



Note

Vegetation Type and Demography of Low Density Willow Ptarmigan Populations

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ABSTRACT The willow ptarmigan (*Lagopus lagopus*) is an economically important and desired game species in Scandinavia. Its abundance varies considerably in time and space, but there has been a long-term population decline over recent decades. Earlier studies demonstrated willow ptarmigan select certain habitat features. We investigated the relationship between area-specific conditions (habitat and ownership status) and 2 variables describing willow ptarmigan demography (adult density and reproductive success). We found no connection between adult density and cover of 6 vegetation types. However, willow ptarmigan had lower reproductive success in survey areas dominated by mountain birch (*Betula pubescens czerepanovii*) forest. The lack of any clear association between willow ptarmigan density and vegetation types could be explained by relatively low population densities in our study areas. Thus, relative to years with higher population levels, resources (e.g., food and shelter) were plentiful and competition was low. We found strong indications in areas of similar vegetation composition that adult density was higher in areas managed by private landowners than on state-owned land. The difference in density was 2.56 birds/km², equivalent to a 46% increase compared to adult density on state-owned land. This difference in density may be due to a difference in hunting pressure. We conclude that management actions to improve habitat will have little effect on willow ptarmigan populations during periods of relatively low densities. © 2016 The Wildlife Society.

KEY WORDS grouse, habitat selection, hunting pressure, *Lagopus lagopus*, landownership, Scandinavia.

Identifying habitat characteristics that improve the distribution and abundance of wildlife species is a central task in wildlife management and conservation. Habitat quality is affected by a suite of environmental conditions (e.g., temperature, precipitation, competitors, predators, availability of food, and cover; Sinclair et al. 2006). Measures of demography or distribution in relation to habitat attributes, especially vegetation, are used to assess habitat quality for birds (Johnson 2007). Habitat quality assessments may then be based on 2 factors. First, habitat selection models (e.g., resource selection functions; Manly et al. 1993) can infer habitat quality from observations where individuals are located (Kastdalen et al. 2003, Nelli et al. 2013). Second, relationships between demographic parameters and vegetation can be used to assess habitat quality (Lande et al. 2014). These approaches assume that individuals more frequently select, settle at higher densities, or produce more offspring in certain habitats, which may be identified by vegetation characteristics.

The willow ptarmigan (*Lagopus lagopus*) is a popular and economically important game species in Norway. Willow ptarmigan population sizes vary considerably in time and space, but over recent decades there has been a long-term decline in abundance (Myrberget 1988, Pedersen 1988, Lehikoinen et al. 2014, Kvasnes et al. 2015). There are indications that willow ptarmigan at the population- and individual-scale select certain areas. Densities in some areas consistently fluctuate around a higher mean density than in others (Kvasnes et al. 2015), and single birds or broods are not randomly encountered with respect to habitat characteristics (Kastdalen et al. 2003, Lande 2011). Consistent difference in abundance between areas over time (Kvasnes et al. 2015) can be attributed to active habitat selection and spatial variation in survival rates that are not related to the physical habitat. Variation in predation rates can alter the survival of birds independently of vegetation composition and structure (Marcstrom et al. 1988). Similarly, harvesting can reduce yearly survival of willow ptarmigan (i.e., additive to natural mortality; Smith and Willebrand 1999, Pedersen et al. 2004, Sandercock et al. 2011). Thus, consistent differences in harvest rates could cause variation in density, and such differences might arise because of management systems that differ between private and state-owned land (Hardin 1968).

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Habitat selection by individual willow ptarmigan has been evaluated at different spatial scales and it has been suggested that birds aggregate in specific vegetation types or areas (Andersen et al. 1984, Steen et al. 1985, Kastdalen et al. 2003, Henden et al. 2011, Lande 2011). Willow thickets (*Salix* spp.), bogs, and dwarf birch (*Betula nana*) are important factors affecting willow ptarmigan distribution (Kastdalen et al. 2003, Henden et al. 2011, Ehrich et al. 2012). The level of saturation of a population can potentially affect distribution across the landscape (Greene and Stamps 2001) and the habitat selection process. Kvasnes et al. (2015) suggested the aggregation of willow ptarmigan populations in Norway could be affected by conspecific attraction (Stamps 1988). The use of conspecifics as guides during settlement can cause preferred vegetation structures to remain unoccupied, reducing the predictability of habitat models (Campomizzi et al. 2008).

Reproductive rates in willow ptarmigan are studied as time series and are related to temporal variation in weather conditions or predation rates (Slagsvold 1975, Steen et al. 1988, Martin and Wiebe 2004, Kvasnes et al. 2014). However, Erikstad (1985) reported evidence of higher survival of broods in areas with high insect larvae densities, and Andersen et al. (1984) reported a preference for eutrophic bogs, areas that also contained more insect food than other areas. In Scotland, Moss and Watson (1984) observed higher reproductive rates for rock ptarmigan

(*Lagopus muta*), an ecologically similar species, in areas overlying base-rich bedrock, suggesting a habitat effect on reproduction. Kvasnes et al. (2015) reported that reproduction rates in willow ptarmigan populations varied more between years than between areas, and that area-specific factors had a small but significant role.

We investigated how density of adult willow ptarmigan and reproductive success varied in relation to habitat, expressed as vegetation types and landownership (i.e., private or state-owned). We predicted that 1) survey areas would vary in terms of vegetation composition and 2) this would partly explain the observed spatial variation in adult densities and reproductive success. We also predicted that 3) privately owned areas would have higher densities than state-owned land because of differences in management regimes. Reproductive rates generally show less spatial variation and are not correlated with adult density (Kvasnes et al. 2015); therefore, we also predicted that 4) the effect of vegetation composition on reproductive rates was different from that affecting adult density.

STUDY AREA

The survey areas for willow ptarmigan were located in alpine tundra and northern boreal habitats (~750–1,100 m ASL) in the south-central and eastern mountain ranges in Hedmark, Oppland, and Sør-Trøndelag counties, Norway (Fig. 1). In general, these mountain ranges are characterized by relatively

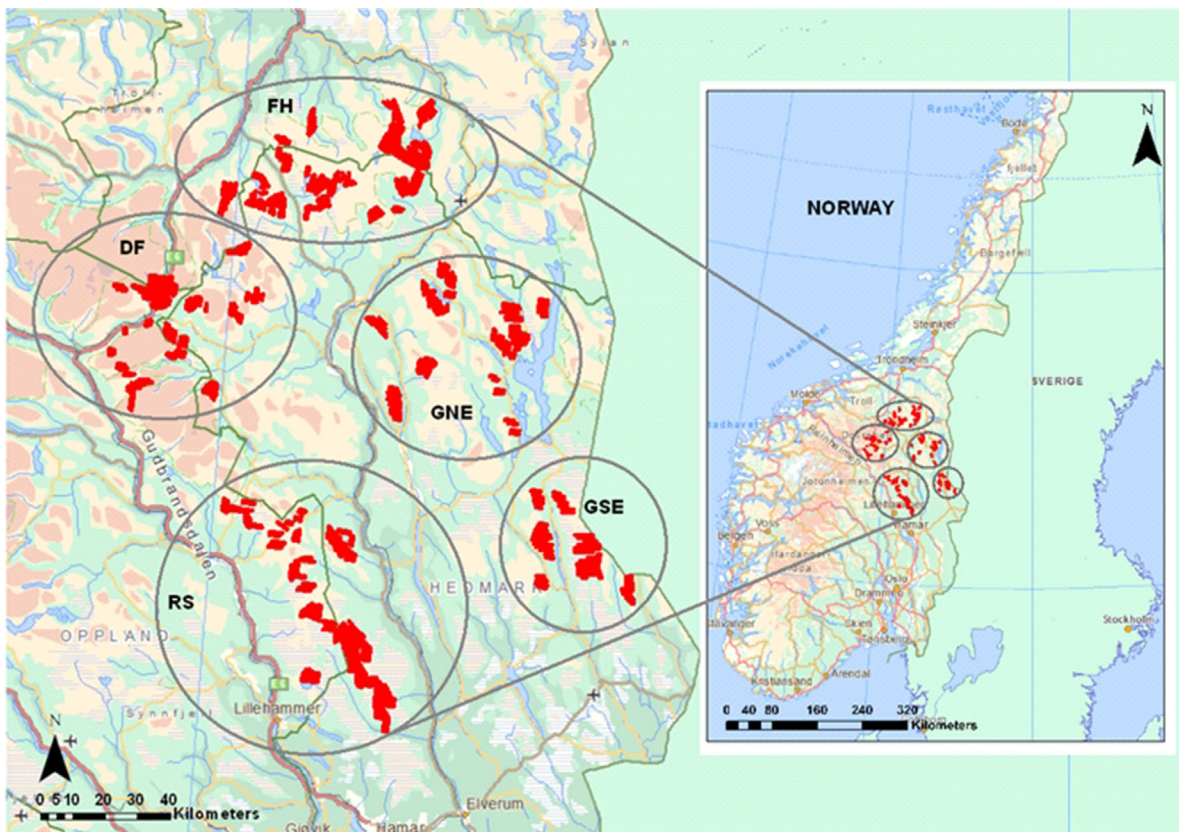


Figure 1. Survey areas (filled areas) for willow ptarmigan within mountain regions (open circles) in south-central Norway, 1996–2011. RS = Rondane, DF = Dovre and Folldal, FH = Forollhogna, GNE = Glomma northeast, GSE = Glomma southeast.

mild mountain slopes. The alpine tundra habitats are dominated by small and medium-sized shrubs (e.g., willow, dwarf birch, and heath [*Vaccinium* spp. and *Caluna* spp.]; Table S1). The northern boreal forests are dominated by birch, Scots pine (*Pinus sylvestris*), and Norway spruce (*Picea abies*). The vertebrate fauna is dominated by large ungulates (wild- and semi-domestic reindeer [*Rangifer tarandus*] and moose [*Alces alces*]), rodents (*Microtus* spp.), and birds (*Passeriformes* spp. and *Lagopus* spp.). Important predator species for willow ptarmigan include red fox (*Vulpes vulpes*), stoat (*Mustela erminea*), pine marten (*Martes martes*), gyrfalcon (*Falco rusticolus*), and rough-legged buzzard (*Buteo lagopus*). Livestock grazing by sheep and cattle is common in most areas during summer (Jun–Aug). The human population within the survey areas is low, limited to only a few permanent homes. However, in some areas there are several cabin villages and isolated cabins, many of which are only seasonally inhabited. The majority of survey areas were located in the transition zone between oceanic and continental climate zones but with a continental-to-ocean gradient from southeast to northwest. Mean annual temperature varied between 0°C and –4.0°C and annual precipitation along the climatic gradient ranged from 500–1,500 mm. Within the general study area, the survey areas were geographically clustered within 5 alpine mountain regions (Fig. 1).

METHODS

Data Collection

Observers conducted line-transect surveys in August from 1996 to 2011. Dog handlers with pointing dogs walked along transect lines and 1 free-ranging dog at a time searched both sides of the line following a distance sampling protocol (Pedersen et al. 1999, 2004; Buckland et al. 2001; Warren and Baines 2011). Observers recorded the number of birds (juveniles, adult M, adult F, birds of unknown sex or age) and the perpendicular distance from the line to the birds (m) at each bird-encounter. Pedersen et al. (2004) provided a detailed description of the robust sampling protocol for estimating willow ptarmigan densities (Pedersen et al. 1999). Further details of survey methods used in this study, including study design, and the estimation of population parameters are described by Kvasnes et al. (2015). This study included 350 estimates of adult density and reproductive success (juveniles/pair) from 40 survey areas from 1996 to 2011. We assigned survey areas to a mountain region based on its geographical location ($n = 5$, Fig. 1) to account for their spatial distribution. Surveys included only fledged willow ptarmigan chicks (>1 month old). The collection of data complied with the Norwegian Biodiversity Act and the Animal Welfare Act; we had exemption from the leash law to use free-ranging dogs in August.

We conducted all surveys within willow ptarmigan management units (i.e., estate boundaries, management boundaries within estates). We defined a survey area as the area (km²) within 250 m of each side of the transect lines. A buffer of 250 m on either side of the transect lines in a survey

area gives little overlap between neighboring lines because most lines in a survey area were 500 m apart (1 line every 500 m north-south or east-west direction on a 1 × 1-km grid; Kvasnes et al. 2015). Also, when using the area within 250 m on each side of the transect lines, rather than the area of a whole management unit, we avoided making inference about sections of the management unit that were not surveyed. We intersected the transect areas of each survey area with the SatVeg vegetation map (Johansen 2009, Johansen et al. 2009). This map consisted of 25 generalized dominant vegetation types covering Norway at a spatial resolution of 30 × 30 m. Ten vegetation types were classified as alpine (classes 12–21; Johansen et al. 2009), but forest vegetation types (classes 1–8) and mire and open swamp vegetation (classes 9–11) were also present in the survey areas (Table S1, available online in Supporting Information). We estimated the proportional cover of each vegetation type within all survey areas based on area surveyed (i.e., the area within 250 m on both sides of all transect lines in the survey areas) and area of each vegetation type in the surveyed area.

Vegetation classes covered the range of willow ptarmigan distribution, from the lowest elevations with sub-alpine mountain birch forests to the highest elevations with snow-bed vegetation, and included open sparsely vegetated areas, densely vegetated open areas, bogs with a sparse field layer, and densely vegetated bogs. Earlier studies of willow ptarmigan reported that broods and individual birds select sites on the basis of availability of food and cover (Andersen et al. 1984, Erikstad 1985, Bergerud and Gratson 1988). We generalized vegetation types into 6 groups with similar attributes to reduce the number of vegetation variables without losing variation in expected density of food and cover (Table S1). We conducted the surveys in sub-alpine areas and it was reasonable to assume that the forest vegetation types with birch (classes 6–8; Table S1) were mountain birch forests near tree-line. We pooled vegetation classes dominated by birch, and did not consider other forest types (classes 1–5; Table S1). The 3 mire and swamp vegetation types were separated by a moisture gradient where shrubs, willows, and heath were more abundant in the driest types (classes 9–10) and graminoids were dominant in the wettest type (class 11; Johansen et al. 2009). We pooled the first 2 into a new variable called bogs with a dense field layer and used the latter as a variable representing swamps and bogs with a sparse field layer. We pooled treeless areas above tree-line (classes 12–21) into 3 variables: 1) sparsely vegetated areas (e.g., ridges and heathland dominated by lichens), 2) heathland dominated by shrubs or herbs, and 3) snow beds dominated by low growth herbs, shrubs, or graminoids (Table S1). The first and third variables representing treeless areas above the tree-line were dominated by low growth vegetation, which we assumed provided less cover and probably less food than the second variable, which was dominated by denser bush and heath vegetation (Johansen et al. 2009). The variables considered as having an effect on reproduction and density were separated by an expected difference in food availability and cover from predators. We had information about

landowner status in all survey areas, and we categorized survey areas as private or state-owned land.

Statistical Analysis

We used generalized mixed effect models to analyze the effect of vegetation types on adult density (birds/km²) and reproductive success (juveniles/pair). We fitted the models with survey area (40 levels), mountain region (5 levels), and year (16 levels) nested within mountain region as random effects. Preliminary modeling based on Akaike's Information Criterion corrected for small samples (AIC_c) and Akaike weights (w_i) indicated a negative relationship between adult density and size of the surveyed areas (model with area size as fixed effect: slope \pm SE = -0.162 ± 0.065 , Δ AIC_c = 0.00, w_i = 0.86; model without area size as fixed effect: Δ AIC_c = 3.64, w_i = 0.14). There were no such relationships between area size and reproductive success. Therefore, we made inferences only about the area surveyed (i.e., considering 250 m on both sides of all lines in the survey areas) and included survey area size (km²) as a fixed effect when modeling adult density. We considered a number of candidate models for adult density with different combinations of plausible explanatory variables, but we analyzed correlated variables (correlation coefficient > 0.4) separately. We conducted the same procedure for reproductive rates but did not include terms for ownership status or survey area size. Because harvesting took place after reproduction, we assumed reproduction was independent of area size and adult density. We used an information-theoretic approach (Burnham and Anderson 2002) to select

the most parsimonious model explaining the variation in adult density and reproduction from a set of candidate models and considered models within 2 AIC_c of the top model to be competitive. The AIC_c weights can be interpreted as a continuous measure of probability that the best candidate model is indeed the best model, given the data and the set of candidate models (Wagenmakers and Farrell 2004).

We conducted all statistical analyses using R (version 3.0.2; R Core Team 2013). We used the lmer function in the lme4 package (Bates et al. 2013) for the mixed effect models and the MuMIn package (Barton 2013) for model selection.

RESULTS

The proportional cover of different vegetation types varied considerably among survey areas (Fig. 2), but there were no differences in the cover of different vegetation types between privately and state-owned lands (Fig. 3). The highest ranked model explaining adult density included the effect of landownership and area size (Table 1). Privately owned survey areas generally had higher adult densities than state-owned survey areas with a mean of 8.54 birds/km² (95% CI = 6.07–11.01) on private lands compared with 5.86 birds/km² (95% CI = 3.23–8.46) on public lands. Four other models were within 2 AIC_c units of this model: the null model (i.e., only area size), a model with a negative effect of snowbed cover, a model with a positive effect of cover of open areas with dense field layer, and a model with a negative effect of mountain birch forest cover (Table 1).

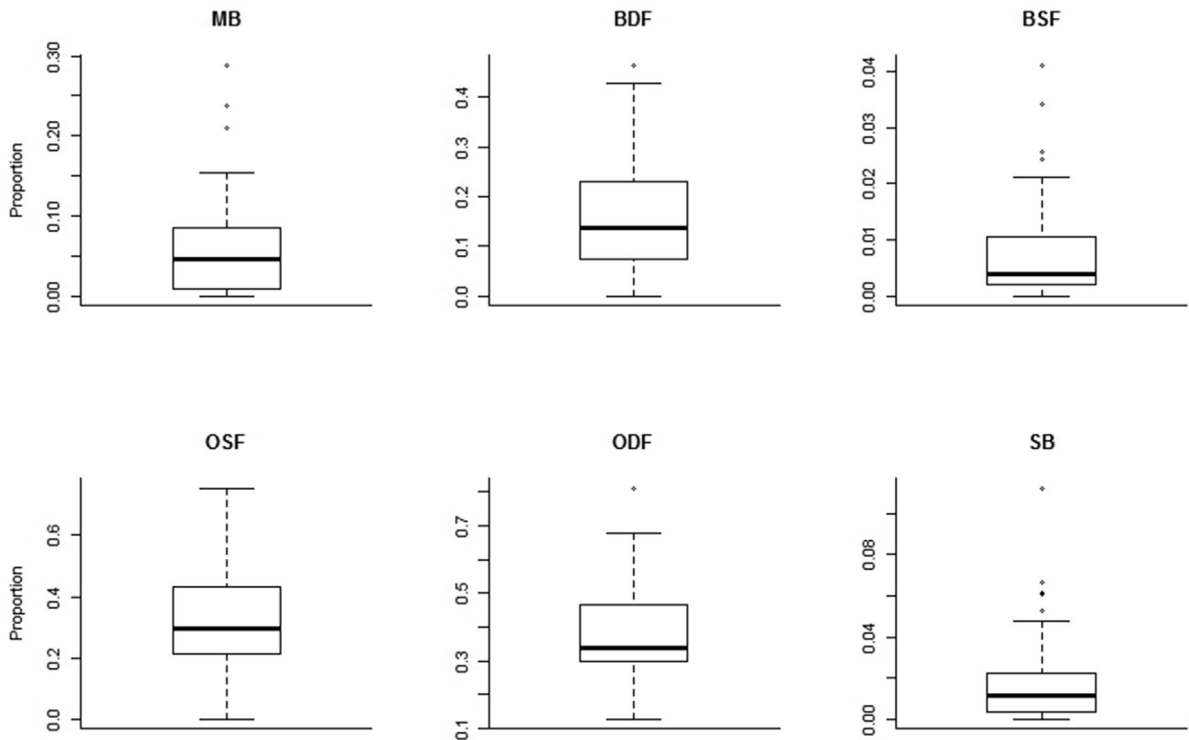


Figure 2. Boxplots showing the proportional cover of different vegetation types across all survey areas in south-central Norway, 2009. Horizontal bold lines indicate median value and the box indicates upper and lower quartile. Different scales on y-axis. MB = mountain birch forest, BDF = bogs with dense field layer, BSF = swamps and bogs with sparse field layer, OSF = open areas with sparse field layer, ODF = open areas with dense field layer, and SB = snowbeds.

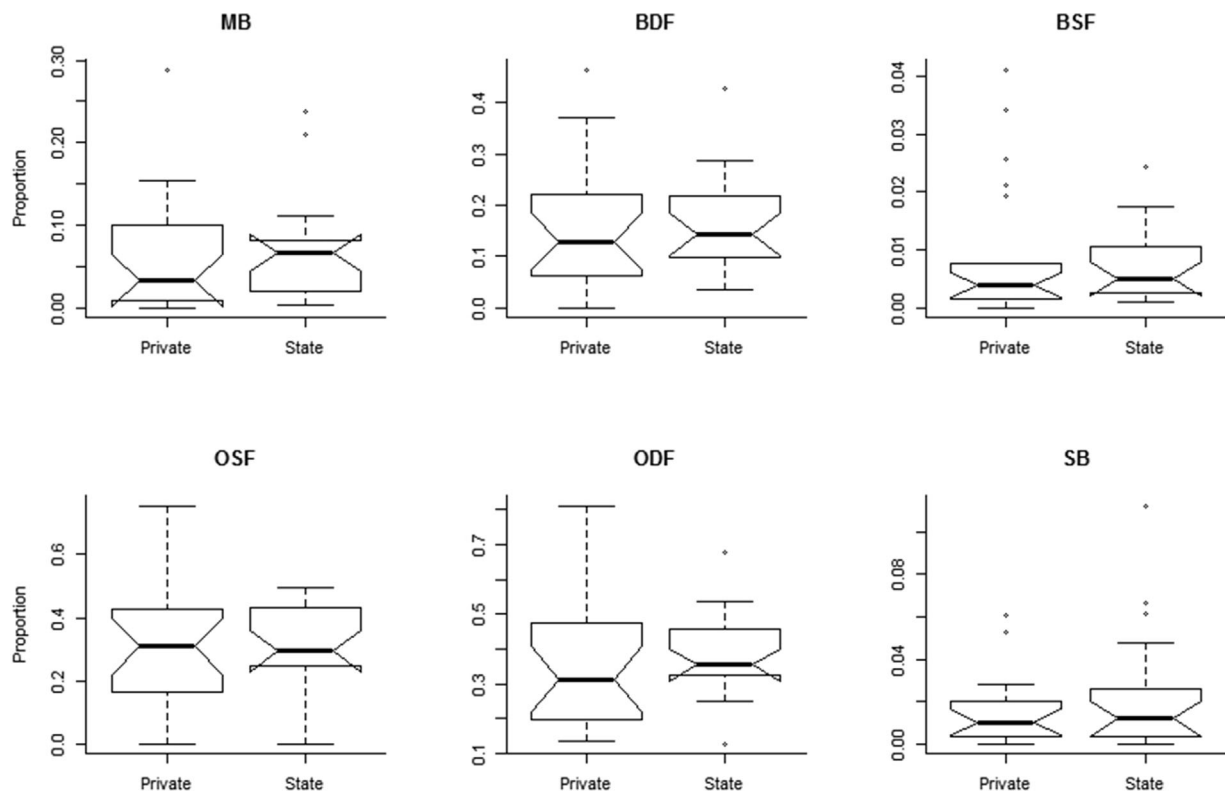


Figure 3. Boxplots with the proportions of different vegetation types by private or state landownership in south-central Norway, 2009. Horizontal bold lines indicate median value, the box indicates upper and lower quartile, and the notches indicate 95% confidence intervals of the median. Notches overlap for all vegetation classes suggesting no significant difference with ownership. MB = mountain birch forest, BDF = bogs with dense field layer, BSF = swamps and bogs with sparse field layer, OSF = open areas with sparse field layer, ODF = open areas with dense field layer, and SB = snowbeds.

The $\Delta AIC_c < 2$ suggests that all models were substantially supported by the data and, based on parsimony we should select the second-ranked model, which was the null model with no explanatory power because it was the simplest model. There were, however, clear indications of an actual effect of landownership. First, the model accounted for 37% of the AIC_c model weights compared to only 18% for the second- and third-ranked models (Table 1). Second, the bootstrapped confidence intervals for effect of state-owned

land in the model with landownership did not overlap 0 (95% CI = -5.61 to -0.09). Third, the difference in effect size was substantial, 2.56 birds/ km^2 , which corresponded to a 46% increase compared to the average density on state-owned land.

There were 5 models within 2 AIC_c units for reproductive success and all were substantially supported by the data (Table 1). The model with the lowest AIC_c included a negative effect of bogs with a sparse field layer and a negative

Table 1. Model selection tables based on Akaike's Information Criterion corrected for small samples (AIC_c) for adult density and reproduction (juveniles/pair) of willow ptarmigan in south-central Norway, 1996–2011. Only models within 2 ΔAIC_c units are presented. We indicate positive (+) and negative (–) effects and specify landownership as a positive effect for privately owned lands (private +).

Variables ^a	df	AIC_c	ΔAIC_c	AIC_c weight
Adult density				
Area (–), landownership (private +)	7	1,996.20	0.00	0.37
Area (–)	6	1,997.70	1.44	0.18
Area (–), landownership (private +), SB (–)	8	1,997.70	1.47	0.18
Area (–), landownership (private +), ODF (+)	8	1,998.20	1.96	0.14
Area (–), landownership (private +), MB (–)	8	1,998.20	1.98	0.14
Juveniles/pair				
BSF (–), MB (–)	7	1,148.20	0.00	0.28
MB (–)	6	1,148.30	0.09	0.27
MB (–), SB (+)	7	1,148.90	0.68	0.20
BSF (–), MB (–), SB (+)	8	1,149.60	1.41	0.14
MB (–), OSF (+)	7	1,149.90	1.72	0.12

^a SB = snowbeds, ODF = open areas with dense field layer, MB = mountain birch forest, BSF = swamps and bogs with sparse field layer, and OSF = open areas with sparse field layer.

effect of mountain birch forest cover. The second-ranked model ($\Delta AIC_c = 0.09$) included mountain birch forest cover, and because it was the only univariate model within $\Delta AIC_c < 2$, parsimony would suggest this was the preferred model. The difference in AIC_c weights between the 2 highest ranked models was only 1%, suggesting that little information was gained by including bogs with a sparse field layer as a term in the model. The negative effect of mountain birch forest cover was the only term occurring in all models within $2 \Delta AIC_c$. The effect size of mountain birch forest cover on reproductive success in the simplest model was -4.85 units (Fig. 4) with bootstrapped confidence intervals not overlapping 0 (95% CI = -7.87 to -1.71).

DISCUSSION

We found differences in vegetation composition among survey areas and the survey areas differed considerably in adult density (prediction 1). We were not able to link adult density to habitat attributes (prediction 2), but privately owned survey areas supported higher densities of willow ptarmigan than state-owned survey areas (prediction 3). There were only weak indications that densities were higher in survey areas rich in open areas with dense field layer and lower densities in areas rich in snow-beds and mountain birch forest (Table 1). We found indications of lower reproduction in survey areas where a high proportion of the area was covered by mountain birch forests (prediction 4).

Our results differ from previous studies, where individual ptarmigan selected specific vegetation types (Andersen et al. 1984, Kastdalen et al. 2003, Henden et al. 2011, Ehrich et al. 2012). Such selection at the individual scale did not affect the density at the population scale in the hunting units surveyed. One possible explanation for the lack of a clear relationship between vegetation composition and adult density in our study was that willow ptarmigan populations in most survey

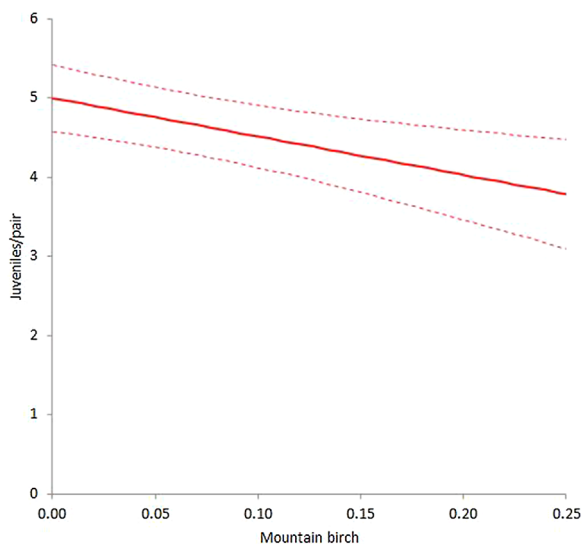


Figure 4. Number of juveniles/pair of willow ptarmigan plotted against the proportional cover of mountain birch forest in south-central Norway, 1996–2011.

areas were below carrying capacity (Myrberget 1988, Pedersen 1988, Lehtikoinen et al. 2014, Kvasnes et al. 2015). Thus, relative to years with higher population levels, food and shelter were plentiful and competition was low. A small proportion of an important habitat component might be sufficient to support relatively high densities. Kastdalen et al. (2003) reported that willow ptarmigan selected willow thickets at relatively high bird densities. However, Henden et al. (2011) reported the same finding at very low ptarmigan densities, indicating that we should also expect evidence for habitat selection. Overbrowsing by large ungulates (i.e., semi-domestic reindeer) caused the landscape variation in the Henden et al. (2011) study area in northern Norway but not in our study area in southern Norway. Ungulates might reduce the quality of tundra habitats to a level where the resources are no longer plentiful even for populations of ptarmigan at low densities, which could affect habitat selection. Earlier studies (Andersen et al. 1984, Steen et al. 1985) reported that vegetation types with willow are important habitat components for willow ptarmigan. Willows occur in bilberry-low fern birch forest within the birch category, tall-grown lawn vegetation within the category for bogs with a dense field layer, and fresh heather and dwarf-shrub communities within the category for heathland dominated by shrubs or herbs (Table S1; Johansen et al. 2009). However, when willows were available in excess, as in our study, we could not document selection for specific vegetation types.

Survey areas with high proportions of mountain birch forest had lower reproductive success. This effect was weak but coincided with the data of Andersen et al. (1984) demonstrating that willow ptarmigan broods avoided mountain birch forests during the first 3 weeks after hatch. Andersen et al. (1984) also reported selection for rich bogs in central Norway, contrary to our study. A possible explanation for the weak relationship between reproductive rates and vegetation cover was the low ptarmigan density and subsequent low competition for brood-rearing habitats. An effect of vegetation composition may be clearer, in theory, at higher densities because of increased competition for optimal habitats (Fretwell and Lucas 1969).

We do not know why we found a difference in density between private and state-owned land. However, there is a general assumption that hunting pressure is greater on state-owned than on private land in Norway (Pedersen and Storaas 2013), and consistent difference in harvest rates among survey areas might cause spatial variation in densities (Smith and Willebrand 1999, Pedersen et al. 2004, Sandercock et al. 2011). However, landownership is not a robust index of hunting pressure, and actual harvest records must be used to estimate harvest rates precisely. Nevertheless, because private- and state-owned areas have similar vegetation composition, the difference in hunting pressures is a possible explanation for the observed differences. Kvasnes et al. (2015) suggested that dispersing juvenile ptarmigan are attracted by established adult conspecifics before choosing where to breed. Single adult males often remain in their former territories and display autumn territoriality when

ptarmigan flock in October (Pedersen et al. 1983, Pedersen 1988), and may sit tight for pointing dogs (M. A. J. Kvasnes, Hedmark University of Applied Sciences, personal observation). More dispersing ptarmigan should be attracted to private land if hunting pressure is higher on state-owned hunting units, especially later in the autumn.

MANAGEMENT IMPLICATIONS

Management to improve habitat will not likely have an effect on the densities of willow ptarmigan populations in Norway during periods of relatively low densities. Further, it will be difficult to identify areas suitable for protection to promote willow ptarmigan. However, restricting human development to areas below the tree-line to mountain birch forest may benefit willow ptarmigan because these areas are less important for reproduction. The lack of a clear effect of habitat composition on breeding density might suggest that other factors than habitat availability are limiting the current population abundance of ptarmigan in Norway.

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