviour of sheep and red deer within natural heather/grass mosaics. J. Appl. Ecol. 36, 133–146.

Lawes Agricultural Trust, 2002. GenStat, 6th ed., Copyright 2002. Lawes Agricultural Trust, Rothhamsted.

Lynch, J.J., Wood-Gush, D.M.G., Davies, H.I., 1985. Aggression and nearest neighbours in a flock of Scottish Blackface sheep. Biol. Behav. 10, 215–225.

Nicholson, I.A., Robertson, R.A., 1958. Some observations on the ecology of an upland grazing in north-east Scotland with special reference to Callunetum. J. Ecol. 46, 239–270.

Oom, S.P., 2003. Spatial Pattern and Process in the Fragmentation of Heather Moorland. PhD Thesis. University of Edinburgh.

Oom, S.P., Hester, A.J., 1999. Heather utilization along paths by red deer and sheep in a natural heather/grass mosaic. Bot. J. Scotland 51, 23–38.

Oom, S.P., Hester, A.J., Elston, D.A., Legg, C.J., 2002. Spatial interaction models: from human geography to plant–herbivore interactions. Oikos 98, 65–74.

Osbourne, B.C., 1984. Habitat use by red deer (*Cervus elaphus* L.) and sheep in the West Highlands. J. App. Ecol. 21, 497–506.

Penning, P.D., 1986. Some effects of sward conditions on grazing behaviour and intake by sheep. In: Gudmundsson, O. (Ed.), Grazing Research at Northern Latitudes, Proceedings of a NATO Advanced Workshop, Hvanneyri, Iceland. Plenum Press Series A: Life Sciences, vol. 108, pp. 219–226.

Sibbald, A.M., Shellard, L.J.F., Smart, T.S., 2000. Effects of space allowance on the grazing behaviour and spacing of sheep. Appl. Anim. Behav. Sci. 70, 49–62.

Sibbald, A.M., Hooper, R.J., 2003. Trade-offs between social behaviour and foraging by sheep in heterogeneous pastures. Behav. Proc. 61, 1–12.

Sibbald, A.M., Hooper, R.J., 2004. Sociability and the willingness of sheep to move away from their companions in order to graze. Appl. Anim. Behav. Sci. 86, 51–62.

Sibbald, A.M., Elston, D.A., Smith, D.J.F., Erhard, H.W., 2005. A method for assessing the relative sociability of individuals within groups: an example with grazing sheep. Appl. Anim. Behav. Sci. 91, 57–73.