Differences in the spacing behaviour of two breeds of domestic sheep (*Ovis aries*) – influence of artificial selection?

Grete H.M. Jørgensen, Inger L. Andersen, Øystein Holand and Knut E. Bøe.

Norwegian University of Life Sciences, Department of Animal and Aquacultural Sciences, P.O. box 5003, 1432 Aas, Norway.

*Corresponding author: Grete H.M. Jørgensen, telephone +47 64 96 51 42, fax +47 64 96 51 01, e-mail: grete.jorgensen@bioforsk.no

ABSTRACT

The aim of this experiment was to investigate differences in spacing behaviour, measured by the individual distance when resting and feeding, between two breeds of sheep with a different selection history. Eight groups of four pregnant ewes from the Nor-X breed (a heavy, composite breed mainly selected for growth and meat quality) and eight groups of four pregnant ewes of the coloured Spæl breed (a light breed, mainly selected for wool quality) were placed in oblong experimental pens for 7 days. The distance between animals was measured from digital video recordings. The heavy Nor-X ewes kept a significantly larger individual distance to their pen mates when resting but not when feeding compared to the lighter Spæl ewes. Spæl ewes also kept a significantly smaller individual distance during resting than during feeding, but this difference was not found in Nor-X ewes. Our results indicate that selection for growth and meat quality might influence spacing behaviour in sheep. Looking at the selection history of these two breeds we discovered differences in how long they had coexisted with large carnivores. The possible effects of previous exposure to carnivores and the role of domestication in modifying spacing behaviour are also discussed.

INTRODUCTION

Flocking behaviour is primarily influenced by resource availability and distribution (Gills & Kramer 1987; Matthiopoulos 2003), or predator pressure (Hamilton 1971). In groups of free-ranging sheep, the use of space varies according to breed, season, topography, forage availability and gender (Grubb & Jewell 1966; Lynch et al. 1992; Meldrum & Ruckstuhl 2009) and can to a large extent be explained by resource availability or distribution as well as the breed's domestication history. Animals that have undergone domestication can be recognized by rapid changes in phenotypic traits (Jensen 2006), the most important behavioural changes being reduced fear and anti-predator responses coupled with increased sociability and longer sensitive periods for socialisation (e.g. Belyaev et al. 1985). Domestic animals display strong social motivation and they are willing to work for access to conspecifics (e.g Adeymo & Heath 1982; Holm 2002; Hovland et al. 2008). Another interesting effect of domestication is a hightened threshold for agonistic behaviours – as reported in studies on Norway rats (Price 1984). More recent experiments on captive fish indicate the opposite, that aggression may increase with artificial selection for fast growth due to a correlation between aggressive behaviour and a prioritized access to resources (larger animals) (Ruzzante 1994). The latter seems to be a more likely effect in fast growing production animals as well, and if so, this may work to increase individual distance between individuals.

Individual distance can be defined as 'the minimal distance that an animal normally keeps between itself and other members of the same species' (Drickamer et al. 2002) and such distances have been observed in several taxonomic groups from insects (Dicke 1986) to fish (Partridge 1980), birds (Keeling & Duncan 1991) and mammals (Rosenblum et al. 1964). Other authors have used different terms, for instance 'social distance' (Lynch et al. 1992) which is defined as the maximum distance of dispersal (group cohesion), or 'personal field' (McBride 1971) which is an area around each animal that is greater in front of the head, and animals actively avoid entering the fields of others. Most avoidance behaviours in groups are linked to reducing the cost of the social lifestyle (Warburton & Lazarus 1991), just as attraction between individuals is linked to the benefits of group living. Indeed, it is imperative that individuals are able to maintain some space between them; enhancing communication transmission, foraging efficiency and escape response when being attacked by an opponent or predator (Krause & Ruxton 2002). However, synchrony is also important in order to maintain group cohesion and stability (Conradt & Roper 2000) and might furthermore be an important feature to ensure an effective anti-predator strategy in groups (Roberts 1996).

One important question that arises is whether individual distance should be regarded as a static or a dynamic entity? If static, one would expect animals to distribute themselves with a fixed individual distance between individuals, like often observed in birds sitting on an electric cable or nesting in a colony (Drickamer et al. 2002). In other species however, the individual distance seems much more dynamic, dependent upon space allowance (cattle: Kondo et al. 1989), familiarity, reproductive state or age difference (e.g. van Dierendonck et al. 2004). Activity also seems to modify the individual distance between animals. Resting animals will for example adjust their distance less frequently than grazing or moving animals, and free ranging sheep have been observed in closer proximity to their nearest neighbours at rest than during grazing (Lynch et al. 1985; Michelena et al. 2008). This phenomenon was explained by the relatively higher risk of predation and increased time to escape when animals were resting. Similar results have been reported in poultry (Keeling & Duncan 1991) but little data on differences in spacing according to activity have been gathered in other ungulates (Walther 1977; Blanc et al. 1999; Shiyomi & Tsuiki 1999; Petherick 2007).

Individual distance and flocking behaviour differ between breeds of sheep. For instance, Mediterranean types of sheep (e.g. Merino) maintain a closer individual distance than English lowland and Scottish hill types of sheep (Dwyer & Lawrence 1999; Fisher & Matthews 2001), which could be related to differences in predation pressure where these breeds have evolved. In predator-rich pastoral systems, artificial selection will focus on flocking behaviour to ease herding and decrease predator success. Sheep in Norway have lived together with predators like wolves and bears until the early 1900s (Swenson et al. 1994), and selection by humans was mostly based on ability to flock and ease of herding. During the 17- and 1800s however, Norwegian farmers started to import sheep from Great

Britain (Drabløs 1997). These British breeds had evolved without the influence of large carnivores for some time, since bears were exterminated during the 10'th century and wolves since the 17'th century in Britain (Schwartz et al. 2003). As the large predators became more and more scarce also in Norway, selection criteria for production traits like fast growth and wool quality got more important than flocking ability, and mainly British breeds were used to create crossbreds (Drabløs 1997) in the 1800's. Some herds of the Norwegian Spæl sheep (Nordic short tail breed group) were however saved by enthusiasts after 1900 with some crossing with similar sheep from the Faroe and Gotland islands and from Iceland, but with minimal influence from other breeds. A previous study indicates that there are behavioural differences between the native short tail sheep and the composite Norwegian White breed today, since the former flocked closer together than the latter, when exposed to predator-related stimuli (Hansen et al. 2001). Such breed differences have never been documented concerning the requirement for social space. Summarizing other data on spacing behaviour in sheep, the same trends occur; breeds which have been heavily selected by man display less gregarious behaviour than breeds that may have been less influenced by humans (Fisher & Matthews 2001). Also differences in flocking behaviour between two breeds of poultry have been explained by adaptations to different predator pressures in the two environments that these poultry breeds have evolved (Keeling & Duncan 1991). Few studies have investigated spacing behaviour in sheep (e.g. Crofton 1958; review: Lynch et al. 1992; Sibbald et al. 2000; Michelena et al. 2005) and none of these involved breed comparison in a controlled environment.

The aim of this experiment was to investigate differences in spacing behaviour, measured by the individual distance when resting and feeding, between two breeds of sheep with a different selection history. Because of earlier findings in both poultry (Keeling and Duncan 1991) and sheep (Hansen et al. 2001) indicating that breeds that have been heavily selected by man display less gregarious behaviour than breeds mainly influenced by natural selection, we hypothesized that the native Norwegian breed (Spæl) would maintain a smaller distance to its pen mates when resting and feeding than ewes from the composite breed (Nor-X). As free ranging sheep have been observed to gather closer together during resting compared to when grazing, we furthermore hypothesized that the ewes would maintain a larger individual distance when feeding than when resting. Finally, we hypothesized that the light breed (Spæl) would have a higher degree of behavioural synchrony than the heavy composite breed (Nor-x), since synchrony might be an important feature of an effective anti-predator behaviour (Roberts 1996).

METHODS

Eight groups of four ewes from the Nor-X breed were tested during four weeks in February/March 2007, and eight groups of four ewes of Spæl sheep were tested during four weeks in January/February 2008. The two breeds were tested in separate years due to restrictions in facilities and the fact that the experimental pens had to be thoroughly cleaned and disinfected before bringing in animals from another farm. Each group was transferred to one of two identical experimental pens for a period of 7 days.

Animals

The 32 ewes from the Nor-X breed, a large, white sheep selected for meat quality (meat line: Kvame 2005; Kvame & Vangen 2007) had a mean body weight of (mean ± STD) 79.6 ± 5.2 kg. It is based on several Norwegian crossbred breeds: Dala, Rygja and others, now grouped as Norwegian White, and has been crossed with imported Texel sheep on several occasions. All the ewes were pregnant in second to third trimester and were selected at random from a population of ewes that were 2 years old (all born in 2005) in order to make sure that they were fertile and had completed at least one pregnancy. Prior to the experiment, the ewes were housed in groups of 20-30 animals with a space of 2.3 –3.4 m^2 per animal on deep straw bedding. Sheep were given *ad libitum* access to silage and fresh water.

The 32 ewes from the coloured Spæl breed, a lighter Norwegian breed (Steinheim et al. 2008), mainly selected for wool quality (Eikje 1979; Drabløs 1997) had a mean body weight of (mean ± STD) 56.9 ± 7.7 kg. All the ewes were pregnant in their second to third trimester (mean age ± STD: 2.3 ± 0.6 years), and some of them had horns. Prior to the experiment the ewes were kept outdoors in groups with free access to shelter, silage and water. In December, the ewes were moved into a sheep barn, on deep straw bedding and kept in groups of 20-25 individuals with a space of 2.4 – 3.0 m^2 per animal. Also indoors the sheep were given *ad libitum* access to grass silage and water.

The mean weight difference between pairs within groups, regardless of breed was (mean ± STD) 6.1 ± 0.08 kg with a range from 0 up to 20 kg. For more information on the Norwegian sheep breeding scheme and genetic differences between the two breeds, refer to Eikje (1979) and Eikje et al. (2008).

Experimental pens

Two identical pens measuring 2.0 m x 12.0 m (24.0 m^2 in total and 6.0 m^2 per animal) were constructed (Fig 1) inside an insulated and mechanically ventilated building at the University campus Aas. The lying area was a raised platform with solid wooden floor running along the whole length of the pen and was 0.6 m wide. The platform was marked with black stripes every 0.5 m so that distance between individuals could be measured from video recordings. Every morning at 09:00 the platform was cleaned and a thin layer of saw dust was provided to insure a dry and non-slippery surface. In order to prevent the sheep from lying in the activity area, grids made of wooden beams (5.0 x 5.0 cm) were placed on the concrete floor between the feed barrier and the resting platform. A continuous horizontal feed opening ran along the other side of the pen, for the entire 12 m length. On top of the feed barrier black stripes were painted for every 0.5 m (Fig 1).

Feeding

The ewes had free access to good quality hay that was evenly distributed along the 12.0 m feed barrier. Every morning the hay residues were removed and a standard concentrate feed for sheep (0.3 kg/day per ewe) was evenly distributed along the feed barrier, before fresh hay was administered. Water was provided *ad libitum* from two buckets, one in each short end of the pen.

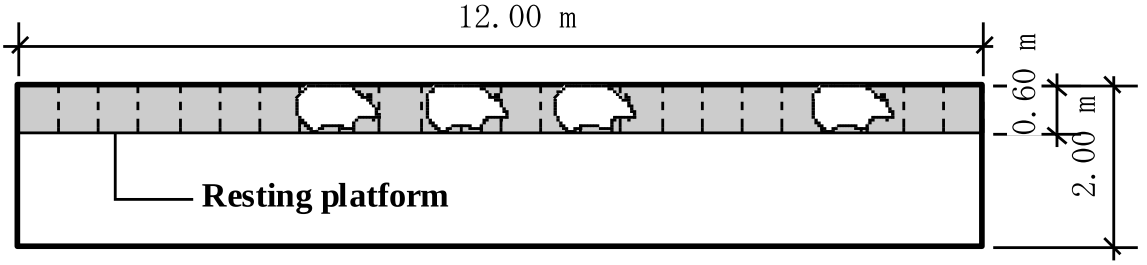

Figure 1. The experimental pen with a wooden platform for resting area (grey), activity area covered with grids and a feeding table.

Behavioural observations

The white Nor-X ewes were individually marked with numbers from 1 to 4 across their backs, with a standard marking spray for animals. Most of the Spæl sheep had coloured wool and was therefore identified by their different markings on the heads, legs or wool colour (brown, black, grey or mixed colour). If two sheep in the same group were hard to tell apart, they were marked using strips of white textile that was tied into their coat of wool (Fig 2b). Four colour cameras were mounted above each pen and connected to a digital video recording system (MSH video system®). The ewes were video recorded for 24 hours on the 7th day of each experimental period.

The distance between the ewes (measured from the closest edges of the two sheep's outlines) and their positions towards other ewes when lying ("Head to Head", "Head to Back" or "Back to Back", Fig 2a) was scored for each of the six possible pairs per group (96 different pairs in total), using instantaneous sampling every 15 minutes from 6 p.m. to 6 a.m. (a quiet period of the 24 hours), giving 50 observations per group.

The distance between the ewes when feeding (Fig 2b) was scored using instantaneous sampling every second minute for four hours (two hours immediately after morning feeding (08:00), and two hours immediately after evening feeding (15:00), giving 120 observations per group.

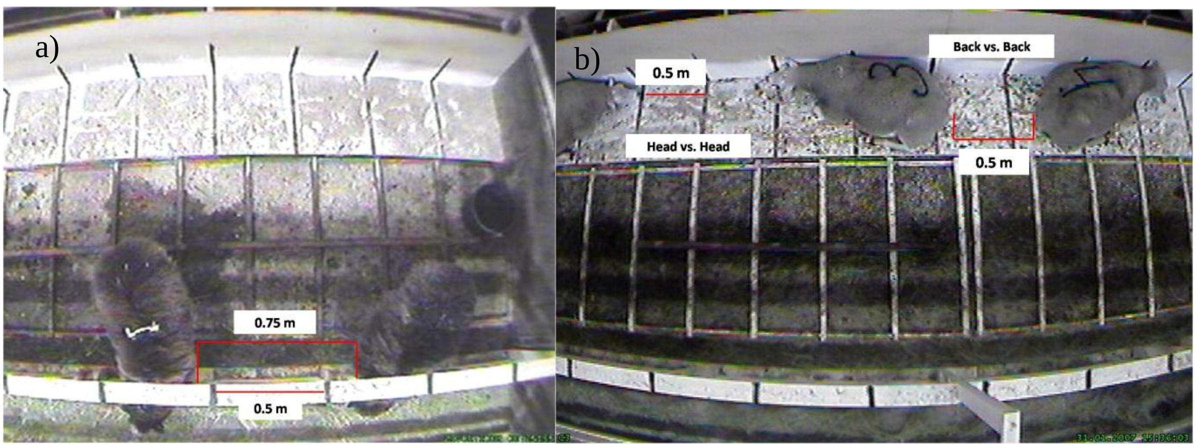

Figure 2a). Experimental pens and examples of measures done between pairs of resting sheep. Figure 2b). Experimental pens and example of measures done between pairs of feeding sheep.

The same person performed all observations and the mean distance between the two individuals in each pair was calculated and used as statistical unit in the datasets.

Coefficient of synchrony

In order to calculate if feeding and resting behaviour was more synchronized than could be expected by chance, we calculated a kappa coefficient of agreement as a coefficient of synchronisation (Rook and Penning, 1994).

Ethical note

A university representative of the National Research Authority (www.FDU.no) approved this experiment, and no ethical concerns were indicated. Animals were minimally handled and kept in pens with lower animal density compared to their normal housing conditions. As soon as each group had spent 7 days in the experimental pens they were returned to their home environment (commercial farming).

Statistical analysis

To test the effects of breed or weight differences on individual distance and CV of individual distance we used a mixed model of analysis of variance, with breed (Nor-X, Spæl sheep), group (1-16), type of activity (resting or feeding) and the interaction between breed and type of activity as class variables. Group nested within breed was specified as a random effect, while weight difference between pairs was included as a continuous variable (SAS Institute Inc. 1989).

The effect of breed and distance on the proportion of resting observations in the different body orientations ("Head to Head", "Back to Back" or "Head to Back") were tested using a a general linear model of analysis of variance with breed, distance category (0-1m; 1-2 m or more than 2m) and the interaction between body orientation and distance category as class variables. Effects of breed on the coefficient of resting and feeding synchrony were tested using a Z test comparing means, as described in detail in Rook and Penning (1991).

Correlations between the mean individual distance during resting and feeding were tested using Pearsons correlations, and least square means were used to verify the differences between means. All analysis were done using the SAS® 9.1 software.

RESULTS

Individual distance

The mean individual distance between group members was 2.2 m during resting and 2.7 m when animals were feeding. The Nor-X sheep kept a significant larger individual distance to their pen mates during resting ($F_{1,27}=18.3$, $P<0.001$) but not when feeding, compared to the Spæl sheep, Figure 3). Spæl sheep kept a larger distance to their group mates when feeding than when resting, but this difference related to activity was not found in the Nor-X sheep (significant interaction effect between breed and activity: $F_{1,27}=11.3$, $P<0.01$, Fig 3). Even though the two breeds differed in body weight, the heavy Nor-X sheep did not occupy more space at the resting area than the lighter Spæl sheep. Individuals from both breeds seemed to take up the space of approximately 1 meter (three painted stripes) when lying on the resting platform, and previous studies on body measurements show that body length changes little according to increased body weight (e.g. Janssens & Vandepitte 2004).

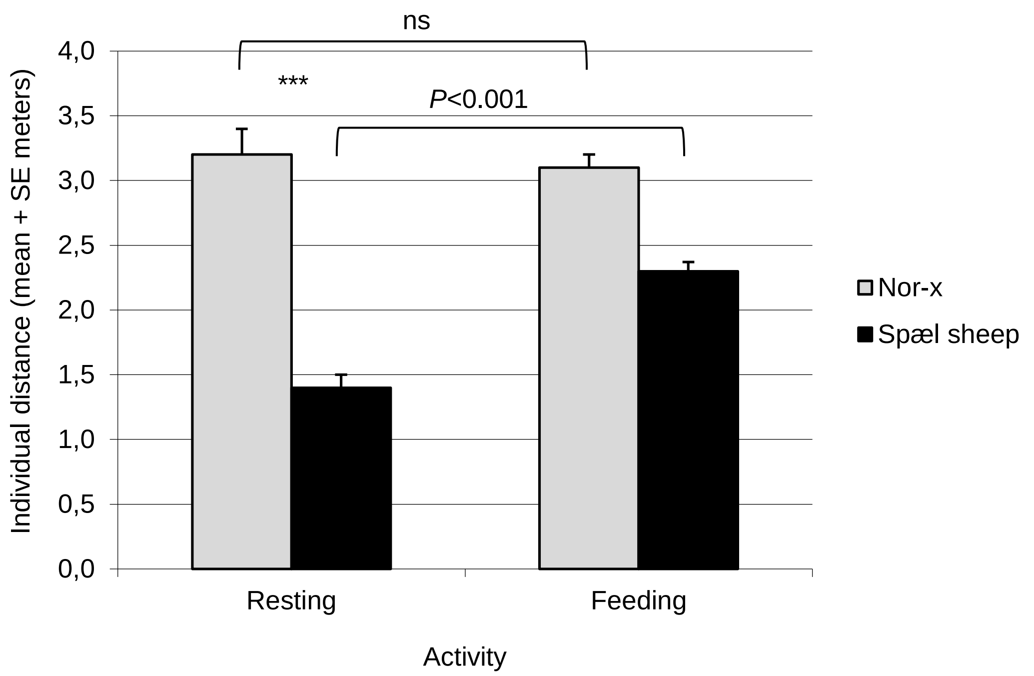

*Figure 3. Mean individual distance according to type of activity and breed. Differences between breeds within activity ***=P<0.0001.*

There was no significant effect of breed on the variation of individual distance. The coefficient of variance was larger when feeding (91.8 ± 2.5%) than when resting (71.7 ± 3.1%) regardless of breed ($F_{1,26}$=52.2; P<0.0001), indicating that the individual distance during feeding was less consistent since sheep changed places more frequently. No significant interaction effect between breed and individual distance or group effect was found for variation in individual distance during feeding or resting.

Pairs of sheep that kept in close proximity to each other during feeding also kept in close proximity to each other during resting (R=0.45, P<0.0001; Fig 4). Individual distance during resting or feeding was not affected by intra-pair weight differences.

Body orientation

More than 50 % of all resting observations were registered as sheep lying “Head to Back” (Fig 5), but the breeds did not differ significantly regarding resting positions. Pairs of ewes orientated Head to Head had in general a larger individual resting distance than pairs oriented either Head to Back or Back to Back (interaction effect between body orientation and individual distance: $F_{4,9}$=7.4; P< 0.0001).

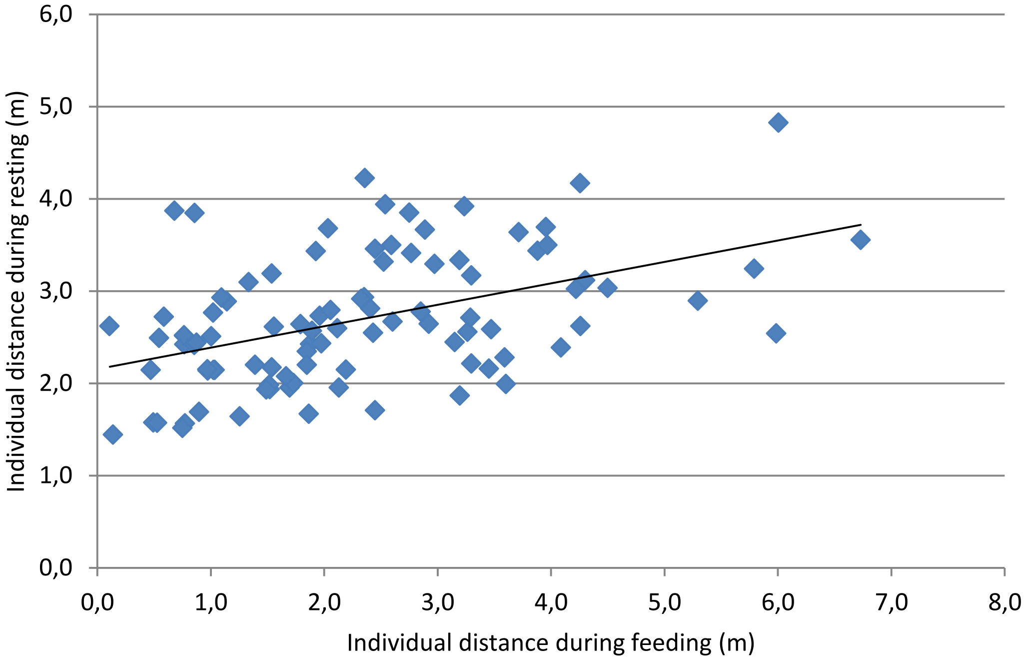

Figure 4. Regression between mean individual distance during feeding and resting activities for the 96 pairs of sheep.

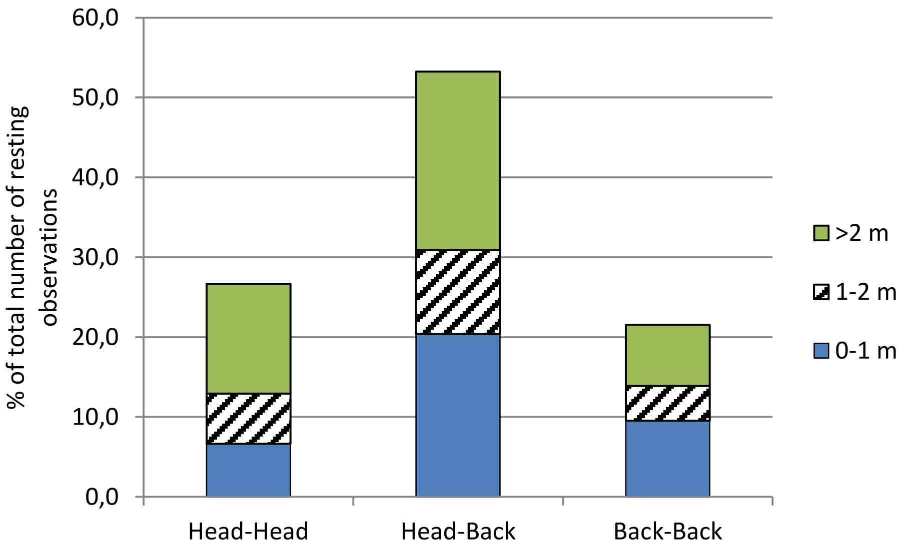

Figure 5. Proportion of resting observations in the different body orientations according to individual distance category.

Synchrony of behaviours

In general, all four group members were resting or feeding simultaneously in more than 60 % of observations (mean ± SE resting: 66.1 ± 3.2 %, feeding: 67.3 ± 2.4 %). In Spæl sheep 70.9 ± 4.7 % of all resting observations were registered in complete synchrony where all four group members rested at the same time, while the corresponding value for the Nor-X sheep was 61.4 ± 3.7 %. When feeding, complete synchrony was scored in 67.7 ± 4.2 % of feeding observations in the Spæl sheep, while this was 66.9 ± 2.7 % in the Nor-X sheep. The Kappa coefficient of synchronisation revealed that Nor-x ewes were more synchronous in resting behaviour than Spæl ewes, but no difference in synchrony was found for feeding behaviour (Table 1).

Table 1. Synchrony of resting and feeding behaviour and the effect of breed on Kappa coefficients of synchronisation.

		Observed proportion of synchronisation P (A)[1]	Expected proportion of synchronisation P (E)[1]	Kappa coefficient of synchronisation K[1]	Var (K)[1]	Z[1]	*P*-value
Resting	Nor-x	0.75	0.46	0.54	0.0055	2.18	0.028
	Spæl	0.70	0.44	0.46	0.0057		
Feeding	Nor-x	0.56	0.35	0.34	0.0032	-1.2	0.22
	Spæl	0.68	0.48	0.39	0.012		

DISCUSSION

As predicted, the Spæl sheep maintained smaller individual distances to their pen mates, both when resting and feeding, compared to ewes from the Nor-X breed. Furthermore, Spæl sheep kept a significantly smaller individual distance during resting compared to when feeding, while no such difference could be found for Nor-X ewes.

Free ranging sheep keep closer to their nearest neighbours when resting than when grazing (Lynch et al. 1985; Michelenea et al. 2008), a behaviour that could be related to anti-predatory strategies. Interestingly, Dwyer & Lawrence (1999) found that light and extensively kept sheep like Blackface were less gregarious than heavy, more intensively kept Suffolk sheep. Grubb & Jewell (1966) in fact suggested that domestication created animals that tolerated crowding to a larger degree and should therefore be more gregarious than animals subjected to natural selection only. One recent experiment on breed differences in anti-predator behaviour however, shows opposite results that correspond well with our findings (Hansen et al. 2001). Hansen et al. (2001) in fact used two breeds that were very similar to the breeds tested in the present experiment. Concurring with earlier findings in sheep (Lynch et al. 1985; Sibbald et al. 2005), we also found that individual sheep actively adjusted their distance to certain other individuals in the group, maintaining closer proximity to some ewes than others.

[1] For definitions and formulas to calculate these proportions and coefficients, please see Rook & Penning 1991.

Maintaining some individual distance is not only important to facilitate an effective fleeing response under predator attack, but it is also necessary to give the animal time to redirect its movement if it comes too close to another individual within the social group (Krause & Ruxton 2002). In sheep, individual distance is influenced by biological states, social relationships, resource distribution and crowding (e.g. Hutson 1984; Gills & Kramer 1987; Sibbald et al. 2000; Matthiopoulos 2003). In the present experiment we found a mean distance between individuals when resting of around 2.2 m, which corresponds well with observations done on free ranging Blackface sheep at rest (Lynch et al. 1985). The difference in individual distance between the two breeds in the present experiment is difficult to explain without noticing the difference in the two breeds' domestication history. Even though the Spæl sheep probably were less influenced by human selection for meat quality than the Nor-X sheep, this breed must still be considered fully domesticated with some human selection criteria being followed (Eikje 1979).

Earlier studies on farmed fish and their wild counterparts have proposed a correlation between artificial selection for growth and a decreased threshold for agonistic behaviour (Ruzzante 1994). In environments where resources are limited in space and monopolizable, animals that show more agonistic behaviours will have an advantage. Furthermore, if this natural selection within the domestic environment is accompanied by an artificial selection for growth, humans unintentionally might have selected for increased aggression (review: Huntingford & Adams 2005) which might also be manifested in increased individual distances as animals try to keep out of each other's way (Ruzzante 1994). On the other hand, articles comparing behaviour in breeds that have been more or less selected for production traits all show a common trend, high yielding breeds are more docile, they spend more time feeding and less time in social interactions (cattle: Sæther et al. 2006). This is explained by the theory of resource allocation that imply that all resources available in a given environment are optimally distributed between important production- and breeding traits (Beilharz et al. 1993; Schütz & Jensen 2001; Mignon-Grasteau et al. 2005).

Due to the cold winter climate and relative low temperatures in early lambing season, sheep husbandry is more or less similar throughout Norway, changing more according to the availability of spring pasture than according to sheep breed. It is therefore not likely that the Spæl sheep have been more exposed to predators the last hundred years, than the Nor-X breed. On the other hand, the Nor-X breed is a composite between Dutch (Texel) and heavy Norwegian sheep breeds with a noticeable influence of British breeds. As previously mentioned, British sheep breeds have been without the influence of large carnivores for more than 300 years (Schwartz et al. 2003) compared to Norwegian breeds that had less than 100 years without substantial influence of carnivores (Swenson et al. 1994). If these breed differences were large enough between the early Spæl sheep and the ancestors of the Nor-X sheep, then these behavioural mechanisms might still be visible today, after a rather limited time under similar intensive husbandry.

Over 50 percent of the resting observations in the present experiment were scored as pairs lying in a "Head to Back" orientation. One might expect that a subordinate ewe would try to maximize her distance to a dominant ewe, especially if they were orientated "Head to Head". This eventual link between individual distance, body orientation and social rank was not investigated in our experiment. Lynch & colleagues (1985) however, described that sheep tried to manoeuvre so that they did not face another sheep when resting, and our data showed that the individual distance depended on body orientation where pairs lying “Head to Head” kept a larger distance to each other than individuals lying “Back to Back”. This effect was also found in the present experiment, and since sensory organs are located on the head, the distance between the pair heads could be more important here than the distance between body outlines.

We did not find any significant breed differences in feeding synchrony, but Nor-x ewes were more synchronous in resting behaviour than Spæl ewes. Focussing on anti-predator strategies, our results are opposite of what we prediced. The effect might also have been suppressed by the relative limitations of the small group size and the pen environments that provided sheep with an overview of each other even though they were not engaged in the same activity. In nature on the other hand, the synchronisation of maintenance behaviours is important for group living animals to synchronize their behaviour in order to maintain group cohesion (Michelena et al. 2006), which in turn is beneficial in relation to anti-predator strategies.

In conclusion, the more selected Nor-X sheep kept a significant larger individual distance to their pen mates than the less selected Spæl sheep during resting. Spæl sheep kept smaller distance to their pen mates when resting than when feeding, while the Nor-X sheep showed no difference in individual distance according to activity.

ACKNOWLEDGEMENTS

The authors would like to thank Øyvind Vartal for help with building the experimental pens. We would also like to thank Johan Persbråten, Berit Morstad, Tone Sondresen, Agnes Klouman, Einar Sørensen and Inger Hansen. Tormod Ådnøy, Odd Vangen, Geir Steinheim and Inger Anne Boman are acknowledged for their valuable comments on breeding and selection history. Torfinn Torp also contributed with statistical advice. The experiment was funded by the Norwegian Research Council.

LITERATURE CITED

Adeyemo, O. & Heath, E. 1982: Social-Behavior and Adrenal-Cortical Activity in Heifers. Appl. Anim. Ethol. **8**, 99-108.

Beilharz, R.G., Luxford, B.G. & Wilkinson, J.L. 1993. Quantitative genetics and evolution: Is our understanding of genetics sufficient to explain evolution? J. Anim. Breed. Genet. **110**, 161-170.

Belyaev, D. K., Plyusnina, I. Z. & Trut, L. N. 1985: Domestication in the silver fox (*Vulpes fulvus desm*): changes in physiological boundaries of the sensitive period of primary socialization. Appl. Anim. Behav. Sci. **13**, 359-370.

Blanc, F, Michel, T. & Brelurut, A. 1999: Effects of mixed-species stocking and space allowance on the behaviour and growth of red deer hinds and ewes at pasture. Appl. Anim. Behav. Sci. **63**, 41-53.

Conradt, L. & Roper, T.J. 2000: Activity synchrony and social cohesion: a fission-fusion model. Proc. R. Soc. Lond. B. **267**, 2213-2218.

Crofton, H.D. 1958: Nematode parasite populations in sheep on lowland farms. VI. Sheep behaviour and nematode infections. Parasitology **48**, 251-260.

Dicke, M. 1986: Volatile Spider-Mite Pheromone and Host-Plant Kairomone, Involved in Spaced-Out Gregariousness in the Spider-Mite *Tetranychus urticae*. Physiol. Entomol. **11**, 251-256.

Drabløs, D. 1997: Soga om smalen (the story of the sheep), 1st edn. AiT Enger AS, Otta Norway.

Drickamer, L. C, Vessey, S. H. & Jakob, E. M. 2002: Animal Behaviour – mechanisms, ecology and evolution, 5th edn. McGraw-Hill, New York, USA.

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.

Eikje, E. D. 1979: Ei jamføring mellom spælsau og dei tyngre rasane Dala og Rygja (A comparison between Spælsau and the heavier breeds Dala and Rygja). Meldinger fra Norges Landbrukshøgskole **58**, 1-10.

Eikje, L. S., Ådnøy, T. & Klemetsdal, G. 2008: The Norwegian sheep breeding scheme: description, genetic and phenotypic change. Animal **2**, 167-176.

Fisher, A. & Matthews, L. 2001: The social behaviour of sheep. In: Social behaviour in farm animals, 1st edn (Keeling, L. J. & Gonyou, H. W., eds). CABI publishing, Wallingford UK, pp. 211-245.

Gills, D. M. & Kramer, D. L. 1987: Ideal interference distributions: population density and patch use by zebrafish. Anim. Behav. **35**, 1875-1882.

Grubb, P. & Jewell, P. A. 1966: Social grouping and home range in feral Soay sheep. Symposia Zool. Soc. Lond. **18**, 179-210.

Hansen, I., Christiansen, F., Hansen, H. S., Braastad, B. O. & Bakken, M. 2001: Variation in behavioural responses of ewes towards predator-related stimuli. Appl. Anim. Behav. Sci. **70**, 227-237.

Hamilton, W. D. 1971: Geometry for the Selfish Herd. J. Theoret. Biol. **31**, 295-311.

Holm, L., Jensen, M. B. & Jeppesen, L. L. 2002: Calves' motivation for access to two different types of social contact measured by operant conditioning. Appl. Anim. Behav. Sci. **79**, 175-194.

Hovland, A. L., Mason, G. J., Kirkden, R. D. & Bakken, M. 2008: The nature and strength of social motivations in young farmed silver fox vixens (*Vulpes vulpes*). Appl. Anim. Behav. Sci. **111**, 357-372.

Huntingford, F. & Adams, C. 2005: Behavioural syndromes in farmed fish: implications for production and welfare. Behaviour **142**, 1207-1221.

Hutson, G. D. 1984: Spacing behaviour of sheep in pens. Appl. Anim. Behav. Sci. **12**, 111-119.

Janssens, S. & Vandepitte, W. 2004: Genetic parameters for body measurements and linear type traits in Belgian Bleu du Maine, Suffolk and Texel sheep. Sm. Rumin. Res. **54**, 13-24.

Jensen, P. 2006: Domestication – From behaviour to genes and back again. Appl. Anim. Behav. Sci. **97**, 3-15.

Keeling, L. J. & Duncan, I. J. H. 1991: Social spacing in domestic fowl under semi natural conditions: the effect of behavioural activity and activity transitions. Appl. Anim. Behav. Sci. **32**, 205-217.

Kondo, S., Sekine, J., Okubo, M. & Asahida, Y. 1989: The effect of group size and space allowance on the agonistic and spacing behavior of cattle. Appl. Anim. Behav. Sci. **24**, 127-135.

Krause, J. & Ruxton, G. D. 2002: Living in groups, 2nd edn. Oxford series in Ecology and evolution, Oxford University Press, UK.

Kvame, T. & Vangen, O. 2007: Selection for lean weight based on ultrasound and CT in a meat line of sheep. Livest. Sci. **106**, 232-242.

Kvame, T. 2005: Selection for slaughter quality in two genetic lines of sheep by the use of computer tomography. Ph.D. Thesis, Norwegian University of Life Sciences, Aas, Norway.

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

Lynch, J. J., Hinch, G. N. & Adams, D. B. 1992: The Behaviour of Sheep – Biological Principles and Implications for Production, 1st edn. CAB International, Wallingford, UK.

Matthiopoulos, J. 2003: The use of space by animals as a function of accessibility and preference. Ecol. Model. **159**, 239-268.

McBride, G. 1971: Theories of animal spacing: the role of flight, fight and social distance. In: The Social Use of Space in Animals and Man, 1st edn (Esser, A.H, ed). Plenum Press, New York, USA, pp 53-68.

Meldrum, G. E. & Ruckstuhl, K. E. 2009: Mixed-sex group formation by bighorn sheep in winter: trading costs of synchrony for benefits of group living. Anim. Behav. **77**, 919-929.

Michelena, P., Henric, K., Angibault, J. M., Gautrais, P., Lapeyronie, R. H., Porter, J. L., Deneubourg, J. L. & Bon, R. 2005: An experimental study of social attraction and spacing between the sexes in sheep. J. Exp. Biol. **208**, 4419-4426.

Michelena, P., Noël, S., Gautrais, J–F., Gerard, J. L., Deneubourg, J. & Bon, R. 2006: Sexual dimorphism, activity budget and synchrony in groups of sheep. Oecologia **148**, 170-180.

Michelena, P., Gautrais, J–F., Gerard, J. L., Bon, R. & Deneubourg, J. 2008: Social cohesion in groups of sheep: Effect of activity level, sex composition and group size. Appl. Anim. Behav. Sci. **112**, 81-93.

Mignon-Grasteau, S., Boissy, A., Bouix, J., Faure, J. M., Fisher, A., Hinch, G. N., Jensen, P., Le Neindre, P., Mormède, P., Prunet, P., Vandeputte, M. & Beaumont, C. 2005: Genetics of adaptation and domestication in livestock. Livest. Prod. Sci. **93**, 3-14.

Partridge, B. L. 1980: The effect of school size on the structure and dynamics of minnow schools. Anim. Behav. **28**, 68-77.

Petherick, J. C. 2007: Spatial requirements of animals: Allometry and beyond. J. Vet. Behav. Clin. Appl. Res. **2**, 197-204.

Price, E. O. 1984: Behavioural aspects of animal domestication. Q. Rev. Biol. **59**, 1-32.

Roberts, G. 1996: Why individual vigilance decline as group size increases. Anim. Behav. **51**, 1077-1086.

Rook, A. J. & Penning, P. D. 1991: Synchronisation of eating, ruminating and idling activity by grazing sheep. Appl. Anim. Behav. Sci. **32,** 157-166.

Rosenblum, L. A., Kaufman, I. C. & Stynes, A. J. 1964: Individual distance in two different species of Macaque. Anim. Behav. **12**, 338-342.

Ruzzante, D. E. 1994: Domestication effects on aggressive and schooling behaviour in fish. Aquaculture **120**, 1-24.

SAS Institute Inc 1989: SAS/STAT® Users's guide, version 6, 4th edn. Cary, NC: SAS Institute Inc.

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**, 753-765.

Schwartz, C. C., Swenson, J. E. & Miller, S. D. 2003: Large carnivores, moose and humans: a changing paradigm of predator management in the 21st century. Alces **39**, 41-63.

Shiyomi, M. & Tsuiki, M. 1999: Model for the spatial pattern formed by a small herd in grazing cattle. Ecol. Model **119**, 231-238.

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., 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.

Steinheim, G., Eikje, L. S., Klemetsdal, G. & Ådnøy, T. 2008: Effect of birth weight, gender and litter characteristics on summer mortality in lambs of Norwegian breeds. Acta. Agri. Sec. A. Anim. Sci. **58**, 45-50.

Swenson, J. E., Sandgren, F., Wabakken, P., Bjärvall, A., Söderberg, A. & Franzen, R. 1994: Bjørnens historiske og nåværende status og forvaltning i Skandinavia (History, current status and management of the bear in Scandinavia). Research report No. 53, Norwegian Instituite for Nature Research, Trondheim.

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

van Dierendonck, M. C., Sigurjónsdóttir, H., Colenbrander, B. & Thorhallsdóttir, A. G. 2004: Differences in social behaviour between late pregnant, post-partum and barren mares in a herd of Icelandic horses. Appl. Anim. Behav. Sci. **89**, 283-297.

Walther, F. R 1977: Sex and activity dependency of distances between Thomson's gazelles (*Gazella thomsoni Günther 1884*). Anim. Behav. **25**, 713-719.

Warburton, K. & Lazarus, J. 1991: Tendency-distance models of social cohesion in animal groups. J. Theor. Biol. **150**, 473-488.