The Secret Life of Icelandic Goats

Activity, group structure and plant selection of the Icelandic goat

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Magister Scientiarum degree in biology

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To my dear friends
Margrét Vilmundardóttir, Bjarni Vilmundarson and Þórður Vilmundarson
who inspired, taught and guided me in life

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General Introduction

General Introduction

The Icelandic Goat Breed

The Icelandic goat (*Capra aegagrus hircus*) is believed to have originated from Norway and been brought to Iceland during 874-930 with the original settlers. There have been no further records of goats being imported to Iceland ever since (Adalsteinsson, 1981).

Goats are distributed in small numbers on farms throughout most of Iceland (Halla Eygló Sveinsdóttir and Ólafur R. Dýrmundsson, 1994). The only Icelandic goats found outside of Iceland are in Scotland. These goats are descendants from individuals exported in the 1980s for a cashmere production crossbreeding programme (Ólafur R. Dýrmundsson, 1990). While goats are found in most parts of Iceland, their numbers have always been small and subject to fluctuation over time. Earliest records on population numbers are from 1703. Since that time the population size has been less than 1000 individuals, with the exception of the period 1915 – 1945; see Figure 1 (Hagstofa, 2013; Ólafur R. Dýrmundsson, 2014; Stefán Aðalsteinsson, 2004). The population has dropped below a hundred individuals twice since 1703; first in 1885 during a cold period in Iceland and again in 1960, partly due to the culling of sheep and goats in order to eradicate maedi visna and other infectious diseases (Dýrmundsson, 2005; Halla Eygló Sveinsdóttir and Ólafur R. Dýrmundsson, 1994). Since then, population numbers have been increasing and in 2012 goats in Iceland were 849 individuals (Hagstofa, 2013; Ólafur R. Dýrmundsson, 2014). The Icelandic goat breed is now highly inbred (Birna Kristín Baldursdóttir, 2010; Stefán Aðalsteinsson, Ólafur R. Dýrmundsson, Sigríður Bjarnadóttir and Emma Eyþórsdóttir, 1994).

During the latter periods, when population numbers declined dramatically, there was a growing concern that the Icelandic goat breed might become extinct. Since 1965 the amendments to the Livestock Act resulted in state conservation grants for each individually recorded goat (Dýrmundsson, 2005). The Goat Breeders Society of Iceland was founded in 1991, and has worked in cooperation with the Farmers Association of Iceland on the conservation of the Icelandic goat breed and the marketing of goat products (Dýrmundsson, 2005Ólafur R. Dýrmundsson, 2014). It is believed that goats have never been as numerous as sheep since their production is not as profitable. Goats were often viewed as the poor man's cow as they need less fodder but milked well (Halla Eygló Sveinsdóttir, 1993). Goats are now mainly kept as pets but few farms keep them for both milk and meat production. The biggest goat herd can be found on Háafell Farm in Borgarfjörður District in West Iceland where around 190 winterfed individuals are kept.

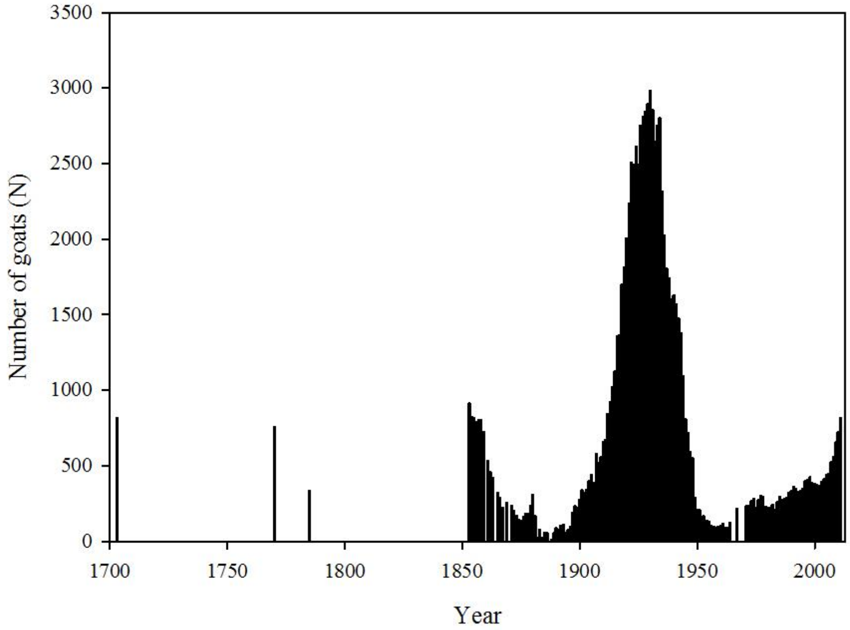

Figure 1 *Population size of the Icelandic Goat Breed for the years 1703-2012 (No information on population size available earlier than 1703 and breaks indicate gaps in records)* (Hagstofa, 2013; Ólafur R. Dýrmundsson, 2014).

Research on goats in Iceland has been very limited and no results from behavioural studies have been published in peer reviewed journals. One master and two bachelor theses have been written at the Agricultural University of Iceland. In 1993, Halla Eygló Sveinsdóttir wrote her bachelor's thesis on the general characteristics of the Icelandic Goat Breed (Halla Eygló Sveinsdóttir, 1993). Lára Hrund Bjargardóttir wrote a thesis in 2010 on the economic value of goats. Her main results were that the economic value of goats in Iceland had been undervalued. She suggested that emphasis should be on increasing their population size (Lára Hrund Bjargardóttir, 2010). Finally, Birna Kristín Baldursdóttir presented her master thesis in 2010 on population genetics, focusing on the genetic diversity of the Icelandic goat breed. Results showed that the population is in a critical state and highly inbred with low genetic diversity (Birna Kristín Baldursdóttir, 2010). So far very limited information is available on goat milk products in Iceland, mainly though on milk (Halla Eygló Sveinsdóttir and Ólafur R. Dýrmundsson, 1994; Ólafur R. Dýrmundsson, Jóhanna B. Thorvaldsdóttir and Thóra S. Kópsdóttir, 2006).

The research reported in this thesis is the first which sheds light on social behaviour, diet selection and grazing ecology of the Icelandic goat breed. The importance of understanding animal behaviour and diet selection for domestic animal husbandry and welfare is well documented internationally. Knowledge of animal behaviour may be more important today than previously as intensive husbandry is increasingly practiced and natural environments frequently unavailable to the animals. Furthermore, increased concerns over animal welfare have led to the need for more information about domestic animal behaviour, their needs and ecological role in their habitat (García, Celaya, García and Osoro, 2012; Jensen, 2006; Shackleton and Shank, 1984).

Description of social behaviour of goats

For the ethogram, aspects of social behaviour were described to estimate activity budget of goats. Goats exhibit a variety of social behaviours. Here the 10 categories which were seen in this study are described:

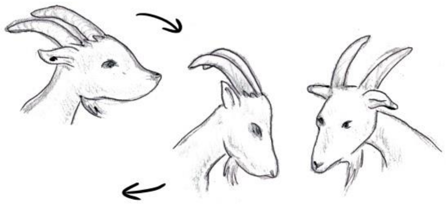

Figure 2 *Example of front butting*

Figure 3 *Example of social interaction of kid on doe*

Front butting: a goat lowers its head towards another goat, the other goat also lowers its head and they butt heads together (see Figure 2);

Butt threat: a goat initiates an antagonistic social interaction where it lowers its head towards and approaches another individual;

Kid on doe: kids interacting with their dams by climbing, standing or lying on them. When lying with their dam, kids sometimes touch their noses and sniff their horns (see Figure 3);

Mating behaviour: Males sniffing the genitals of a female and/or chases the female around the enclosure (no actual mating occurred during the study);

Nose to horn and nose to nose: one individual sniffs the horn or nose of another (this is a way to recognize individuals) (see Figure 4);

Play: two or more kids butt heads together similar to front butting or butt threats;

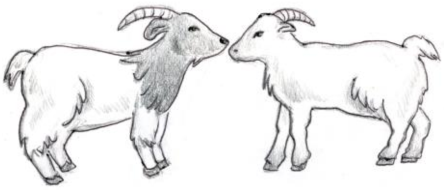

Figure 4 *Example of nose to nose*

Figure 5 *Example of submission*

Sideways butting: a goat lowers its head quickly and thrusts it upwards to the side of another goat, which typically results in the other goat retreating;

Submission: a goat first raises its head and points it away from the assailant (see Figure 5), then retreats by moving away;

Suckling: kid suckles a doe.

Social behaviour

The nature of social organization is one of the most fundamental features in animal societies (Tanner and Jackson, 2012). As predicted from the behavioural ecology theory, sociality evolves when the benefit of group-living exceeds the cost (Krause and Ruxton, 2002) and is expected to vary across species and habitats. In mammals, sociality can be beneficial as it provides greater protection against predators, better access to resources and increases mating opportunities. At the same time, sociality can promote intraspecies competition over access to resources and mating opportunities, as well as increased visibility to predators. (Kutsukake, 2009; Silk, 2007; Tanner and Jackson, 2012; Valone, 1989). When sociality is favoured, mammals may form groups ranging from small pair bonded units to big aggregations (Silk, 2007; Tanner and Jackson, 2012). All farm animals, for instance, are social with a strong tendency to form groups (Estevez, Andersen and Nævdal, 2007). It is believed that domestication has had little effect on their social behaviour and if opportunities arise as in the case of feral situations, the social organization which characterizes the wild species will form (Jensen, 2006; Jensen, 2009; O’Brien, 1988; Shackleton and Shank, 1984). Although domestic herbivores often differ morphologically from their wild or feral relatives, no evidence has been found indicating that their basic social behaviour has changed due to domestication and the social organization which characterizes the wild species will form (Jensen, 2006; Jensen, 2009; Shackleton and Shank, 1984).

Nature of groups and their formation

In order to be able to live in groups, individuals must find a balance within the group to minimize conflicts between individuals. Through repeated contest, a hierarchy is established within the group (East and Hofer, 2010). In general, the existence of a linear hierarchy decreases the frequency of aggressive behaviour between individuals in a group. Antagonistic behaviour varies considerably among species but dominance hierarchy will exist in any group of animals. Outcome of social conflicts between individuals in a group depends on variables such as age, sex and relatedness as well as on environmental factors such as access to food and other resources (Clutton-Brock, 2009; Kutsukake, 2009).

The nature of group formation varies greatly; an aggregation is considered a group of animals which are bonded to each other while a congregation is typically described as a casual or demographic animal group (Dunbar and Shultz, 2010). These distinctions focus on the difference between loose herds of the kind seen in many grazing ungulates on one hand and, on the other, more formal groups that can be seen in many primate species (Dunbar and Shultz, 2010). As stated previously, farm animals are social and have a strong tendency to form groups which are aggregations rather than congregations (Estevez *et al.*, 2007). Domestic herbivores, such as goats, form variously sized groups in response to local environmental conditions and habitat characteristics (O’Brien, 1988; Shackleton and

Shank, 1984; Shi, Dunbar, Buckland and Miller, 2005). Goats typically form groups of 4 – 10 individuals with a maximum size of 100 – 150 (O'Brien, 1988; Shackleton and Shank, 1984; Shi *et al*., 2005) depending on population density and habitat characteristics (Silk, 2007). For goats, as with other herbivores, habitat structure plays an important role in group size, with larger groups occurring in areas with more open terrain. Although most domesticated herbivores live in controlled environments, where antipredatory behaviour should be less relevant, domestic animals nevertheless maintain strong antipredator behaviour that shapes their social features (Estevez *et al*., 2007). Being in a group reduces fearful behaviour in novel situations. In addition, for domestic herbivores such as goats, individuals are continuously regrouped during rearing for management purposes leading to social instability and stress (Estevez *et al*., 2007). However, when the herd roams freely over a long period of time stability can be expected.

Many ungulates form casual or demographic congregations that do not build on strong social relationships (Dunbar and Shultz, 2010). Females can either form unstable groups that consist primarily of unrelated individuals that can lack stable membership or live in stable groups consisting of mainly related individuals (Clutton-Brock, 2009). Species such as wildebeest (*Connochaetes taurinus*) and reindeer (*Rangider tarandus*) live in loose herds while many equids and social carnivores such as hyenas (*Crocuta crocuta*) demonstrate strong bonds between individuals in their groups (Dunbar and Shultz, 2010). Research has also shown that domestic cows (*Bos primigenius*) (Coulon, Baudoin, Abdi, Heyman and Deputte, 2010; Greek and Greek, 2002) and domestic sheep (*Ovis aries*) form tight groups built on kinship (Hafdís Sturlaugsdóttir, 2008; Nituch, Schaefer and Maxwell, 2008). Shi *et al*. (2005) reported that feral goats (*Capra hircus*) on the Isle of Rum in Scotland form sexually segregated groups where males stay in one group and females and their offspring in another. Mixed-sex groups were occasionally recorded throughout the year but their frequency increased considerably in August and September during the rut period. During that time, bucks would join the females in polygynous foraging groups. The foraging groups were of various sizes and composition as individuals joined and left without any obvious reaction from other group members. Consequently the group size may vary over time as foraging groups fuse, fission or dissolve (Shi *et al*., 2005).

Fission-fusion group dynamics

Fission-fusion group type was first described for highly social species, such as the chimpanzees and bottle nosed dolphin, which are known for their social nature and intelligence (Bearzi and Stanford, 2008). Fission-fusion group type has now been described for several ungulates including: red deer (Conradt and Roper, 2000), African elephants (Archie, Moss and Alberts, 2006), Grevy´s zebra (Sundaresan, Fischhoff, Dushoff and Rubenstein, 2007), giraffes (Carter, Brand, Carter, Shorrocks and Goldizen, 2013) and feral goats (Shi *et al*., 2005). Goats have demonstrated the ability to discriminate between group members (Keil, Imfeld-Mueller, Aschwanden and Wechsler, 2012), locate food with cues from other individuals (Kaminski, Riedel, Call and Tomasellu, 2005) and follow gaze directions towards outside objects at the same level as primates (Kaminski *et al.*, 2005). This suggests that goats possess cognitive skills that enable them to live in complex fission-fusion societies (Kaminski, Call and Tomasello, 2006).

Fission-fusion societies are based on larger groups, known as ‘parent groups’, which fissure into smaller, flexible subgroups over the course of the day depending on activity and resources (Aureli *et al.*, 2008). There can be fluid movements of group members between subgroups resulting in changing sizes and composition. Subgroups are reflections of the fact that individuals synchronize their behavioural activity (Conradt and Roper, 2000; Dunbar and Shultz, 2010). Absence of behavioural synchrony may lead to separation of individuals and for groups to dissolve (Dunbar and Shultz, 2010). It can be costly for individuals to forgo an activity that would be individually beneficial in order to remain a part of the group. Individuals with similar needs and requirements are therefore more likely to synchronize their behaviour (Archie *et al.*, 2006; Conradt and Roper, 2000; Dunbar and Shultz, 2010). Age, sex and body size can affect behavioural synchrony and cause separation in the group (Conradt and Roper, 2000; Ruckstuhl and Neuhaus, 2000).

Sexual segregation

It is common for goats and other ungulates to form sexually segregated groups where females remain in groups with kids and males form single sex groups (Calhim, Shi and Dunbar, 2006; Main and Coblentz, 1990; O’Brien, 1988; Shackleton and Shank, 1984; Shi *et al.*, 2005). Sexual segregation greatly influences foraging behaviour of the sexes on pasture. Shackelton and Shank (1984) stated that sexual segregation seems primarily dependent on the seasonality of breeding. In milder climates, goats tend to breed periodically all year round and have more mixed groups. In less favourable climates, feral goats tend to breed only once a year and are sexually segregated for the rest of the year. The same pattern has been found with wild and feral sheep. Human controlled breeding in domesticated sheep follows a similar structure (O’Brien, 1988). Domestic goats have less space to form sexually segregated groups but when they do roam freely, this segregation takes place (Shi *et al.*, 2005).

Many hypotheses have been proposed explaining sexual segregation of ungulates, and specifically goats (Calhim *et al.*, 2006; Dunbar and Shi, 2008; Main and Coblentz, 1990; Main, Weckerly and Bleich, 1996; O’Brien, 1988; Ruckstuhl and Neuhaus, 2000). The most recent is the activity budget hypothesis which implies that the activity pattern between the sexes becomes desynchronized. The basic assumptions of this hypothesis are that sexual differences in body size lead to sexual differences in nutritional requirements which in the end lead to differences in foraging behaviour (Ruckstuhl and Neuhaus, 2000). Mooring *et al.* (2005) found that bison’s (*Bison bison*) were sexually segregated due to the males’ larger size. Research on feral goats supports both the activity budget hypothesis and the social preference model where same sex individuals are more likely to associate with each other (Calhim *et al*., 2006). Dunbar and Shi (2008) found that the activity budget of feral goats on the Isle of Rum was different between the sexes as they were not synchronized in their behaviour and therefore did not spend significant time together on pasture.

Activity budget

The life of all free ranging animals is divided into periods of rest and activity. It has been demonstrated that the activity budget varies between species and is expected to exhibit daily and even seasonal activity pattern (Shi, Dunbar, Buckland and Miller, 2003). The activity pattern of animals reflects a complex compromise between optimal foraging time, social activities and environmental constraints (Shi, *et al*., 2003). As animal populations show adaptations to their environment in maximizing energy intake, their behaviour can be a sensitive indicator of forage quality and quantity. Changes in activity patterns would be expected if the quantity and quality of forage resources change. Much of the work in this area is on domesticated species as it is more practical than studying their wild counterparts (O'Brien, 1988; Shi and Dunbar, 2009).

Goats are small ruminants which spend considerable time foraging as they have periods of ruminating and grazing. Their digestive system requires them to ruminate between foraging periods to digest (Heitschmidt and Stuth, 1991) while single stomached ungulates such as horses can go on foraging. Foraging is the dominant activity of all free-ranging ungulates as they typically devote around 40 – 60% of their day to that activity (Belovsky and Slade, 1986). Lu (1988) reported that a major proportion of goats' day is occupied in the activity of foraging and rumination.

Goats spend considerably more time foraging than sheep and less time ruminating (Kronberg and Malechek, 1997; Lu, 1988). They eat faster than sheep, spend relatively more time on plant selection and travel great distances during foraging (Lu, 1988). Therefore they select quality diet which requires less ruminating. Travelling on pasture and resting are considered to be the second most dominant behavioural categories after foraging. Other behaviours that free-ranging ungulates invest their time in are, for example, social interactions, grooming and excretion.

El Aich *et al.* (2007) found that on average goats in Morocco seemed to spend 70% of their time foraging while Solanki (2000) found goats in India spending on average 60% of their time foraging. Animut *et al.* (2005a) found that goats in Oklahoma spent slightly less time foraging or around 55% and similar results were found in the study by Stronge *et al*. (1997) on goats in New Zealand. They also reported that females spent significantly more time foraging than males. Similar results have been reported for sheep in Iceland where females spent significantly more time foraging than males as they need to produce milk for offspring (Anna Guðrún Thórhallsdóttir and Ingvi Thorsteinsson,1993). Orihuela and Solano (1999) showed that goats in Mexico spent more than 90% of their time foraging and only 4% on other types of behaviour. They concluded that this was possibly due to the fact that the goats spent only one hour each day on pasture and therefore used that time for foraging, the animals appeared highly motivated to forage during this time (Orihuela and Solano, 1999). Difference in foraging time of goats around the world is probably due to differences in pasture quality. Goats would spend more time foraging on a sparsely vegetated pasture while a productive pasture would require less foraging time (Papachristou, Dziba and Provenza, 2005).

Spatial distribution

In a natural heterogeneous environment, patches come in all shapes and sizes and differ in their spatial arrangements, so predicting where animals are likely to forage becomes difficult (Sibbald, Oom, Hooper and Anderson, 2008). During foraging, goats and other herbivores travel around pasture searching for desirable patches containing favourable species. The extent of travelling during foraging depends on forage availability, water sources, comfortable resting area, season and size of the goat, along with other physical factors (Lu, 1988). Environmental factors such as weather, topography and the risk of predation influence group distribution on pasture (Sibbald *et al.*, 2008). Howery *et al.* (1998) found cattle to be faithful to areas they were reared in and peers and environmental factors influence foraging decision as well. Yearlings tended to associate with each other rather than older ones and location on foraging patches shifted according to that (Howery, Provenza, Banner and Scott, 1998). Cattle (Howery, Provenza, Banner and Scott, 1996) and horses (Sigurjonsdottir, Thorhallsdottir, Hafthorsdottir, and Granquist, 2012) have been reported to occupy a certain home range when foraging on pasture. Foraging location of sheep is influenced by distance to other animals, group size and preferable patches (Dumont and Boissy, 2000). Sheep are highly gregarious animals and social motivation remains strong when foraging on pasture (Michelena, Sibbald, Erhard and McLeod, 2009). Sheep in Iceland have been reported to have large home ranges where related individuals forage and are faithful to areas they were reared in (Hafdís Sturlaugsdóttir, 2008). Wild or feral goats tend to gather at night in specific areas which serve the purpose of both shelter and night camp (O’Brien, 1988; Shi *et al.*, 2005). While travelling between foraging patches and shelters, goats are exposed to wide variety of plant species (Animut *et al.*, 2005b; Kronberg and Malechek, 1997).

Selective foraging

Herbivores are faced with numerous foraging choices each day and this selective foraging behaviour has resulted in an evolutionary adaptation in their digestive morpho-physiology. Hofmann (1989) describes three feeding types among ruminants: roughage feeders, concentrate selectors and intermediate selectors. Roughage feeders (grazers) have a relatively large rumen, small salivary glands, inert lips and tongue which give a well suited digestive system to cope with fibre rich nutrition like monocots. Concentrate selectors (browsers) have a relatively small rumen, large salivary glands, mobile lips and tongue and their digestive system is therefore adapted to nutritient rich, fibre poor forage, potentially with plant defences like dicots (Hofmann, 1989; Robbins, Spalinger and van Hoven, 1995). A big proportion of ruminants are morphopo-hysiologiaclly intermediate between roughage feeders and concentrate selectors. Intermediate mixed feeders are selective, choose mixed diet and are considered opportunistic (Hofmann, 1989).

Research shows that most herbivores forage selectively (Hofmann, 1989; Papachristou *et al.*, 2005). Foraging in a selective way is influenced by both external and internal factors. Selectivity depends on animal type and experience, nutritional need, peer pressure and plant community. Large herbivores generally forage on widely dispersed resources and therefore it has been suggested that aggression between group members is relatively unimportant (Shi and Dunbar, 2006). Small herbivores are more selective than larger ones with a similar digestive system as their energy requirements are proportionally higher.

Goats have been classified as intermediate mixed feeders as they are neither exclusively grazers nor browsers (Hofmann, 1989; Papachristou *et al.*, 2005). Smaller ruminants like goats have relatively higher energy requirements than bigger ones but at the same time they have smaller rumen. Because of this, smaller ruminants must be more selective on more digestible forage (Hofmann, 1989). Goats therefore spend more time foraging in shorter intervals compared to both cattle and sheep, and as previously said, foraging is considered a dominant activity (Belovsky and Slade, 1986). In months when favoured species abundance is high, goats selectively feed on these species, whereas during months when species abundance is low, goats adapt their foraging behaviour to consume a wider variety of species to meet their dietary requirements (Barroso, Alados and Boza, 2000). Goats are considered highly flexible and are known for their adaptability and efficient selective behaviour (Silanikove, 2000).

Plant selection

Goats and other herbivores are faced with numerous foraging choices in a highly variable environment, both in space and time (Provenza and Balph, 1988). They are known to be selective and to utilize wide variety of plant species (Animut and Goetsch, 2008). Unlike cattle and sheep, goats are able to assume both bipedal and aerial stance while foraging (El Aich, El Assouli, Fathi, Morand-Fehr and Bourbouze, 2007; Orihuela and Solano, 1999). Goats have proline-rich protein producing salivary glands which allows them to consume more tannin rich nutrition (Hofmann, 1989; Lamy *et al*. 2011; Makkar, 2003; Papachristou *et al.*, 2005; Robbins *et al.*, 1995). Dietary choices can be based on individual information, social information as well as being a post-ingestive feedback (Provenza and Balph, 1988;

Provenza, 1995; Provenza, Villalba, Cheney and Werner, 1998; Thorhallsdottir, Provenza and Balph, 1987). Goats favour browse species such as trees, shrubs and forbs regardless of availability (Heitschmidt and Stuth, 1991) but increase proportion of grasses in the absence of browse (Ferreira *et* al., 2013; Malechek and Leinweber, 1972). Plants that are selected proportionally more than their abundance are referred to as favoured species (Heitschmidt and Stuth, 1991). Plant selection among goats is dependant on both external factors (species availability, topography of pasture, season and weather condition) and internal factors (nutritional requirements and physiology) (Animut and Goetsch, 2008; Glasser *et al*., 2009; Hofmann, 1989; Robbins *et al*., 1995).

Although foraging preferences may vary according to location, goats can consume up to 50% of browse species (Odo *et al*., 2001). Mellado *et al*. (2006) found that lactating goats in Mexico did not differ in their plant selection during different stages of lactation. Grasses and browse accounted for more than 67% of the total forage eaten. Grasses were not abundant but still highly important in their diet (Mellado *et al*. 2006). Malechek and Leinweber (1972) reported that grasses accounted for 50 – 90% of the goats’ diet on a Texas rangeland while browse species were frequently less selected. Odo *et al*. (2001) found that goats in Nigeria seemed to graze more than browse which differs from other studies but that can be related to relative abundance of grass species. Few studies have been conducted on goat plant selection in West Europe or Scandinavia and Iceland.

Study objective

The main objective of this study was to study the social structure, activity budget and plant selection of Icelandic goats. Sub-objectives were firstly to describe group formation within two herds, i.e. find out if the herds are aggregations (close knit community), or fission-fusion congregations (casual or demographic community). Secondly, to describe the nature of social bonds during foraging by testing correlations between bonds and kinship, and correlations between bonds and age. Thirdly, to estimate activity budgets to determine how goats spend their time on pasture in a large free roaming herd compared to a smaller more confined one. For this purpose an ethogram for the Icelandic goat was constructed. Fourthly, to analyse plant selection during foraging and distribution on pasture to determine what kind of feeders Icelandic goats are. Finally, diet selection was compared to that of sheep in Iceland.

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Manuscript I

Social behaviour and activity budget of Icelandic goats

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Abstract

Farm animals are social with a strong tendency to form groups of various sizes. Goats form dynamic foraging groups in response to local environmental conditions and habitat characteristics. Lives of group living animals are divided into periods of rest and activity which results in a compromise between optimal foraging, social activities and environmental constraints.

The objectives of this study were to (i) assess the nature of the social structure of the biggest goat herd in Iceland (N = 186 adult goats), and (ii) to obtain information on the activity budget of this herd and to compare it with a smaller, more confined herd.

This study strongly supports a fission-fusion group type among goats. Results show mean group size in the large herd to be 5.3 in August and 6.1 in September and skewed towards 1 – 5 individuals. Number of groups was highest in the middle of the day and most foraging groups were found at 40 – 60 m above sea level, typically around the farm. Distribution of groups was found to be random in all but two cases (N = 64 scans). Formation of groups seemed neither to be based on kinship nor age as no significant correlation was found between bonded individuals and these variables. In both August and September, foraging was the principal activity and accounted for 70.1% and 71.3% respectively of overall activity of the big herd. The small, confined herd spent significantly less time foraging than the larger more dispersed herd. Activity budget analysis shows similar results to those reported in other studies on goats.

Keywords: Icelandic goats, social structure, fission-fusion, activity budget.

Introduction

Sociality among mammals evolves when benefits of group-living exceed the costs (Krause and Ruxton, 2002; Silk, 2007). When sociality is favoured, mammals can form groups ranging from small bonded units to big aggregations or congregations (Silk, 2007; Tanner and Jackson, 2012). Aggregations are considered a group of animals which are bonded to each other while congregations are typically described as casual or demographic. These distinctions focus on the difference between loose herds of the kind often seen in grazing ungulates and more formal groups seen in many primate species (Dunbar and Shultz, 2010). All domestic farm animals, for instance, are social and have a strong tendency to form groups (Estevez, Andersen, and Nævdal, 2007). Domestic herbivores, such as goats, form various sized groups in response to local environmental conditions and habitat characteristics (Shackleton and Shank, 1984; Shi, Dunbar, Buckland and Miller, 2005).

Fission-fusion group type structure was first described for highly social species, such as the chimpanzee (*Pan troglodytes*) (Aureli *et al*., 2008) and bottle nosed dolphin (*Tursiops spp.*) (Connor, Wells, Mann and Read, 2000), that are known for their social nature and intelligence. Fission-fusion group type seems to characterize several ungulates including: red deer (*Cervus elaphus*) (Conradt and Roper, 2000), African elephants (*Loxodonta spp.*) (Archie, Moss and Alberts, 2006), Grevy´s zebra (*Equus grevyi*) (Sundaresan, Fischhoff, Dushoff and Rubenstein, 2007) and giraffes (*Giraffa camelopardalis*) (Carter, Brand, Carter, Shorrocks and Goldizen, 2013). Evidence suggests that feral goats also fall into this category. They are highly social and intelligent (Kaminski, Riedel, Call and Tomasello, 2005; Keil, Imfeld-Mueller, Aschwanden and Wechsler, 2012; Roitberg and Franz, 2004), have the ability to discriminate between group members (Keil *et al*., 2012), locate food using cues from other individuals (Kaminski *et al*., 2005) and follow gaze directions towards outside objects at the same level as primates (Kaminski *et al*., 2005). This suggests that goats possess cognitive skills that enable them to live in complex fission-fusion societies (Kaminski, Call and Tomasello, 2006).

Fission-fusion societies are based on parent groups that fracture into smaller, flexible subgroups over the course of the day depending on activity and resources (Aureli *et al*., 2008). Fluid movements of group members between subgroups are common, resulting in changing group size and composition. Subgroups tend to form as a result of individuals synchronizing behavioural activities within their habitats (Conradt and Roper, 2000; Dunbar and Shultz, 2010). Absence of behavioural synchrony can lead to formation of unstable sub-groups within the larger flock (Dunbar and Shultz, 2010). It can be costly for an individual to postpone an activity that would be personally beneficial in order to stay within a group. Individuals with similar needs and requirements are therefore more likely to synchronize their behaviour (Archie *et al*., 2006; Conradt and Roper, 2000; Dunbar and Shultz, 2010). Age difference, sex and body size can affect behavioural synchrony and cause group fragmentation (Conradt and Roper, 2000; Ruckstuhl and Neuhaus, 2000).

Sexual segregation occurs widely among ungulates where males stay in one or more groups and females with their offspring in others (Calhim, Shi and Dunbar, 2006; Main and Coblentz, 1990; O'Brien, 1988; Shackleton and Shank, 1984; Shi *et al.*, 2005). Many hypotheses have been proposed to explain sexual segregation in ungulates (Calhim *et al.*, 2006; Dunbar and Shi, 2008; Main and Coblentz, 1990; Main, Weckerly, and Bleich, 1996; O'Brien, 1988; Ruckstuhl and Neuhaus, 2000), but the most recent is the activity budget hypothesis (Yearsley and Perez-Barberia, 2005). This hypothesis implies that the activity pattern between the sexes becomes desynchronized, and this is usually believed to be the result of differences between the sexes in their foraging requirements, movement rate, behavioural patterns and size (Ruckstuhl and Neuhaus, 2000). Work by Dunbar and Shi (2008) on feral goats on the Isle of Rum on the west coast of Scotland supported this hypothesis. The activity budget hypothesis could therefore both predict sexual segregation and fission-fusion group structure.

Shi *et al.* (2005) reported that goats on the Isle of Rum on the west coast of Scotland formed sexually segregated groups with males in one group and females and their offspring in another. Mixed-sex groups were occasionally recorded throughout the year but their frequency increased considerably in August and September during the rutting period. At this time, bucks would join females in polygynous foraging groups (Saunders, McElligott, Safi and Hayden, 2005). The foraging groups' size and composition varied throughout this period, as individuals joined and left, without any obvious reaction from other group members. Goats typically form groups of 4 – 10 individuals with a maximum group size of 100 – 150 individuals (Shackleton and Shank, 1984). Consequently foraging group size may vary over time as groups disintegrate and reunite during foraging on pasture (Shi *et al.*, 2005).

Lives of all free ranging animals are divided into periods of rest and activity. Activity patterns are a function of trade-offs between optimal foraging, social activities and environmental constraints (Shi, Dunbar, Buckland and Miller, 2003). Foraging is considered the dominant activity of all free ranging ruminants (Belovsky and Slade, 1986), and goats spend 50% - 70% of their time devoted to this activity (Lu, 1988). Time spent on other activities ranges from 10 to 25% (Animut *et al.*, 2005; El Aich, El Assouli, Fathi, Morand-Fehr and Bourbouze, 2007; Solanki, 1994; Stronge, Fordham and Minot, 1997).

The objectives of this study were: (i) to assess the nature of the social structure of the biggest goat herd found in Iceland, and (ii) to obtain information on the activity budget of this herd and compare it to a smaller, more confined herd. We hypothesized that the goats would show a fission-fusion type social structure and that within sub-groups, goats would prefer to associate with a) individuals of similar age and b) related individuals. We also predicted that the goats in the big herd would spend more time foraging than those in the smaller herd that inhabited a more confined and botanically less diverse area.

Methods

Study site I – Háafell Farm

Háafell Farm is located at 64°42’N latitude and 21°15’W longitude. The study area is ca. 300 ha in size and characterized by a hill which is 348 m high (Figure 1). It is defined by two gullies on either side on the borders of neighbouring farms. The hill is heterogeneously vegetated with some regions of gravel beds and sparse vegetation. Hummocks are quite common in the study area and usually covered with moss and other vegetation. Goats were brought into the area in 1989 and in the group are 186 winterfed individuals. During summer, following the birthing season, the population nearly doubles to around 350 individuals. A proportion of these leaves the farm area and roams the hill from May through September. In August 2012, proportion of free-romaing goats was 110 with this number dropping to 80 in September. During this time, silage bale was provided near a shed positioned beside the farmhouse at the foot of the hill (Figure 1). The goats at Háafell Farm had unlimited access to the shed and cultivated farmland around the farm, and supplementary silage bales. Water was not provided as it was readily available in small streams throughout the study area. This area was shared with a population of roughly 60 sheep. At Háafell Farm, both measurements on group structure and activity budget were carried out.

Study site II – Brennistaðir Farm

Brennistaðir Farm is located at 64°37’N latitude and 21°21’W longitude, ca. 23 km distance from Háafell. The study site is rather small, ca. 1.6 ha in size and defined by a fence (see Figure 2). The vegetation inside the fence is quite homogeneous with low species diversity. The plant composition is mainly grasses and sedges. External silage bales were brought in as a supplementary food source. Within the fence is an open barn where goats can enter and exit at will. Measurements of activity budget were made on Brennistaðir Farm and an ethogram created. The herd on Brennistaðir Farm consisted of 20 adult individuals. At the time of study there were 40 – 42 individuals present including kids.

Ethogram

An ethogram was constructed for Brennistaðir following the definitions proposed by Shank (1972) and Shi *et al*. (2003). These definitions are based on observations of feral goats on Saturna Island in British Columbia, Canada, and on feral goats on the Isle of Rum by the west coast of Scotland (Shank, 1972; Shi *et al*., 2003). Ethograms have not been constructed for the Icelandic goat before. A simplified ethogram was used to describe the goats’ activity budget on Háafell Farm and this was used for comparison between the two farms. The ethogam for Brennistaðir Farm included 25 defined behavioural classes:

Unsocial:	*disturbance*: human presence; *drinking*: self-explanatory; *eating:* eating from a silage bale; *excretion:* self-explanatory; *foraging:* standing still or moving around pasture with head stooped; *lying down:* sternal recumbence without rumination; *play:* kids jump, climb or run around; *rumination:* rumination in sternal recumbence or while standing; *running:* moving rapidly around pasture; *self-grooming:* scratching with hooves, horns or teeth; *sleeping:* sternal recumbence or standing with eyes closed; *standing:* standing still and/or alert with upright head and open eyes without rumination; *standing up*: standing up from sternal recumbence; *walking:* walking around pasture with upright head; *other:* behaviour not included in above categories.
Social:	*front butting*: goat butts another goat, *butt threat*: threatening to butt another goat; *kid on doe:* kid climbing, lying or standing on doe; *mating behaviour:* male goat sniffing genitals and/or chasing a female; *nose to horn:* sniffs and/or touches horn of another; *nose to nose:* sniffs and/or touches nose of another; *play:* kids butt heads together; *sideways butting*: goat butt another goat to the side; *submission:* goat retreats by backing away with head erect and pointed away, *suckling*: kid suckling on a doe.

The ethogram at Háafell Farm included five categories: *foraging:* standing still or moving around pasture with head stooped; *lying down:* sternal recumbence with or without rumination; *standing:* standing still or alert with upright head; *walking:* includes walking and travelling with head upright (higher than the back); and *other:* behaviour not included in above categories such as running, grooming, excretion and social interactions. For comparison a similar classification was also made for the Brennistaðir Farm data.

Social structure

Instantaneous scans (Altmann, 1974; Lehner, 1979) were made at one hour intervals during daylight hours on the 9th to 11th of August 2012 and the 11th to 13th of September 2012 (total 64 hours) at Háafell Farm. During each scan, a 3 km section of the road was surveyed (road within red box seen in Figure 1) and observations made every 600 m with a powerful William Optics scope. This allowed an area of approximately 300 ha to be covered. During these scans the position of each group and number of individuals (adults and kids) was noted. In September, marked individuals were recorded for group composition (see below).

Group structure and distribution

Distribution of groups and number of goats in each group was marked on a Garmin© map of the area. The number of groups and size of groups with respect to both time of day and height above sea level were analysed by combining the scans from August and September. The distribution of groups within the habitat was analysed. To test the hypothesis that the distribution of groups was significantly different from random, Chi-square (Molles, 2012) and d- values for a large sample size were calculated for the central 2x1 km area in 10x10 plots (df = 99) for each scan (total = 64). The statistical program SigmaPlot™ (version 11.0) was used for plotting grouping patterns and spatial distribution of the groups was plotted with ArcGIS 10.2 (Geographic Information System).

Group composition

During the 11th – 13th of September 2012, 34 does were randomly selected to be colour marked and released on Háafell Farm. Kids were captured alongside the selected adults although only adult individuals were marked. Kids were released at the same time as the adults. The does were marked with a specific colour and a pre-determined sign. The colours used were green, red/pink and yellow. The signs were: a circle (○), a minus (–), a square (☐), a triangle (△) and X. The complete list of markings can be found in Appendix I. Among the marked individuals there were three pairs of sisters and four pairs of mothers and their four daughters. During all scans it was noted which marked individuals formed groups.

Using this method it was clear which marked goats formed groups during foraging. Preferred associates of marked individuals were those that had Chi-square values which were significantly larger than the null-hypothesis of random association predicted. SocProg (version 2.4) was used to map the social structure of the group where the association indices were the calculated Chi-square values.

Information on relatedness between the marked goats was obtained from the owner who maintains a thorough record of lineage. Relatedness was calculated with ENDOG (version 4.8) and the partial inbreeding coefficient between the does estimated. The program MatMan® was used to do tau (τ) KR permutation tests (de Vries, 1993) for correlations between matrices. Two correlations were tested: the association matrix (where each cell showed how often individuals of the relevant pair were found together and (i) relatedness between the same dyads and (ii) age (the cell value was the difference in age of the two goats of the dyad).

Activity budget – Háafell Farm

Data to calculate the activity budget at Háafell was collected with the instantaneous scan sampling method once every hour from daybreak until nightfall (as described previously) and the behaviour of all individuals observed in the 300 ha area was recorded on a dictaphone. There were two study periods: the 9th – 11th of August 2012 and the 11th – 13th of September 2012 (total 64 hours). A Chi-square test was used to compare allocation of time (percentage) across behavioural categories in the two herds studied.

Activity budget – Brennistaðir Farm

Instantaneous scans were made more frequently than at Háafell Farm or at 15 minute intervals during daylight hours in three study periods; the 22nd – 24th of July 2012, the 12th – 13th of August and the 1st – 3rd of October 2012 (total 70 hours). If any part of the herd was inside the barn at the time of scans, records were made both inside and outside.

The statistical programs R (version 3.0.2) and SigmaPlot™ (verison 11.0) were used for analysis of activity budget data and plotting.

Results

Social structure

Group structure and distribution

The goats gathered overnight to rest in a cave within a gully or in a barn near the farm. At daybreak, a proportion of the goats left their shelter to forage during the day. The groups split up into smaller subgroups which changed throughout the day. The same pattern could be seen during periods of rain when the goats would gather at the shelters and remain there until rain ceased.

On average, 12 groups were seen on the hill in any one scan in August and 5.5 in September. Average group sizes were 5.3 individuals in August and 6.1 in September. Group size ranged from 1 to 39 individuals with a skewed distribution towards 1 – 5 goats (Figure 3). A group of two goats was most frequently observed, accounting for 24.9% of all groups seen. Groups of three and four were second most common, accounting for 14.6% and 15.1%, respectively. Groups of 2 – 4 constituted 54.6% of groups but large groups were rare (groups of >20 individuals accounted for 1.9% of all groups). The stability was rather low as shown by the variation in number of groups according to time of day shown in Figure 4.

Number of groups varied considerably by time of day. In general, fewer groups were observed early in the day, with group numbers increasing until midday and then decreasing again in the evening (Figure 4). More groups were observed in August than in September when daylength decreases and fewer goats were roaming the pasture after rounding up for winter. The foraging pattern with respect to altitude was similar in August and September. A large proportion of the goats foraged at 40 – 60 m above sea level, where the farm and the cultivated pasture are located. Fewer groups were seen at altitudes between 160 – 180 m above sea level and the number of groups continued to decline as elevation increased above 180 m. Few groups were recorded at 260 – 300 m above sea level (Figure 5).

The distribution of goats within the study area was found to be random for all observations (N = 64) ($d < 1.96$) excluding two scans in September made at daybreak ($d > 1.96$) and were clumped (Figure 6A and 6B).

Group composition

The sociogram (Figure 7) shows significant bonding between the 34 marked individuals with bond strength represented by line thickness. The mean number of significant associations between individual goats was 2. Two of the tested goats did not display any preference towards associates (Ljúfa and Rós).

Correlation tests between matrices showed (i) that the goats did not on the whole associate more with more related individuals ($\tau = 0.0019$, KR = 22, $p = 0.516$) and (ii) individuals close in age did not prefer to associate with each other ($\tau = -0.039$, KR = -508, $p = 0.154$).

Activity budget

In both August and September, foraging was the principal activity of the goats at Háafell Farm and accounted for 70.1% and 71.3% of the overall activity, respectively. Walking was the second most common activity among the goats, accounting for 13.5% and 20.3% in August and September, respectively. The remaining time was devoted to: lying down (9% in August and 5.3% in September), standing (2.4% in August and <1% in September) and other activities (4.2% in August and 2.2% in September), including social interactions which were rarely observed. A diurnal pattern could be seen in foraging time for goats at Háafell Farm in August. Foraging was most common in the afternoon and decreased in the evening (Figure 8A). The diurnal pattern was not clear for September (Figure 8B).

A different activity pattern could be seen at Brennistaðir Farm (complete data in Figure 9A and 9B). The goats spent similar time foraging (38.95%) and lying down (34.7%). Analysing the data with respect to month shows that in both July (Figure 8C) and August (Figure 8D*)*, foraging was the principal activity and accounted for 38.1% and 49.6% of the goats' time and lying down was the second most common or 34.9% and 22.4%, respectively. In October, however, the main activity was lying down which accounted for 42.8% while foraging constituted 29.8% (Figure 8E*)*. The remaining time was devoted to: standing (16.3% in July, 19.4% in August and 18.4% in October), walking (7.1% in July, 6.2% in August and 6.7% in October) and other behaviours (3.6% in July, 2.4% in August and 2.3% in October). A diurnal pattern could be seen in foraging at Brennistaðir Farm in July and August. The goats foraged early in the morning in July and rested in the afternoon but foraging then increased slightly in the evening. An opposite pattern could be seen in August where the goats foraged primarily in the afternoon and less in the early morning and late evenings. No visible diurnal pattern could be seen in October.

Other behavioural categories at Brennistaðir included playing, self-grooming, sleeping and social interactions (Figure 9A and 9B). Unsocial play was <1% for July and August and none in October. Self-grooming accounted for 1.19%, 0.38% and 0.75% in July, August and October respectively. Social interactions accounted for 1.15%, 0.46% and 0.57% of overall activity in July, August and October. In July, social play was the most common behaviour. In August, antagonistic behaviour accounted for 80%. In October, however, mating behaviour of bucks was the most common or in 63.3% of cases.

Comparison of activity patterns can be seen in Figure 8F. Chi-square analysis on the activity budget shows that the goats at Háafell Farm spent more time foraging than the ones at Brennistaðir Farm ($\chi^2 = 833.02$, df = 1, $p < 0.0001$). The goats at Brennistaðir Farm, however, spent significantly more time lying down ($\chi^2 = 904.70$, df = 1, $p < 0.0001$). Less time was spent lying down during summer than in the autumn at Brennistaðir Farm ($\chi^2 = 109.37$, df = 1, $p < 0.0001$). Goats at Háafell Farm spent similar time on foraging in August and September ($\chi^2 = 1.26$, df = 1, $p < 0.5$).

Discussion

Group formation and structure

The goats at Háafell Farm showed clear signs of a fission-fusion group type. They spent the night around the farm in a barn or in a cave within a gully. Early in the day they left their shelter to forage around the hill. The groups travelled from the parent group and fractured into smaller subgroups that dispersed around the pasture to forage (Figure 6A and 6B). The goats often sought shelter during rain and large parent groups could be seen leaving the shelter when rain ceased, these groups then divided into smaller units as the day progressed. These areas have been referred to as permanent night-camps where the herd stays each night and during extreme weather (O'Brien, 1988). Similar results have been recorded for feral goats on the Isle of Rum in Scotland (Shi *et al*., 2005). The groups which the goats formed during foraging were neither based on kinship (Figure 7) nor composed of individuals of similar age. Goats on the Isle of Rum, likewise, did not associate randomly but seemed to have preferred associates and actively sought them out (Stanley and Dunbar, 2013).

The goats seemed to form sexually segregated groups on pasture. The sixteen free-ranging males formed one group which roamed the same hill throughout the study and did not return to the same shelters as the females during night-time. As mentioned earlier, numerous explanations have been suggested as to why females would rather associate with each other and offspring rather than males (Calhim *et al*., 2006; O'Brien, 1988). One hypothesis implies that sexual segregation is an antipredatory behaviour (Main *et al*., 1996; Ruckstuhl and Neuhaus, 2000). In Iceland, few species can be categorized as natural predators but they include the arctic fox (*Vulpes lagopus*) and ravens (*Corvus corax*). Since they are neither big in size nor prone to attacking goats it can be concluded that their presence would neither affect group size nor density. Another idea refers to sexual size dimorphism as a reason for sexual segregation as physiological factors influence nutritional requirements (Main *et al*., 1996; Ruckstuhl and Neuhaus, 2000). As mentioned earlier, the most recent hypothesis implies that the activity pattern between the sexes becomes desynchronized, because of differences of the sexes in their foraging requirements, movement rate, behavioural patterns and size (Ruckstuhl and Neuhaus, 2000; Yearsley and Perez-Barberia, 2005). Calhim, Shi and Dunbar (2006) concluded that the activity hypothesis and social preference model could be applied to the feral goat population on the Isle of Rum. Shi *et al*. (2003), however, suggest an alternative explanation, i.e. females are avoiding males due to their harassment. Male sexual harassment towards females was noted several times in the herd at Brennistaðir Farm which included three males and 18 – 20 females. The enclosure was small and offered no opportunity for the females to avoid males when harassed. The males chased the females until they managed to hide in an old shed inside the enclosure. Similar harassment was noted with young males towards older females at Háafell Farm during marking in September. However, no conclusions can be drawn from these findings as no males were marked or recorded specifically.

The analyses showed that groups were distributed randomly over the habitat. The fact that the numbers of groups change with time of day, month and altitude (Figure 4, 5, 6A and 6B) shows how unstable they are. The majority of groups were recorded at altitudes between 40 – 60 m above sea level which indicates that they spent substantial time foraging around the farm, located at that same altitude (Figure 5, 6A and 6B). At the same time, groups seemed to forage at higher altitudes early in the morning and disperse to lower altitudes during the day. The goats therefore seemed to start foraging at high altitudes of the pasture and later in the day foraged on cultivated farmlands around Háafell Farm. The same pattern can be seen for both August and September where groups are fewer early in the day with a peak in the afternoon. The number of groups decreases as the goats start to find shelter for the night (Figure 4). Fewer groups were recorded in September as rounding up had already taken place and marked goats and their offspring were only released onto the hill for the present study (Figure 6B). With regard to group size, the high occurrence of groups comprising 2 – 5 individuals and rarity of larger groups at Háafell Farm (Figure 3) echo the findings of Shi *et al.* (2005) for the feral population on the Isle of Rum population, where group size was highly skewed towards 1 – 3 individuals. Thus, the results of this study support the conclusion of Shi *et al.* (2005) that the social structure of goats can be classified as a fission-fusion group type.

Activity budget

The goats at HáafellFarm and Brennistaðir Farm showed dissimilarities in their activity patterns during the study periods (*Figure 8A, 8B, 8C, 8D*, and *8E*). The goats at Háafell Farm spent considerably more time foraging than those at Brennistaðir Farm. The Háafell Farm goats have the opportunity to travel longer distances between desirable patches on pasture while those at Brennistaðir Farm are in a confined enclosure. The free roaming herd at Háafell Farm spent, on average, approximately 70% of the day foraging and 15% of the day walking. Consequently, other behaviours comprised only a small part of the goats' daily activity. Goats, like other ruminants, need to rest between foraging periods. Alternating between rest and foraging is a typical activity pattern in ruminants. A diurnal pattern where goats forage early in the morning and late afternoon has been recorded (Stronge *et al*., 1997). A diurnal pattern is not clear with goats at Háafell Farm as has been reported in feral goats in New Zealand (Stronge *et al*., 1997) and feral goats on the Isle of Rum in Scotland (Shi *et al*., 2003). Daylenght in Iceland differs from other studies which in turn can influence foraging activity. Conversely, the goats at Brennistaðir Farm showed similar diurnal pattern in July to feral goats in New Zealand (Stronge *et al*., 1997) and feral goats on the Isle of Rum in Scotland (Shi *et al*., 2003) where foraging activity was recorded higher in the afternoon. In August, diurnal behaviour patterns of goats at Brennistaðir Farm were similar to those of goats at Háafell Farm. Activity budget at Brennistaðir Farm in October differed from any other study period where considerably less foraging activity was recorded, accounting for only 29.9% of their time budget. More time was spent lying down and resting during that month.

Social interactions were found to be a small proportion of the overall activity budget at Brennistaðir Farm (Figure 9A and 9B). This included antagonistic behaviour, play and mating behaviour. Aggressive behaviour was most common around the feeding rack where goats would threaten to butt or butt other individuals for better access to the silage bale. Tölü and Savaş (2007) found that horned individuals were more likely to show antagonistic behaviour towards other goats than the polled ones. Aggressive behaviour was expected to increase with a higher dominance rank (Barroso, Alados, and Boza 2000; Tölü and Savaş, 2007). Andersen *et al*. (2011) reported that social interactions (positive and negative) declined with increased group size among goats. Jørgensen *et al*. (2007) and Van *et al*.

(2007), however, reported more aggressive behaviour with increased group size at feeding places. Aggressive behaviour at Brennistaðir Farm was initiated more frequently by older more dominant individuals towards the younger ones. Although not measured quantitatively, it was clear that bucks outranked does regardless of age and size, even though some does were larger than the youngest males. The antagonistic behaviour would typically end when one goat would show submission by retreating or backing away before actual conflict took place. These findings are similar to those for the feral goats of the Isle of Rum (Shi and Dunbar, 2006). Interestingly, two older does showed more antagonistic behaviour than the others towards young does and kids around the feeding rack.

As expected, kids showed more playful behaviour than adult goats at Brennistaðir Farm (Spinka, Newberry and Bekoff, 2001). Both unsocial play, where kids would climb on rocks and smalls hills and jump on corrugated iron, and social play was recorded, which entailed butting heads together. The adaptive value for play in mammals has been subject to some debate among scientists. It has often been suggested that play serves as a physical exercise and that it is good for mental development where young animals learn necessary aspects of survival through the act of playing (Held and Spinka, 2011; Spinka, Newberry and Bekoff, 2001), with flow-on effects for fitness maximization. The goats showed fewer signs of play behaviour after most kids had been removed from the parent group in October (Figure 9A and 9B). Mature kids were found to form their own groups rather than stay with their dam. Similar results have been reported for kids in California where they formed peer groups (Lickliter, 1987).

Conclusions

The study strongly supports the hypothesis that goats at Háafell Farm have a fission-fusion group type similar to the feral goats on the Isle of Rum. Large groups would divide into smaller subgroups and fuse again later in the day or dissolve entirely. Foraging groups did not seem to be based on kinship nor age, as preferred associates were neither related nor close in age. The diurnal pattern observed in foraging differed markedly from that found in other goat populations in other countries, where activity is highest early in the day and late evenings. Foraging was found to be the dominant activity among the goats which is consistent with other studies. The goats at Háafell Farm spent more time foraging than the ones at Brennistaðir Farm, where there was very limited opportunity for them to travel around the pasture. Social interactions constituted only a small proportion of overall activity among the goats.

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Figures

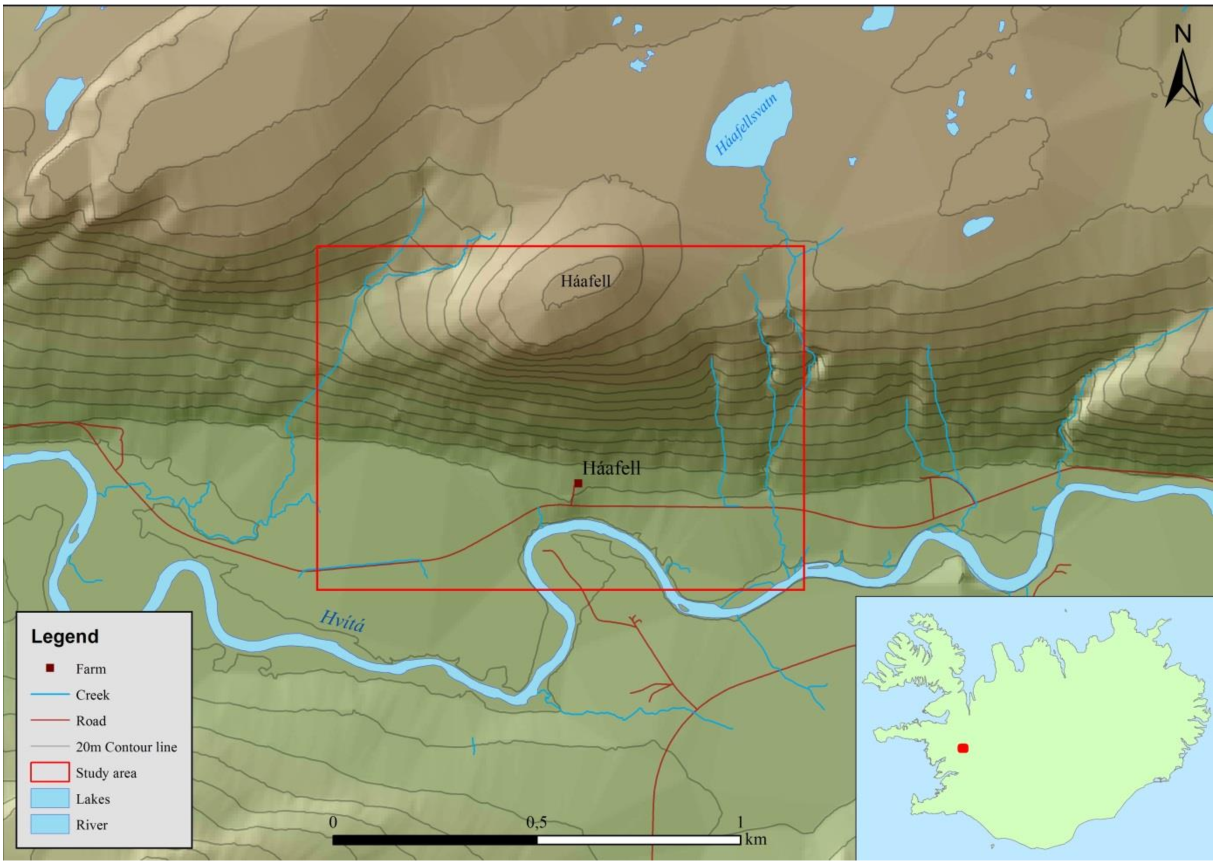

Figure 1 *Study area at Háafell Farm (64°42'N latitude and 21°15'W longitude).*

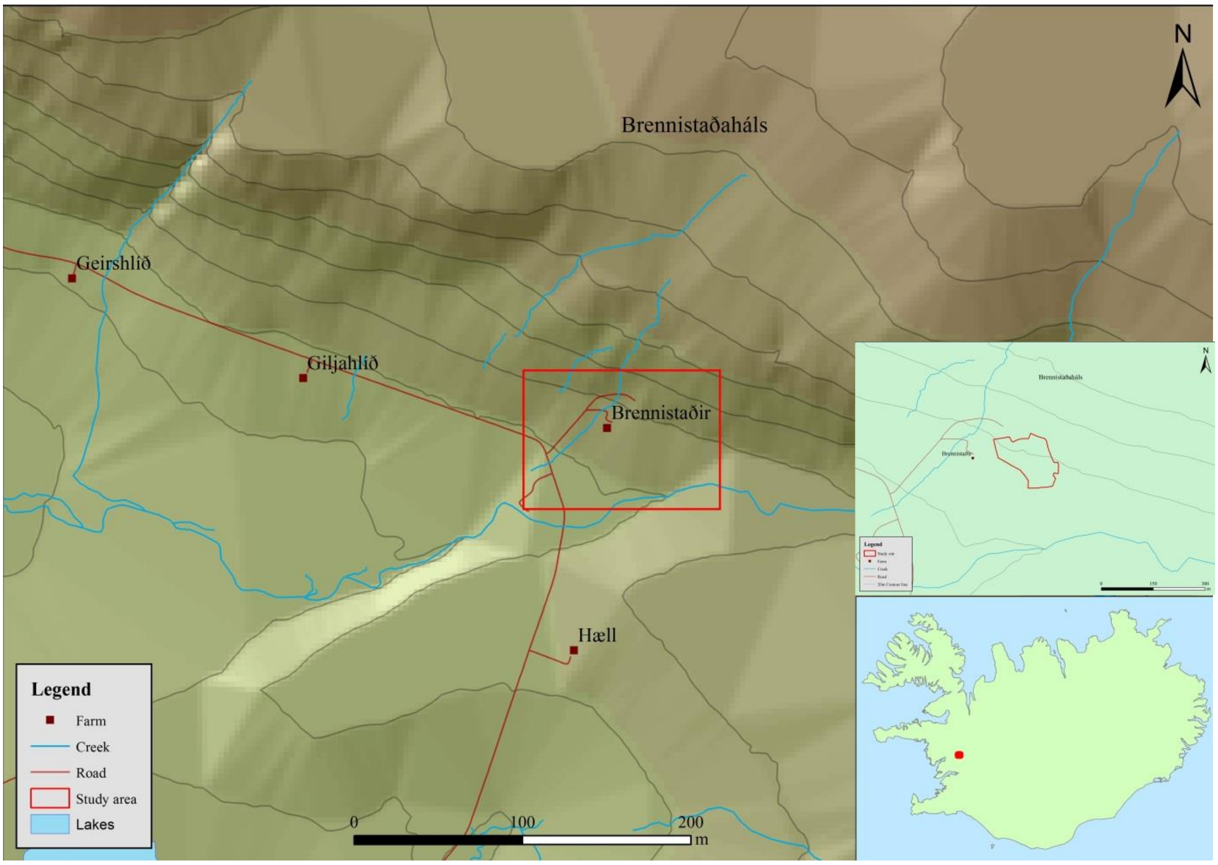

Figure 2 *Study area at Brennistaðir Farm (64°37’N latitude and 21°21’W longitude).*

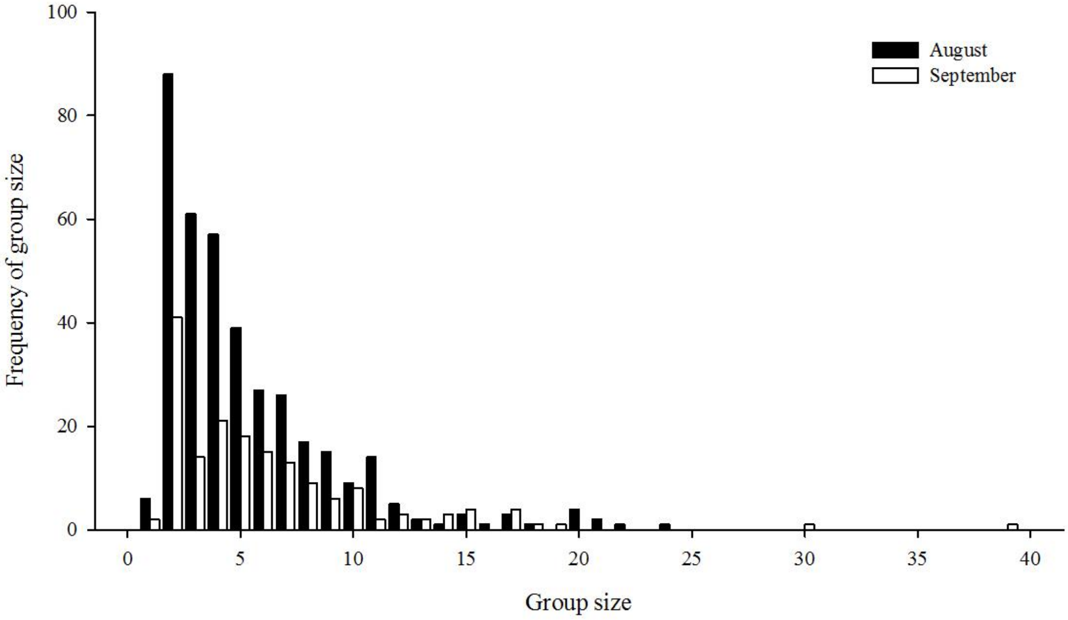

Figure 3 *Combined data on frequency of group sizes in August and September at Háafell Farm.*

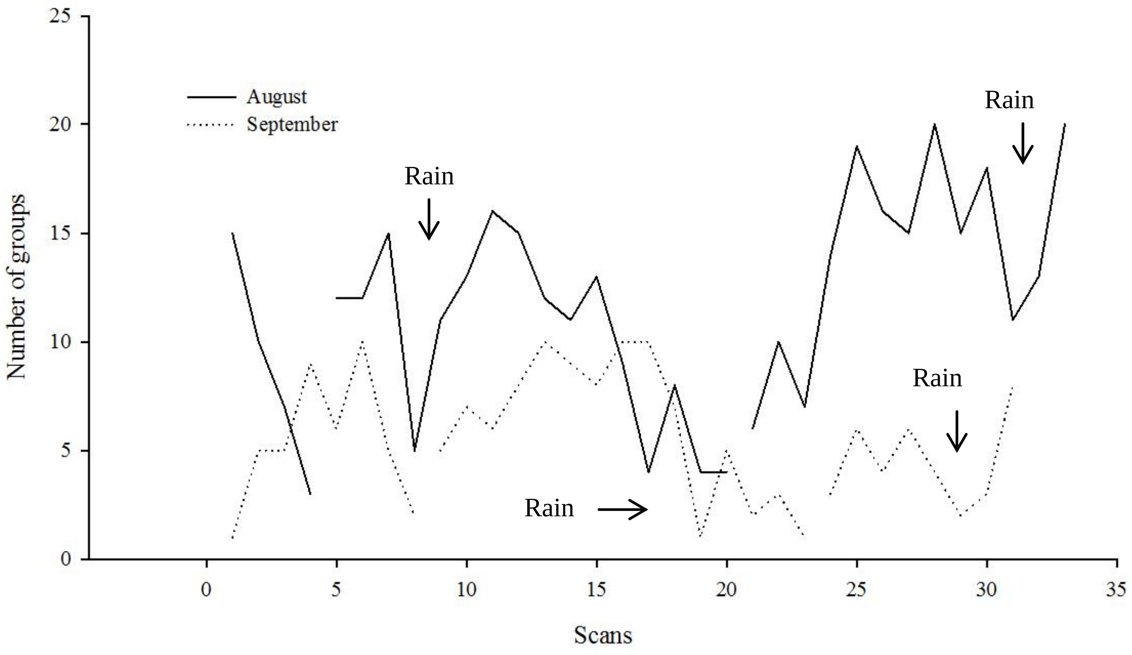

Figure 4 *Number of groups observed at Háafell Farm during August (31 scans made over three days) and September (33 scans made over three days). Each line represents a single day of scans made at one hour interval within each month. Rain is indicated with arrows.*

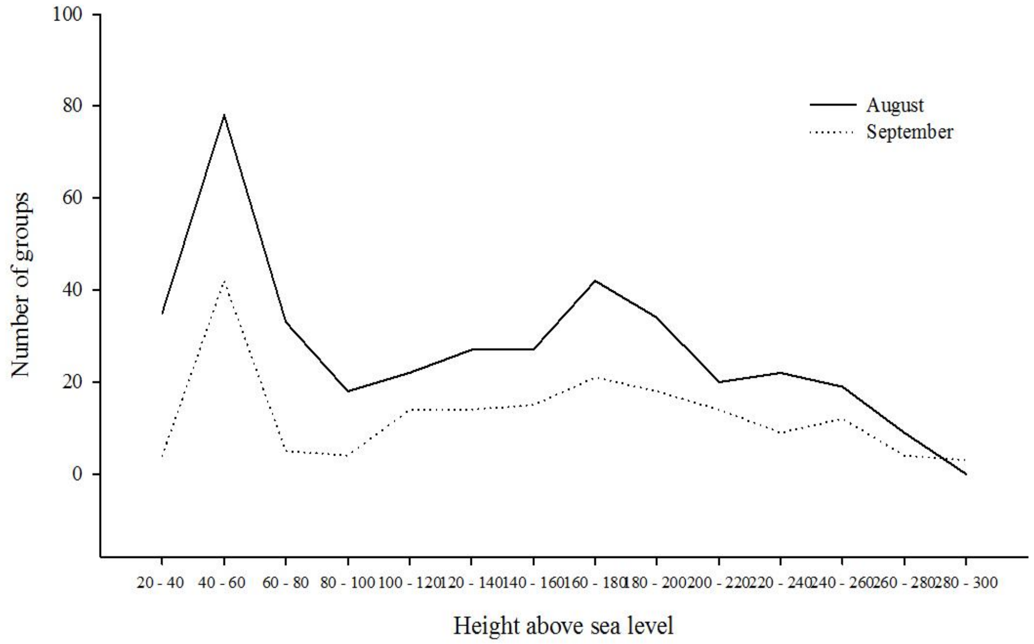

Figure 5 *Combined data for August (31 scans in 3 days) and September (33 scans in 3 days) showing the number of observed groups in relation to altitude at Háafell Farm.*

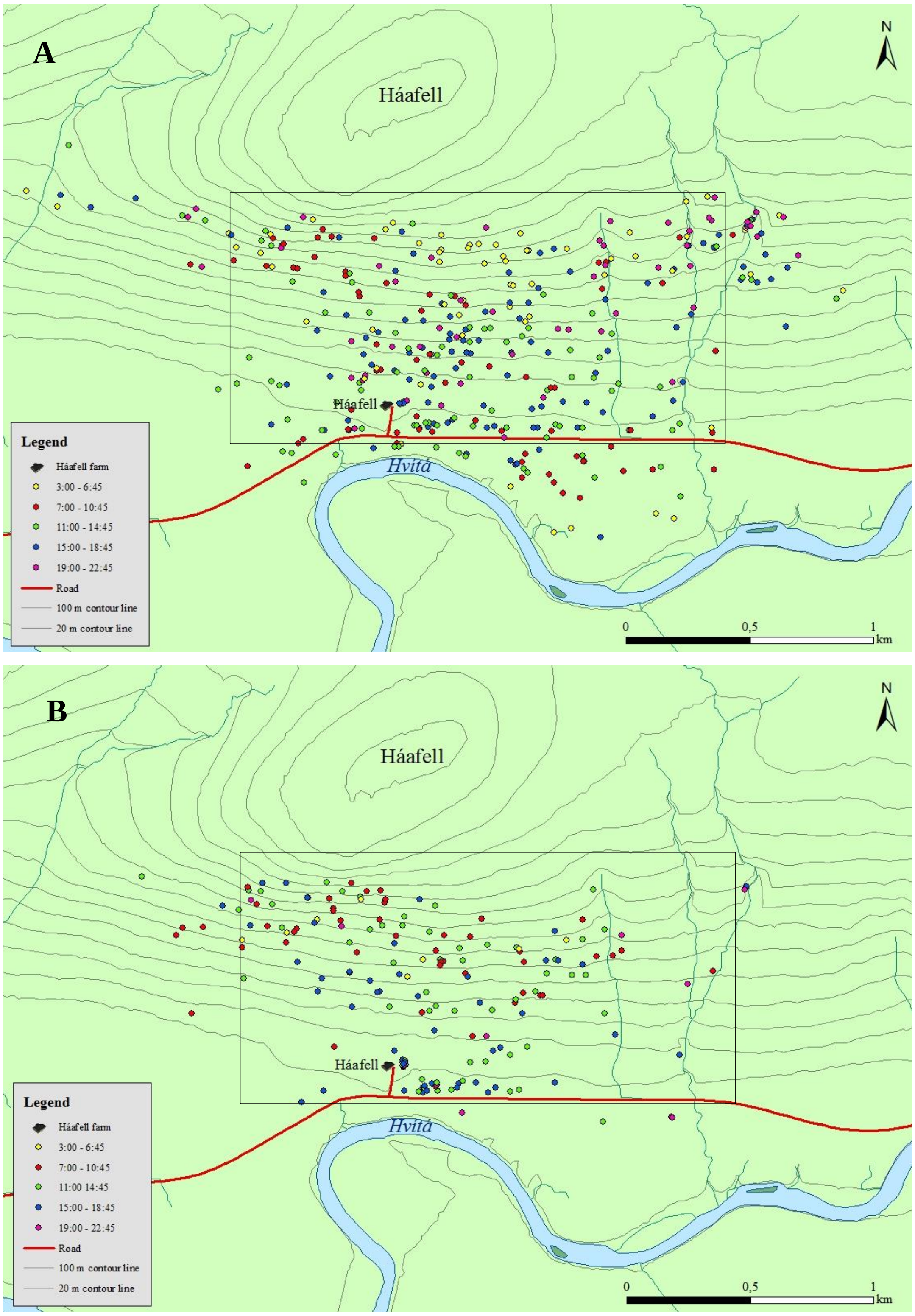

Figure 6 *Distribution of goat groups within the study area at Háafell Farm in A) August and B) September with respect to time of day where yellow = 3:00 – 6:45, red = 7:00 – 10:45, green = 11:00 – 14:45, blue = 15:00 – 18:45 and pink = 19:00 – 22:45 hours. The black square specifies a 100h central plot for distribution measurements for both August and September.*

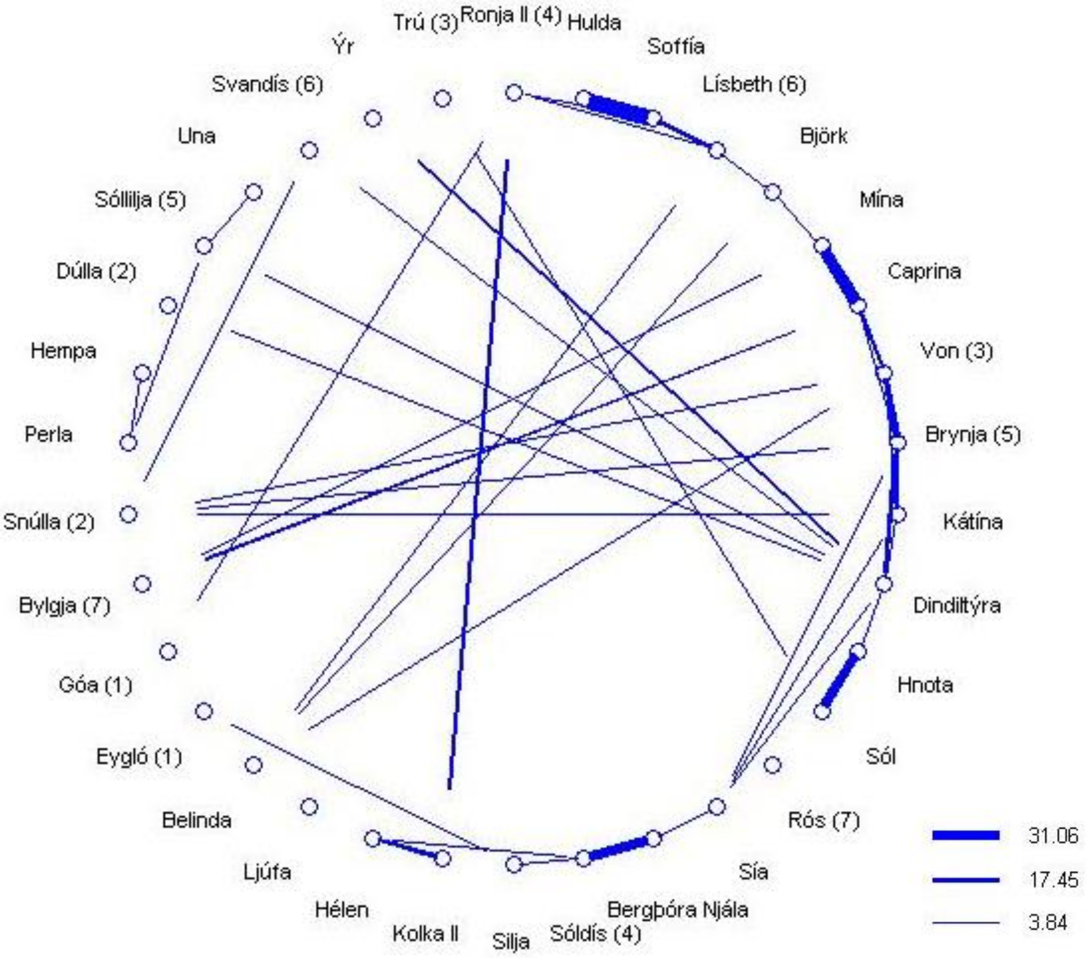

Figure 7 *Sociogram for 34 marked females based on association indices where H_0: each goat equally likely to be found with any other goat (Chi-square values: 3.84= p< 0.05, 17.45= p< 0.01, 31.06= p < 0.001). Goats marked (1), (2), (3) are three pairs of sisters and (4), (5), (6), (7) are four mothers and their four daughters.*

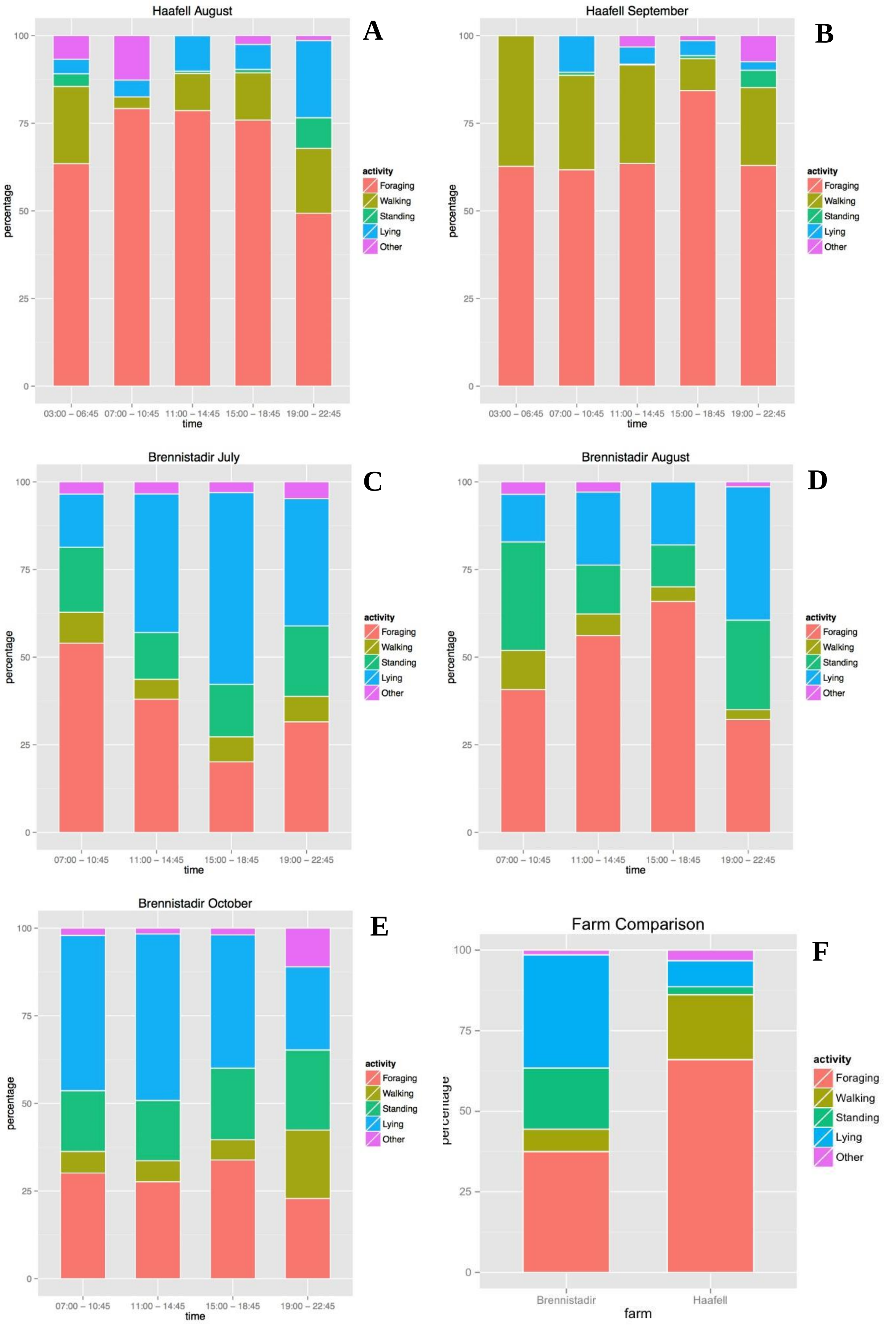

Figure 8 Daytime activty budget of goats at Háafell Farm in August (A) and September (B), Brennistaðir farm in July (C), August (D) and October (E) and combined data for both farms (F) where red = foraging, yellow/brown = walking, green = standing, blue = lying and pink = other behaviour.

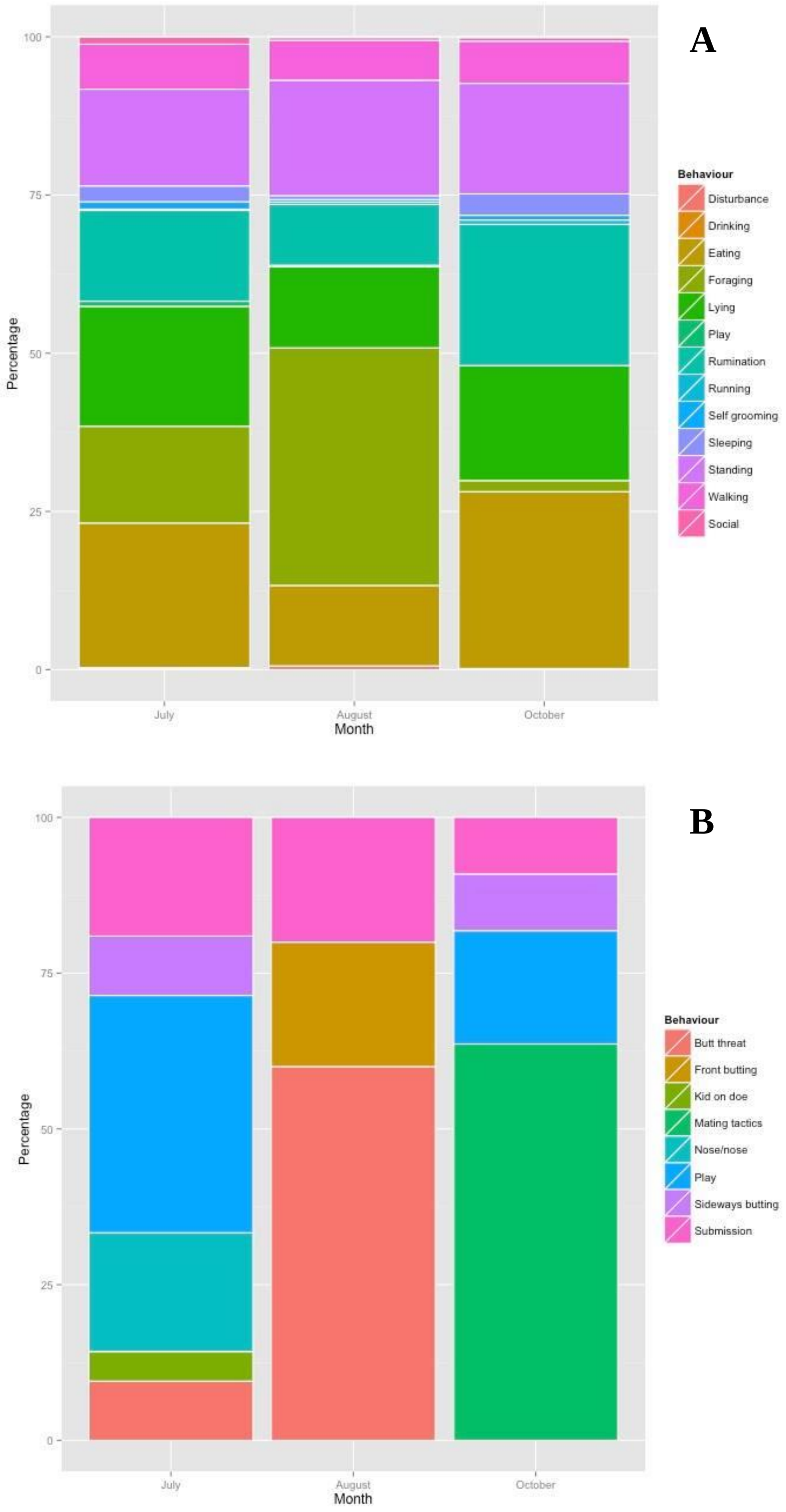

***Figure 9** Combined data for unsocial (A) and social (B) activity budget of goats at Brennistaðir Farm according to month.*

Manuscript II

Pasture utilization and plant selection of Icelandic goats

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Abstract

Goats and other free-ranging ruminants spend most of their time foraging and moving around pasture. Goats have been described as intermediate mixed feeders and are known to be highly flexible in their foraging selection.

The aim of the study was to investigate plant selection and pasture utilization of a free roaming goat herd in Iceland.

Results of microhistological analysis of goat faeces showed that grasses were dominant in the diet (70%) while other plant types were found in lower proportions (forbs: 10%, shrubs: 5% and sedges and rushes <5%). Different digestibility of plants can be expected to bias the results, as grasses are less digestible than both forbs and small shrubs. Supplementary silage was assumed to have influenced the proportion of grasses in faeces. The goats were found to utilize most of the area but one small region (10%) was noticeably less used without any obvious reasons, as it did not differ from others. The goats spent from 20 to 90% of their time foraging, a behaviour pattern that was influenced by weather conditions. Typically they spent 40 – 60% of their time foraging. The study shows that the goats are able to switch to grasses in the absence of browse, indicating flexibility and adaptation to the food resource. That supports the classification of goats as intermediate mixed feeders rather than strict browsers.

Keywords: Icelandic goats, plant selection, faeces samples, foraging behaviour, pasture utilization.

Introduction

Free-roaming ruminants spend most of their time foraging, moving between feeding stations and choosing desirable plant species (Stuth, 1991). Ruminants forage selectively which has resulted in an evolutionary adaptation in their digestive morpho-physiology (Hofmann, 1989; Papachristou, Dziba and Provenza, 2005). According to ruminant digestive morpho-physiology, Hofmann (1989) described three feeding types: roughage feeders, concentrate selectors and intermediate selectors. Roughage feeders (grazers) have a relatively large rumen, small salivary glands, inert lips and tongue which give a well suited digestive system to cope with fibre rich forages like monocots. Concentrate selectors (browsers) have a relatively smaller rumen, large salivary glands, mobile lips and tongue which is a digestive system adapted to nutrient rich, fibre poor forage, potentially with plant defences, like many dicots (Hofmann, 1989; Robbins, Spalinger and Vanhoven, 1995). A big proportion of ruminants are morpho-physiologically intermediate between roughage and concentrate selectors. These intermediate mixed feeders are selective, choosing a mixed diet and are considered opportunistic (Hofmann, 1989).

Goats have been classified as intermediate mixed feeders as they are neither exclusively grazers nor browsers (Hofmann, 1989; Papachristou *et al*., 2005). Goats differ morpho-physiologically from sheep and cattle, both of which are considered grazers. Smaller ruminants like goats have relatively larger energy requirements, the same time their smaller rumen can assimilate less nutrition at a given time (Clauss *et al*., 2003; Hofmann, 1989). Therefore, goats must be more selective, spend more time foraging and forage in shorter intervals than cattle and sheep (Heitschmidt and Stuth, 1991). Goats are faced with numerous foraging choices dependent on both external factors; species availability, topography of pasture, season and weather condition, and internal factors; nutritional requirements and physiology (Animut and Goetsch, 2008; Hofmann, 1989; Provenza and Balph, 1988; Robbins *et al*., 1995). As a result, goats are highly flexible in their foraging requirements and have adaptive behaviours to meet these requirements, for example, travelling great distances on pasture (Silanikove, 2000). In months when favoured species abundance is high, goats selectively feed on these species, whereas during months when species abundance is low, goats adapt their foraging behaviour to consume a wider variety of species to meet their dietary requirements (Barroso, Alados and Boza, 2000; Heitschmidt and Stuth, 1991).

Goats as intermediate selectors have comparatively large salivary glands, producing proline-rich proteins (PRP) which bind to tannins in the forage. This allows them to consume species fairly high in tannins (Hofmann, 1989; Lamy *et al*. 2011; Makkar, 2003; Papachristou *et al*., 2005; Robbins *et al*., 1995; Shimada, 2006). Goats favour browse species, such as trees, shrubs and forbs, regardless of availability (Heitschmidt and Stuth, 1991). Dietary choices made by each individual will, in the end, be based on personal information, social information as well as post-ingestive feedback (Provenza, 1995; Provenza and Balph, 1988; Provenza, Villalba, Cheney and Werner, 1998; Thorhallsdottir, Provenza and Balph, 1987).

The aim of the study was to investigate plant selection and pasture utilization of a free roaming goat herd in Iceland.

Methods

Study location

The study was conducted at Háafell Farm, located at 64°42'N latitude and 21°15'W longitude in West Iceland (Figure 1). The study took place between the 19th – 21st of July 2012, the 9th – 11th of August 2012 and the 11th – 13th of September 2012. Weather data for those dates can be found in *Table 1*. The study area is a south facing hill, 348 m high, defined by two gullies on either side on the borders to neighbouring farms and approximately 300 ha in size. The hill is heterogeneously vegetated with regions of gravel beds with sparse and patchy vegetation, especially in the upper regions. Hummocks are quite common in the study area and are usually covered with mosses and other vegetation.

Animals

Goats were brought into the area in 1989. Today, the whole group consists of 190 winterfed individuals. During summer, the population nearly doubles following the birthing season. In the summer of 2012, the total number of adults and kids was around 350. A proportion of these were allowed to roam freely on the hill during the summer. In 2012, this proportion was 110 individuals in August and 80 in September. During that time, a silage bale was provided near a shed positioned beside the farmhouse at the root of the hill (Figure 1). The free roaming goats had unlimited access to the shed, a small part of cultivated farmland and the supplementary silage bale. Drinking water is abundant in small streams throughout the study area. The area is shared with a population of roughly 60 sheep (ewes, lambs and rams).

Vegetation composition

Vegetation composition in the study area was assessed with the Braun-Blanquet method (Mueller-Dombois and Ellenberg, 1974) on the 1st of September 2013. Four zones were selected on the hill and vegetation composition and availability was assessed; three in frequently visited areas and one known to be less popular by the goats (Figure 2).

Within each zone, two transects were selected based on different vegetation types considered representative of the vegetation in the area. Along a 50 m long transect, 10 50x50cm quadrats were placed at 10 m intervals. Species composition within each quadrat was determined according to the book Flowering Plants and Ferns of Iceland (Hörður Kristinsson, 2010). Only cardiovascular plants were determined to species. Total vegetation, including mosses and lichens, along with bare ground and stones was set to 100%. Species abundance was classified to five categories according to quantity within each quadrat: 5 (>75%), 4 (50 – 75%), 3 (25 – 50%), 2 (5 – 25%) and 1 (<5%). Overall abundance of each species in the study area was calculated by taking the average of combined proportion within every quadrat from all transects. From this average, plant species abundance was classified into three categories: dominant (>50%), common (5 – 50%) and rare (<5%).

Plant selection

A total of 38 samples of fresh faeces from individual animals were collected at three separate occasions at Háafell and frozen for later analysis: the 19th – 21st of July 2012 (N = 9), the 9th – 11th of August 2012 (N = 17) and 11th – 13th of September 2012 (N = 12). Samples were collected on and near a frequently travelled track leading to and from the shed which served as night camp for the goats (Figure 2). This prevented the possibility of collecting faeces samples from sheep as they stay on the hill during night. Faeces samples were dried in a forced air oven at 70°C for 72 hours. The oven dried faeces samples were stored in plastic bags. Samples were ground with a grinder and sifted through a 1 mm mesh to remove large fragments. Slide preparation followed the procedure first described by Baumgartner and Martin (1939), later modified by Sparks and Malechek (1968) and Holechek (1982). Each plant sample was bleached for two minutes and cleaned with distilled water. A microscope slide was prepared for each faeces sample and Hoyer´s mounting solution was used to mount cover slips on the slides (Marie-Luise Øllgaard Meyhoff, 2003).

Fresh plant samples, for comparison with the faecal samples, were collected on Háafell on the 9th – 11th of August 2012 and the 11th – 13th of September 2012 and dried for later analysis. These samples were identified according to Flowering Plants and Ferns of Iceland (Hörður Kristinsson, 2010). The plant samples were treated in the same way as the faeces samples, with the exception that the plant samples were dried at 40°C temperature. Two microscope slides were prepared for each plant sample as references. Reference slides were used to identify epidermal fragments recovered in faeces samples. Fragments were identified to family level (Hansen, Foppe, Gilbert, Clark and Reynolds, 1976; Howard and Samuel, 1979). Unidentified fragments were not included in final results count as they were within bounds noted by Hansen *et al*. (1976). The statistical program R (version 3.0.2.) was used for plotting the proportion of plant types in faeces into five categories: forbs, grasses, rushes, sedges, shrubs and other (e.g. seeds and ferns).

Pasture utilization and foraging time

Instantaneous scans (Altmann, 1974; Lehner, 1979) were recorded twice for three consecutive days at one hour interval during daylight hours between the 9th – 11th of August 2012 and the 11th – 13th of September 2012 (64 hours in total) to estimate foraging time and distribution in the study area. During each scan, a 3 km section of the road below the farm was surveyed and observations made every 600 m with a powerful William Optics scope, thus covering the 300 ha (road within red box in Figure 1). In each scan, position of each group, number of individuals in a group (adults and kids) and activity was recorded on a dictaphone and marked on a Garmin© map of the area. The statistical program SigmaPlot™ was used to plot foraging time and distribution with ArcGIS (version 10.2).

Results

Vegetation composition

The grasses *Argrostis capillaris and Deschampsia cespitosa* were dominant in the sward of the study area, while *Anthoxanthum odoratum*, *Avenella flexuosa*, *Carex bigelowii*, *Festuca rubra richardonii*, *Festuca vivipara*, *Juncus trifidus* and *Kobresia myosuroides* were classified as common. Common forbs were *Alchemilla alpine* and *Thymus praecox arcticus* and common small shrubs were *Empetrum nigrum*, and *Vaccinium uliginosum*. A complete list of species and their estimated availability in the study site can be seen in Table 2.

Plant selection

Microhistological analysis showed grasses to constitute the highest proportions of plant types in the faeces samples for all three months (Figure 3). Grasses were found to account for 69.4% in July, 78.1% in August and 79.2% in September. Forbs were second most common, constituting 11.2% in July, 12.8% in August and 8.6% in September. Sedges were the third most common plant type that accounted for 10.7% in July but only 4.5% in August and 5.4 % in September. The remaining proportion in samples included small shrubs (8.1% in July, 3.8% in August and 5.2% in September) and rushes (<1% in July and August and 1.6% in September). Monocots therefore constituted 80 – 86% in the samples and dicots around 13 – 19% (Table 3).

The dominant plant types in the faeces samples were the grasses *Avenella flexuosa, Deschampsia cespitosa* and *Festuca spp*. Other frequent species seen in samples were the grasses *Anthoxanthum sp.*, *Agrostis spp.* and *Phleum sp.* The sedges *Kobresia myosuroides*, *Carex spp.*, *Luzula spp.* and *Juncus spp.* were also fairly common. Forbs found in faeces included *Achillea ssp., Alchemilla ssp., Rumex ssp., Bistoria sp.* and *Leontodon.* The small shrub *Vaccinium uliginosum* was fairly common, whilst *Empetrum nigrum* and *Thymus praecox arcticus* were rarely seen. *Vaccinium uliginosum* was found in high proportions in two samples (32.81% and 19.48%). *Kobresia myosuroides* was found in eight samples and accounted for <5%.

Pasture utilization and foraging time

In both August and September the goats appeared to occupy higher altitudes earlier in the day and lower altitudes in the afternoon and evening (Figure 4A and 4B).)The goats seemed to forage mostly at 40 – 60 m above sea level, where the farm is located and the cultivated pastures are (Figure 5). Groups were commonly seen at altitudes between 160 – 180 m above sea level but rarely at 180 m above sea level or higher. Few groups were recorded at 260 – 300 m above sea level. Some individuals were typically found near the farm eating from the silage bale that was kept there for the goats. Number of goats foraging between scans varied greatly (10 – 90%) but on average they spent 40 – 60% on that activity (Figure 6A and 6B).

Discussion

Plant selection

Microhistological analysis of faeces from the goats at Háafell Farm showed grasses to be dominant in samples (Figure 3, Table 2). Forbs were the second most common type for all three months, although this was less apparent in September when many species are fading and become less nutritious and palatable for foraging animals. Other plant types such as rushes, sedges and small shrubs were in lower proportions, never exceeding 11% in all three months, indicating a lower foraging preference for these plant types by the goats. The goats appeared to actively seek out certain rare species whilst at the same time avoiding certain common ones (Table 2). *Alchemilla spp.*, *Empetrum nigrum*, *Juncus trifidus, Kobresia myosuroides*, *Thymus praecox articus* and mosses appeared to be avoided by the goats as these species were common in the study area. Conversely, *Leontodon autumnalis* and *Luzula spp.* were rare in the study area but common in faeces. Goats have demonstrated to be selective of browse species regardless of availability (Heitschmidt and Stuth, 1991). The study area had little coverage of small shrubs and it would have been costly for the goats to actively seek them out (Stuth, 1991). Of the four small shrubs in the area, *Empetrum nigrum* and *Vaccinium uliginosum* were common and *Calluna vulgaris* and *Salix herbacea* were rare. Goats are known to increase proportion of grasses in diet if browse availability is limited (Malechek and Leinweber, 1972; Ferreira *et al*. 2013).

Malechek and Leinweber (1972) reported that grasses constituted for 50 – 90% of the goats' diet while browse species were less frequently selected. A study on goats on the Isle of Rhum in Scotland revealed that the sexes utilized the pasture differently (Gordon, 1989). Females were most commonly found in species-rich *Agrostis – Festuca* grassland and species-poor *Agrostis – Festuca* grassland while males were found in wet heath and seaweed communities (Gordon, 1989). Female goat diet on the Isle of Rhum showed similar results as those found in this study, where grass species were the most important plant type in their diet. Although grasses constituted the greatest proportion of faeces, individual preferences were noted in two samples from Háafell Farm. In both of these samples, *Vaccinium ulignosum*, appeared in unexpected proportions (Figure 3).

A study on sheep plant selection in Iceland showed similar tendencies where individual preferences were noted (Anna Guðrún Thórhallsdóttir and Ingvi Thorsteinsson, 1993). In that study, two sheep grazing in forest enclosures preferred *Betula pubescens* and *Vaccinium uliginosum*, while four others did not select these species.

Goats have been reported to avoid sedges belonging to the genus *Nardus* (Illius, Gordon, Elston and Milne, 1999) and sheep in Iceland were found to circumvent the sedge *Kobresia myosuroides* (Anna Guðrún Þórhallsdóttir, 1981). *Kobresia myosuroides* was conversely found, although in low proportions, in several faeces samples in all three months. Species such as *Nardus stricta* and *Kobresia myosuroides* are relatively low in nutrition and therefore less selected unless other abundant species have declined or faded before winter sets in. Studies on goat diet have reported less selectivity during autumn and wintertime (Barroso *et al*., 2000; Gordon, 1989; Malechek and Leinweber, 1972) as plant species become less nutritious and of poor quality. In autumn, ruminants can be expected to be less selective as plant species become less nutritious and abundant (Anna Guðrún

Þórhallsdóttir, 1981; Barroso *et al*. 2000; Heitshmidt and Stuth, 1991). This selective behaviour was not clear on Háafell Farm as no samples were gathered early in the season that could show seasonal differences (May or June). Grasses were dominant in all the samples, but were least visible in the samples from July (Figure 3), although this difference was not significant.

Proportion of grasses and other plant types in faeces samples reflect the goats´ diet to some extent but microhistological analysis, as was used in this study, has some limitation. The main disadvantages of this method are that identification of epidermal fragments can be problematic, an extensive reference plant collection is required, some species may become unidentifiable in faeces, and there is different digestibility of plant species (Alipayo, Valdez, Holechek and Cardenas, 1992; Anthony and Smith, 1974; Bartolome, Franch, Gutman and Seligman, 1995; Holechek, Vavra and Pieper, 1982; Smith and Shandruk, 1979; Vavra and Holechek, 1980).

Plant species are digested differently (Buxton and Redfearn, 1997) which can result in biased outcomes of microhistological fragment identification (Mayes and Dove, 2000). Plants low in fibre such as shrubs and forbs (i.e. dicots) are more digestible than fibre rich plants such as grasses and sedges (i.e. monocots) (Heitschmidt and Stuth, 1991). Presence of shrubs and forbs in faeces samples can therefore be expected to be underestimated because of their digestibility. Forbs and shrubs can be lost in the faeces while fibre rich plants are more likely to be found in accurate proportions. The dominant plant types in samples were grasses which are less digestible than both small shrubs and forbs. Presence or absence of mosses in faeces can be anticipated to be accurate as they are not readily digested.

Plant digestibility, supplementary feeding silage bale and access to cultivated pastures are three factors that most likely affect proportions of grasses in faeces samples. Proportion of the goats chose to eat from the supplementary silage bale or forage the cultivated pasture available to them. However, availability of grasses was also dominant on the hill (Table 2). Certain grasses are mostly found on pasture while others are mainly found on cultivated lands. *Anthoxanthum odoratum* and *Avenella flexuosa* are only found on pasture while *Deschampsia cespitosa* and *Festuca spp.* are found both on cultivated land and on pasture. *Argrostis spp.* and *Phleum spp.* are, however, merely found on cultivated land and therefore in supplementary silage bale. The proportion of these species in faeces can consequently be explained by the supplementary silage bale provided for the goats and access to cultivated lands. Malechek and Leinweber (1972) found that goats eat more grasses when browse species were limited. The goats at Háafell Farm might therefore be displaying flexibility in foraging requirements by increasing the proportion of grasses in the diet. It can therefore be concluded that all three factors affected the quantity of grasses found in the faeces. The findings indicate that goats, as intermediate mixed feeders, are opportunistic and adaptable regarding the areas and species they consume (Hofmann, 1989; Robbins *et al*. 1995).

Pasture utilization and foraging time

While foraging, the goats travelled widely around the hill at Háafell Farm. The largest proportion of groups were recorded at altitudes between 40 – 60 m above sea level indicating substantial time spent foraging around the farm on cultivated farmland, located at that same altitude (Figure 5). The goats seemed to forage at higher altitudes early in the day and disperse to lower altitudes later in the day. Goats were rarely seen between 260 and 300 m above sea level, and never higher than 300 m. Different vegetation appears in higher altitudes where mosses are dominant and other species rare. Most of the hill was occupied at some point by the goats apart from one area that was not utilized by the goats at any time. This area does not differ botanically from the others and thus it is inconclusive why it was avoided (Figure 4A and 4B).

The herd at Háafell Farm spent a large proportion of the day foraging but activity levels varied considerably. Foraging activity was most commonly found to take between 40 – 60% of the goats' time which differs from sheep in Iceland that have been recorded to spend less than half of their day foraging (Anna Guðrún Thórhallsdóttir and Ingvi Thorsteinsson, 1993). This dissimilarity can be explained by morpho-physiological differences between goats and sheep (Hofmann, 1989). Goats have relatively larger energy requirements compared to sheep and select more nutritious and easily digestible forage requiring less rumination. Goats therefore spend more time foraging and, accordingly, less time ruminating. Earlier studies have shown that goats follow a diurnal pattern, foraging early in the morning (at dawn) and late afternoon (at dusk) (Ferreira *et* al., 2013; Shi, Dunbar, Buckland and Miller, 2003; Stronge, Fordham and Minot, 1997). Feral goats on the Isle of Rum and goats in New Zealand showed such patterns (Shi *et al.*, 2003; Stronge *et al.*, 1997). The goats at Háafell Farm, conversely, did not show such a pattern (Figure 6A and 6B). External factors such as weather can affect foraging activity as goats are know to avoid rain. During the study period, heavy rain showers were recurrent (Figure 6A and 6B). Rain showers seemed to influence foraging activity of the goats greatly as the percentage of goats foraging on pasture was reduced considerably during showers. It can be concluded that weather influences could to some degree explain the unusual diurnal pattern recorded at Háafell Farm.

Conclusions

The results of this study indicate that the goats at Háafell Farm are opportunistic and flexible in foraging choices which supports the general idea that goats are intermediate mixed feeders. Certain abundant species on pasture did not appear in faeces whilst other rare ones were relatively common. The most prominent species in samples were grasses indicating that goats can effectively thrive on them in the absence of browse which is consistent with other studies. The goats spend most of their day foraging and foraging time was found to be different from sheep in Iceland where goats spent more time foraging than sheep. Diurnal patterns observed were found to be different from those in other studies as the goats seemed to forage in the middle of the day. This contrasts with the goats on the Isle of Rum in Scotland which show diurnal patterns where foraging activity peaks early in the day and late in the evening. Heavy rain showers during observations seemed to influence foraging activity where goats did not forage during rain, indicated by greatly reduced numbers foraging during showers. Thus it is concluded that weather explains the unusual diurnal pattern recorded among the goats at Háafell Farm. Foraging time was found to be a dominant activity which is consistent with other studies.

Acknowledgements

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Figures

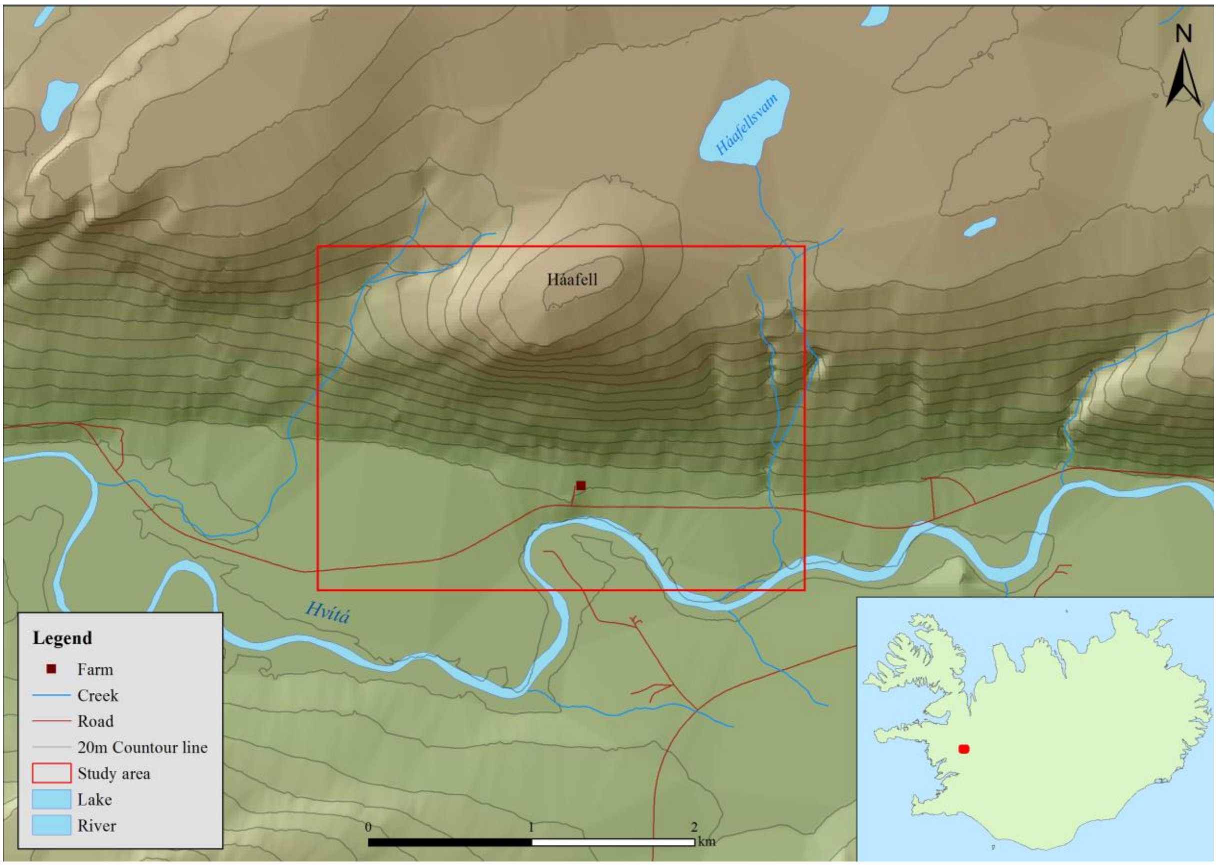

***Figure 1** Study site at Háafell Farm (64°42’N latitude and 21°15’W longitude).*

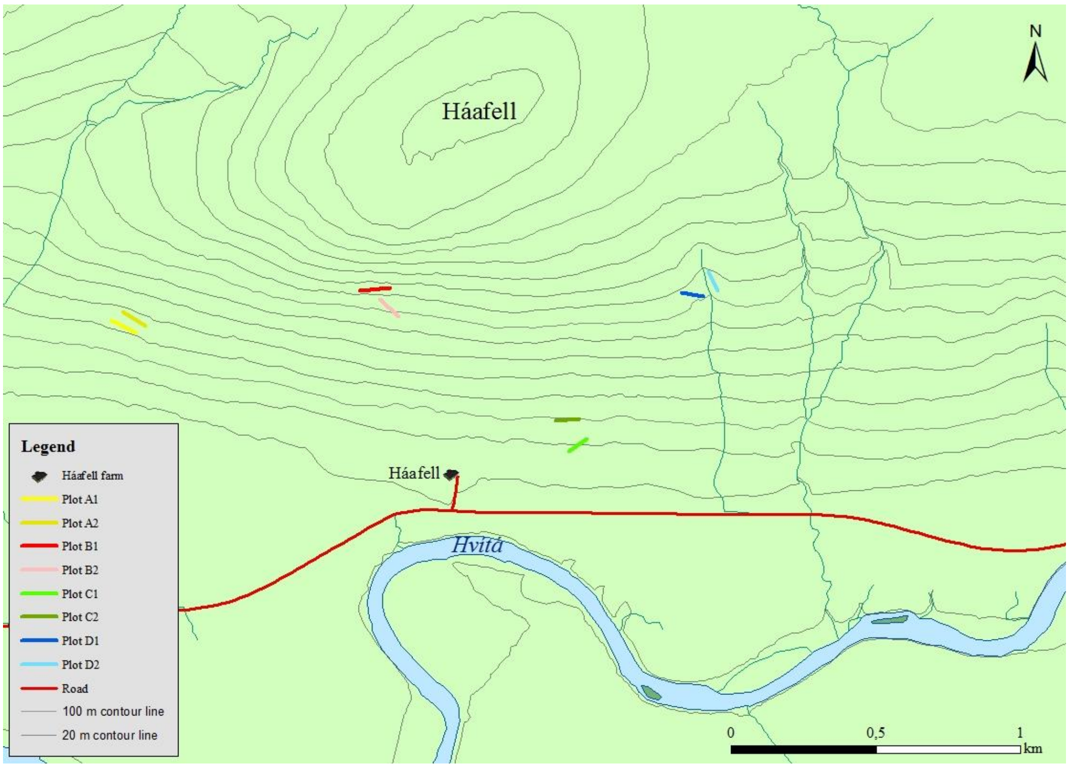

Figure 2 *Eight transects for vegetation composition stationed at 10 m intervals in four zones, three in frequently visited areas (red, green and blue) and one known to be less popular by the goats (yellow).*

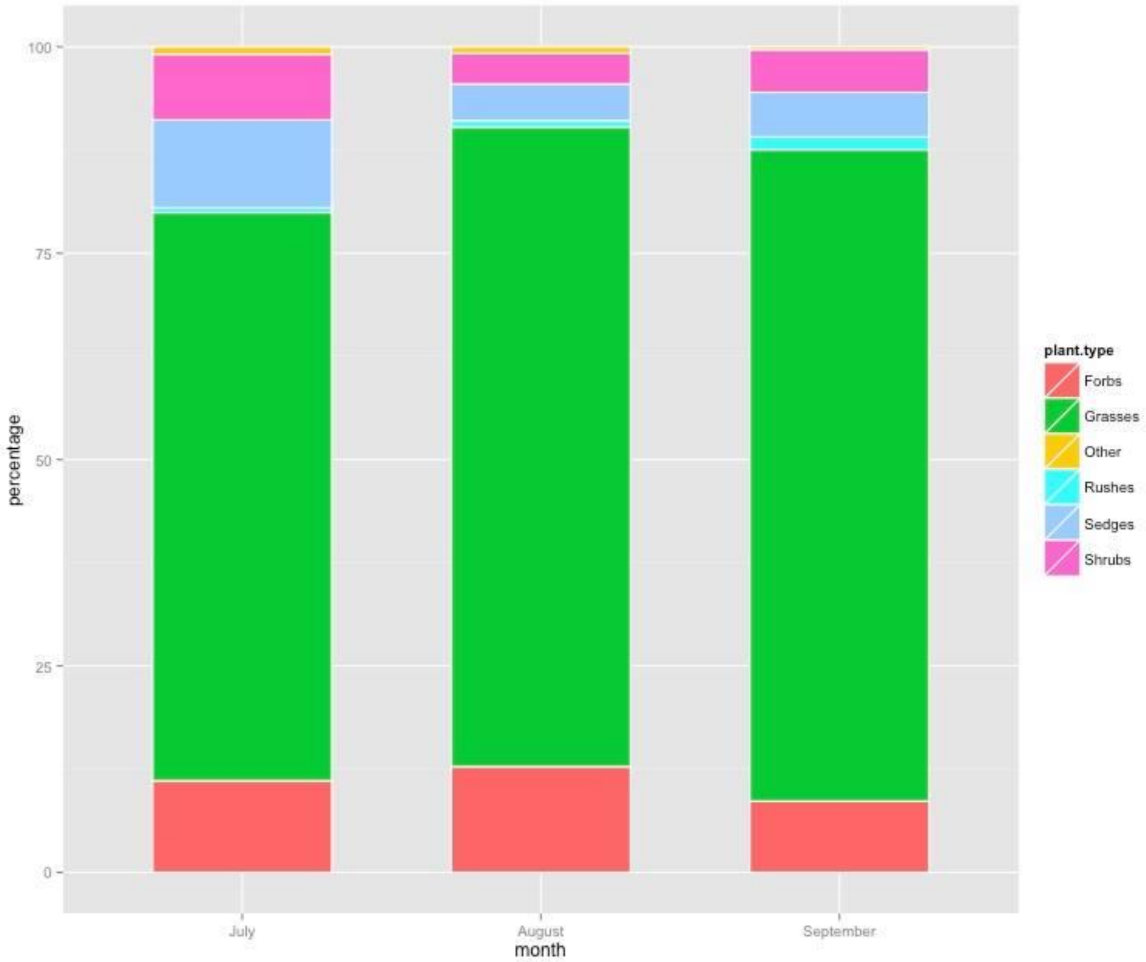

Figure 3 *Proporiton of plant categories in faeces samples of goats at Háafell Farm where red = forbs, green = grasses, yellow = other, light blue = rushes, dark blue = sedges and pink = shrubs.*

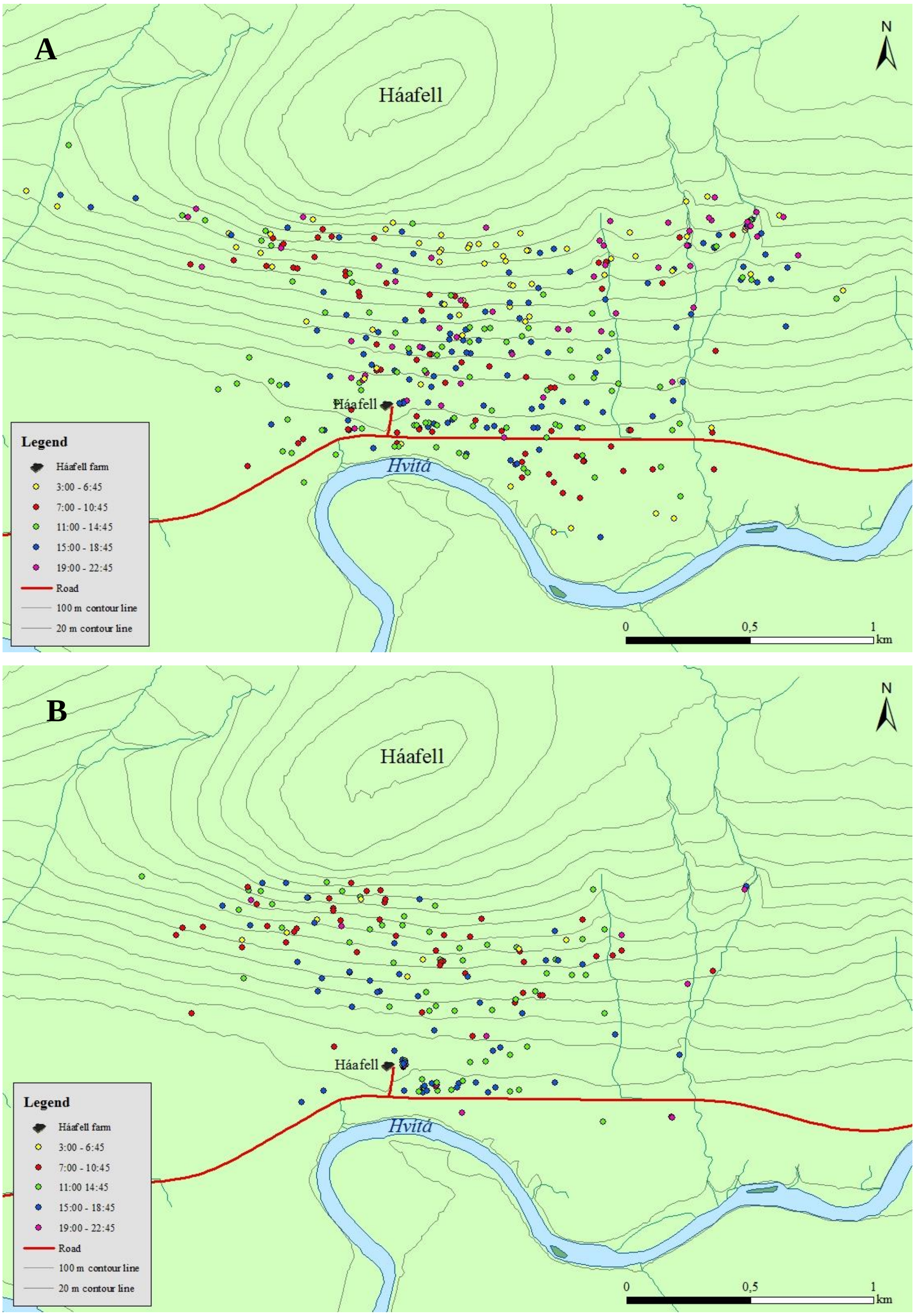

Figure 4 *Distribution of goat groups within the study area at Háafell Farm in (A) August and (B) September with respect to time of day where yellow = 3:00 – 6:45, red = 7:00 – 10:45, green = 11:00 – 14:45, blue = 15:00 – 18:45 and pink = 19:00 – 22:45 hours.*

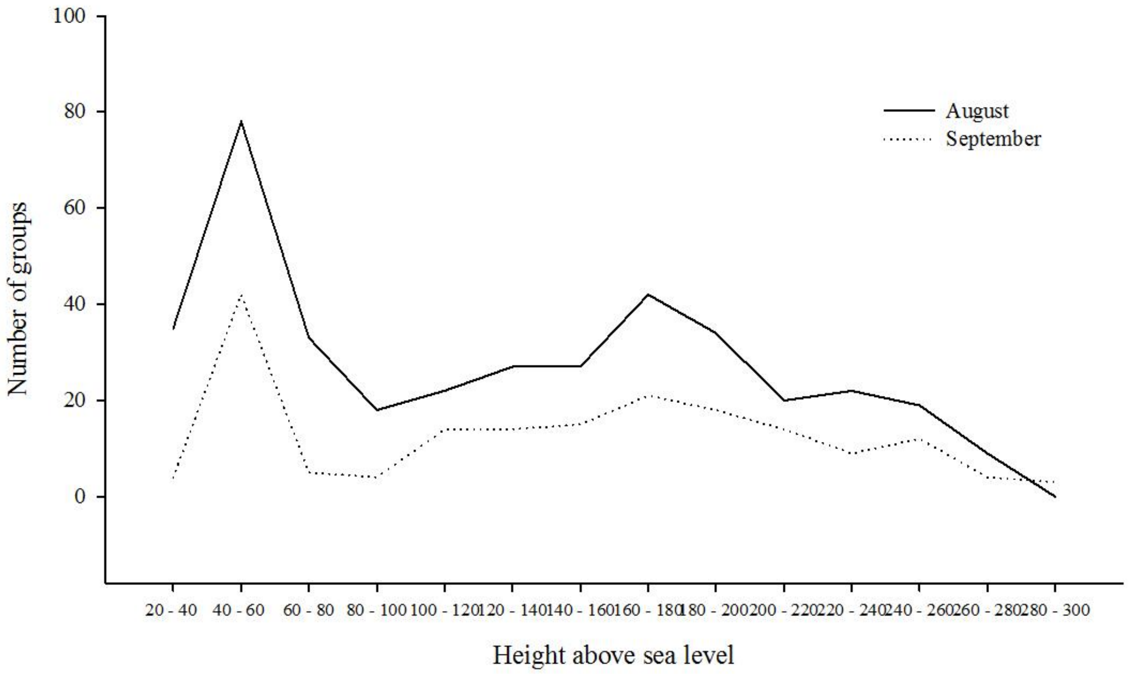

Figure 5 *Combined data for 31 scans in August (3 days) and 33 in September (3 days) showing number of recorded groups in relation to altitude at Háafell Farm.*

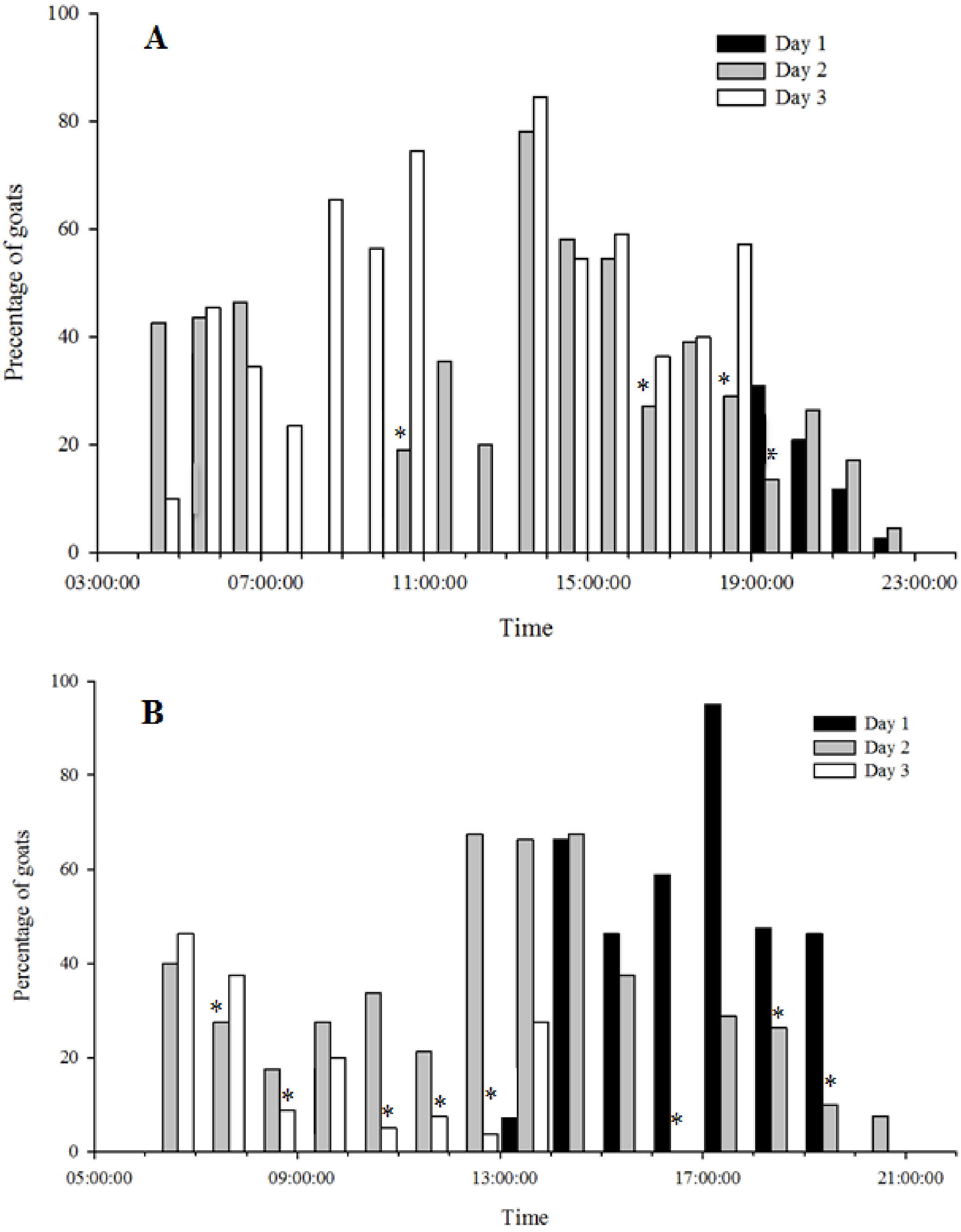

Figure 6 *Percentage of goats foraging (foraging time) at Háafell Farm in (A) August and (B) September where * indicates rain.*

Tables

***Table 1** Weather conditions for the 19th – 21st of July 2012, the 9th – 11th of August 2012 and the 11th – 13th of September 2012 at Háafell farm.*

	Month		
	July	August	September
Mean cloud cover (%)	90.1	91.6	69.1
Mean temperature (°C)	11.5	14.2	6.5
Mean wind speed (m/s)	4.2	4.0	4.0
Precipitation (mm)	3.7	14.3	7.1

***Table 2** Complete list of species found in the study area, type of plant, their abundance and proportion in faeces samples. Plant types are marked with codes Fo (forbs), Fe (Fern), Gr (grasses), Le (legumes), Ru (Rushes), Se (sedges), Sh (small shrubs). Availability and proportion in samples are marked with D = dominant, C = common, R = rare, N/A = not available where * indicates avoidance and ** choice.*

Species	Plant type	Availability	Proportion in samples	Species	Plant type	Availability	Proportion in samples
Agrostis spp.	Gr	D	D	*Kobresia myosuroides*	Se	C	R *
Alchemilla spp.	Fo	C	R *	*Leontodon autumnalis*	Fo	R	C **
Anthoxanthum odoratum	Gr	C	C	*Luzula spp.*	Ru	R	C **
Arabidopsis petraea	Fo	R	R	Moss	-	D	R *
Avenella flexuosa	Gr	C	D	*Myosotis arvensis*	Fo	R	R
Bistorta vivipara	Fo	R	R	*Nardus stricta*	Se	R	N/A
Botrychium lunaria	Fe	R	N/A	*Parnassia palustris*	Fo	R	N/A
Calluna vulgaris	Sh	R	R	*Phleum spp.*	Gr	R	C **
Cardamine pratensis	Fo	R	N/A	*Plantago maritima*	Fo	R	N/A
Carex spp.	Se	C	C	*Poa spp.*	Gr	R	R
Cerastium spp.	Fo	R	N/A	*Potentilla crantzii*	Fo	R	N/A
Deschampsia cespitosa	Gr	D	D	*Rumex spp.*	Fo	R	R
Draba incana	Fo	R	N/A	*Salix herbacea*	Sh	R	N/A
Dryas octopetala	Fo	R	N/A	*Silene acaulis*	Fo	R	N/A
Empetrum nigrum	Sh	C	R *	*Taraxacum spp.*	Fo	R	N/A
Epilobium palustre	Fo	R	N/A	*Thalictrum alpinum*	Fo	R	N/A
Equisetum spp.	Fe	R	R	*Thymus praecox arcticus*	Fo	C	R *
Euphrasia frigida	Fo	R	N/A	*Tofieldia pusilla*	Fo	R	N/A
Festuca spp.	Gr	C	D	*Trifolium repens*	Le	R	N/A
Galium spp.	Fo	R	N/A	*Trisetum spicatum*	Gr	R	N/A
Geranium sylvaticum	Fo	R	R	*Vaccinium uliginosum*	Sh	C	C
Juncus trifidus	Ru	C	R *	*Viola canina*	Fo	R	N/A

Table 3 *Proportion of dicots and monocots in plant selection without unidentified fragments according to months.*

	Month		
Plant group	July	August	September
Dicots (%)	19.21	16.67	13.82
Monocots (%)	80.79	83.33	86.18

Appendix I

No	Name	Year born	Marking	Comments
1	Mína	2005	○ **I**	-
2	Ljúfa	2008	□ **I**	-
3	Belinda	2008	□ **II**	-
4	Eygló	2007	□ **III**	Sister of Góa (5)
5	Góa	2007	□ **IV**	Sister of Eygló (6)
6	Björk	2010	△ **I**	-
7	Sól	2006	△ **II**	-
8	Bylgja	2009	△ **III**	Mother of Rós (28)
9	Silja	2009	**X I**	-
10	Kátína	2011	**X II**	-
11	Soffía	2011	**X III**	-
12	Snúlla	2007	**– I**	Sister of Dúlla (15)
13	Sóldís	2010	**– II**	Daugher of Ronja II (25)
14	Perla	2010	□ **I**	-
15	Dúlla	2007	□ **II**	Sister of Snúlla (12)
16	Sóllilja	2010	□ **III**	Daughter of Brynja (33)
17	Una	2011	**X I**	-
18	Svandís	2007	**X II**	Mother of Lísbeth (32)
19	Ýr	2011	**X III**	-
20	Trú	2010	△ **I**	Sister of Von (23)
21	Hélen	2010	△ **II**	-
22	Bergþóra – Njála	2008	△ **III**	-
23	Von	2010	**– I**	Sister of Trú (20)
24	Hempa	2008	**– II**	-
25	Ronja II Ræningjadóttir	2009	**– III**	Mother of Sóldís (13)
26	Hnota	2011	**X I**	-
27	Caprina	2007	**X II**	-
28	Rós	2010	**X III**	Daughter of Bylgja (8)
29	Dindiltýra	2010	□ **I**	-
30	Sía	2011	□ **II**	-
31	Hulda	2009	□ **III**	-
32	Lísbeth	2009	△ **I**	Daughter of Svandís (18)
33	Brynja	2008	△ **II**	Mother of Sóllilja (16)
34	Kolka II	2010	△ **III**	-