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The effects of castration, sex ratio and population density on social segregation and habitat use in Soay sheep

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Abstract We analysed 16 years of census data gathered on the island of Hirta (archipelago of St. Kilda) to investigate the effects of castration, population density, sex ratio, season and group type on habitat use and social segregation of Soay sheep. From 1978 to 1980, 72 male lambs were castrated. We used this experiment to study how a change in reproductive status could affect sociality and habitat choice of these males. Males, females and castrates were all segregated outside the rutting season in autumn. Castrates were the least segregated from females in spring and summer but were most segregated from them during the pre-rut. The more equal the sex ratios, the higher was the degree of social segregation. The three sex classes used similar habitat types, namely, *Holcus agrostis*, *Agrostis festuca* and *Calluna* habitats. *Holcus agrostis* and *Agrostis festuca* were top- and second-ranked in female and castrate habitat use, while *Holcus agrostis* and *Calluna* were the two top habitat types used by rams. It is unclear why males included *Calluna* heath habitats, but it cannot be excluded that they might have shifted their use depending on forage availability. A lack in differences in habitat use between castrates and females suggests that body size differences alone cannot be the driving factor for habitat segregation in male and female Soay sheep and that there are reasons other than body size that

could motivate reproductive males to use additional habitat types, such as *Calluna* heath. Although habitat use shifted from one habitat type to the next between low- and high-population-density years and between seasons, there was no clear link between population density and how different groups (male, female or castrate) used these areas. We discuss effects of reproductive status, population density and sex ratio on social segregation and habitat use and suggest that these factors need to be taken into account when investigating causes of sexual segregation in ungulates.

Keywords Social segregation · Habitat choice · Sex ratio · Population density · Soay sheep

Introduction

Males and females of most sexually dimorphic ungulates segregate by sex outside the rutting season (Main and Coblentz 1990; Main et al. 1996). Four hypotheses have been investigated in greatest detail: the predation risk, the forage selection, the activity budget and the social factors hypothesis (for a detailed description and review see Ruckstuhl and Neuhaus 2000 and Ruckstuhl and Neuhaus 2002). While the first two hypotheses predict sexual differences in predation risk and forage selection to lead to habitat segregation, the latter two hypotheses predict that sexual differences in activity budgets or same-sex attraction and opposite-sex avoidance lead to social segregation between the sexes. Sexual segregation can hence occur on two different levels: socially or by habitat (see Bowyer et al. 1996; Conrard 1999; Bowyer and Kie 2004 or Ciuti et al. 2004) for a discussion on differences between habitat, social and spatial segregation).

In ungulates, sexual segregation has commonly been attributed to sexual differences in habitat use, with social segregation being treated as a by-product of sexual segregation by habitat (Bowyer et al. 2001; Bowyer et al. 2002; Kie and Bowyer 1999; Bowyer 2004), while in carnivores and primates, the occurrence of all-male groups has always been attributed to social factors rather than to sexual differences in space or habitat use (Caro 1994; Pusey and Packer 1987). A

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recent experimental study on Soay sheep (*Ovis aries*) showed that social attraction to the same sex promotes cohesion of single-sex groups and might lead to sexual segregation (Pérez-Barbería et al. 2005). There have been various papers investigating whether social factors, such as same-sex attraction or opposite-sex avoidance, could cause sexual segregation in ungulates (Bon and Campan 1996; Le Pendu et al. 2000; Weckerly et al. 2001; Michelena et al. 2004). Traditionally, causes of segregation have been investigated by looking at behavioural differences between males and females. However, behavioural differences were always linked to sex and sex to body size dimorphism or reproductive status, factors that cannot be manipulated. In our study, we are using data from an experiment that was initiated in 1978 on the island of Hirta. The experiment involved castrating lambs to measure costs of reproduction on survival and longevity in Soay sheep. We are using data collected during this experiment to test how changes in reproductive status in these males can affect social segregation and habitat use. The castrates provide us with an excellent opportunity to look at effects of body size and behavioural changes on social segregation and habitat use, without sex as a confounding factor.

As castrates were reported to be different in body size (Clutton-Brock et al. 1990) and behaviour (Jewell 1997) from entire rams and ewes, we predicted that they would segregate from others and form castrate-only groups, as it is known that differences in body size can lead to differences in activity budgets (Ruckstuhl 1998), bite rates (Ruckstuhl and Festa-Bianchet 2003) and forage selection (Bowyer 1984), which in turn can lead to social or habitat segregation. Castrates were reported to be less aggressive and to avoid fights with other males (Jewell 1997). Differences in behaviour between castrates and entire rams or ewes could therefore affect social compatibility or preferences and hence lead to social segregation. We do not have data on social preferences, aggressiveness or activity budgets and are therefore unable to test this hypothesis. We instead focus on investigating differences in habitat selection of the different sex classes and the degree of social segregation between them.

The Soay sheep of Hirta (also known as St. Kilda) are well known for their fluctuations in population size and sex ratio (Jewell et al. 1974; Clutton-Brock et al. 1991; Clutton-Brock et al. 2004). These fluctuations are therefore a good opportunity to examine the ways in which animal numbers and sex ratio affect the degree of social segregation and habitat use in the different sex classes. Large-scale changes in population density and sex ratio are likely to affect the degree of social segregation. When population density is high and sex ratio close to equality, we expect an increased level of social segregation because the number of individuals of the same sex increases and with it the opportunity to group with them. In social species, optimal group sizes usually form as a trade-off between competition for food and predator protection through higher numbers (Krebs and Davies 1993; Dehn 1990; Risenhoover and Bailey 1985). Conversely, if sex ratio is heavily skewed towards one sex or if animal numbers are low (low population density), we expect social sexual segregation to decrease and animals to form groups with the opposite sex more often, as not enough suitable partners of the same sex are

available to form large unisex groups. As the Soay sheep population experiences regular crashes, and old males are the first to die, we also expected social segregation to be less pronounced in low-population-density years because the surviving young males might still be associated with female groups. Although Soay sheep on Hirta do not have natural predators, anti-predator behaviour such as group formations often remain an integral part of a species' social make-up, long after predators have disappeared from their range (Byers 1997).

Body size is thought to be an important factor driving social and habitat segregation (Ruckstuhl and Neuhaus 2002). Soay sheep are sexually dimorphic in body size, with males being on average 44% heavier than females. Males weigh around 36 kg and females around 25 kg. Because of their larger size and greater daily requirements for food, we expect castrates and males to be less selective feeders than females (Pérez-Barbería and Gordon 1999; Clutton-Brock et al. 1987; Demment 1982; McCullough 1979; Short and Balaban 1994). Females, however, are expected to be more selective than males because they are usually either lactating or pregnant and therefore have a high energy demand. We also expected rams and castrates to be less selective in their habitat use than ewes and to change their use of habitat types in years when population density and grazing pressure in certain areas were high.

Methods

Study area and species

The feral population of Soay sheep on the island of Hirta, St. Kilda, in the Outer Hebrides, Scotland, has been intensively studied since 1959 (Clutton-Brock and Pemberton 2004; Jewell et al. 1974). Standard censuses on foot were carried out each year in spring, summer and in autumn (approximately ten censuses each) on an area of about 175 ha in Village Bay, which includes a former settlement. Groups were located, and group compositions, including animal identities, location, and vegetation type, were noted. Detailed accounts of the study area, the sheep and census methods are given in Jewell et al. 1974, Jewell (1997) and Clutton-Brock et al. (1992). More than 80% of the sheep were individually recognisable through ear tags. We analysed census data collected between 1985 and 2000.

In 1978, 1979 and 1980, 72 male lambs were castrated immediately after birth, by applying a rubber ring around their scrotum, in order to study the cost of reproduction in rams (Jewell 1997). Of these castrates, 19 survived to be censused from 1985 onwards. According to osteology data, castrates had up to 5% longer femurs (indication of body size) than normal males and 11% longer femurs than females. Their mandibles were up to 12% longer than in either entire males or females (Clutton-Brock et al. 1990). That is why we consider them here as a third sex class. Over the 16 years of the study, we had 5,399 sightings of female groups, 3,332 sightings of male groups, 64 of castrate-only groups, 7,418 of mixed-sex groups, 112 of females-with-castrate groups and 57 of males-

with-castrates groups. Data on castrates were limited in later years, as the last ones died in 1993 (Table 1).

Habitat types within the census area were determined by using the vegetation classification and distribution on the map of St. Kilda (in Jewell et al. 1974). Habitats were classified into six types: HA=*Holcus agrostis* grassland, AF=*Agrostis festuca* grassland, FE=*Festuca* grassland, MO=*Molinia* grassland, CA=*Calluna*, dry and wet heath, O=others (bogs and mires, maritime communities, minor communities and unclassified areas such scree, sand etc., comprising about 12% of the study area). We then calculated how many times female, male, and castrate groups were found in these different habitat types over the 16 years of censuses.

Data handling and analyses

Social segregation

We only used data from sheep that were at least 3 years of age for both sexes as we were only interested in social segregation between adults. We used 3 years as a cut-off point in these sheep because heft fidelity (fidelity to the group they were born into) by male offspring drops after 2 years of age (Coltman et al. 2003). Social segregation coefficients (SC) between females and males, females and castrates, and males and castrates were calculated separately for each census day. Details of this coefficient are described in Conradt's (1999) paper and will not be repeated here, as it is well known and used. The index ranges from 0 to 1, from no to complete social segregation of the sexes.

To avoid pseudo-replication and to minimize problems of data dependence, we first averaged social segregation indices between each sex and reproductive class for each month and season (spring, summer, autumn), instead of using indices for every census day or sighting. All segregation indices were arcsine-square-root-transformed prior to analyses. The effect of season, month, population density, segregation type

(between ewes and rams or between ewes and castrates or between rams and castrates) and adult sex ratio [calculated as the number of adult males (aged >2 years) per female (aged >2 years)] in a given year on social segregation indices was tested using GLM (SPSS 8); we also tested for all levels of interactions between the different variables in the model.

Population density and sex ratio in the Soay sheep were highly correlated ($r_{\text{pearson}}=0.69$, $p<0.01$, $N=16$ years) due to high mortality of males in crash years (Jewell 1997). In years of very high population density (around 600 adult and juvenile sheep in Village Bay), the sex ratio value was high, with about 40 rams per 100 ewes. After crashes, population density and sex ratio values were both low (Table 1). As the two variables were highly correlated, we only used one of them in each analysis: For the analyses on habitat use, we used population density, instead of total number of adults, as a variable in our analyses because food availability will mainly depend on the total number of sheep in the area rather than the total number of adults only. Adult sex ratio, however, was the more appropriate variable to use when investigating social segregation, as we assumed that individuals would be attracted by other animals of similar age (adults) and sex. While we used number of sightings of different group types for our analyses on social segregation, we will use number of sightings of a particular group (identified by a group ID; see below) in our analyses of habitat use.

Habitat use

When analysing the behaviour of an individual animal, it is customary to use identity as a random factor in the model to account for repeated measures. It is much less clear how to solve the problem of pseudo-replication when the unit of the analysis is a group of individuals (Aebischer et al. 1993), especially when group membership is ephemeral as in the Soay sheep. Soay sheep live in a fission–fusion society, and group membership is not stable (Jewell et al. 1974). To

Table 1 Number of adult Soay sheep females, males and castrates, adult sex ratio (adults are 3 years and older), total adults and population size from 1985 to 2000 on the island of Hirta

Year	Ewes	Rams	Castrates	Adult sex ratio (M/F)	Total adults	Population size
1985	165	50	19	0.30	234	509
1986	110	17	18	0.15	145	211
1987	111	17	17	0.15	145	331
1988	131	42	17	0.32	190	457
1989	100	15	13	0.15	128	211
1990	111	11	10	0.10	132	290
1991	128	31	9	0.24	168	414
1992	143	47	5	0.33	195	321
1993	159	31	3	0.19	193	443
1994	180	73	0	0.41	253	435
1995	188	47	0	0.25	235	357
1996	202	71	0	0.35	273	575
1997	238	77	0	0.32	315	542
1998	247	99	0	0.40	346	591
1999	171	24	0	0.14	195	325
2000	184	29	0	0.16	213	461

M Males, F females

account for the fact that individuals were censused multiple times, we used cluster analysis to define groups. We defined dissimilarity between pairs of group sightings using asymmetric binary distances. The number of individuals that were present in only one of the two sightings was divided by the numbers of individuals present in at least one of the two sightings. We then used hierarchical cluster analysis to define the relationships among group sightings.

Because of the fission–fusion nature of the social system in Soay sheep, the appropriate threshold of dissimilarity among sightings that should be used to identify a group is not obvious. We used three arbitrary levels of dissimilarity that should allow us to explore the effect of the grouping criterion on our results: 0.5 indicates low dissimilarity, so only sightings that shared most individuals were defined as the same group, producing 5,993 groups; 0.7 represents medium dissimilarity, producing 3,537 groups; and 0.9 means a high dissimilarity threshold, so that sightings that shared very few individuals were still defined as belonging to the same group. With this threshold, 986 different groups were produced. The analysis (see below for details) was repeated with the three different classification criteria, fitting the group ID as a random factor in our models. Since the qualitative nature of the results did not vary within the different similarity indices, we only present the output of the models with the highest, and thus most conservative, dissimilarity threshold. This is the most conservative approach as we are basically attributing the same group ID to a group until 90% of its members have changed. This allows us to test for problems of pseudo-replication by repeatedly sampling the same groups.

To look at habitat use by different groups of Soay sheep, we used the approach outlined by Aebischer et al. (1993). For each group identified in the cluster analysis, we calculated per cent habitat use for the six different habitat types. The dependence across percentages from a given group was eliminated by using a log-ratio transformation with respect to the use of the “other” habitat, i.e. $\log(x_i/x_o)$, where x_i is the percentage use of the habitat of interest and x_o is the percentage use of the “other” habitat. Conveniently, the “other” habitat class was a collection of habitats unsuitable for foraging, and its use was thus not influenced by any of the investigated factors. A multivariate linear mixed model was fitted on the five log ratios, with group ID as a random factor. We looked at the following predictors: population density, group type (male, female or castrates) and season (spring, summer and autumn), as well as their first-order interactions. A minimal model was obtained using a backward stepwise procedure.

Habitat choice

During the sheep censuses, the location of each sighted group was noted on a 100×100-m grid system superimposed on the map of the Island. To calculate total habitat availability and availability within each grid square, we used the GIS programme ArcView 3.2 from ESRI, with Spatial Analyst 1.0. For digitising the map and geo-referencing, we used ArcGIS 8.0.

To look at habitat choice, we again referred to the approach outlined by Aebischer et al. (1993). Since individual sheep moved through the whole available habitat, we only compared habitat used by the group with the total available habitat, which would be an indication of choice and potentially indicate a preference. Log ratios for all possible habitat combinations were computed for each individual group. We run a separate analysis for each type of group (i.e. male, female or castrate groups): we tested both for an overall deviation from random use of all habitats, as well as for individual habitat pairs. For details on the methodology, see Aebischer et al. (1993). Due to the large number of groups and the distribution of the log-ratios not deviating significantly from Gaussian, we adopted a parametric approach to test the significance of both the overall Λ as well as the individual t estimates for each habitat contrast for male and female groups. A randomization approach with 1,000 runs had to be adopted to look at habitat choice in castrates.

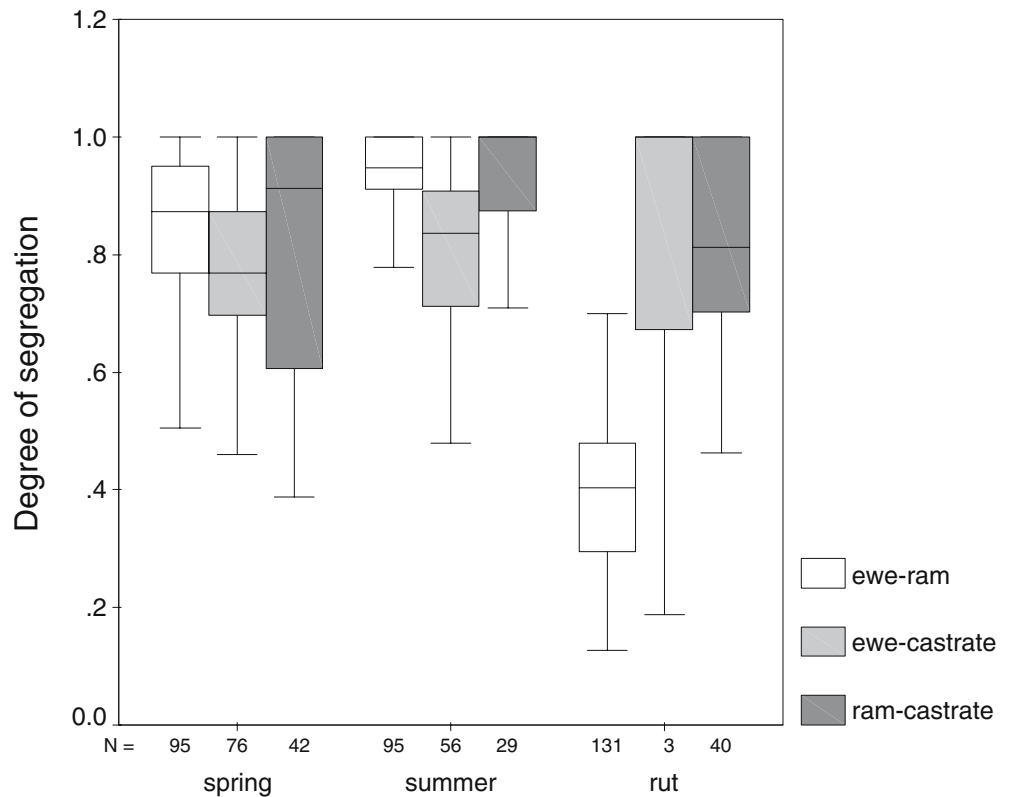
Results

Seasonal changes in social segregation and sex ratio effects

Overall, Soay sheep showed a high degree of social segregation outside the rutting (autumn) season ($F_{2,114}=7.32$, $p<0.01$) (Fig. 1). However, ewes and castrates were significantly less segregated (Scheffé post hoc test $p<0.01$) than either ewes and rams or castrates and rams, which showed similarly high degrees of segregation ($p=0.69$) (Fig. 1). Season significantly affected social segregation between all three sex classes, except between ewes and castrates (overall $F_{2,176}=32.69$, $p<0.001$; segregation between ewes–rams: $F_{2,87}=125.76$, $p<0.001$; between ewes–castrates: $F_{2,43}=1.12$, $p=0.33$; between rams–castrates: $F_{2,40}=6.12$, $p<0.01$) (Fig. 1). The degree of social segregation found between ewes and rams changed significantly in each season (all post hoc comparison $p<0.001$), whereas the only significant difference in the degree of social segregation between rams and castrates was between summer and autumn ($p<0.01$); in autumn, rams and castrates were less segregated than in summer (Fig. 1).

The month of the year also significantly affected the degree of segregation found between ewes and rams ($F_{7,81}=38.72$, $p<0.001$), with a peak of social segregation in July and August, while segregation decreased by October, before the rutting season. The degree of social segregation between rams and castrates also varied between months ($F_{5,41}=16.37$, $p<0.001$). They were most segregated from March to August and much less segregated from October to December (post hoc test for all comparisons between October, November, December and the rest of the year $p<0.001$). Although the degree of social segregation between rams and ewes was not significantly related to population density and adult sex ratio at social segregation coefficients smaller than 0.69 (regression $F_{2,376}=1.18$, $p=0.31$; $t_{\text{pop dens}}=0.85$, $p=0.40$; $t_{\text{sex ratio}}=-1.53$, $p=0.13$), sex ratio positively affected the degree of social segregation for segregation coefficients between 0.69 and 1

Fig. 1 Degree of social segregation between ewes and rams (*open box*), ewes and castrates (*light grey box*) and rams and castrates (*dark grey box*) according to seasons (spring, summer and autumn). Averages are displayed with quartiles and 95% confidence interval of the mean. *N*=number of censuses



(maximum): the more equal the sex ratio, the bigger the degree of social segregation ($F_{3,303}=8.74$, $p<0.001$).

Habitat use: effects of season, population density and group type

Between 1985 and 2000, the Soay sheep of Hirta experienced strong fluctuations in numbers from 700 to 2,000 sheep on the whole island, and from 210 to 590 sheep in the Village Bay population, where the censuses took place. Population density and season (Wald $\chi^2=032.56$, $df=10$, $p<0.001$), as well as group type and season (Wald $\chi^2=44.47$, $df=20$, $p=0.001$) interacted significantly with each other when we investigated their effects on habitat use. Therefore, we present the following results on habitat use by showing separate figures for the two interactions. *Holcus agrostis*, *Calluna* and *Agrostis festuca* were the most used habitat types. Population density significantly affected use of *Holcus agrostis*, *Calluna* and *Agrostis festuca*, whereas it did not seem to affect use of *Molinia* or *Festuca* habitats (Fig. 2a). In spring, use of *Holcus agrostis* habitats decreased as population density increased, while *Agrostis festuca* and *Calluna* habitats were used more heavily in high-population-density years than in lower-density years (Fig. 2a). However, in summer and autumn, the trend was reversed with respect to population density: there was an increased use of *Holcus agrostis* habitats with an increase in population density in summer and autumn and a corresponding decrease in use

of *Calluna* habitats for the same seasons and with increasing population density (Fig. 2a).

All three group types (ewes, rams and castrate groups) used *Holcus agrostis* habitats the most, while *Calluna* and *Agrostis festuca* experienced intermediate use and *Molinia* and *Festuca* habitats were only very little used by all groups. The different groups used the habitats differently according to season, with *Holcus agrostis* being used less and *Agrostis festuca* and *Calluna* habitats being used more in fall than in spring or summer (Fig. 2b). In autumn, castrates drastically reduced use of *Holcus agrostis* habitats, which was the most chosen/used habitat type (see results on use below) for all sheep (Fig. 2a,b). Castrates shifted their use to *Agrostis festuca* and *Calluna* habitats. While ewes and rams also decreased their use of *Holcus agrostis* habitat, it was still the most used type for both genders (Fig. 2b). Interestingly, the levels of use for ewes were intermediate in value between that of rams and castrates for all habitat types (Fig. 2b), and only in autumn did rams and ewes match in their levels of habitat use in all five habitats.

Habitat availability and use/choice

We detected a significant overall choice in habitat use for both female ($\Lambda=0.031$, $\chi^2=2772.84$, $p<0.001$) and male groups ($\Lambda=0.124$, $\chi^2=256.76$, $p<0.001$), but not for castrates ($\Lambda=0.243$, randomization test $p=0.062$). Allowing for the availability of the different habitat types and their use by the different sex classes, females, males and castrates all chose

Fig. 2 **a** Predicted mean use by Soay sheep of different habitat types depending on population density and season and **b** predicted mean use of the different habitat types depending on group type and season. Use is given as the log-ratio of proportional habitat use (see Aebischer et al. 1993). Habitat types are *Holcus agrostis* grassland, *Agrostis festuca* grassland, *Festuca* grassland, *Molinia* grassland and *Calluna* dry and wet heath. In figures under **(a)**, the predicted means refer to the average use by ewe groups (values for rams or castrates would follow the same trends), while under **(b)**, the values are centred on the mean population density

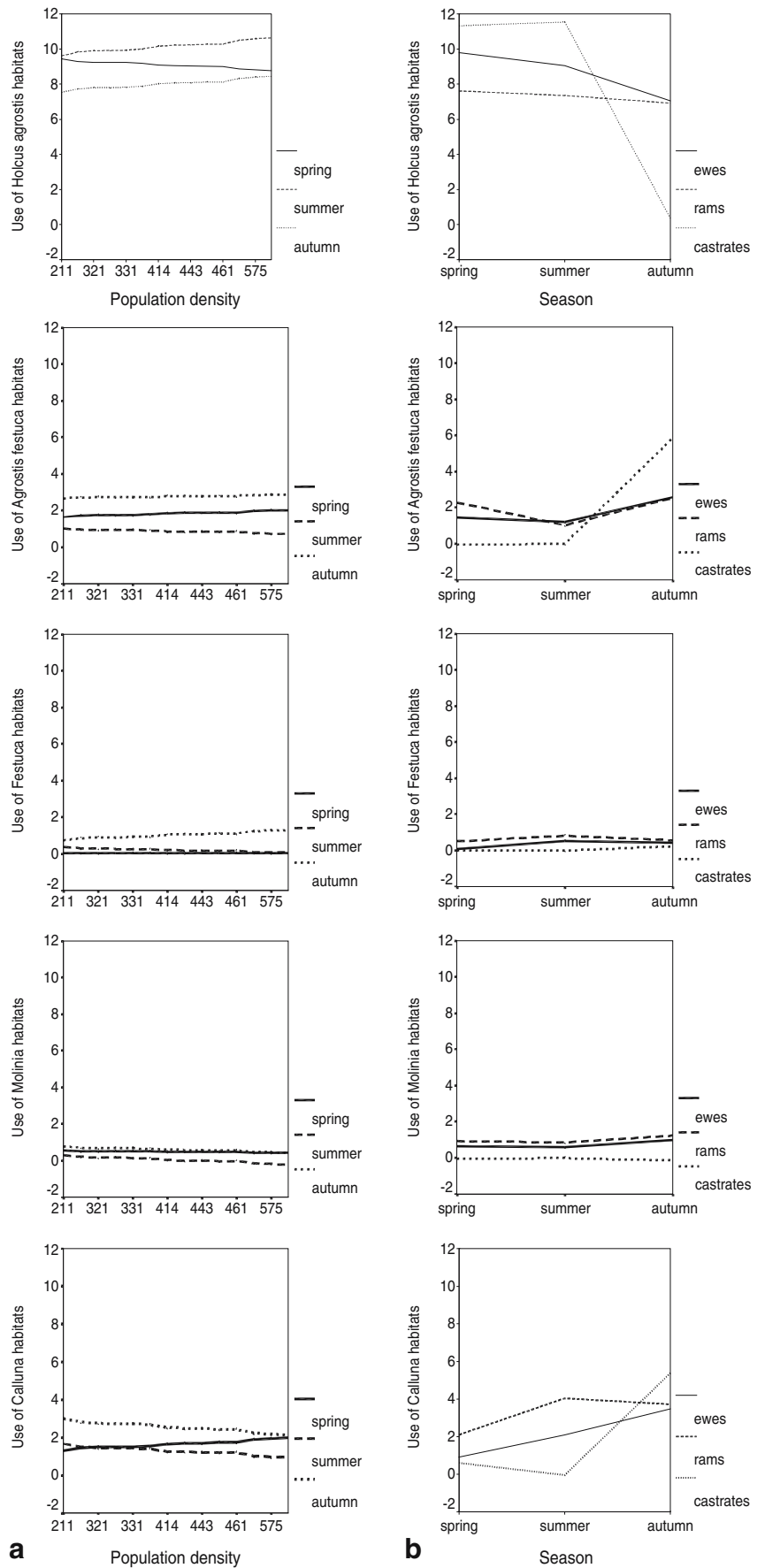


Table 2 Relative habitat use by Soay sheep ewes, rams and castrates on the island of Hirta

	HA	AF	FE	MO	CA	O	Rank
Ewes							
HA		+++	+++	+++	+++	+++	5
AF	—		+++	+++	+++	+++	4
FE	—	—		+++	—	+++	2
MO	—	—	—		—	+++	1
CA	—	—	+++	+++		+++	3
O	—	—	—	—	—		0
Rams							
HA		+++	+++	+++	+++	+++	5
AF	—		+	+++	—	+++	3
FE	—	—		+	—	+++	2
MO	—	—	—		—	+++	1
CA	—	+	+++	+++		+++	4
O	—	—	—	—	—		0
Castrates							
HA		+	+++	+++	+	+++	5
AF	—		+	+	+	+	4
FE	—	—		+	—	+	2
MO	—	—	—		—	+	1
CA	—	—	+	+		+	3
O	—	—	—	—	—		0

Not all habitats were equally abundant. We therefore looked at habitat use and choice by each sex class, controlling for the availability of each habitat type. '+' indicates that the habitat listed in the row is used more than the one in the column, but not significantly so. '+++' indicates a significantly higher use of a particular habitat within a pair. To clarify, the '+++' between HA and AF, for example, means that sheep significantly selected HA over AF (although HA habitat is less abundant than AF). '-' indicates that one habitat is used less than the one in the column with respect to availability, but not significantly so. '—' indicates a significantly different use of the habitat listed in the column. The '-' signs are therefore the mirror image of the '+' signs in this table. Rank represents the overall bias in habitat use, with 5 being the most and 1 being the least used/selected habitat type

HA *Holcus agrostis* grassland, AF *Agrostis festuca* grassland, FE *Festuca* grassland, MO *Molinia* grassland, CA *Calluna* dry and wet heath, O rest of habitat

the same habitats and showed a clear bias towards *Holcus agrostis*, *Agrostis festuca* and *Calluna* habitats, whereas *Molinia* grassland and *Festuca*, or the remaining habitats (category 'O') were less selected (Table 2). *Holcus agrostis* was chosen most often by all group types. Castrate and female groups were also significantly biased towards *Agrostis festuca* habitats, while rams chose *Calluna* habitats over *Agrostisfestuca* (Table 2, see sub-table for rams).

Discussion

Changes in social segregation: effects of sex class, season and sex ratio

Here we demonstrate clear social segregation between sex classes without any substantial difference in habitat choice, and how habitat use in three different groups of sheep (castrates, entire males and females) respond in the same way to changes in population density and sex ratio. Soay sheep of St. Kilda showed a high degree of social segregation by sex as well as by reproductive status (castrates and normal rams). The castration experiment therefore clearly showed that a change in reproductive status, behaviour and physiology can

lead to social segregation, without leading to habitat segregation or a change in diet choice.

Outside the breeding season, segregation indices were highest between males and castrates, intermediate between males and females and lowest between females and castrates. That segregation was least between females and castrates is surprising and could be due to castrates being phenotypically different from normal rams (Clutton-Brock et al. 1990). Jewell (1997) also reported that, during the rut, castrates spent most of their daytime grazing, with activity patterns similar to those of females, whereas normal rams were continuously moving and involved in fights and mating. It is well known that males sometimes segregate into similar-age groups (e.g. Bon and Campan 1996; Ruckstuhl and Festa-Bianchet 2001) and a study on African buffalo (*Syncerus cafer*) has shown that males in poor condition segregate from other males and female groups (Prins 1989). It is therefore possible that castrates segregated themselves from entire males and sometimes from females due to social factors or incompatibilities of activity budgets with either entire males or females.

Studies on bighorn sheep, for example, have shown that females socially segregate from males—and subadult males segregate from females and males—because they

all greatly differ in their activity budgets (Ruckstuhl 1998; Ruckstuhl 1999; Ruckstuhl and Festa-Bianchet 2001). Within male bighorns, body mass and dominance status seem to be an important determinant of activity budgets outside the rutting season, with dominant and heavier animals spending significantly less time foraging and more time lying than subordinate and lighter individuals (Pelletier and Festa-Bianchet 2004). Unfortunately, we do not have data on social attraction or activity budgets to test whether social factors or differences in activity budgets could have led castrates to segregate from normal rams and females, but this would be an area well worth investigating in future studies.

Although some of the castrates were associating with females on a regular basis, it is worthwhile pointing out that on average, segregation indices remained high between all groups outside the breeding season. Social segregation only dropped significantly in the fall during the pre-rut. At that point, castrates and females were the most segregated, males and castrates were found in the same group more often, while males and females aggregated into mixed-sex groups.

That castrates were less segregated from some males during breeding than from females could be because not all rams were in female groups at all times during the rut, and therefore encounters between rams and castrates were possible. Castrates may further have avoided breeding areas during the rut (Jewell 1997), which would have distanced them from adult females. Although social segregation by sex (Main and Coblentz 1990; Main et al. 1996; Pérez-Barbería and Gordon 2000), age (Cransac et al. 1998; Le Pendu et al. 2000; Ruckstuhl and Festa-Bianchet 2001; Villaret and Bon 1995) and reproductive state (Main et al. 1996; Bleich et al. 1997; Miquelle et al. 1993) have been documented for several ungulate species, this is the first experiment to demonstrate that an alteration in reproductive state by castration, with its associated changes in physiology, growth, metabolism and endocrinology, leads castrates to markedly socially segregate from normal rams. Whether this segregation was an active choice of castrates or the result of passive mechanisms is unclear and should be investigated further.

As expected, social segregation indices increased for all sex and reproductive classes when adult sex ratio increased, probably because there were more individuals of the same sex available to form peer groups in years of high density than in years of low density and low sex ratio values, especially for rams.

High population density, starvation and bad winter weather on Hirta regularly lead to high winter mortality, which mostly affects old, young and male individuals (Clutton-Brock et al. 2004). As male mortality is higher than female, population density and male numbers are always relatively low after a crash (Stevenson 1994), limiting the number of suitable group peers for males, but not necessarily for females. Ruckstuhl and Festa-Bianchet (2001) found a similar result in Rocky Mountain bighorn sheep (*Ovis canadensis*), where in high-population-density years, with many subadults, subadult rams were more likely to form peer groups than in low-population-density years, with only few subadults.

Effects of sex class, population density and season on habitat use

Sexual differences in forage selection have been put forward as an important determinant of sexual segregation by habitat in many ungulate species (Jakimchuk et al. 1987; Koga and Ono 1994; McShea et al. 2001), and also, for example in giant petrels (*Macronectes halli*) (Gonzalez-Solis et al. 2000), Northern elephant seals (*Mirounga angustirostris*) (Le Boeuf et al. 2000; Steward 1997), sharks (Sims et al. 2001) and Anoline lizard (*Norops humilis*) (Parmelee and Guyer 1995). Although Conradt (1999) reported high degrees of habitat segregation between male and female Soay sheep on St. Kilda, our study did not find marked differences in proportional habitat use by the different sex classes. This could be because calculations of spatial and habitat segregation are scale-dependent and the results therefore are affected by the sampling scale. In our study, we simply noted the vegetation type where the sheep groups were present during censuses, a sampling method that is not scale-dependent and does not describe habitat segregation, only habitat use.

Rams, ewes and castrates used *Holcus agrostis* grassland more than other habitat types, although *Holcus agrostis* grassland was much less abundant than for example *Calluna* wet and dry heath, which covered more than half of the census area. While castrates and ewes showed the exact same orders of proportional habitat use, it is interesting that rams also used *Calluna* habitats, which were used the second highest by rams. That castrates and females used the same areas was surprising because they are the most dimorphic in body size, and indicates that differences in habitat use are not primarily influenced by body size and digestive efficiency, but that there are other motivations that cause reproductive males to segregate and at times use different habitats (e.g. *Calluna* heath) than females and castrates. Males might have modified their habitat use to include *Calluna* heath in response to forage availability, which would presumably be influenced by grazing pressure. However, we do not have data on forage biomass to test this idea.

All types of sheep used grassland more often than any other vegetation types, which was not surprising as sheep are mainly grazers. However, the most used habitat type, *Holcus agrostis*, was found in the former settlement within Village Bay. The former settlers cultivated the fields surrounding the village area, rendering the soils more fertile than the surrounding hillsides (Jewell et al. 1974). These areas therefore attract many sheep and form one of the main grazing sites for the Soay sheep in the census area.

Crawley et al. (2004) reported that the higher the Soay sheep density on Hirta, the lower the available forage biomass. Males might therefore be expected to leave heavily frequented areas because they are able to digest lower-quality (less preferred) foods more efficiently than females (Clutton-Brock et al. 1987; Barboza and Bowyer 2000, 2001; Demment 1982; McCullough 1979). However, we did not find that males were choosing different habitats, except for an increase in the use of *Calluna* heath, when

density was high. This contrasts with studies on red deer (*Cervus elaphus*) (Clutton-Brock et al. 1987; Conradt et al. 1999; Conradt et al. 2001) and suggests that changes in male habitat use are not a consequence of high density or competition with females.

A study on white-tailed deer found that at high population density, both spatial and dietary overlap between males and females decreased (Kie and Bowyer 1999). However, female white-tailed deer, which are mainly browsers, were in poorer condition in high-density years than males, suggesting that in this species too, females did not drive spatial segregation by being better competitors on preferred feeding sites. Analyses of available forage and height of the standing crop in the different habitat types on Hirta in low- and high-population-density years are needed to verify whether males and female could differ in their forage selection on the micro-scale and how population density might affect gender differences in forage selection.

Like many other ruminants [e.g. mouflon (*Ovis aries*) (Cransac and Hewison 1997), Cantabrian chamois (*Rupicapra pyrenaica parva*) (Pérez-Barbería et al. 1997), or waterbuck (*Kobus ellipsiprymnus*) (Wirtz and Kaiser 1988)], Soay sheep habitat use varied with season. Although there was a shift in the use of *Holcus agrostis* to *Agrostis festuca* and *Calluna* habitats with an increase in population density, the reverse was true for summer and autumn. The lack of any clear seasonal pattern between spring, summer and autumn is probably linked to a lack of seasonal variation in the relative quality of habitats. The climate of St. Kilda is temperate oceanic, and changes in temperature and rainfall that might induce changes in habitat quality are relatively small. There is also a small altitudinal range, 430 m, compared with that experienced by many mountain ungulates, and on St. Kilda, the best quality grazing is usually found close to sea level in all seasons.

Conclusions

Although changes in population size have been used to look at shifts in habitat use and dietary niche selection in white-tailed deer (Kie and Bowyer 1999) and Bowyer et al. (1996, 2002) emphasized the importance of evaluating effects of population density on segregation by space and habitat, studies incorporating population density and sex ratio as driving factors in models of social segregation are lacking. However, this study shows that population density and sex ratio are important variables that need to be taken into account when interpreting social and habitat segregation in ungulates. This study also highlights that not only population density and sex ratio, but also intrinsic (i.e. reproductive state) and phenotypic factors (body size or behaviour) could potentially be important in driving social segregation in Soay sheep, and possibly in other ungulates as well. It is well worth looking at any evidence of differences in body size or age, as has been done in various studies, within a sex and how changes in population density affect habitat use, activity patterns and group choice.

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