Effect of group size on the consistency of movement direction among cows in a small grazing group

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Abstract

This study investigated the effect of group size on the consistency of movement direction among grazing cows in a small group by analyzing their intra- and inter-patch movement behaviour. Three (GROUP-3) and 6 (GROUP-6) cows grazing in a 1.6-ha pasture were observed. The positions of cows were recorded at 1-s intervals by GPS, and the feeding station (FS) and steps between FSs was observed. A patch was defined as a cluster of FSs. For each intra- and inter-patch movement, actual distance moved (ADM), and distance moved in a consistent direction (DMCD: ADM \(\times \cos(\alpha)\)), where \(\alpha\) is the angular difference in movement direction between the focal animal and group members' center coordinate) were calculated. The ratio of \(\Sigma[DMCD]\) to \(\Sigma[ADM]\) (DMCD-Ratio) was also calculated. For intra-patch movement, ADM, DMCD, and DMCD-Ratio were similar between GROUP-3 and GROUP-6. For inter-patch movement, both ADM and DMCD were greater for GROUP-6 than for GROUP-3 \((P < 0.01)\), and DMCD-Ratio was higher for GROUP-6 than for GROUP-3 \((P < 0.05)\). The large group size enhanced the consistency of inter-patch movement direction among grazing cows and increased their inter-patch movement distance. The increase of the spatial group cohesion was also observed in the large group.

Key Words: cattle; grazing behaviour; group size; movement direction

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Introduction

Foraging is the process of searching for and eating food resources, and largely affects both an animal's fitness and the environment (Stephens \textit{et al.}, 2007). In grazing systems, grazing behaviour (i.e. foraging behaviour of grazing herbivores) have a key role for productivity (Bailey \textit{et al.}, 1996). That is, the movement behaviour of grazing herbivores is closely related to their grazing site selection, and thus the spatial heterogeneity of swards would be affected (Parsons & Dumont, 2003). The spatial heterogeneity of swards can in turn influence grazing site selection by herbivores (Dumont & Gordon, 2003). Spatial utilization of environments is reflected by movement behaviour during grazing. Thus, understanding the factors affecting the movement behaviour of grazing herbivores is an important step in improving grazing management and foraging efficiency.

In group-living herbivores, their gregarious tendency should largely contribute to movement behaviour (Gompper 1996; Ramseyer \textit{et al.}, 2009a, b), and would also affect movement behaviour during grazing (Dumont & Boissy, 2000; Sibbald & Hooper, 2003). The leader-follower relationship is the typical pattern of behaviour in group-living animals, and spatial leadership, as a different concept of social leadership, was observed among dairy cows in movements between a barn and a paddock (Kondo \textit{et al.}, 1980). Some authors have implied that spatial leadership played a key role in the movement of animals during actual grazing (Sato 1982; Dumont \textit{et al.}, 2005; Sárová \textit{et al.}, 2010). Although spatial leadership could explain the mechanism of group cohesion, it does not explain how herbivores modulate movement behaviour while grazing as a group. Herbivore groups are stable only if group members synchronize their activity (Conradt & Roper 2000). Thus, for herbivores grazing in a group, the consistency of movement direction among group members may be important for group cohesion. However, studies of such social interactions for herbivores during actual grazing sessions are limited.

One of the factors affecting the consistency of movement direction may be group size. For instance, assuming that animals in a group adjust their movement direction with respect to nearby animals (similar to the assumption of some modeling
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approaches; e.g., Viscido et al., 2002), such adjustment opportunity of the animal would increase when group size is large, because the large group size increases the opportunity of approaching group members. Or more simply than that, extra movement may be needed to maintain group cohesion when the group size is large. Thus, it is hypothesized that the consistency of movement direction among cows during grazing required to maintain group cohesion increases with group size. Initially, these investigations should be conducted using small groups to avoid the splitting of a group into subgroups (which makes the interpretation of the consistency of movement direction difficult).

As the patch of grazing herbivores can be defined as a sequence of steps with eating (Bailey et al., 1996), movement behaviour can be divided into continuous steps with eating (intra-patch movement) and continuous steps without eating (inter-patch movement). Herbivores modulate these movement behaviours as different processes (Shingu et al., 2010). This study investigated the effect of group size on the consistency of movement direction among grazing cows to verify the behavioural modulation of herbivores in a group.

Materials and Methods

The grazing experiment was conducted at the Experimental Farm (43° 05' N, 141° 20' E) of the Agro-Ecosystem Research Station, Field Science Center for the Northern Biosphere, Hokkaido University, Sapporo, Hokkaido, Japan. The present study was approved by the Technical Committee for Experiments on Animals at Hokkaido University.

1. Pasture, animals, and their management

A 1.6-ha pasture (163 m × 55 m + 88 m × 80 m) was used in this study. The pasture supported perennial ryegrass (Lolium perenne L.), orchard grass (Dactylis glomerata L.), and a small amount of white clover (Trifolium repens L.). Before the experimental period in October, the pasture had been continuously grazed by experimental cows as a group from May. The pasture was fertilized with 27.3 kg N/ha and 68.4 kg P2O5/ha in May and with 50.9 kg N/ha, 9.2 kg P2O5/ha, 40.0 kg K2O/ha in each of July, August, and September.

Six Holstein Friesian cows that were accustomed to grazing the experimental pasture were used. Mean weight and age of these cows was 778 kg (SD 60.0) and 7.1 years old, respectively. Three cows were selected as focal animals, and these focal animals and the others were balanced according to weight and age. On October 13, 15, 17, 19, 21, and 23, the 3 focal cows were allowed to graze in the experimental pasture (GROUP-3), while the remaining 3 cows grazed in another pasture. The pastures were located near to one another and the cows could see each other. However, aggregation of the focal animals with the other cows through a fence, or any leading-following behaviour among them, was not observed. Therefore, the behaviour of each group was considered to be independent. On October 12, 14, 16, 18, 20, and 22, the remaining 3 cows were also allowed to graze in the experimental pasture with the focal animals, forming a group of 6 cows (GROUP-6). Grazing was limited to 5 h (from 08:00 to 13:00) per day to observe the active grazing behaviour of the cows. At all other times, cows were kept in a paddock and were fasted (i.e., no supplemental feed was provided) to ensure active grazing during the observation periods. Free access was given to water and mineral blocks for these cows while they were kept in the paddock.

2. Measurements

2.1. Sward height, herbage mass, and compressed sward height

On October 11, sward height was measured using a ruler at 5 points in each of 17 quadrats (50 × 50 cm) and grass in the quadrat was cut to ground level. These samples were oven-dried at 60°C for 48 h to estimate herbage mass (t DM/ha).

To evaluate the heterogeneity of the pasture, compressed sward height, which is an index of the herbage mass at the measurement point (Michell, 1982), was measured using a rising plate-meter (Ashgrove, Hamilton, New Zealand). The measurements were made at every 3 steps of an observer (the same observer throughout the experiment) walking across the whole pasture. In total, approximately 500 measurements were recorded.

2.2. Grazing behaviour

The animal observations were conducted during the first 2 h of each grazing period (from 08:00 to 10:00), when animals grazed actively. Any agonistic behaviour among experimental cows were not observed during the observation period. For each observation day, one trained observer recorded the grazing behaviour of 1 of the 3 focal cows using a video camera. Two repeated measurements were performed per cow and treatment. Thus, the total experimental period was 12 days. A feeding station (FS) was defined as the area from which an animal was able to graze without moving its forelegs (Bailey et al., 1996). In this study, a patch was defined as a sequence of FSs. To define the intra- and inter-patch movement (see 3.2.), each FS and the step taken between adjacent FSs were quantified from the videos by recording the universal time in which the animal moved its forelegs.

At the same time, the positions of all cows in a group were recorded at 1-s intervals using a global positioning system (GPS). A GPS receiver (DG-100, GlobalSat, New Taipei City, Taiwan) was placed on top of the animal’s head using a halter, which allowed to record the spatial position of the head without disturbing normal grazing activity. The measurements
of fixed points by the GPS unit showed a dispersion of 1.3 m around the mean value. Though this accuracy of the GPS may seem to be insufficient for observing fine-scale behaviour, it was sufficient to generate the movement vectors of patch scale behaviour (see results, Table 1 and 2). That is, the mean distance of both intra- and inter-patch movement were sufficiently larger than this dispersion (26.6 m and 9.7 m, respectively; estimated using more precise GPS corrected by differential signal). The movement vectors of intra- and inter-patch movement can be generated by synchronizing videos and GPS data (see 3.2.).

3. Data analysis
3.1. Analysis for inter-individual distance
The distance from each cow to its nearest neighbor during the observation period was calculated at 1-min intervals from the GPS data. Mean values over each observation period were calculated for statistical analysis. To evaluate group cohesion, nearest-neighbor distance was also calculated when the animals were distributed randomly. Random number generation in Microsoft Excel (Microsoft Corporation, Redmond, WA, USA) was used for this purpose. Random x-y coordinates (that express virtual cows) were generated and plotted in a virtual experimental pasture 500 times for each group-size treatment. The nearest-neighbor distances for each of the 500 cases were then calculated.

The mean of the calculated distances was 36.4 m for GROUP-3, and 21.1 m for GROUP-6. These values were compared to the actual mean nearest-neighbor distance.

3.2. Definition of intra- and inter-patch movement
From the view point of the behaviour of herbivores, patch can be defined as the cluster of FSs (Bailey et al., 1996). In this study, the threshold step number between FSs delimiting among patches was determined by log-survivor analysis (Shingu et al., 2010). The concept of this determination was based on the method of Tolkamp et al. (1998) and DeVries et al. (2003), which was developed for determining meal criterion. In this method, the criterion was calculated by fitting a combination of two Poisson distributions to the distributions of log-transformed lengths of the intervals between eating visits, on the assumption that the distribution was a mixture of 2 random processes. In the present study, the first distribution showed the steps within patches and the second one represented those between patches. Maximum likelihood estimation was used to fit the combined distributions. The criterion was determined as the point at which the distribution curve of inter-patch steps intersected the distribution curve of intra-patch steps. The threshold step numbers of each cow were calculated for each observation day and animal. On the basis of this criterion, the FSs were

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<th>Table 1. Intra-patch movement behaviour of grazing cows</th>
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<td>GROUP-3</td>
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<td>Number of steps within patch</td>
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<td>ADM (m)</td>
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clustered into patches. That is, taking fewer steps between adjacent FSs than those of the threshold step numbers was regarded as the animal having moved within an patch, and taking more steps between adjacent FSs than those of the threshold step numbers was regarded as the inter-patch movement.

3.3. Evaluation of the consistency of movement direction

The consistency of movement direction was evaluated using a method modified from that of Focardi and Pecchioli (2005). For each intra- and inter-patch movement of the focal animal, the movement vectors of the animal itself and the group members' center coordinate during the same time period were generated (Figure 1). The initial point of the vector of intra-patch movement was the point where the animal starts to forage a new patch, and the terminal point was the point where the animal leaves for the next patch. This was vice versa for the movement vector of inter-patch movement. The center coordinates of group members were calculated as the mean of their coordinates. As this generating process is based on the movement of a focal animal, the movement of group members during this time period was not matched with their intra- and inter-patch movement for most cases. From these vectors, actual distance moved (ADM) and distance moved in a consistent direction (DMCD: ADM × COS[α], where α is the angular difference in movement direction between the focal animal and group members) were calculated. For example, when all the members in a group move in the same direction, α equals 0 and COS[α] equals 1; hence ADM equals DMCD. In contrast, when the angular difference in movement direction among animals is large, COS[α] and the consequent DMCD would have low values. Since the DMCD is largely affected by the ADM and may not express the consistency of movement direction, the ratio of ∑[DMCD] to ∑[ADM] (DMCD-Ratio) was also calculated. This value is an indicator of the extent of movement that contributed to the consistency of movement direction. The higher the consistency of movement direction among cows, the greater the DMCD-Ratio. Mean values of these parameters over each observation period were calculated for statistical analysis.

It could be considered that the DMCD and the DMCD-Ratio were inevitably higher for GROUP-6 than for GROUP-3 because the large group size might increase the possibility of the accidental consistency of movement direction with any group members. To verify the validity of these parameters, the DMCD and the DMCD-Ratio were also calculated when the group of 3 or 6 animals move randomly. Random number generation in Microsoft Excel (Microsoft Corporation, Redmond, WA, USA) was used for define the x-y coordinates of the animals before and after the movements. These movement simulations indicated that the DMCD and the DMCD-Ratio were similar between the groups of 3 or 6 animals when they move randomly. Therefore, the large group size did not necessary result in high values of these parameters.

4. Statistical Analysis

General linear mixed models were used to investigate the effect of group size on the consistency of movement direction. As repeated sampling of the same individual animals was performed, the individual animal was included as a random effect to avoid pseudoreplication (Hurlbert, 1984). General linear mixed models, including the animal as a random effect and group size (GROUP-3 or GROUP-6) as a fixed effect, were constructed and analyzed using the lmer function of R 2.6.2 statistical software (R Development Core Team, 2008). For the fraction data (DMCD-Ratio), a generalized linear mixed model with a Gamma distribution was applied.

Results

1. Sward height, herbage mass, and compressed sward height

Mean sward height was 15.6 cm and herbage mass was 1.9 t DM/ha. Mean compressed sward height was 13.5 cm and its coefficient of variation was 38.6%.
2. Nearest-neighbor distance and grazing behaviour

The distance from a cow to its nearest neighbor was greater in GROUP-3 than in GROUP-6 (27.4 m vs. 18.0 m; \( P < 0.05 \)). For both group size treatments, the nearest-neighbor distance was shorter than the distance calculated when the animals were distributed randomly \( (P < 0.01) \), indicating that group cohesion was sustained for both groups. The mean amount of time for which any cows were isolated from a group (i.e., for which the nearest-neighbor distance was greater than the calculated distance that assumed random spatial distribution of cows) was 22.5% of the total observed period for GROUP-3 and 23.9% of the total observed period for GROUP-6.

The threshold step number between FSs delimiting among patches was similar between GROUP-3 and GROUP-6 (2.7 steps vs. 2.3 steps). The intra-patch movement behaviour of cows is shown in Table 1 and inter-patch movement behaviour is shown in Table 2. There was no significant difference in the number of steps within patch movement between the treatments, although the number of steps between patches tended to be greater for cows in GROUP-6 than for cows in GROUP-3 \( (P = 0.07) \). For intra-patch movement, ADM, DMCD, and DMCD-Ratio were similar between GROUP-3 and GROUP-6. For inter-patch movement, both ADM and DMCD were greater for GROUP-6 than for GROUP-3 \( (P < 0.01) \), and the DMCD-Ratio was higher for GROUP-6 than for GROUP-3 \( (P < 0.05) \).

Discussion

Since the pasture in this study showed relatively high spatial homogeneity (Our unpublished data showed that the CV of compressed sward height ranged from 25.4 % to 78.1 % through the grazing season), the spatial heterogeneity of swards should not characterize the movement of grazing cows. Our results demonstrate that for the inter-patch movement of grazing cows, distance moved in a consistent direction with group members (inter-patch DMCD) and the ratio to total movement distance (inter-patch DMCD-Ratio) were both greater when the group size was large. This suggests that the relatively large group size enhanced the consistency of inter-patch movement direction among grazing cows.

In terms of the social interaction that affects movement behaviour during grazing, the present study has provided a new perspective - the consistency of movement direction. Affiliative relationships between individuals had been considered to be important for the movement behaviour of herbivores in a group. For example, Hayasaka et al. (1986) reported that individual cow in a group had a strong tendency to spatially associate more closely with other companions that have same growth history than with individuals that have different growth history. Ramseyer et al. (2009) found that ewes often recruited/followed their preferential partners for group movements. However, in this study, experimental cows formed a group for a long period, and affiliative relationships seemed to be similar among all pairs of group members. Therefore, affiliative relationships cannot explain the difference of the consistency of movement direction between the group size treatments.

One explanation for the difference in the consistency of movement direction between treatments can be related to the group cohesion during grazing. If animals forage solitarily, they would compete for a limited food resource with other solitary foragers (Beauchamp & Ruxton, 2005). In contrast, foraging as a group has been proposed to be efficient as individuals in groups are less likely to revisit patches that have already been exploited recently by others (Beauchamp & Ruxton, 2005). Estevez et al. (2007) discussed that as group size increases, more individuals will benefit from not getting involved in competition since individuals that do not participate in the competition can acquire more resources than those who participate in it. In groups of weaned calves, an increased group size resulted in little aggressive behaviour among animals (Færevik et al., 2007). In our case, cows in GROUP-6 had more competitors than cows in GROUP-3 for acquiring food resources. Thus cows in GROUP-6 might avoid competition by means of grazing as a group. In fact, large group size resulted in a decrease in nearest-neighbor distance in our study, and it indicated the higher group cohesion in GROUP-6 than in GROUP-3. The consistency of movement direction among cows should promote the animals to move a new foraging site with their group members, and it might play an important role for such group cohesion during grazing.

One issue that should be addressed for our analysis is the interpretation of how grazing animals matched their movement direction with group members. In this study, we calculated the mean movement direction of all group members to evaluate the consistency of movement direction. However, the assumption that grazing cows always react to all group members' movements is not realistic. In a study of a bird flock, it was shown that each bird interacts with a fixed number (6 to 7) of its neighbors to maintain the flock's cohesion (Ballerini et al., 2008). Although the behaviour of birds and grazing herbivores should not be directly compared, such an analysis of interactions between each pair of individual animals in the group may provide further insight.

Laca et al. (2009) pointed out that even with the same animal density, bite distribution on swards may differ if the group size is different. Our results would support their suggestion, and it is an important point to consider for grazing management. As animal density (i.e., stocking rate) determines herbage allowance per animal, it has been represented as one of the main factors affecting herbage intake of grazing herbivores (e.g., Stockdale & King, 1983; Kennedy et al., 2007).
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However, the present study indicates that group size affects not only herbage allowance but also grazing movement behaviour. The spatial heterogeneity of sward and consequent herbage intake of herbivores may be affected by group size. Because this study was performed using the same paddock area, an experiment in which the paddock area is changed in relation to group size is needed to demonstrate such an effect of group size.

In conclusion, our study showed that large group size could enhance the consistency of inter-patch movement direction among grazing cows. This behavioural modulation may help to maintain group cohesion spatially.

References


短期数の放牧牛群においてグループサイズが移動方向の一致の程度に及ぼす影響

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要約

短期数の放牧牛群においてグループサイズが他個体との移動方向の一致の程度に及ぼす影響を、バッテ内移動、バッテ間移動を解析することで検討した。1.6haのイネ科主体草地にホルスタイン種乳牛3頭もしくは6頭を1日5時間放牧した。供試牛にGPSを装着し1秒間隔で位置データを得た。本論文ではバッテはフィーディングステーション（前肢を動かさずに採食できる範囲、FS）の集合と定義し、バッテ内移動とバッテ間移動を区分するためにFSおよびFS間移動を観察した。個々のバッテ内、バッテ間移動について、実際の移動距離（ADM）および他個体の移動方向と一致した方向への移動距離（DMCD：ADM×COS[α]、αは対象牛の移動方向と群他個体の中心座標の移動方向との角度差）を算出した。総DMCDが総ADMに占める割合（DMCD割合）も算出した。バッテ内移動では、ADM、DMCDおよびDMCD割合のいずれにも3頭群と6頭群とに差はみられなかった。バッテ間移動では、ADM、DMCDともに6頭群で3頭群より長く（P<0.01）、また、DMCD割合は6頭群で3頭群より高かった（P<0.05）。すなわち、比較的グループサイズが大きい場合、バッテ間移動における他個体との移動方向の一致の程度は高く、また、これにはバッテ間移動距離の増加が伴った。このとき群構造は空間的に維持された。

キーワード：ウシ、食草行動、グループサイズ、移動方向

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