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

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Abstract

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

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

Introduction

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

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

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

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

Study area

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

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

Methods

Study Design and Field Protocol

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

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

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

Data Analysis

Breeding density

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

Replacement of ptarmigans

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

Population sex ratio

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

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

Population age ratio

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

Male body mass

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

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

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

Common aspects for all models

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

Results

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

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

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

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

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

Discussion

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

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

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

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

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

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

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

Management implications

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

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

which will influence the number of surplus birds available for hunting. Estimates of demographic parameters are essential to integrate in harvest models to evaluate and predict results from different harvesting strategies (e.g., Chapman et al. 2009; Brøseth et al. 2012). Although, the present knowledge about the demography of the Svalbard rock ptarmigan is insufficient to suggest a specific upper maximum threshold for harvesting to be sustainable, our results still suggest that this sub-species of the rock ptarmigan, despite its low densities, can sustain harvesting at present levels in Svalbard. Today most harvest takes place in the vicinity of the largest local settlement, Longyearbyen (78°20´N, 15°60´ E), where 200 – 300 hunters annually harvest 500 – 2300 ptarmigans during the hunting season (10 September – 23 December; however, the hunting season lasts in reality to mid November due to the Polar night with 24 h darkness; Fuglei and Pedersen 2013). Annual monitoring of males in spring for more than 10 years, in the areas where most ptarmigan are hunted, shows no consistent declining trend in numbers (Pedersen et al. 2012a). Our conclusion might be conservative because the experiments removed adult birds with high intensity in spring, in contrast to the autumn harvest where a large proportion of offtake is chicks with expected higher natural mortality (Steen and Unander 1985; Cotter 1999). Normally, removing an individual late in the harvest season causes a larger reduction in the population than if the individual had been removed earlier in autumn (Kokko 2001). The fact that removal of birds in spring did not affect the size of the breeding population gives strong support for the existence of surplus male and female Svalbard rock ptarmigan. Our results have limited consequences for harvest planning of Svalbard rock ptarmigan since harvest of the autumn population likely will have little effect on the breeding population.

Still, the rapid ongoing climate change might have unknown effects on this high-arctic ecosystem, and the ptarmigans' ability to tolerate harvest. Indeed, a recent study has shown that the entire resident vertebrate community in Svalbard, is strongly impacted by climatic events (Hansen et al. 2013). Therefore, our results must be treated with precaution and may not apply in the future, which suggests that the Svalbard rock ptarmigan population should be monitored annually.

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FIGURE CAPTIONS

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

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

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

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

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

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

Black line represents median, boxes first and third quartiles, whiskers either maximum values or 1.5 times inter-quartile range (whichever is smaller) and points outliers. Numbers in parenthesis below the boxes are sample 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^2)	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	- [2]	- [2]	-
		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)	- [1]
		1985	Pairs	9 (8)	9 (7)	0.50	9 (2)	4 (1)	8
		1986	None	12	9	0.43	- [2]	- [2]	9
Blomstrandhalvøya	Control	1984	None	18	13	0.41	-	-	14
		1985	None	16	9	0.36	-	-	15
		1986	None	24	18	0.43	-	-	20
Engelskbukta	Control	1984	None	27	17	0.39	-	-	17
		1985	None	21	16	0.43	-	-	15
		1986	Both	25	23	0.48	14	9	17 [2)]

1. The population was not surveyed before the end of July and information on the replaceded population was not available.
2. Here the entire pre-breeding population was entirely removed in spring. The reproductive population was not surveyed during summer 1986. The reproductive population reported here is that of before removal experiment, from 24 May. We treated data in the analyses of breeding density as a 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).

			Male			Female		
Area	Year	Date	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

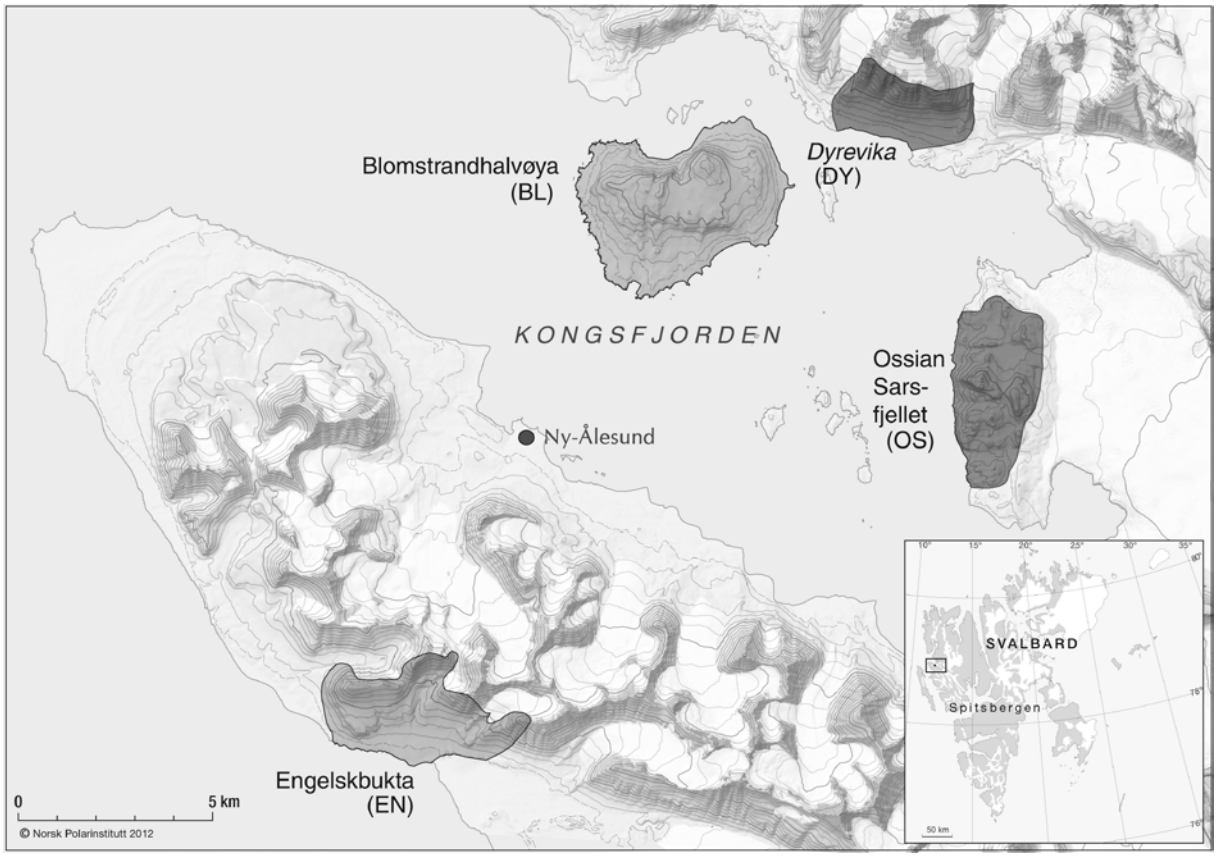
Table 4 Effect of previous year's harvest on the Svalbard rock ptarmigan population sex ratio (proportion of females in the population) in the experimental study loactions, Svalbard, Norway (1984-1986). The table shows effect size estimates for the intercept and the predictor variables, with 95 % confidence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

Table 5 Effects of experimental harvest on the Svalbard rock ptarmigan male age (adult ≥ 1 year; juvenile ≤ 1 year) and body mass in Svalbard, Norway (1984-1986). 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 quasi-binomial models (population level models), the column 'Residual' represents residual degrees of freedom and residual deviance and the column 'R^2' represents Nagalekerke's pseudo-R^2. For the linear mixed effect model (third model from the top), the column 'Residual' represents residual standard deviation; at the intercept line is 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, the column 'Residual' represents residual degrees of freedom and residual standard deviation and the column 'R^2'represents adjusted R^2. Statistically significant estimates are indicated by bold.

Sampling unit	Response	Coefficient	Estimate (95% CI)	Residual	R^2
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)	**-28.53 (-42.91, -12.89)**		
		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)	**-18.51 (-33.08, -3.95)**		
		Primary male (yes)	**15.63 (0.76, 30.49)**		

Figure 1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fjellet
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SVALBARD
Spitsbergen
Engelskbukta
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© Norsk Polarinstitutt 2012

Figure 2

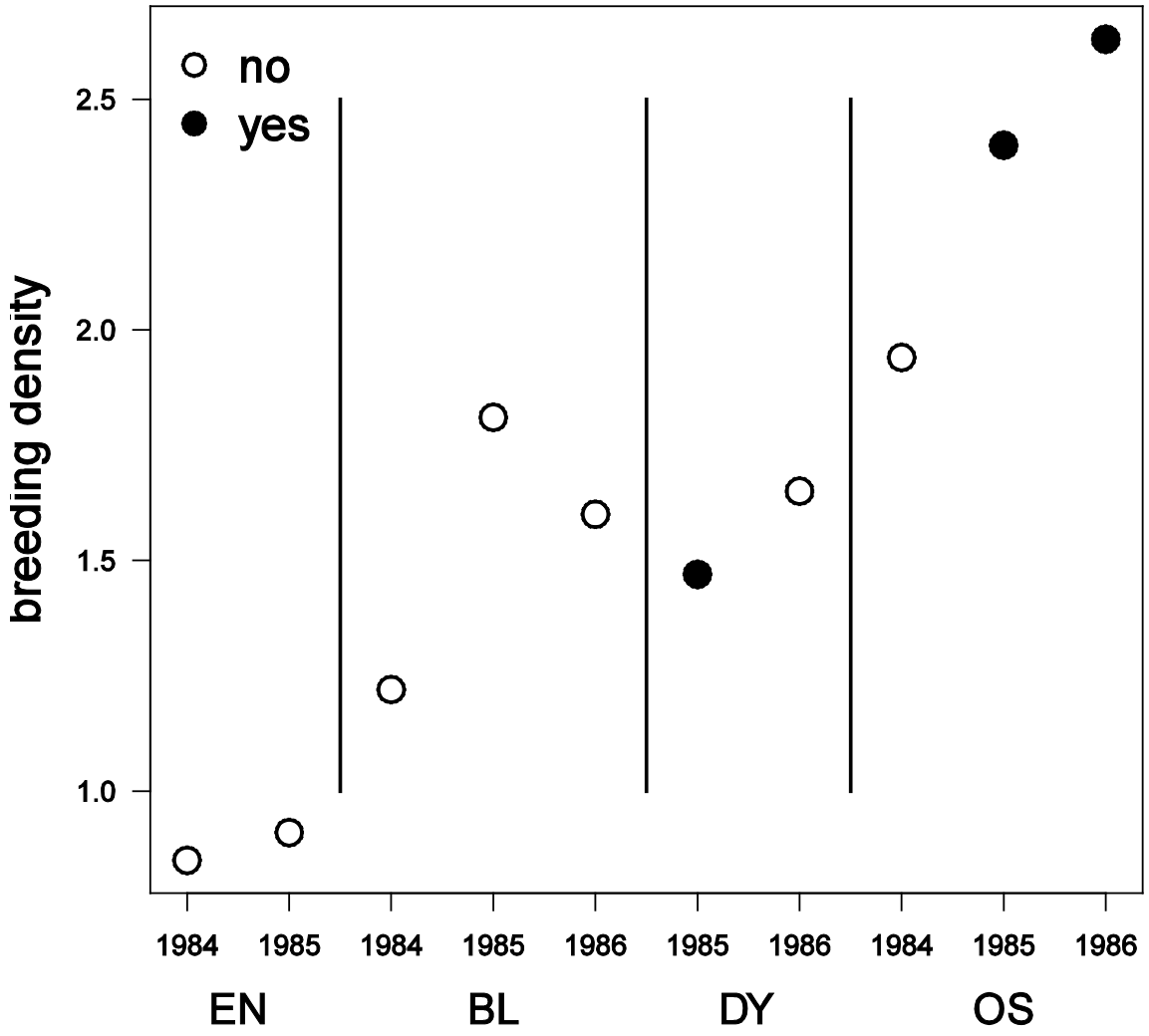
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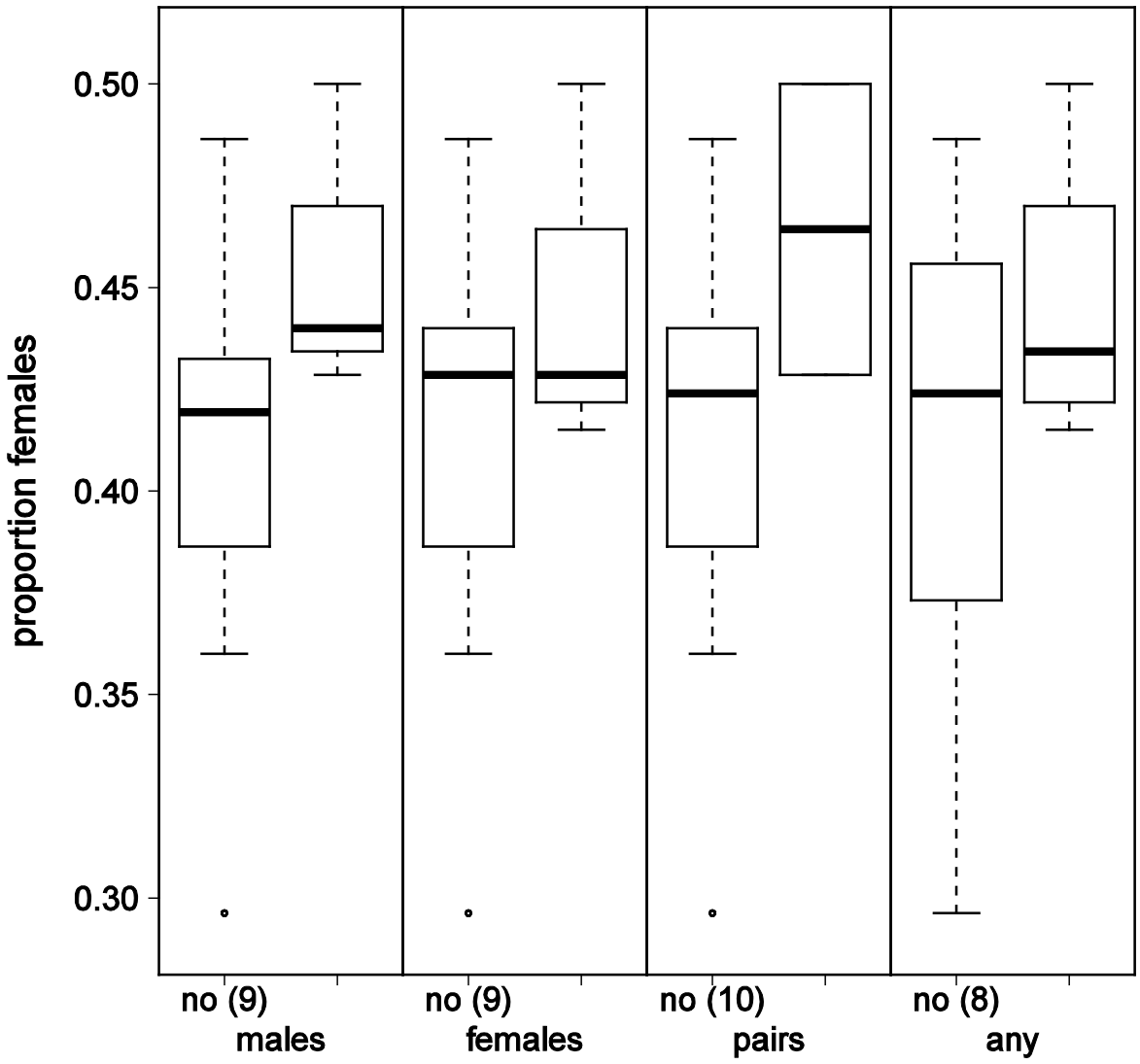
Figure 3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0.45
0.40
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0.30
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males
no (9)
females
no (10)
pairs
no (8)
any

Figure 4

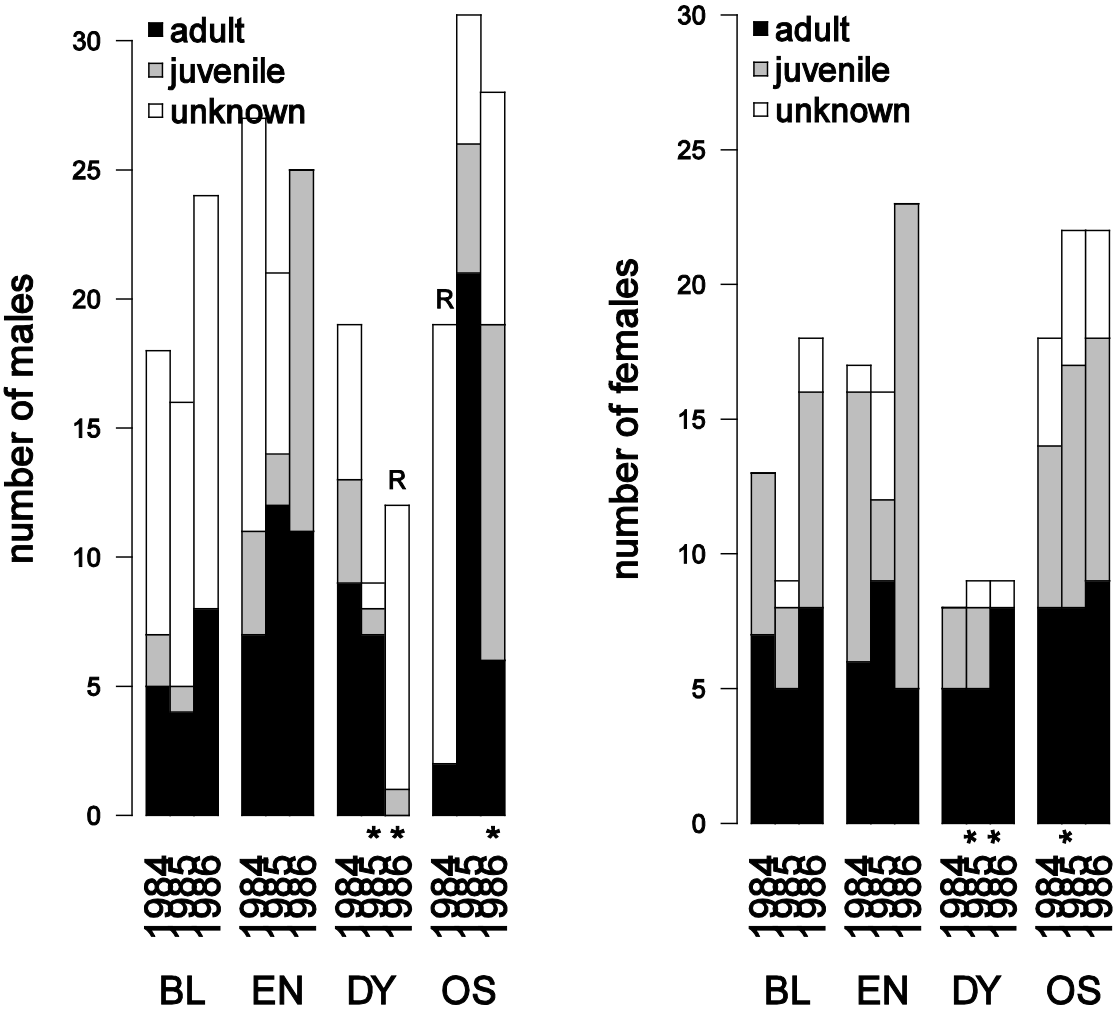
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Figure 5

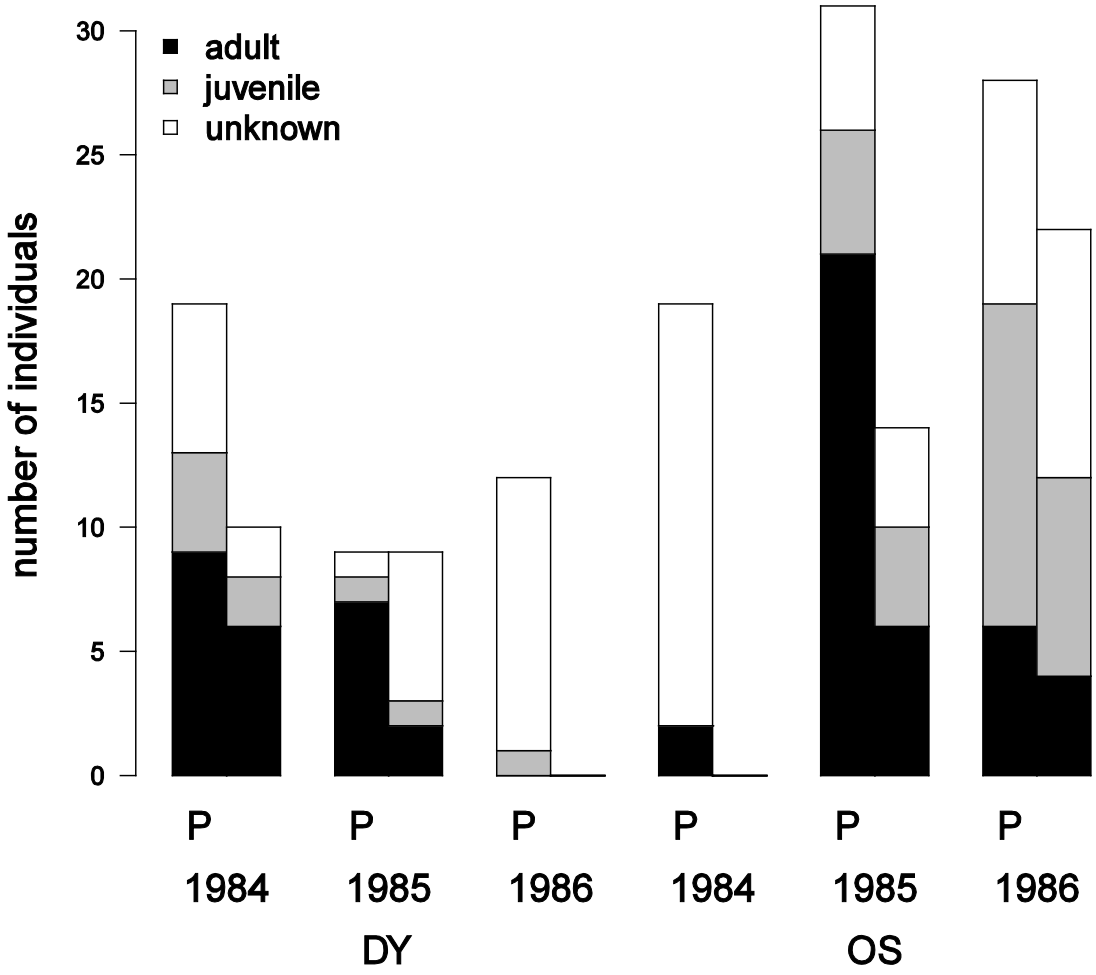
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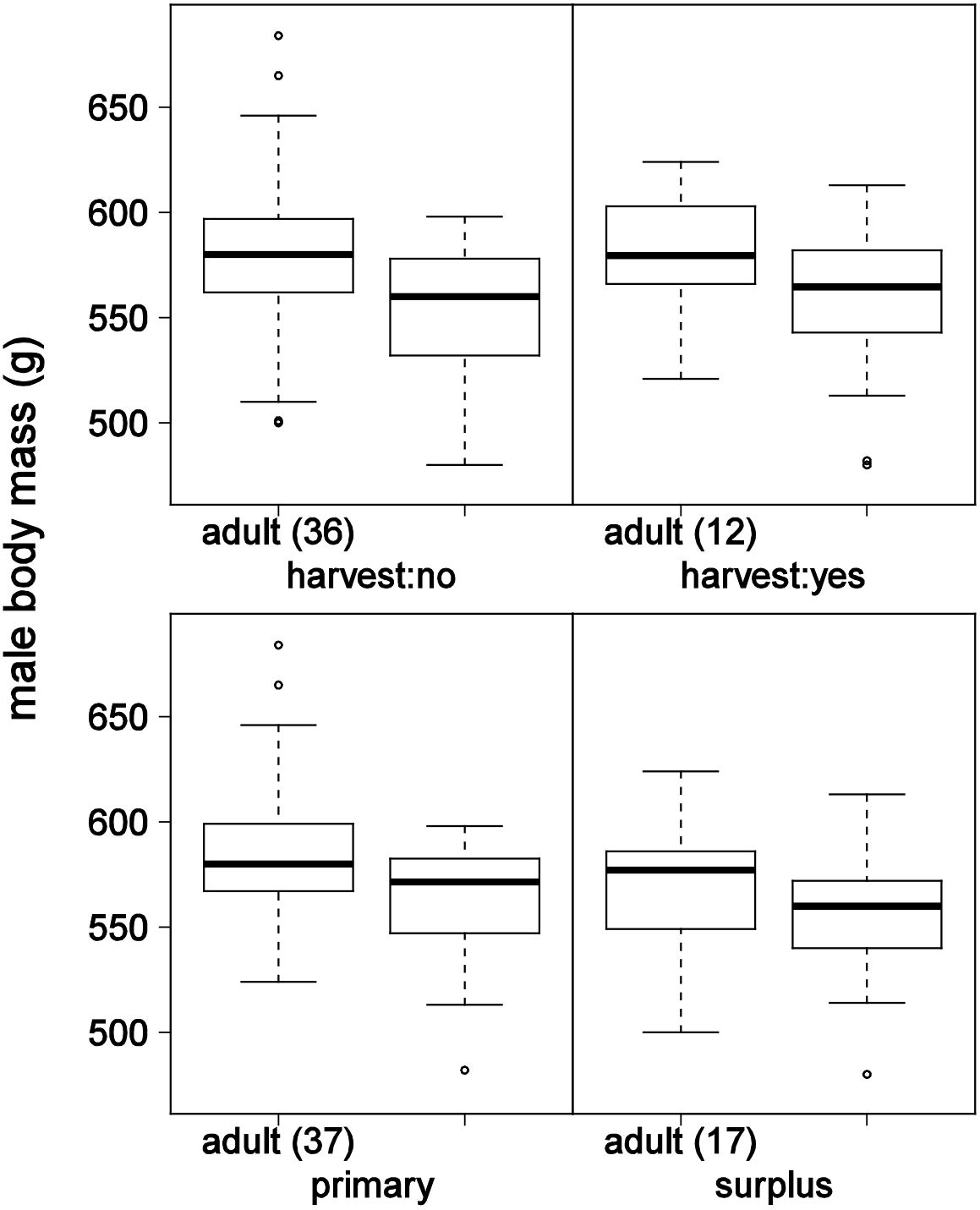
Figure 6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600
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adult (37)
primary
adult (17)
surplus