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2 **Experimental harvest reveals the importance of territoriality in limiting the breeding population of**  
3 **Svalbard rock ptarmigan**

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12 **Abstract**

13 The Svalbard rock ptarmigan (*Lagopus muta hyperborea*) is an endemic sub-species of rock ptarmigan  
14 inhabiting the high-Arctic archipelagos of Svalbard and Franz Josefs Land. This ptarmigan species exists at low  
15 population densities, with little interannual variations in population numbers, and limited habitat for breeding  
16 with less than 5% of the land area in Svalbard constituting medium to high quality breeding habitat. Unander and  
17 Steen (1985) hypothesized, based on a descriptive study, that territories sufficiently attractive for breeding could  
18 be a limiting factor of the Svalbard rock ptarmigan population. Here we use experimental data from a three-year  
19 removal experiment (1984-1986) to test their hypothesis by comparing breeding density, demography (sex and  
20 age ratios) and body mass of birds between experimental removal plots and control locations. We found  
21 evidence of surplus birds by showing that both sexes of Svalbard rock ptarmigan replaced quickly in vacant  
22 territories after removal of the resident birds, and that breeding densities were similar for the experimental and  
23 control populations. Replaced males in the breeding population weighed less than males in the initial breeding  
24 population, and tended to be younger. Experimental harvest during the preceding spring had no effect on male  
25 body mass, population sex-ratio or the proportion of juvenile males in the pre-breeding population the following  
26 spring. The documented surplus of male and female Svalbard rock ptarmigan and a lack of impact on breeding  
27 densities from removal of birds, leave a proportion available for harvest.

28 **Key words** *Lagopus muta hyperborea*, management, removal experiment, surplus birds.

29 **Introduction**

30 The role of territorial behavior as a mechanism limiting population size is central in avian population ecology  
31 (Newton 1992). Charles Darwin noted the presence of “wandering males” rapidly replacing mates if one in a pair  
32 was lost (Darwin 1871). Because a territory or lek is a pre-requisite for breeding in grouse species, territorial  
33 behaviour in both the breeding and non-breeding season can limit the density of breeders (Newton 1992). Birds  
34 lacking a territory, often called ‘floaters’ or the ‘non-breeding surplus’, must either find a territory elsewhere to  
35 breed (e.g., in poorer habitat) or remain non-breeders. Whether territorial behaviour in grouse species limits the  
36 breeding density has been debated in the literature (Hannon 1986; Bergerud et al. 1985; Watson and Mossop  
37 1987), and many studies have addressed the intrinsic population regulation hypothesis related to spacing  
38 behaviour (Wynne-Edwards 1962). Results vary with species and timing of the study (see Newton 1992), but  
39 removal experiments of rock ptarmigan (*Lagopus muta*) and willow ptarmigan (*Lagopus lagopus*) have given  
40 almost consistent results with the intrinsic population regulation hypothesis (e.g., Watson 1965; Watson and  
41 Jenkins 1968; Hannon 1983; Pedersen 1984; Unander and Steen 1985; Pedersen 1988). However, Blom and  
42 Myrberget (1976) and Gardarsson (1977) found that willow- and rock ptarmigan were not replaced after a  
43 removal experiment or after natural removal by the specialist predator, gyrfalcon (*Falco rusticolus*).

44 The rock ptarmigan is a circumpolar herbivore species inhabiting alpine and arctic tundra regions  
45 (Storch 2007a; Watson and Moss 2008). The high-arctic archipelago, Svalbard, Norway, houses the endemic  
46 sub-species, the Svalbard rock ptarmigan (*Lagopus muta hyperborea*), which is the only resident terrestrial bird  
47 within the archipelago (Løvenskiold 1964). The Svalbard rock ptarmigan is migratory and uses separate habitats  
48 in the winter and the breeding season (Unander and Steen 1985; Fuglei and Pedersen 2011). When returning  
49 from the wintering grounds in April, the males establish and defend a territory ranging from 3 to 50 hectares  
50 (Unander and Steen 1985). The males show territorial behavior until hatching of chicks in July (Unander and  
51 Steen 1985), which is in contrast to other grouse species (e.g. red grouse *Lagopus lagopus scotica* and willow  
52 ptarmigan), defending a territory in both spring and autumn (Watson and Jenkins 1968; Pedersen 1984). In  
53 Svalbard, the ptarmigan has been a popular small game since the island was first discovered in the 16<sup>th</sup> Century  
54 (Løvenskiold 1964). Currently, the ptarmigan is the most popular small game species in Svalbard and annual  
55 harvest varies between 500 and 2300 individuals (Governor of Svalbard 2012). Knowledge of factors impacting  
56 population dynamics is scarce (Pedersen et al. 2012a). Steen and Unander (1985) described nest predation from  
57 the main predator, the arctic fox (*Vulpes lagopus*) (see also Prestrud 1992), and weather conditions (i.e., snow  
58 falls during incubation and right after hatching) as important factors impacting reproductive success. Less than

59 5% of the land area in Svalbard constitute medium to high quality breeding habitat (Pedersen et al. 2007), and  
60 rock ptarmigan densities in spring are low (1 – 3 males/km<sup>2</sup>) with limited interannual population size variability  
61 (Pedersen et al. 2012). There is no evidence of cyclic population dynamics (Pedersen et al. 2012) as found in  
62 other parts of the breeding distribution range of the rock ptarmigan (Nielsen 1999; Weeden and Theberge 1972;  
63 Watson et al. 2000). Low population densities raise the question whether the Svalbard rock ptarmigan could be  
64 regulated by male spacing behaviour to the same extent as other ptarmigan species with much higher breeding  
65 densities (e.g., Watson 1965; Watson 1968; Hannon 1983; Pedersen 1988). Males compete for access to females,  
66 but females can also compete for resources necessary for incubation or care of their young with other females  
67 (Hannon 1983). Svalbard rock ptarmigan males can be facultative polygynous (Unander and Steen 1985) and  
68 given that habitats are limited and both males and females defend resources, the effect of removing individuals  
69 should be similar for both sexes even if population densities are low.

70 Unander and Steen (1985) described, based on a two year experimental removal study of males and  
71 females in spring, the presence of surplus Svalbard rock ptarmigan individuals of both sexes in the breeding  
72 season and recruitment of birds to vacant territories. Thus, they concluded that shortage of males and/or  
73 territories sufficiently attractive for breeding was a limiting factor of the breeding population (Unander and Steen  
74 1985). However, their study did not include statistical analyses of possible changes in breeding density,  
75 demographic composition and body mass as an indicator of physical condition. Here we use unpublished  
76 experimental data from a three-year field experiment (1984-1986) conducted by S. Unander to re-examine their  
77 hypothesis. If territoriality is a limiting factor for Svalbard rock ptarmigan, we predicted that a removal  
78 experiment would have little impact on the population breeding density or sex-ratio if vacant territories were  
79 quickly re-occupied. We further predicted that experimentally harvested populations would be comprised of  
80 younger males and females with lower body mass compared with birds in the non-harvested populations.

### 81 **Study area**

82 In the high-arctic archipelago of Svalbard, Norway (62 700 km<sup>2</sup>), only 15% of the land area is vegetated, the  
83 remaining being covered mostly by glaciers and barren ground (Johansen et al. 2012). During 1980-1982  
84 (Unander and Steen 1985; Steen and Unander 1985) and 1984-1986 S. Unander conducted observational and  
85 experimental studies on the Svalbard rock ptarmigan in the region of Kongsfjorden and the Brøgger peninsula  
86 (78°55'N, 11°56' E). The study area is situated in the high- Arctic tundra zone where the landscape is dominated  
87 by alpine, steep mountains, glaciers and barren rocky or sparsely vegetated ground, except for the lush bird cliff  
88 vegetation (Walker et al. 2005). Plants are short-statured and rarely taller than 5 cm, except for graminoids, and

89 the vegetation is dominated by mosses, lichens, dwarf willow *Salix polaris*, purple saxifrage *Saxifraga*  
90 *oppositifolia* and graminoids (Elvebakk 1999; Hansen et al. 2007). The four study locations included two  
91 experimental areas (locations with removal of ptarmigans), Dyrvika (hereafter DY) and Ossian Sarsfjellet (OS),  
92 and two control areas (locations without removal of ptarmigans), Blomstrandhalvøya (BL) and Engelskbukta  
93 (EN) (Fig.1). The study locations are surrounded by sea and glaciers and were isolated from other surrounding  
94 areas. Based on a habitat suitability model for territorial Svalbard rock ptarmigan males (Pedersen et al. 2012b;  
95 see also Pedersen et al. 2007), the study locations comprised 29% high, 26% fair, 11% low and 34% unsuitable  
96 ptarmigan habitat, respectively (see Table 1 for details on the locations). During the time the removal experiment  
97 was conducted (1984-1986), the overall autumn harvest by hunters in the study locations and surrounding areas  
98 ranged from 40 to 130 ptarmigans (S. Unander, unpublished data). Presently, there is no harvest of ptarmigan in  
99 the area.

## 100 **Methods**

### 101 *Study Design and Field Protocol*

102 We mapped territories of the Svalbard rock ptarmigan as occupied by pairs or single males in the four study  
103 locations in May by observing agnostic behaviour, territorial display and boundary disputes according to  
104 Unander and Steen (1985). Birds settled and paired by the end of May were considered to belong to the pre-  
105 breeding population (i.e. population before egg-laying). The removal experiment was conducted in two of the  
106 four study locations, OS and DY (Fig. 1, Table 2 and 3) after the pre-breeding census. However, in 1986  
107 removal experiment was extended to a third location, BL (see Table 2 for details). During two-week periods  
108 between May 25<sup>th</sup> and June 11<sup>th</sup>, pairs or only males or females were shot and the treatments differed between  
109 the four study locations and the three study years according to Table 2 and 3. After the removal experiment (late  
110 June and July) both males and females which had newly established in the vacant territories were surveyed by  
111 mapping territories.

112 We obtained demographic data on individual ptarmigans (sex, age and body mass) from the shot birds  
113 and by catching newly settled individuals in the study locations. Birds were captured by placing a fish net in a V-  
114 shape close to the birds, herding them into it, and catching them by hand or a dip net. Birds were marked by  
115 patagial wing-tags with 7x1 cm coloured plastic bands on either one or both wings (Höglund 1952; Safety Flag  
116 Company of America). Different colour bands were used in each study location and year for individual  
117 identification. Chicks were marked with a foot-ring on one of the legs. All birds were aged (Bergerud et al.  
118 1963), sexed by inspecting the plumage and weighted to the nearest 1 g. Age of the birds (adult  $\geq$  1 year or

119 juvenile  $\leq 1$  year; born previous year) was determined by the pigmentation method (Bergerud et al. 1963) by  
120 comparing the amount of dark pigment on primaries 8 and 9. Adults had the same amount or less pigment on  
121 primary 9 than 8 whereas juveniles had more on primary 9 than 8. Unander and Steen (1985) and (Parker 1985)  
122 showed that age determination by this method alone was unreliable, resulting in an overestimate of adult birds.  
123 We used an additional criterion to reduce the risk of erroneous age determination by visually inspecting the  
124 amount of wear on primary 9 and 10, which appear to be more pronounced for juveniles than for adults returning  
125 from wintering grounds. We always classified birds as adults when they had moulted the primaries during their  
126 second summer.

## 127 **Data Analysis**

### 128 *Breeding density*

129 We calculated breeding density (pair/km<sup>2</sup>) for the four study populations, based on the number of occupied  
130 territories by pairs (or a male with several females), surveyed in the time period between replacement and  
131 hatching of chicks (see Table 2). We studied the effect of harvest on the breeding density using a linear mixed  
132 effect model, using *breeding density* as response variable and *harvest of males during the same spring*, with  
133 levels ‘yes’ and ‘no’, as a fixed predictor variable. In addition, we included year (three levels) and study  
134 locations (four levels) as random predictor variables in the model. We were not able to test the effect of female  
135 harvest on breeding density because of the low sample size (Table 3).

### 136 *Replacement of ptarmigans*

137 We calculated the mean number of days between the start of the experimental harvest and the arrival of a new  
138 individual to vacant territories to assess how fast birds re-occupy territories after the experimental harvest. Birds  
139 that arrived after July 1 were excluded because the Svalbard rock ptarmigan starts incubation on average during  
140 the latter half of June (Steen and Unander 1985). Thus, we assumed that birds arriving in July did not contribute  
141 to the breeding population. For males, we calculated the proportion of juveniles in both the pre-breeding  
142 population (hereafter ‘primary males’) and the replaced population. We were not able to analyse this relationship  
143 because we lacked adequate sample size from all of the study locations populations (see Fig. 4). Due to lack of  
144 information on dates for newly established females, age-ratio before and after the experimental harvest could not  
145 be compared.

### 146 *Population sex ratio*

147 We studied the effect of previous year’s experimental harvest on population sex ratio (see Table 2) using  
148 binomial generalized linear models (GLM) with logit link where the population *sex-ratio* (proportion of females

149 in the pre-breeding population before treatment) was the response variable. Five different models were tested,  
150 four of them including one of the following factorial predictor variables: *Males harvested previous year, females*  
151 *harvested previous year, pairs harvested previous year or any harvest previous year* (i.e., either males, females  
152 or pairs harvested previous year) (see Table 2). All of these variables had two levels, ‘yes’ and ‘no’. The fifth of  
153 the tested models was a null model without any predictor variable. We assessed model support using an  
154 information theoretic approach (Akaike’s Information Criterion corrected for small sample size (AICc);  
155 Burnham and Anderson 2002) and considered predictor variables to be meaningful if 95% confidence intervals  
156 of the  $\beta$  coefficients did not overlap zero.

#### 157 *Population age ratio*

158 We studied the effect of previous year’s experimental harvest on the age of males and females separately by  
159 using the pre-breeding population data (see column ‘pre-breeding’ in Table 2). We used binomial GLM with  
160 logit link where *male age ratio* and *female age ratio* (proportion of juveniles of all observations of the sex in  
161 question) were the response variables. We tested whether the age ratio was affected by *previous year’s*  
162 *experimental harvest of males or females*, respectively, where the factorial predictor variables had two levels;  
163 ‘yes’ and ‘no’. For the analysis of males, we excluded OS (1984) and DY (1986) because < 30% of males had  
164 been aged. We fitted the models using a quasi-binomial error structure because both models were over-dispersed  
165 (residual deviance being larger than residual degrees of freedom).

#### 166 *Male body mass*

167 To assess the effect of previous year’s experimental harvest on male body mass, we used data from birds  
168 observed in the pre-breeding populations (column ‘pre-breeding’ in Table 2). Body mass was not available for  
169 all birds and we therefore excluded the BL study location due to low sample size ( $n = 1$ ). We used a linear mixed  
170 effects model, individual male as the sampling unit and male *body mass* as the response variable. As fixed  
171 predictor variables, we used two factorial variables; *age* (levels ‘adult’ and ‘juvenile’) and *previous year’s*  
172 *experimental harvest of males*, i.e. whether or not the male came from an area where males had been harvested  
173 the year before (levels ‘yes’ and ‘no’). Initially, we included an interaction term between the predictor variables  
174 in the model, but as this was not significant we removed it. We included *study location* and *year* as random  
175 predictor variables in the models.

176 We also assessed whether males that had established a territory in spring (column ‘pre-breeding’ in  
177 Table 2) were heavier than males which replaced in vacant territories (column ‘replaced’ in Table 2) in the  
178 experimental populations. We used a linear model, individual male as sampling unit and male *male body mass* as

179 the response variable. We used two factorial predictor variables; *bird status* (levels ‘primary’ or ‘replaced’) and  
180 *age* (‘adult’ and ‘juvenile’). We initially included an interaction between the predictor variables in the model, but  
181 as this was not significant we removed it. We also attempted including *study location* and *year* as random  
182 variables using a linear mixed effects model. However, variance related to both of these variables was assessed  
183 to be zero, and we therefore removed the random part and present a linear model.

#### 184 ***Common aspects for all models***

185 The statistical software R version 2.14.0 (R Development Core Team 2012) was used for all analyses. All  
186 binomial models were implemented using *glm*-function of the R-package *nlmer* (Pinheiro et al. 2013), while all  
187 linear mixed effects models were implemented using *lmer*-function of the R-package *lme4* (Bates et al. 2008).  
188 We used diagnostic plots, i.e., constant variance and approximate normality of residuals as well as presence of  
189 outliers, to check model fit and assumptions. We considered a coefficient to have a statistically significant effect  
190 when its 95% CI did not include zero. For all mixed effect models we calculated 95% confidence intervals (CI)  
191 for the fixed parameters using Markov Chain Monte Carlo estimation (with 100 000 replicates), implemented  
192 with *mcmc* –function in R (Bates et al. 2008). For all binomial models, we first attempted to include the  
193 effects of year and study location as random variables, fitting the models as generalized mixed effect models  
194 (GLMM) using the *glme*-function of the R-package *lme4* (Bates et al. 2008). However, several of these models  
195 estimated the random variable contribution to variance to be zero, indicating that the data set did not encompass  
196 a long enough time frame or enough study sites to appropriately assess temporal or spatial variance. Based on the  
197 limited size of our dataset and in order to keep the models comparable, we chose to analyze all of our binomial  
198 models without random effects. Goodness of fit for binomial or quasi-binomial models was assessed by  
199 calculating Nagelkerke’s  $R^2$ , which quantifies the proportion of the total variance explained by the model  
200 (Nagelkerke 1991).

## 201 **Results**

202  
203 Experimental harvest of males during spring had no significant effect on breeding density in the subsequent  
204 summer. Non-harvested populations had a mean (95% CI) breeding density of 1.65 (0.82, 2.07) pairs/km<sup>2</sup>. The  
205 effect of harvest was a slight non-significant increase of pairs/km<sup>2</sup> (effect size [95% CI]; 0.13 [-0.22, 1.51]).  
206 Both study location and year had an effect on the breeding density (Fig. 2; the standard deviance of the random  
207 effect variance being 0.58 for area, 0.16 for year and 0.10 for residual). Hence, area explained 90% and year 7%



208 of the variance in the breeding density (calculated as proportion of the variance not accounted for by fixed effect  
209 [harvest of males during the same spring], see Zuur et al. 2009).

210 A total of 65 males replaced in vacant territories after removal of 88 primary males from the pre-  
211 breeding populations in the experimental study locations over the study years (Table 3). The mean (SD) arrival  
212 for replaced males was 9.32 ( $\pm$  4.33) days ( $n$  = 65) after experimental harvest commenced. Some birds arrived  
213 shortly after primary male was removed, as demonstrated by 25% of the new males were replaced within 5 days  
214 after beginning of the experimental harvest. Because the experimental harvest was conducted over several days  
215 (see Table 3 for successive removal dates), vacant territories appeared also at later dates than the initial start date  
216 of the experiment since the observations were conducted by one person, hence, all study sites could not be  
217 visited every day. Thus, the average of 9.32 days is a conservative estimate and probably higher than the actual  
218 number of days elapsed between a territory becoming vacant and re-occupied. A total of 32 females were  
219 removed over the study years. We were able to determine that 16 ( $n$  = 3 [DY 1985];  $n$  = 4 [DY 1984];  $n$  = 9  
220 [EN1986]) females established themselves at the vacant territories within the breeding season (Table 2 and 3).  
221 For these females, the mean arrival date was 9.44 ( $\pm$  2.63) days ( $n$  = 16) after the experimental harvest  
222 commenced. We were only able to document breeding for one replaced female (DY 1985) due to limited number  
223 of marked females. During the same time-period (i.e., after the removal experiment), no new males arrived to the  
224 control study locations which were not harvested.

225 All of the study populations consisted of more males than females in the territories during the pre-  
226 breeding population census (Table 2). None of the four tested predictor variables had significant effect on the  
227 population sex ratio (Table 4, Fig. 3). Neither had we evidence for any of the models being better than the others  
228 (Table 4).  $AIC_c$  for all models with a predictor variable ranged between 55.5-55.7, whereas the null model  $AIC_c$   
229 was 53.8 (i.e. approximately two units lower). Previous year's experimental harvest had no effect on the age  
230 composition of either males or females in the pre-breeding population the year after the experimental harvest  
231 (Table 5, Fig. 4 and 5).

232 Juvenile males weighed less than adult males (Table 5, see also Steen and Unander 1985), and newly  
233 established males weighed less than primary males after controlling for age in the models (Table 5, Fig. 6).  
234 However, previous year's harvest had no effect on male individual body mass (Table 5, Fig. 6).

## 235 **Discussion**

236 This study documents the presence of surplus birds in the Svalbard rock ptarmigan populations because both  
237 sexes replaced quickly in vacant territories after removal of the resident birds, and breeding densities were

238 similar for the control and experimental populations. Replaced males had lower body mass compared to males in  
239 the pre-breeding population, and were mainly juveniles. Experimental harvest in the preceding spring had no  
240 effect on male body mass, population sex ratio, or the proportion of juvenile males in the population the  
241 following spring.

242         The rapid replacement of both males and females after the removal experiment (i.e., surplus of both  
243 sexes) and no changes in the breeding density between the experimental and control areas support the spacing  
244 behaviour hypothesis (Wynne-Edwards 1962). Our result confirm the earlier findings by Unander and Steen  
245 (1985), and correspond to results from other rock ptarmigan removal experiments demonstrating territoriality to  
246 be a limiting factor for this species (Watson 1965). Pedersen et al. (2012a) found limited inter-annual population  
247 size variability, which is a characteristic of bird species limited by territorial behaviour (Newton 1992). Our  
248 removal experiment fulfils several conditions essential to demonstrate that territorial behaviour limits the  
249 breeding population of ptarmigans (Hannon 1986; Newton 1992). First, a proportion of the potential breeders  
250 (i.e., surplus ptarmigans) were prevented from establishing a territory, as indicated by the replacement after  
251 removal. Second, when resident males were removed, replacement males established themselves quickly in  
252 vacant territories. Third, all potential territories, as expressed by limited change in breeding density related to  
253 experimental manipulation, were occupied. And last, the effect of removals was similar for both males and  
254 females. Subsequently, we conclude that surplus Svalbard rock ptarmigans of both sexes exist in these low-  
255 density populations.

256         Few removal experiments have attempted to determine whether surplus birds of both sexes exist (but  
257 see Bendell et al. 1972; Zwickel 1972, 1980), nor has the effect of removal of one sex on the density of the other  
258 been investigated (but see Hannon 1983). Here we demonstrate a surplus of both sexes by replacement within  
259 approximately 9 days after experimental removal before breeding in spring. Hannon's (1983) removal  
260 experiment on willow ptarmigan indicates a large number of females, primarily yearlings, available to replace  
261 resident hens and breed, and most of them came from other areas than from territories on or directly surrounding  
262 the removal areas. Most removal experiments on avian species are made in high quality habitats where the  
263 density of animals is high, and a general criticism is that the origin and fate of the replacement birds are  
264 unknown (Hannon 1986; Newton 1992). The limited availability of breeding habitat in Svalbard makes it  
265 reasonable to assume that few of the surplus birds were able to breed elsewhere. Dispersal is often sex-biased in  
266 grouse and females move longer distances than males (e.g., Schroeder 1986; Martin and Hannon 1987; Small  
267 and Rusch 1989; Warren 2002; Holmstad et al. 2004). In Svalbard, Unander and Steen (1985) found that only

268 4% of marked Svalbard rock ptarmigan juveniles returned to the same breeding grounds in the following spring.  
269 Knowledge about rock ptarmigan movements between seasons is limited, but some subspecies in Iceland,  
270 Greenland, Russia and Italy move long distances (up to 1000 km) (Gudmundsson 1972; Del Hoyo et al. 1994;  
271 Favaron et al. 2006; Storch 2007b). Observational data (Unander and Steen 1985), anecdotes (Løvenskiold 1964)  
272 and a recent pilot study using satellite transmitters on Svalbard rock ptarmigan (Fuglei and Pedersen  
273 unpublished) indicate that the Svalbard rock ptarmigan disperse over large areas. Our data indicate that local  
274 intensive harvest in spring is compensated within relatively short time. We lack data to investigate the  
275 mechanisms behind this response (e.g., heterogeneity in inherent mortality risk (Sedinger et al. 2010; Sedinger &  
276 Herzog 2012)), but it is most likely due to immigration from surplus birds because there were no changes in the  
277 density of the breeding population the same summer and the replacement happened shortly after removal.

278 In our study replacement males had lower body mass than males before removal, indicating that the  
279 newly established population consisted of younger males (Unander and Steen 1985), which corresponds to other  
280 studies of ptarmigan (e.g., Pedersen 1984). However, even if the replacement males were lighter and younger we  
281 cannot be certain whether they were of lower quality than the territorial males before removal, and we do not  
282 know if they could have bred elsewhere if the experiment had not occurred. The body mass of ptarmigan females  
283 relates to reproductive success (Steen and Unander 1985, but see Cotter 1999, Wilson et al. 2007; Brittas 1988),  
284 start of egg-laying, clutch size and chick body mass (Steen and Unander 1985; Robb et al. 1992), and the  
285 likelihood of re-nesting after failure (Wiebe and Martin 1998). The Svalbard rock ptarmigan has a unique ability  
286 to build fat reserves (Grammeltvedt and Steen 1978) and the fat storage dynamics corresponds with the breeding  
287 biology of the species (Steen and Unander 1985). Steen and Unander (1985) found body mass of juvenile hens to  
288 be less than for adult Svalbard rock ptarmigan and a positive correlation between body mass and clutch size.  
289 Here, we were only able to show that the replaced males weighed less than the males in the pre-breeding  
290 population, and males are less likely to impact the reproductive success and recruitment. Although many females  
291 were individually marked in our study, we were not able to estimate the reproductive success for a large enough  
292 sample to compare the control and experimental locations. Our results do, however, suggest that the  
293 experimental spring harvest only had short-term effects on the demography of breeding Svalbard rock  
294 ptarmigan; age structure of the population and body mass of males the same year were altered, but there were no  
295 effect on the demographic parameters the following year. Due to lack of data we were not able to assess whether  
296 the removal experiment caused changes in female reproductive success at a short term (i.e. within season).

297 The limited human impacts in our remote study locations still makes our experimental data  
298 representative of ptarmigan demography, even if they were collected in the mid-1980's. Our breeding densities  
299 (Fig. 2) are unchanged compared to the newly reported ones by Pedersen et al. (2012a) in a 10-year study from  
300 2000-2009. Thus, this study clearly show the existence of surplus birds of both sexes in Svalbard rock  
301 ptarmigan, and hence limitation of the breeding density by territorial behaviour.

### 302 **Management implications**

303 A prevailing assumption for the management of grouse species has been that as long as surplus birds exist, it is  
304 possible to harvest from that surplus by compensation for other types of mortality. How wild animal population  
305 sizes vary in response to harvest mortality may depend on life-history strategies and density regulations (Péron et  
306 al. 2012). Timing of harvest is important for the effect of the removal of individuals (Brøseth et al. 2012). We  
307 conducted intensive spring harvest right before the reproductive season and documented compensation within a  
308 relatively short time. A documented surplus of male and female Svalbard rock ptarmigans and a lack of impact  
309 on breeding densities from removal of birds, leaves a proportion available for harvest. Harvest mortality can be  
310 substantial in hunted ptarmigan populations, and different studies have suggested that harvest is completely or  
311 partially compensated (e.g., Jenkins et al. 1963; Myrberget 1985; Ellison 1991; Sandercock et al. 2011) or even  
312 completely additive (e.g., Smith and Willebrand 1999; Pedersen et al. 2004; Sandercock et al. 2011). Early  
313 studies report that removal of up to 40% of the rock ptarmigan autumn populations did not affect spring breeding  
314 densities (Weeden 1972; McGowan 1975), but autumn harvest led to a higher proportion of yearlings in the  
315 spring breeding population (McGowan 1975). However, Magnússon et al. (2004) argued that increased harvest  
316 pressure of the Icelandic rock ptarmigan is the probable cause behind population declines from 1981 and  
317 onwards. Despite contradictory effect of harvest mortality, it seems likely to assume that when strong density  
318 dependence acts in the breeding season and excludes some birds from breeding, moderate harvest levels seems to  
319 be completely compensated (Ellison 1991).

320 Models for red grouse (*Lagopus lagopus scoticus*) suggested harvesting of almost all males that  
321 potentially joined the non-territorial (surplus) male population to obtain maximum yield and a safe long-term  
322 strategy (Chapman et al. 2009). Chapman (2009) argued that this threshold would depend on; 1) the number of  
323 territories the landscape can contain, 2) the breeding productivity and 3) seasonal survival rates. Where this  
324 threshold is for the Svalbard rock ptarmigan population is not known, and we lack detailed information on  
325 breeding productivity, recruitment (including dispersal) and survival from autumn to spring to determine this  
326 threshold. To provide evidence-based advice, we recommend future studies to focus on demographic parameters

327 which will influence the number of surplus birds available for hunting. Estimates of demographic parameters are  
328 essential to integrate in harvest models to evaluate and predict results from different harvesting strategies (e.g.,  
329 Chapman et al. 2009; Brøseth et al. 2012). Although, the present knowledge about the demography of the  
330 Svalbard rock ptarmigan is insufficient to suggest a specific upper maximum threshold for harvesting to be  
331 sustainable, our results still suggest that this sub-species of the rock ptarmigan, despite its low densities, can  
332 sustain harvesting at present levels in Svalbard. Today most harvest takes place in the vicinity of the largest local  
333 settlement, Longyearbyen (78°20' N, 15°60' E), where 200 – 300 hunters annually harvest 500 – 2300  
334 ptarmigans during the hunting season (10 September – 23 December; however, the hunting season lasts in reality  
335 to mid November due to the Polar night with 24 h darkness; Fuglei and Pedersen 2013). Annual monitoring of  
336 males in spring for more than 10 years, in the areas where most ptarmigan are hunted, shows no consistent  
337 declining trend in numbers (Pedersen et al. 2012a). Our conclusion might be conservative because the  
338 experiments removed adult birds with high intensity in spring, in contrast to the autumn harvest where a large  
339 proportion of offtake is chicks with expected higher natural mortality (Steen and Unander 1985; Cotter 1999).  
340 Normally, removing an individual late in the harvest season causes a larger reduction in the population than if  
341 the individual had been removed earlier in autumn (Kokko 2001). The fact that removal of birds in spring did not  
342 affect the size of the breeding population gives strong support for the existence of surplus male and female  
343 Svalbard rock ptarmigan. Our results have limited consequences for harvest planning of Svalbard rock ptarmigan  
344 since harvest of the autumn population likely will have little effect on the breeding population.  
345 Still, the rapid ongoing climate change might have unknown effects on this high-arctic ecosystem, and the  
346 ptarmigans' ability to tolerate harvest. Indeed, a recent study has shown that the entire resident vertebrate  
347 community in Svalbard, is strongly impacted by climatic events (Hansen et al. 2013). Therefore, our results must  
348 be treated with precaution and may not apply in the future, which suggests that the Svalbard rock ptarmigan  
349 population should be monitored annually.

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491 **FIGURE CAPTIONS**

492 **Fig. 1** The study areas in Blomstrandhalvøya (BL), Dyrvika (DY), Engelskbukta (EN) and Ossian Sarsfjellet  
493 (OS), Svalbard, Norway (1984-1986). The removal areas (OS and DY) are marked dark grey and the control  
494 areas (BL and EN) light grey on the map. Illustration: Oddveig Øien Ørvoll, Norwegian Polar Institute 2013.

495 **Fig. 2** Breeding density (number of territories occupied by a pair or a male with several females per km<sup>2</sup>) of  
496 Svalbard rock ptarmigans in the four study areas (BL=Blomstrandhalvøya and EN=Engelskbukta [control];  
497 DY=Dyrvika and OS=Ossian Sarsfjellet [experimental]), Svalbard, Norway (1984-1986). Symbols refer to no  
498 treatment (denoted by 'no') or the experimental harvest treatment the same spring (denoted by 'yes'). See Table  
499 2 and 3 for details regarding sample sizes and treatments.

500 **Fig. 3** Effect of the experimental harvest the preceding year on Svalbard rock ptarmigan population sex ratio  
501 (proportion of females in the population), Svalbard, Norway (1984-1986). The labels on the X-axis refer to the  
502 type of experimental harvest conducted previous year (i.e., only males, only females, pairs or any of these  
503 treatments). The black line represents median, boxes first and third quartiles, whiskers either maximum values or  
504 1.5 times inter-quartile range whichever is smaller) and points outliers. The numbers in parenthesis gives the  
505 sample sizes.

506 **Fig. 4** Age composition of the pre-breeding population of Svalbard rock ptarmigan in the four study locations,  
507 Svalbard, Norway (1984-1986). Left panel shows males and right panel females. The study areas are abbreviated  
508 at the x-axis (BL=Blomstrandhalvøya and EN=Engelskbukta [control]; DY=Dyrvika and OS=Ossian Sarsfjellet  
509 [experimental]). Bars marked with \* denote populations where the sex in question was harvested the previous  
510 year, and bars marked with 'R' denotes where data was removed from the statistical analysis owing to low  
511 sample size of males with known age.

512 **Fig. 5** Age composition of Svalbard rock ptarmigan males, Svalbard, Norway (1984-1986). Each pair of bars  
513 represents one study area during one year. To the left (marked with P) are males belonging to the primary spring  
514 population and to the right (marked with S) are 'replaced males (i.e., males which established territories after the  
515 removal experiment). The study locations are abbreviated at the x-axis; DY=Dyrvika and OS=Ossian Sarsfjellet.

516 **Fig. 6** Body mass (g) of Svalbard rock ptarmigan males in the four study locations, Svalbard, Norway (1984-  
517 1986). The upper panels compare body mass data from populations where males were not harvested the  
518 preceding year (left) and populations where experimental removal of males was conducted the preceding year  
519 (right). The lower panels compare body mass of individual males which had established a territory in the primary  
520 spring population (left) and replaced males which arrived to the location after the experimental removal (right).

521 Black line represents median, boxes first and third quartiles, whiskers either maximum values or 1.5 times inter-  
522 quartile range (whichever is smaller) and points outliers. Numbers in parenthesis below the boxes are sample  
523 sizes of males.

524 **Table 1** Habitat quality, based on a predictive habitat model by Pedersen et al. (2012a) for territorial males, in percent of total area surveyed during the pre-breeding census in  
 525 the four study locations, Svalbard, Norway (1984-1986) 'Type' denotes treatment.

Study area	Type	Area (km <sup>2</sup> )	Habitat quality				
			High	Fair	Low	Very low	Unsuitable
Ossian Sarsfjellet	Experimental	8.75	25.7	28.8	7.1	1.4	37.0
Dyrvika	Experimental	5.45	18.7	6.2	5.5	11.4	58.2
Blomstrandhalvøya	Control	16.4	30.6	37.6	17.7	5.0	9.2
Engelskbukta	Control	9.39	34.1	16.4	5.8	11.2	32.6

526

527 **Table 2** Overview of the Svalbard rock ptarmigan removal experiment in the four study locations in Svalbard, Norway (1984-1986). ‘Type’ denotes whether the population  
528 was experimental (E) or control (C). ‘Pre-breeding’ refers to number of territorial males and females during the spring population census (25 May - 2 June) and the number in  
529 parenthesis gives the number of removed individuals. ‘Sex-ratio’ gives the proportion of females in the pre-breeding population. ‘Replacement’ refers to birds that established  
530 a territory after the removal experiment commenced and the number in parenthesis denotes the number of replaced birds that further were removed by experimental harvest.  
531 See Table 3 for details on the timing of the experimental removal. ‘Reproductive’ gives the number of territories occupied by a pair (or a male with several females) surveyed  
532 after the experimental harvest and birds had replaced.

Area	Type	Year	Removal treatment	Pre-breeding		Sex-ratio	Replaced		Reproductive
				♂	♀		♂	♀	
Ossian Sarsfjellet	Experimental	1984	Females	19 (2)	18 (14)	0.49	- <sup>2</sup>	- <sup>2</sup>	-
		1985	Males	31 (17)	22	0.42	11 (7)	4	21
		1986	Males	28 (18)	22	0.44	21(13)	0	23
Dyrvika	Experimental	1984	Pairs	19 (13)	8 (8)	0.30	10 (8)	3(2)	- <sup>1</sup>
		1985	Pairs	9 (8)	9 (7)	0.50	9 (2)	4 (1)	8
		1986	None	12	9	0.43	- <sup>2</sup>	- <sup>2</sup>	9
Blomstrandhalvøya	Control	1984	None	18	13	0.41	-	-	14
		1985	None	16	9	0.36	-	-	15
		1986	None	24	18	0.43	-	-	20
Engelsbukta	Control	1984	None	27	17	0.39	-	-	17
		1985	None	21	16	0.43	-	-	15
		1986	Both	25	23	0.48	14	9	17 <sup>2)</sup>

533

1. The population was not surveyed before the end of July and information on the replaced population was not available.

534

2. Here the entire pre-breeding population was entirely removed in spring. The reproductive population was not surveyed during summer 1986. The

535

reproductive population reported here is that of before removal experiment, from 24 May. We treated data in the analyses of breeding density as a

536

population which had not been harvested.



537 **Table 3** Number of Svalbard rock ptarmigan removed at the two experimental study locations in Svalbard, Norway (1984-1986).

Area	Year	Date	Male			Female		
			Adult	Juvenile	Unknown age	Adult	Juvenile	Unknown age
Ossian Sarsfjellet (OS)	1984	June 1-2	2	0	0	8	6	0
	1985	May 28-30	18	4	0	0	0	0
		June 7	1	1	0	0	0	0
	1986	May 25-26	2	11	0	0	0	0
		May 30	2	3	2	0	0	0
		June 3-5	5	6	0	0	0	0
Dyrvika (DY)	1984	May 31	9	4	0	5	3	0
		June 10	6	2	0	1	0	1
	1985	May 27	7	0	0	3	3	0
		June 1	2	0	0	0	1	0
		June 11	0	1	0	1	0	0
Total			54	32	2	18	13	1

538

539 **Table 4** Effect of previous year's harvest on the Svalbard rock ptarmigan population sex ratio (proportion of females in the population) in the experimental study loactions,  
 540 Svalbard, Norway (1984-1986). The table shows effect size estimates for the intercept and the predictor variables, with 95 % confidence interval in parenthesis.  $R^2$  is  
 541 Nagelkerkes pseudo-  $R^2$ .

Predictor variable	Intercept	Predictor estimate	Residual (Df)	Residual deviance	$R^2$	AICc
Null model	0.30 (0.11, 0.50)	-	11	4.24	0.00	53.80
Males harvested previous year	0.33 (0.12, 0.54)	-0.13 (-0.59, 0.35)	10	3.97	0.08	55.55
Females harvested previous year	0.31 (0.10, 0.53)	-0.05 (-0.51, 0.42)	10	4.20	0.01	55.77
Pairs harvested previous year	0.32 (0.11, 0.52)	-0.16 (-0.82, 0.51)	10	4.01	0.06	55.59
All types of harvest previous year	0.33 (0.09, 0.56)	-0.07 (-0.47, 0.34)	10	4.13	0.03	55.70

542

543 **Table 5** Effects of experimental harvest on the Svalbard rock ptarmigan male age (adult  $\geq$  1 year; juvenile  $\leq$  1 year) and body mass in Svalbard, Norway (1984-1986).  
544 Estimates are differences (contrasts) between the intercept and the estimated effect. Statistically significant effects (95% CI not crossing zero) are indicated with bold. For the  
545 quasi-binomial models (population level models), the column 'Residual' represents residual degrees of freedom and residual deviance and the column 'R<sup>2</sup>' represents  
546 Nagalekerke's pseudo-R<sup>2</sup>. For the linear mixed effect model (third model from the top), the column 'Residual' represents residual standard deviation; at the intercept line is  
547 noted the actual residual standard deviation of the model and at the random effect lines are the standard deviations related to each of these. For the last model,  
548 the column 'Residual' represents residual degrees of freedom and residual standard deviation and the column 'R<sup>2</sup>' represents adjusted R<sup>2</sup>. Statistically significant estimates are  
549 indicated by bold.

Sampling unit	Response	Coefficient	Estimate (95% CI)	Residual	R <sup>2</sup>	
Male population	Proportion of juveniles	Intercept	0.87 (0.21,1.61)	8, 24.54	0.40	
		Males harvested previous year (yes)	-0.95 (-2.43, 0.50)			
Female population	Proportion of juveniles	Intercept	-0.07 (-0.60, 0.45)	10, 23.24	0.14	
		Females harvested previous year (yes)	0.43 (-0.51, 1.39)			
Individual male	Body mass	Intercept	589.56 (547.97, 624,75)	31.21		
		Age (juvenile)	<b>-28.53 (-42.91, -12.89)</b>			
		Males harvested previous year (yes)	-0.12 (-22.26, 18.37)			
		Random: year				6.66
		Random: area				0.000001
Individual male	Body mass	Intercept	568.26 (554.71, 581.81)	84, 33.03	0.10	
		Age (juvenile)	<b>-18.51 (-33.08, -3.95)</b>			
		Primary male (yes)	<b>15.63 (0.76, 30.49)</b>			

550