Scale-dependent effects of summer density on autumn mass in reindeer

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Abstract: The ongoing dispute about reindeer overabundance in the West Finnmark (Norway) herding region has accentuated the need for an in-depth understanding of the density-dependent and -independent processes driving this pastoral system, as well as the spatial and temporal scale(s) they operate on. Using 20 604 records of individual male reindeer yearlings we assessed the spatial and temporal variation in animals' performance (measured by their autumn carcass mass), and investigated summer density dependent effects on autumn carcass masses at different scales. We defined three spatial scales; a regional scale represented by the whole summer range of West Finnmark, a sub-regional scale represented by the mainland (14) and the island (11) summer districts, and a fine scale represented by eight individual summer districts. We defined two temporal scales; the whole collection phase (13 years) and a temporal dimension based on the three periods of population growth. We found carcass masses to be higher at island than at mainland and to vary among districts. Effect of period was found at the regional, sub-regional and often at the district scale. The autumn carcass masses were sensitive to density at West Finnmark and mainland scales, but not at island scale, the effect being negative. This suggests intra-specific competition for summer forage due to consistent higher density resulting in reduced range quality at mainland as compared to island. On the finest scale the density effect was highly variable. Response of carcass mass to density appeared to be scale dependent both in space and time at regional and sub-regional scales. These findings underline the importance, for skilful management, of site specific biological understanding of (1) the density dependent processes and (2) the spatial and temporal scales these processes are operating on. Adaptive management strategies for sustainable use of the summer forage resources in West Finnmark have therefore to be district specific.

Key words: density dependence, *Rangifer tarandus*, reindeer husbandry, scale effect.

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Introduction

The Norwegian Reindeer Husbandry Administration (Reindriftsforvaltningen) has since the early 1980s been claiming the number of semi-domestic reindeer in West Finnmark, a reindeer management herding region in the northernmost part of Norway, to be far above the level for sustainable management (Riseth, 1987; Ims & Kosmo, 2001). This claim has been based upon deterioration of the winter lichen pastures (reviewed by Johansen & Karlsen, 2005), low carcass masses, a highly variable population size due to variable recruitment and survival rate resulting in a fluctuating production output the last decades (Reindriftsforvaltningen, 2008). The Norwegian Reindeer Herders' Association (NRL) agrees that some of the winter as well as summer pastures

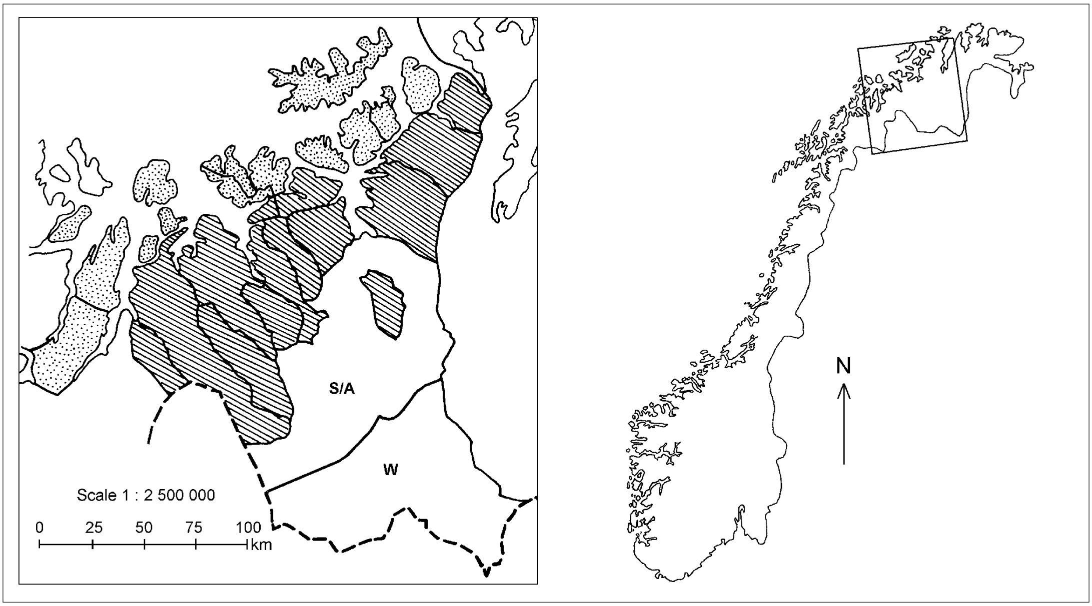

Fig. 1. Seasonal distribution of the ranges in West Finnmark, displaying the different summer herding districts (black signatures) and spring/autumn (S/A) and winter (W) (white areas) ranges further south. The summer herding districts are further divided into mainland districts (stippled) and island districts (dotted).

in West Finnmark have been overstocked, but argues, that the highly stochastic environment, especially the winter snow condition, is the main driver of the availability of winter forages (Ulvevadet, 2000). This results in a highly variable winter carrying capacity and hence fluctuations in the population size and production output, which accords with the non-equilibrium approach (reviewed by Behnke, 2000).

In 2002 the Reindeer Husbandry Board (Reindriftsstyret) agreed upon a reduction scheme in order to stabilize the population of around 63 700 heads in West Finnmark within 5 years (Holand, 2003). To implement the plan each of the 26 summer herding districts representing the operative administrative units within the region, were given a target population size based on empirical data on carcass masses, summer density estimates and interdistrict comparisons (Ims & Kosmo, 2001). However, mismatch in conception between state authorities and herders on which spatial and temporal scales these expected density dependent processes are operating on and the importance of density independent processes, has torpedoed the implementation of the plan, the outcome being an increased population size since the Board's decision in 2002 (Reindriftsforvaltningen, 2008).

Indeed, the winter snow condition varies greatly and has been reported to influence large northern herbivores' performance through forage availability (e.g. Skogland, 1985; Loison *et al.,* 1999; Kumpula & Colpart, 2003; Tveraa *et al.,* 2007) as well as cost of locomotion (Fancy & White, 1985). Several studies have also shown negative summer density-dependent effects on body mass of large temperate and northern herbivores (Hjeljord & Histøl, 1999; Stewart *et al.,* 2005; Herfindal *et al.,* 2006), including reindeer (Lundqvist, 2007). The main suggested mechanism being intraspecific competition for forage, which may operate at multiple spatial scales (Senft *et al.,* 1987). The temporal dimension may also vary as consistent high grazing pressure over time may induce

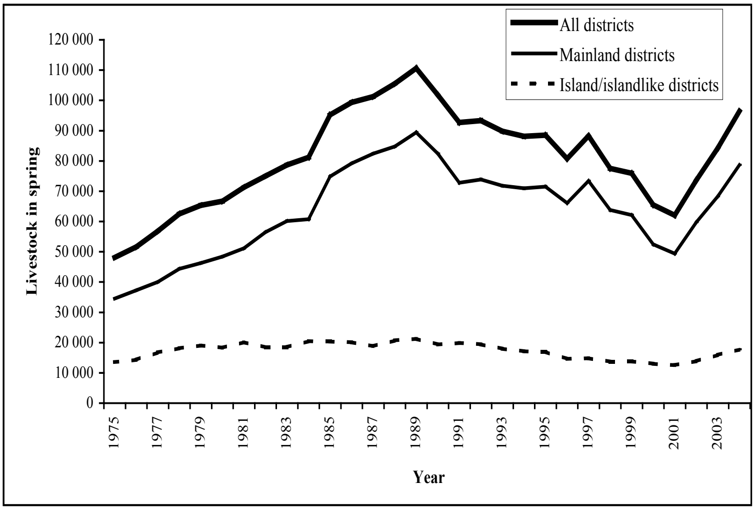

Fig. 2. The fluctuations in the reindeer spring population in West-Finnmark (1975 - 2005) (continuous bold line) and for mainland (continuous line) and island (discontinuous line) districts separately (Reindriftsforvaltningen, 2005).

neutral, facilitating or retarding vegetation productivity (Simberloff, 2004). Actually, homogenisation (i.e. reduced abundance of productive and preferred plants/plant groups) of the summer range in Finnmark at high reindeer grazing pressure has been reported (Bråthen *et al.,* 2007). This will lead to an accumulated density effect which can be hard to disentangle from the current density effect. Consequently, the summer density dependent effect may vary spatially and temporally according to climate (Herfindal *et al.,* 2006), management practice and other abiotic as well as biotic factors (Sæther, 1997; Hobbs, 2003; Ims *et al.,* 2007). Understanding these ecological processes and the scales they are operating on are therefore critical for skilful management of this extensive pastoral production system.

Based on records of individual carcass masses and density estimates spanning 13 year (1983-1987 and 1996-2004) in West Finnmark we assessed the spatial and temporal variation in animals' performance (measured by their pre rut carcass mass). Further we investigated whether the summer density effect, if any, would be scale dependent in space and time.

Study area

The data used in this study are from the West Finnmark reindeer-herding region, which totally encompasses around 24 000 km^2 in the northernmost part of Norway (Fig. 1). The reindeer husbandry in the region is characterized by a semi-nomadic seasonal grazing system where the herds migrate from the summer ranges at or close to the coast to the interior winter ranges, a distance of 100 – 350 km. The summer grazing areas are characterized by nutrient-rich bed rocks and rather high annual precipitation whereas the winter ranges are found on nutrient-poor bed rocks low in annual precipitation including winter precipitation as snow. The spring and autumn ranges represent a transition zone between the two main seasonal ranges. The summer ranges of West Finnmark are divided into 26 summer herding districts (administrative units). The winter, spring and autumn ranges have been defined administratively as commons, although traditionally each summer herding group is split into smaller winter herding groups (winter-siidas) with their defined grazing areas (Paine, 1994).

The reindeer husbandry authorities have since the early 1980s made various attempts to control and reduce the number of reindeer (Riseth, 1988; Ims & Kosmo, 2001; Reindriftsforvaltningen, 2005). This strategy, combined with several severe winters in the late 1990s, led to a reduction of the reindeer number by almost 50% from 1989 (110 000 heads) to 2001 (62 000 heads) (Reindriftsforvaltningen,

2008) (Fig. 2). Since then the population has again increased reaching 96 000 individuals in spring 2004 (Reindriftsforvaltningen, 2008) probably due to several favourable winters and summers in a row causing reduced pre-weaning calf mortality as well as reduced winter mortality, combined with moderate numbers of reindeer being slaughtered. In spring 2008 the population estimate was 94 000 heads (Reindriftsforvaltningen, 2008).

Table 1. Mean yearly carcass mass ± standard error in kg, sample size (n) provided in brackets and annual net density by sub-region.

Year	Mainland		Island	
	Carc. Mass ± SE (*n*)	Net density	Carc. mass ± SE (*n*)	Net density
1983	29.1 ± 0.45 (74)	6.3		
1984	26.2 ± 3.90 (1)	6.4		
1985	24.9 ± 0.16 (562)	7.8	24.0 ± 2.30 (4)	6.0
1986	24.5 ± 0.11 (1266)	8.3	26.9 ± 0.42 (120)	5.8
1987	24.0 ± 0.08 (2352)	8.6	25.2 ± 0.21 (491)	5.6
1996	23.9 ± 0.12 (1122)	6.9	29.4 ± 0.34 (185)	4.6
1997	23.2 ± 0.10 (1381)	7.7	27.2 ± 0.45 (105)	4.4
1998	22.5 ± 0.10 (1374)	6.8	27.2 ± 0.25 (340)	3.1
1999	22.3 ± 0.09 (1704)	6.5	28.5 ± 0.22 (412)	3.2
2000	25.0 ± 0.19 (420)	5.5	27.6 ± 0.37 (157)	3.8
2001	26.6 ± 0.16 (610)	5.2	29.3 ± 0.47 (97)	3.8
2002	27.7 ± 0.08 (2660)	6.3	32.6 ± 0.26 (323)	4.1
2003	27.4 ± 0.09 (1820)	7.2	30.6 ± 0.24 (305)	4.8
2004	24.1 ± 0.08 (2323)	8.3	30.2 ± 0.25 (341)	5.3

Material and methods

Reindeer data

We collected available age- and sex-specified slaughter data (i.e. carcass mass representing live body mass minus head, skin, viscera, blood and hoofs from the wrist and down) from all summer herding districts in West Finnmark, except one district without available data, representing periods of rise (1983-87 and 2002-2004) and fall (1996-2001) in population size (Fig. 2). We focused on carcass masses of yearling male reindeer, which represent a homogenous group and traditionally constitute the most important segment of the herd being slaughtered, consisting of more than 67 000 carcass masses from the 3 actual periods. The animals in this group are in their growth phase and hence sensitive to environmental factors. As our main goal was to scrutinize potential density effect of the summer ranges, we used only pre-rut (i.e. September to early October) carcass masses before or just after the animals normally leave the summer ranges. Further, in the final analyses we dropped year 1984 and the island's carcasses in 1985 due to very few observations (Table 1), thereby reducing the data set to 20 604 carcasses.

Annual net densities for each summer district (fine scale density) were calculated based on the reported number of animals each spring (March 31st) and the estimated net summer range area (i.e. total area minus impediments) (Ims & Kosmo, 2001) corrected for number of summer grazing days (if any) spent outside the defined summer range for each district during the summer grazing period (May 15th to September 15th, i.e. 120 days). In order to investigate scale effects we also calculated the aggregated annual net summer density for West Finnmark region (coarse scale density), as well as for the two sub-regions (mainland and island) separately (medium scale density) (Table 1). Island also included the peninsula districts (Fig. 1) where geomorphologic characteristics and management practises are very much alike the island districts (Ims & Kosmo 2001). The annual variation in calf production (number of females, out of the total number of females, having calf at heel in autumn) within a district was pronounced as well as the between districts variation for a given year. Also the herd structure (i.e. sex ratio) will influence the number of calves produced. Indeed, the number of calves will greatly influence summer plant biomass off-take. Summer density calculated based on the reported number of animals each spring may therefore not be accurate, but the best available estimate.

Statistical analyses

We used linear mixed models (Mixed procedure in SAS; SAS, 1999) to assess the effect of density on carcass mass of yearling male reindeer, with "year" entered as random term. Male yearlings have been exposed to two summer seasons, both influencing their pre-rut carcass mass. However, the relative strong correlations of density between years (year of slaughter *vs.* year of slaughter – 1) at West Finnmark (r = 0.65) and mainland (r = 0.58) / island (r = 0.79) scales confirm that using the spring density the year of slaughter is satisfactory, especially since the range condition (incl. density) the second summer will influence the carcass mass of yearlings strongest.

We defined three spatial scales; a regional scale represented by the whole West Finnmark summer range region, a sub-regional scale represented by the mainland and the island districts respectively, and a fine scale represented by the individual summer districts. We defined two temporal scales; the whole collection phase (13 years) and a temporal dimension based on the two distinct periods of population rise; period 1 (1983-1987) and period 3 (2002-2004), and one period of decline; period 2 (1996-2001) (Fig. 2). For each of the spatial and temporal scales we ran one set of analyses.

Independently of the scale of investigation, "slaughter date" restricted to the pre-rut period was included in all models as covariates to account for temporal change in body mass. We also included the winter (December – March) NAO-index (www.cgd.edu/cas/jhurell/indices.html) as a covariate to account for yearly variations in winter range conditions (reviewed by Mysterud *et al.,* 2003, Weladji & Holand, 2006). Inclusion of period and lower level spatial scale and the interaction between density and "period", between density and "sub-region" (i.e. mainland and island), or between density and "district" were performed to assess temporal and spatial variation in density dependency respectively. All analyses were performed in SAS (SAS, 1999), and significance was accepted at 5% level.

West Finnmark scale: In addition to slaughter date and winter NAO-index, predictor variables in the models included the "coarse scale density", with and without the variable "sub-region" and period and their interaction with density, thereby testing the scale dependent density effect. Hence, the full model was:

Carcass mass =
density + sub-region(mainland and island) + period + slaughter date + NAO + density*sub-region + density*period + e

We assumed spatial and/or temporal scale-dependent density effect if, the inclusion or not of the lower level, here "sub-region" i.e. mainland vs. island and/or period, and their interactions with overall density yielded different density effect and affected the accuracy and sign of the parameter estimates differently. While the interaction between density and sub-region describe the spatial variability in the density dependency, its interaction with period would describe the temporal variation in the density effect. Sub-region and period were entered as categorical variables, all other variables being continuous.

Table 2. Parameter estimates with standard errors (SE) and *P*-values for the mixed linear models fitting the autumn carcass masses (kg) of male yearlings at the coarse density scale (i.e. **West Finnmark**) without sub-region (mainland: M and island: I) and period (P1: 1983-86, P2: 1996-2001; P3: 2002-2004) and theirs interactions with density (***A:***), including sub-region and density by sub-region interaction (***B:***), without period and density by period interaction (***C:***), and with sub-region and period and theirs interactions with density (***D:***). Slaughter date and winter NAO are entered as covariates in the models.

	Without Sub-region and Density x Sub-region			**Including Sub-region and Density x Sub-region**		
	Estimate	*SE*	*P-value*	*Estimate*	*SE*	*P-value*
Without Period and Density x Period	*A:*			*B:*		
Intercept	27.2719	3.8363	<0.001	36.0121	4.1034	<0.001
Slaugther date	0.05803	0.0048	<0.001	0.01776	0.0047	<0.001
Winter NAO	0.2260	0.3203	0.4806	0.2152	0.3401	0.5270
Density	-0.5028	0.5898	0.3940	-1.1607	0.6312	0.0660
Sub-region (M-I)				-9.3559	0.5601	<0.001
Density x Sub-region (M-I)				0.8183	0.0855	<0.001
Including Period and Density x Period	*C:*			*D:*		
Intercept	38.6826	4.0878	<0.001	48.5184	4.1178	<0.001
Slaughter date	0.05828	0.0048	<0.001	0.01798	0.0047	<0.001
Winter NAO	-0.2632	0.1477	0.0748	-0.3323	0.1476	0.0244
Density	-1.9700	0.6176	0.0014	-2.7982	0.6223	<0.001
Period						
(P1-P2)	13.1130	5.1595	0.0107	18.2958	5.1196	<0.001
(P1-P3)	7.4454	6.0417	0.2178	10.2403	6.0092	0.0884
(P2-P3)	-5.7237	4.8518	0.2381	-8.0555	4.8651	0.0978
Sub-region (M-I)				-9.3709	0.5600	<0.001
Density x Period						
(P1-P2)	-1.2441	0.7470	0.0958	-1.9715	0.7423	0.0079
(P1-P3)	-0.9986	0.8621	0.2467	-1.3483	0.8583	0.1162
(P2-P3)	0.2456	0.7693	0.7496	0.6232	0.7693	0.4179
Density x Sub-region (M-I)				0.8205	0.0855	<0.001

Mainland/Island scale: We ran similar models as at the West Finnmark scale, but using the “medium scale density”, and the lower level scale i.e. with and without the variable “district” within sub-region and period and theirs interaction with density, thereby testing for scale dependency and differential spatial and temporal responses to density.

The mainland full model was:

Carcass mass =
density(mainland) + district(mainland) + period + slaughter date + NAO + density*district + density*period + e
and the island full model was:

Carcass mass =
density(island) + district(island) + period + slaughter date + NAO + density*district + density*period + e

District and period were entered as categorical variables, all the rest being continuous.

District scale: The linear mixed models ran for specific districts using “fine scale density” were:

Carcass mass =
density(specific district) + period + slaughter date + NAO + density*period + e

Because of the limitation of the data, analyses were restricted to only 8 districts with at least 10 years of pre rut carcass mass and at least 7 observations per year. Six mainland (Fiettar, Lákkonjárga, Orda, Ábborassa, Seainnus/Návggastat, and Joahkonjárga) and two island (Fálá and Ivguláhku) districts were included. All variables, except period, were entered as continuous.

Results

West Finnmark scale

The full model including both period and sub-region and their interactions with overall density in West Finnmark, yielded carcass mass of male yearlings higher at island as compared to mainland ($F_{1,\ 21000}$ = 280.01, $P < 0.001$, Table 2D), and a fixed effect of period was found ($F_{1,\ 21000}$ = 6.63, P = 0.001) the mass being highest in the late 1980s, i.e. period 1 (Table 2D). Further, the carcass mass was negatively influenced by the overall density in West Finnmark ($F_{1,\ 21000}$ = 54.95, $P < 0.001$, Table 2D, Fig. 3a). Density had a significant interaction with sub-region ($F_{1,\ 21000}$ = 92.04, $P < 0.001$) and with period ($F_{2,\ 21000}$ = 3.54, P = 0.029). The effect of the random term “year” was significant (variance estimate ± SE = 0.6079 ± 0.3555, Z = 1.71, P = 0.044). In the stripped model excluding both sub-region and period and their

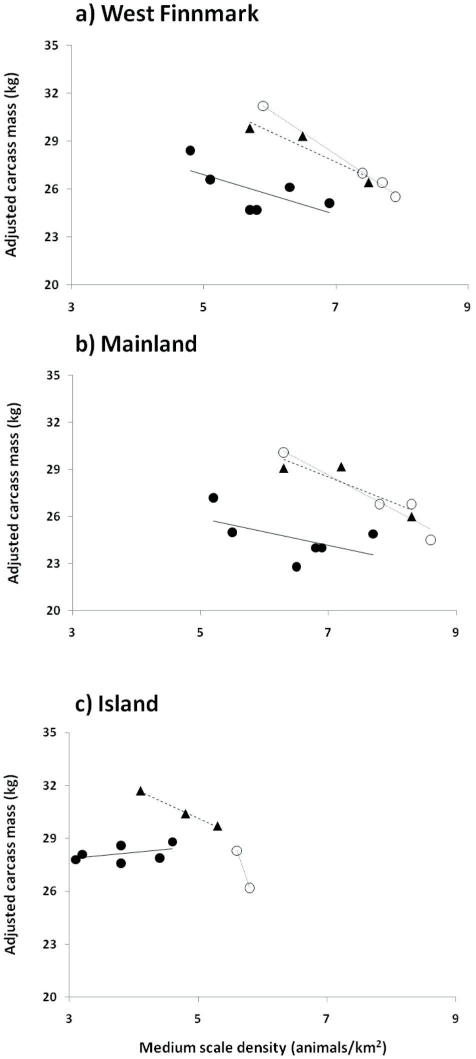

Fig. 3. LS means carcass mass of male yearlings adjusted for slaughter date, period and sub-region (mainland and island) plotted against annual net summer density at West-Finnmark scale (a) and LS means carcass mass of male yearlings adjusted for date of slaughter, period and districts plotted against annual net summer density at mainland (b) and island (c) scales. White symbols represent period 1 (1983-1987, missing data for year 1984), black filled symbols represent period 2 (1996-2001) and black filled triangles represent period 3 (2002-2005). The clear dashed line is the fitted line for period 1, the solid line is the fitted line for period 2, while the weak spotted line is the fitted line for period 3.

Table 3. Parameter estimates with standard errors (SE) and *P*-values for the mixed linear models fitting the autumn carcass masses (in kg) of male yearlings at the medium density scale (i.e. **mainland**) without district and period and theirs interactions with density (*A:*), including district within the sub-region and density by district interaction (*B:*) (for the main effect and the interaction the ANOVA results are presented in italic), with period (P1: 1983-86, P2: 1996-2001; P3: 2002-2004) and density by period interaction (*C:*), and including district and period and theirs interactions with density (*D:*). Slaughter date and winter NAO are entered as covariates in the models.

	Without District and Density x District			**Including District and Density x District**		
	Estimate	*SE*	*P-value*	*Estimate*	*SE*	*P-value*
Without Period and Density x Period	*A:*			*B:*		
Intercept	28.8011	4.1430	<0.001	68.0906	7.1199	<0.001
Slaughter date	0.01630	0.0050	0.0010	-0.0544	0.0055	<0.001
Winter NAO	0.2060	0.3345	0.5380	0.3068	0.3767	0.4154
Density	-0.6035	0.5803	0.2884	-4.8493	0.9196	<0.001
District*				$F_{12,18000}$=	*30.87*	<0.001
Density x District*				$F_{13,18000}$=	*26.69*	<0.001
Including Period and Density x Period	*C:*			*D:*		
Intercept	40.0437	4.8289	<0.001	81.0019	8.4573	<0.001
Slaughter date	0.01662	0.0050	<0.001	-0.0543	0.0055	<0.001
Winter NAO	-0.2466	0.1699	0.1466	-0.1745	0.2292	0.4463
Density	-1.9210	0.6594	0.0036	-6.3479	1.1014	<0.001
Period						
(P1-P2)	13.1439	5.6216	0.0194	5.4957	7.4297	0.0370
(P1-P3)	5.9543	6.7622	0.3786	5.6901	9.0101	0.5277
(P2-P3)	-7.1896	5.6130	0.2003	-9.8056	7.5991	0.1969
District*				$F_{12,18000}$=	*30.58*	<0.001
Density x Period						
(P1-P2)	-1.1895	0.7508	0.1131	-1.5079	0.9967	0.1303
(P1-P3)	-0.7344	0.8910	0.4098	-0.7488	1.1905	0.5293
(P2-P3)	0.4551	0.7947	0.5669	0.7590	1.0759	0.4805
Density x District*				$F_{13,18000}$=	*26.69*	<0.001

*Because of limited data from many districts and space limitations we report only the *F*-values for the district effect and the interaction density x district.

interactions with overall density, carcass mass of male yearlings were not influenced by the overall density in West Finnmark ($F_{1,\ 21000}$ = 0.75, P = 0.39, Table 2A). That the parameter estimate of overall density changed from “no effect” to “significant negative effect” depending on whether “sub-region” and “period” and their interactions with overall density were included (Table 2D) in the model or not (Table 2A), suggested a scale dependent density effect. We thus investigated this scale further by separating the effect of space and time.

Comparing the non-significant overall density estimate in West Finnmark in the stripped model (Table 2A) to the significant negative estimate of carcass mass in the model including only sub-region and its interaction with overall density (Table 2B) suggests spatial scale dependence. Further, comparing the non-significant estimate of density in West Finnmark in the stripped model (Table 2A) with its negative estimate in the model including only period and its interaction (Table 2C) suggests temporal scale dependence.

Mainland scale

In the full model, including both period and district (altogether 14 districts) and their interactions with mainland density, carcass mass of male yearlings differed between districts ($F_{12, 18000} = 30.58$, $P < 0.001$) whereas no significant effect of period was detected ($F_{2, 18000} = 2.44$, $P = 0.087$). Further, carcass mass was negatively influenced by the mainland density ($F_{1, 18000} = 21.08$, $P < 0.001$; Table 3D; Fig. 3b). Density had a significant interaction with district ($F_{13, 18000} = 26.69$, $P < 0.001$), but not with period ($F_{2, 18000} = 1.16$, $P = 0.31$). The effect of the random term "year" was significant at mainland scale (variance estimate ± SE = 1.158 ± 0.092 Z = 1.72, $P = 0.043$). In the stripped model, excluding both period and district and their interactions with mainland density, the non-significant density estimate of carcass mass of male yearlings (Table 3A) suggested a scale dependent density effect at this level.

The parameter estimate of mainland density did changed depending on whether "district" and its interaction with density were included in the model or not (Table 3B), suggesting spatial scale dependence. Further, temporal scale dependence was found when comparing the non-significant estimate of density in the stripped model (Table 3A) with the negative mainland density estimate of carcass mass in the model including only period and its interaction with density (Table 3C).

Island scale

In the full model, including both period and district (altogether 11 districts) and their interactions with island density, carcass mass of male yearlings differed between districts ($F_{10, 2901} = 33.10$, $P < 0.001$), and significant effect of period was detected ($F_{2, 2901} = 49.52$, $P < 0.001$). Carcass mass was not negatively influenced by the island density ($F_{1, 2901} = 1.12$, $P = 0.29$), although the parameter estimate was highly significant (Table 4D, Fig. 3c). The interaction between density and district was significant ($F_{10, 2901} = 27.62$, $P < 0.001$), as well as the interaction between density and period ($F_{2, 2901} = 33.76$, $P < 0.001$). The variance estimate of the random term "year" equalled zero at island scale. That the parameter estimate for the variable "density" change depending on whether "district" and its interaction with density were included in the model (Table 4B) or not (Table 4A), suggested spatial scale dependent density effect. Further, temporal scale dependence was also found (Table 4A, C).

District scale

The two island districts (Fálá and Ivguláhku) and one mainland district (Orda) showed a negative density effect ($F_{1, 578} = 5.51$, $P = 0.019$ and $F_{1, 748} = 39.28$, $P < 0.001$ and $F_{1, 3250} = 4.15$, $P = 0.042$, respectively). The five others mainland districts showed an indifferent density pattern. Three mainland (Seainnus/Návggastat, Ábborassa and Orda) and one island district (Ivguláhku) showed an effect of period ($F_{2, 1869} = 2.98$, $P = 0.051$, $F_{2, 2412} = 4.15$, $P < 0.001$ and $F_{2, 3250} = 4.91$, $P = 0.007$ and $F_{2, 748} = 37.89$, $P < 0.001$, respectively).

Discussion

There are no indications that the island sub-region has generally better winter ranges than the mainland (Bernt Johansen, personal communication). We therefore ascribe the higher average carcass mass at the island as compared to the mainland sub-region (Table 2D) to differences in summer range conditions in ac-

Table 4. Parameter estimates with standard errors (SE) and *P*-values for the mixed linear models fitting the autumn carcass masses (in kg) of male yearlings at the medium density scale (i.e. **island**) without district and period and theirs interactions with density (***A:***), including district within the sub-region and density by district interaction (***B:***) (for the main effect and the interaction the ANOVA results are presented in italic), with period (P1: 1983-86, P2: 1996-2001; P3: 2002-2004) and density by period interaction (***C:***), and including district and period and theirs interactions with density (***D:***). Slaughter date and winter NAO are entered as covariates in the models.

	Without District and Density x District			**Including District and Density x District**		
	Estimate	*SE*	*P value*	*Estimate*	*SE*	*P value*
Without Period and Density x Period	*A:*			*B:*		
Intercept	28.3170	4.0831	<0.001	54.0198	4.1945	<0.001
Slaugther date	0.0825	0.0158	<0.001	-0.1097	0.0237	<0.001
Winter NAO	-0.2028	0.4738	0.6686	-0.3846	0.4221	0.3623
Density	-0.4383	0.9045	0.6280	-6.2050	0.9691	<0.001
District*				$F_{10,2903}$=	*31.82*	<0.001
Density x District*				$F_{10,2903}$ =	*27.02*	<0.001
Including Period and Density x Period	*C:*			*D:*		
Intercept	40.8174	4.8310	<0.001	61.4395	2.4462	<0.001
Slaughter date	0.0838	0.0158	<0.001	-0.1046	0.0226	<0.001
Winter NAO	-0.3885	0.2167	0.0731	-0.2381	0.0816	0.0036
Density	-2.4536	1.0123	0.0154	-7.2399	0.6034	<0.001
Period						
(P1-P2)	83.7906	36.981	0.0235	86.0698	14.9375	<0.001
(P1-P3)	-97.795	36.907	0.0081	72.5215	14.906	<0.001
(P2-P3)	-14.004	5.5207	0.0112	-13.548	1.5912	<0.001
District				$F_{10,2901}$=	*33.10*	<0.001
Density x Period						
(P1-P2)	14.3933	6.5632	0.0284	-15.8478	2.6673	<0.001
(P1-P3)	16.5903	6.5077	0.0108	-13.393	2.6402	<0.001
(P2-P3)	2.1971	1.2551	0.0801	2.4548	0.3798	<0.001
Density x District*				$F_{10,2901}$=	*27.62*	<0.001

* Because of limited data from many districts and space limitations we report only the *F*-values for the district effect and the interaction density x district.

cordance with Klein's (1970) hypothesis (i.e. the summer range condition is decisive for the growth of northern large herbivores). This finding contrasts the general heavier carcass masses of male yearlings in mainland districts as compared to island districts in the early 1960s (1960-63, i.e. before the summer ranges, especially at the mainland, were exposed to the high densities; Movinkel & Prestbakmo, 1968). The consistently higher density at mainland as compared to island the last decades (Table 1) may have induced a homogenisation of the vegetation (see Bråthen *et al.,* 2007), and hence reduced the summer range quality at the mainland as compared to the island sub-region, resulting in mainland having lower mean carcass mass than island in the late 1990s (period 2) and early 2000s (period 3) (Table 1). Indeed management practises may add to the spatial variation in carcass masses observed. However, there are no indications that the practise, except stocking rate, has changed considerably more at the mainland as compared to the island sub-region the last four decades. Since the summer herding groups normally are divided into smaller winter siidas (Paine, 1994) and spread out on different winter ranges, the spatial variation between districts within sub-region observed in pre-rut carcass mass is also ascribed to inter-district variation in summer range quality, as well as management practice, including stocking rate. Also level of human disturbance (Vistnes & Nellemann, 2001) and predator pressure (Tveraa *et al.,* 2003) may add to the between district variation observed.

At West Finnmark scale the fixed effect of period was manifested as higher autumn carcass mass estimate during the first period of population rise (period 1) as compared to the clear decline in period 2 and the lower, but not significant, estimate in period 3 (Table 2D). This indicates a general accumulated density effect (i.e. homogenisation of the vegetation). Surprisingly the effect of period was only clearly expressed at the island scale ($P < 0.001$) as compared to the mainland scale ($P = 0.087$), however, the island carcass estimate being heavier in the early 2000s (period 3) as compared to the late 1980s (period 1) and late 1990s (period 2) (Table 4D). The higher estimate in the late 1980s than in late 1990s at mainland (Table 3D) confirms a different temporal dynamic at the island as compared to the mainland sub-region and hints again to an accumulated density effect at the mainland sub-region. The relatively lower interannual variation in mean reindeer carcass mass at island (CV = 7.2%) as compared to the mainland sub-region (CV = 11.9%) suggests a lower between year summer climatic stochasticity at island, probably due to the proximity of the ocean “buffering” the annual climatic variation. Indeed this will result in a lower yearly variation in summer forage growth and quality and a less prominent yearly variation in insect harassment (Colman, 2001; Weladji *et al.,* 2003b). In addition, the pronounced homogenisation effect at the mainland indicates that this sub-region is more sensitive to annual climatic stochasticity as compared to the island, as also reported at consistently high moose densities (Herfindal *et al.,* 2006). Temporal (at period scale) variation in carcass mass was found in four districts out of the eight used in the analyses. Significant yearly correlations in mean carcass masses between districts were found in 30 district pairs out of the 56 potentials (between 23 mainland pairs out of 30 potentials). This strong annual synchrony between mainland districts is probably driven by their general higher annual climatic variation and is amplified by their higher sensitivity to stochastic weather parameter(s) due to the general homogenisation of the vegetation, as compared to the island districts.

Reindeer is classified as a highly selective intermediate forager (Hofmann, 2000). We therefore expect that reindeer performance is sensitive to density, especially animals in their growth stage as male yearlings. This was confirmed by the drop in performance at the West Finnmark scale with densities ranging from 5 to 8 animals (1 yr and older) per km^2 (Fig. 3a) and also seen at the mainland sub-regional scale with densities between 5-9 per km^2 (Fig. 3b), but not at low densities (3-6 per km^2) at the island scale (Fig. 3c). Actually the generally lower annual calf production at island as compared to mainland (Ims & Kosmo, 2001; Reindriftsforvaltningen, 2008) will amplify the "real" density difference between the two sub-regions. The interaction between regional density and sub-region was significant, the parameter estimate of the difference being positive (Table 2D), and confirms that the negative effect of density was pronounced at mainland as compared to island. However, the effect of density varied with period at island scale (Fig. 3c), but not at mainland (Fig. 3b). The lack of intra-specific competition for summer forages at the island scale points to a sustainable stocking rate of the summer ranges in contrast to at the mainland scale where a consistently high stocking rate has resulted in reduce range quality. As the interactions between both mainland and island density and district, within mainland and island, respectively were significant (Tables 3D & 4D) the effect of density did differ between districts within sub-regions. Surprisingly both island districts showed a negative density effect, as compared to only one out of six mainland districts. The island district Fálá was consistently exposed to high density (mean 6.0 animals per km^2) compared to most other island districts, whereas the opposite was true for Ivguláhku (2.6 per km^2). The lack of density effect among the five mainland districts could be attributed to strong homogenisation of the forages at these, suggested by their consistently high densities (mean density ranging from 6.5-9.9 animals per km^2). This may lead to a less sensitive density dependent response as the reindeer are not able to fully express their selective feeding potential at ranges dominated by species with low quality and palatability. Indeed, these highly variable density responses at district scale reflect inter-district variations in summer range condition as well as management practice, including current stocking rate and accumulated density effects, and concurs with the general context-dependent response and low predictability of herbivore impacts at fine spatial scales (Noda, 2004). Sustainable management of the summer forage resources in West Finnmark has therefore to be district specific.

At the West Finnmark scale the effect of density on carcass mass changed from "no-effect" to "significant negative effect" when sub-region and its interaction with density, period and its interaction with density, as well as both sub-region, period and theirs interactions with density were included in the model (Table 2B, C, D) as compared to the stripped model (Table 2A) suggesting spatial and temporal density dependence. The same was seen at the mainland and island scales when district and its interaction with density, period and its interaction with density and district and period and theirs interactions with density were included (Tables 3B, C, D & 4B, C, D) as compared to the stripped models (Tables 3A & 4A). That density may act differently at different scales as also reported earlier in other ungulates (e.g. Coulson *et al.,* 1999; Mysterud *et al.,* 2000), underlines the man made as well as natural spatial and temporal heterogeneity of the West Finnmark summer range and the relative and multidimensional role of density. Caution should therefore be taken when trying to predict density effects across spatial and temporal scales.

Managed ungulate populations are regulated and limited through a combination of food limitations, climatic effects and predation in addition to harvesting scheme (Sæther, 1997; Tveraa *et al.*, 2007). Obviously there are difficulties in managing large herbivores populations in highly variable environments (Côté *et al.,* 2004; Warg, 2009). The highly variable density effect and the spatial and temporal variation in carcass mass among districts implies that adaptive management strategies for sustainable use of the summer forage resources have to be site-specific and calls for a target carcass mass at the functional management unit (i.e. district/siida) reflecting an appropriate stocking rate of the specific summer range. In several districts we recommend a reduction of the summer stocking rate by the herders followed by a monitoring of the medium to long term feedback on carcass mass. Hence management becomes an active process of learning by doing, based on long time series of carcass masses and animals counts on district level, involving both herders and managers. We therefore urge all to continue participating in the ongoing reporting of key production parameters (i.e. carcass mass, number of animals and calf production) as well as management regime.

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Skala-avhengige virkninger av antallet rein på høstslaktevektene i Vest-Finnmark

Abstract in Norwegian / Sammendrag: Den stadig pågående diskusjon omkring reintall og overbelastning av beitene i Vest-Finnmark krever en bedre forståelse av tetthetsavhengige, så vel som tetthetsuavhengige prosesser som påvirker dette beitesystemet og på hvilke skalaer disse opererer. Vi benyttet 20 604 slaktevekter av varit (1,5 års gamle bukker) før brunst for å undersøke variasjonen i tid og rom i disse, og om sommerbeitebelegget på ulike skalaer påvirket vektene. Vi definerte tre romlig skalaer: 1) hele sommerbeiteområdet i Vest-Finnmark, 2) to underregioner: innlandsdistriktene samlet og øy/halvøydistriktene samlet og 3) det enkelte sommerbeitedistrikt. På distriktsnivå ble bare slaktedata fra 8 distrikt benyttet. Videre ble to tidsskalaer definert: 1) hele perioden samlet, 2) tre perioder basert på utviklingen i reintallet i Vest-Finnmark - økning i periode 1 (1983-87) og i periode 3 (2001-2004) og nedgang i periode 2 (1996 -2000). Slaktevektene var høyere for øy/halvøydistriktene sammenlignet med innlandsdistriktene samlet og varierte mellom distrikt. Periode påvirket også slaktevektene regionalt, subregionalt og ofte på distriktsnivå. Vi fant en negativ tetthetsavhengig effekt på slaktevektene for Vest-Finnmark samlet. Det samme gjaldt for innlandsdistriktene samlet, men ikke for øy/halvøydistriktene samlet. Dette forklares ved fødekonkurranse på innlandsdistriktenes sommerbeiter, sannsynligvis på grunn av at vedvarende høye tettheter har forringet beitekvaliteten, sammenlignet med øy/halvøydistriktene samlet. På distriktsnivå varierte effekten av tetthet. Resultatene tyder videre på skala-avhengige tetthetseffekter i tid og rom, i Vest-Finnmark samlet, så vel som på innlands- og øy/halvøynivå. Tetthet er et mangesidig og komplekst begrep som ikke kan sees uavhengig av skala. Det er derfor viktig å analysere slike prosesser på flere skalanivå for bedre å kunne forstå samspillet mellom vegetasjon og beitedyr. Dette innebærer i praksis at hvert sommerdistrikt (siida), som er den funksjonelle enheten i forvaltningssammenheng, må behandles uavhengig og danne grunnenheten i en fornuftig forvaltning.