Old bilberry forest increases likelihood of Capercaillie (*Tetrao urogallus*) lek occupancy in Southern Norway

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Capercaillie *Tetrao urogallus* prefers old forest, and bilberry *Vaccinium myrtillus* is a key dietary component. This study aimed to explore lek occupancy and size in relation to those habitat qualities (old forest proportion and type), by examining 246 leks situated in south-eastern Norway. Lek occupancy, lek size and proportion old forest/old bilberry forest were estimated within 0.3 and 1 km radius respectively. Our results showed that lek occupancy and size depended strongly on the proportion of old bilberry forest. Other old forest had no effects on lek occupancy or size after accounting for the effects of old bilberry forest. These findings can be implemented in forest management plans to improve lek habitats and population size.

Key words: grouse; boreal forests; wildlife; conservation; management

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INTRODUCTION

Capercaillie *Tetrao urogallus* is an old forest species and a flagship species for hunters and conservationists (Rolstad & Wegge 1989, Pakkala *et al*. 2003). Population declines and range contractions have been documented for several bird species connected to old-growth forests in northern Europe (Helle & Järvinen 1986, Kouki & Väänänen 2000, Brotons *et al*. 2003, Hanski & Walsh 2004) including the Capercaillie (Rolstad & Wegge 1989, Pakkala *et al*. 2003). Capercaillie abundance correlates with several environmental factors, such as ground vegetation, predation, forest structure, forest age or climate (Slagsvold & Grasaas 1979, Kurki *et al*. 2000, Selås 2000, 2006, Borchtchevski *et al*. 2003, Baines *et al*. 2004). Many negative effects are induced by modern forestry and they co-vary on both temporal and spatial scales, such as the forestry-induced increase in egg and chick predation with reduction of favourable habitat characteristics (old forest) (Storaas & Wegge 1987, Rolstad & Wegge 1989, Kurki *et al*. 1997, 1998, 2000, Storaas *et al*. 1999).

Several studies show that Capercaillie is an old forest species, which thrives in productive old forests in spring-summer and prefers Scotch pine *Pinus sylvestris* for winter diet (Rolstad & Wegge 1987, Storch 1993, Swenson & Angelstam 1993, Kurki *et al*. 2000, Baines *et al*. 2004). Further, the bilberry plant and insects living on this vegetation are an important dietary component for the

Capercaillie (Spidsø & Stuen 1988, Picozzi *et al.* 1999, Baines *et al.* 2004, Summers *et al.* 2004, Wegge *et al.* 2005). Old bilberry forest or bilberry vegetation has also been linked to population density, lek presence or individual habitat use in Capercaillie (Storch 1993, Selås 2000, Baines *et al.* 2004, Summers *et al.* 2004). Selås (2000, 2001) reported a match between mast years of bilberry and population density. Baines *et al.* (2004) revealed that breeding success increased with bilberry cover at least up to 15-20% (maximum bilberry cover in this study was 24%). From current knowledge we expect that increased old bilberry forest proportion will increase likelihood of lek occupancy, because more males settle down in an area with more preferred habitat. Moreover, an area of good quality is expected to produce more chicks and have higher individual survival, and in the end therefore produce more territorial and displaying males.

In this study we link Capercaillie lek occupancy and size to forest type on a local scale (± 1 km). Our goal is to find easy and cost-effective management tools suitable to recognize important habitat qualities for Capercaillie. From knowledge of habitat preferences we expect that increased old forest proportion in the landscape increases likelihood of lek occupancy (Wegge & Rolstad 1986, Rolstad & Wegge 1987). As bilberry vegetation has been shown to be important, we specifically test the importance of old bilberry forest in predicting lek occupancy. We ask whether it is more likely that a lek site will be occupied if the proportion of old bilberry forest increases on a local scale.

MATERIAL AND METHODS

Our main aim was to study the influence of specific environmental gradients and not to document exact values of population densities or environmental states. Therefore, we needed to sample a large number of leks, and we chose an expert opinion approach (see Johnson & Gillingham 2004, Seoane *et al.* 2005) which is not compared to or scaled to other methods which are usually used in Capercaillie research (see Discussion). However, we emphasize that to give good estimates, the observers' decisions (expert opinion) should be based upon the same judgement and criteria. Criteria used to determine forest quality and lek occupancy are treated in the next paragraphs. These criteria are easily recognized by skilled wildlife biologists with Capercaillie experience.

To test the hypothesis of «old bilberry forest» dependence we selected 217 lek sites registered in the 1980s. The Norwegian Directorate for Nature Management gathered information on Capercaillie leks in the 1980s, and in many cases the regional game authorities took the initiative to visit and map leks. We used mapped registrations from these projects. During three consecutive spring seasons, 2003-2005, we revisited all leks in eight representative regions (municipalities) of south-eastern Norway (Table 1, Fig. 1).

The oceanic influence increases slightly towards the south-west in our study area (Esseen *et al.* 1997, Fremstad 1997). All leks were located in coniferous forest ranging from nutrient-poor lichen-pine forests to productive herb-rich bilberry spruce forest. All study regions are intensively managed by modern forestry methods and less than 30% old semi-natural forest remains, especially on more productive soils (Framstad *et al.* 2002, Rolstad *et al.* 2002). In this study we use the term «old forest», which in most cases is old semi-natural forest (see distinctions in Rolstad *et al.* 2002).

Two observers revisited 217 Capercaillie leks and also included 29 newly discovered leks (Table 1). The inventory was done from March to May when male Capercaillie are distributed in their spring territories around the lek (Finne *et al.* 2000, Hjeljord *et al.* 2000, Wegge *et al.* 2003). As this study strived to find easy and cost-effective techniques which could be used in practical management, we used methods of semi-quantitative character which included visual

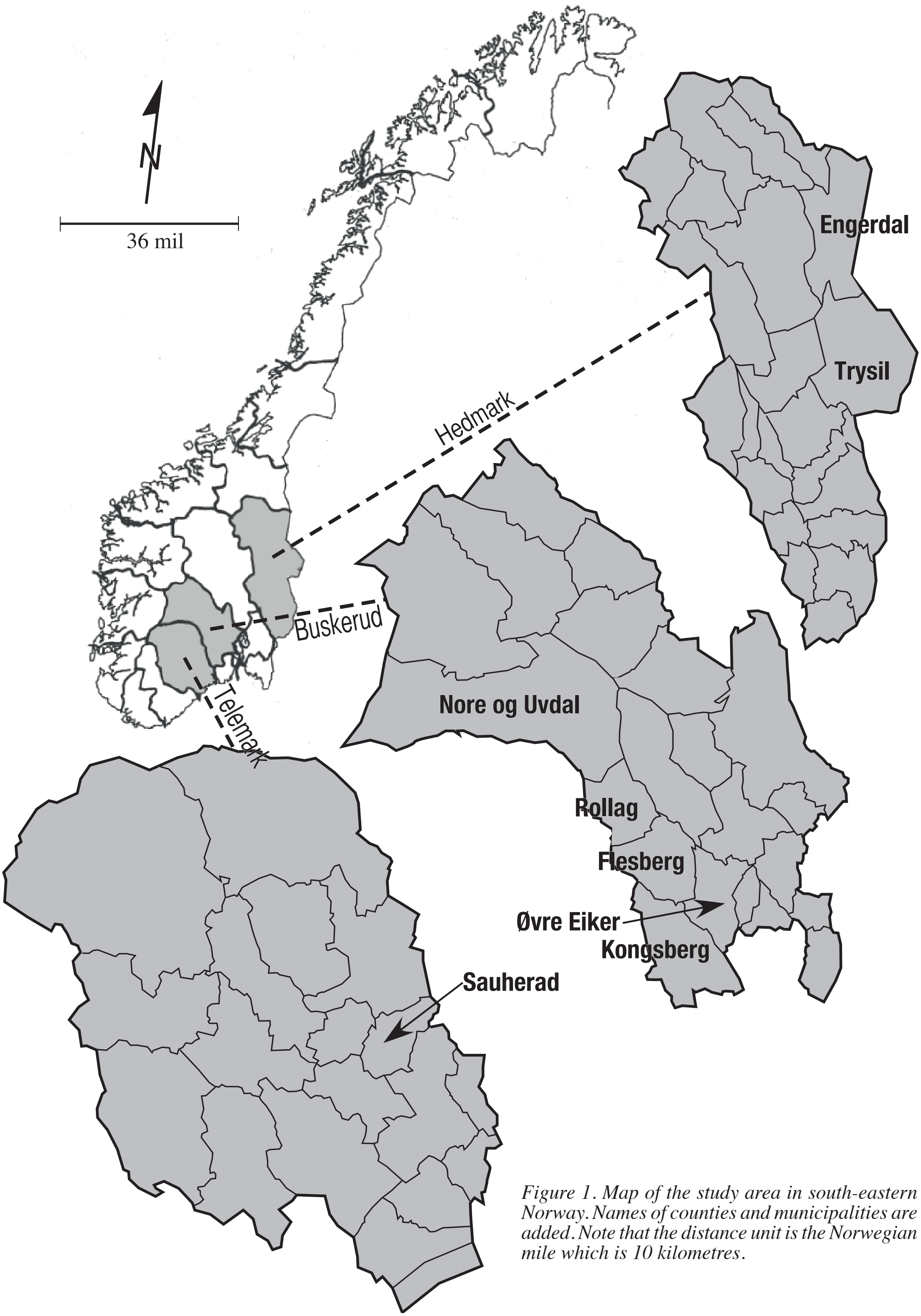

Figure 1. Map of the study area in south-eastern Norway. Names of counties and municipalities are added. Note that the distance unit is the Norwegian mile which is 10 kilometres.

interpretation. Most observations were done with partial snow cover, increasing the detectability of traces of Capercaillie. We subjectively estimated (expert opinion) based on own observations from the inventory: i) either the old forest (N = 194) or the old bilberry forest (N = 123) proportion, or both (N = 73), within a circle of 1 km radius around each lek and: ii) the likely occupancy of Capercaillie cocks at the lek. The display areas are centred in the inner 300 metres of a Capercaillie's daytime territory with a radial extension of 1 kilometre (Rolstad *et al*. 2007).

Lek occupancy was noted if we recorded male Capercaillie activity within a 0.3 km radius around lek centre according to the registered coordinates (see footnote Table 1). The observer started observations at the centre of the lek and systematically circled (spiralled) out to a radius of 0.3 km. All observations of Capercaillie activity were recorded, such as territorial markings (faeces, tracks and feathers), signs of foraging activities (clipping of pines), roosting trees, sound and visual observations of Capercaillie. Such a visit could take from half an hour to several hours depending on accessibility. For leks with Capercaillie activity, lek occupancies were verified more accurately by visual observations during display in early morning.

Old forest and old bilberry forest proportion were visually estimated within a circle of 1 km radius around each lek, as previous studies have shown that territories surrounding a lek most probably lie inside this circle (Rolstad & Wegge 1987, Picozzi *et al*. 1992, Hjeljord *et al*. 2000, Wegge *et al*. 2003). The forest should consist of old (mature forest, above age of growth deceleration (>60-70 years)) semi-natural coniferous forest not affected by modern forestry, according to Capercaillie preferences (Rolstad & Wegge 1987, Storch 1993). However, younger forests which are managed by thinning to sustain the field layer (bilberry cover) can also serve as low-density Capercaillie habitat (Rolstad *et al*. 2007). The old bilberry forest, being the most productive and moist old forest, is a richer subsample of old forest. This old bilberry forest is similar to well-defined forest vegetation types such as bilberry woodland (type A4, according to Fremstad 1997), preferentially including aspen *Populus tremula* and a mosaic of richer vegetation types (small fern woodland; vegetation type A5) and swamp woodland (vegetation type E; Fremstad 1997), in line with Capercaillie spring-summer habitat preferences (Storch 1993, Picozzi *et al*. 1999, Baines *et al*. 2004, Summers *et al*. 2004, Wegge *et al*. 2005).

We tested for a relationship between Capercaillie lek occupancy and size and forest type by using either logistic or linear regression (SAS 2003). Because old bilberry forest is a subsample of old forest, we used leks where both forest types were surveyed in order to separate the effects of old bilberry forest from other old forest, this being old forest minus old bilberry forest. We introduced old bilberry forest, other old forest and observer in the same model, either logistic (occupancy) or linear (lek size). By adding observer as a dummy variable, we investigated the observational precision. The linear model violated assumptions of normality (even when log-transformed), indicated by a lack-of-fit test ($p = 0.02$), but this does not affect our predicted values. Due to dominance of lower values the distribution is skewed downwards (variance: 10.34, Skewness: 2.44, Kurtosis: 8.28, CV (coefficient of variation): 168).

RESULTS

Seventy-three percent of Capercaillie leks were categorized as unoccupied, and regionally this varied between 63 and 82% (Table 1). The proportions of old forest and old bilberry forest were significantly lower on unoccupied (31.1% and 9.6%, respectively) leks compared to occupied (52.9% and 20.2%) leks (Table 1, Fig. 2). Both lek occupancy and lek size increased with proportion of both forest types (Fig. 3). Both lek occupancy and size were higher and increased more rapidly for old bilberry forest compared to old forest in

Table 1. Regional summary statistics of Capercaillie lek occupancy and forest type proportions in this study (mean ± STD).

Municipality	Original leks	New leks[1]	Leks used in habitat analysis	Unoccupied leks[2]	Old bilberry forest proportion in the surroundings (± 1 km) of a lek and in parenthesis values for unoccupied/occupied leks.	Old forest proportion in the surroundings (± 1 km) of a lek and in parenthesis values for unoccupied/occupied leks.
Kongsberg	50	6	56	78%		33.3% ± 16.3 (29/48*)
Sauherad	24	3	27	63%	9.6% ± 5.5 (7/13*)	
Øvre Eiker	30	6	36	77%	14.4% ± 8.8 (10/20*)	36.4% ± 17.7 (31/49*)
Flesberg	28	6	34	64%	18.7% ± 9.2 (13/25*)	30.6% ± 18.4 (25/43*)
Rollag	22	1	23	73%	14.3% ± 11.9 (8/25*)	40.7% ± 20.8 (36/50)
Nore og Uvdal	30	1	31	73%	14.0% ± 8.6 (10/22*)	43.6% ± 21.7 (37/59*)
Trysil	15	0	15	77%	10.0% ± 5.3 (8/15*)	
Engerdal	17	6	23	82%		
Total	**217**	**29**	**246**	**73%**	**14.0% ± 9 (10/20*)**	**36.0% ± 19.0 (31/53*)**

[1]The newly discovered leks did not differ from the other leks in their forest type-lek occupancy/size associations, therefore this sample was added to our material. [2] As a lek displaying area is within the 300 meter radius we treat movement out of this zone as a new lek, and therefore the original lek as unoccupied. The distance moved is correlated to reduction in proportion of old forest in central areas of the original lek (unpublished data). * Significant difference by a t-test ($p < 0.05$).

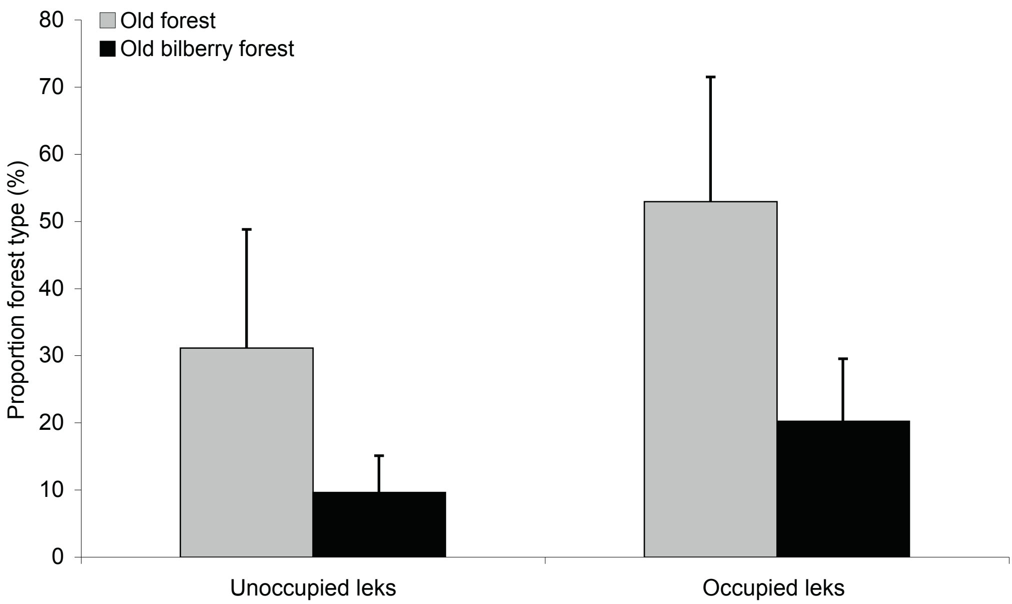

Figure 2. The difference in proportion of old bilberry forest and old forest on occupied and unoccupied leks (mean ± STD).

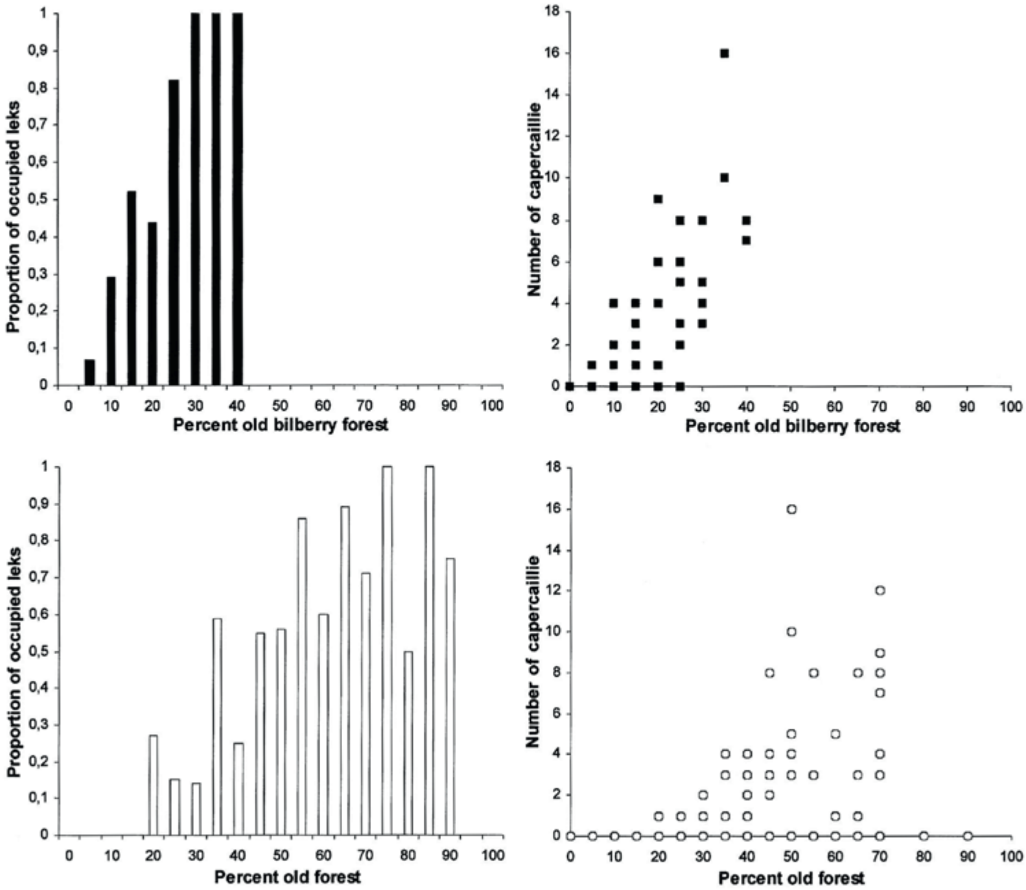

Figure 3. Observed proportion of occupied leks (left column) and observed lek size (right column) as a function of proportion of either old bilberry forest (Upper row; n = 123) or old forest (Lower row; n = 194).

general. Comparing the shape and position for the two curves we see that adding bilberry in the old forest will effectively shift the curves up towards higher probability of lek occupancy or larger lek sizes (Fig. 3).

In cases where both forest types were surveyed we could analyse the separate effects of old bilberry forest and other old forest (i.e. old bilberry not included). Other old forest was insignificant in predicting lek occupancy or size (p = 0.50, p = 0.69) when introduced in the same model as old bilberry forest (Table 2). This is interpreted as indicating that it is the bilberry component in the old bilberry forest which best predicts the Capercaillie lek occupancy. For these data there were no significant effects of observer difference (Table 2, p = 0.95 and 0.55).

Old bilberry forest predicted Capercaillie lek occupancy with high precision (Table 2, Fig. 4). Capercaillie lek occupancy increased logistically with the proportion of old bilberry forest, with most of the increase in occupancy occurring as the proportion of old bilberry forest increased from 10 to 30%. Beyond 30% old bilberry

Table 2. Test statistics for two models fitted either to predict likelihood of Capercaillie lek occupancy (logistic regression) or lek size (linear regression) as a function of old bilberry forest, other old forest and observer (N = 73). Due to the non-normal distribution of the response in the linear model the model suffers from lack-of-fit (p = 0.02), but this does not conflict with the parameter results we present. The response in the linear model is natural log-transformed.

Model	**Source**	**Test statistic**	**p**	**Parameter estimates ± SE**
logistic model (Chi square,	Intercept	18.46	<0.0001	4.23 ± 0.98
$\chi^2 = 34.12$, $R^2 = 0.36$,	Old bilberry forest	18.08	0.0003	-0.18 ± 0.05
$p < 0.0001$; N = 73)	Other old forest	0.45	0.50	-0.01 ± 0.02
	Observer	0.0038	0.95	-0.02 ± 0.38
linear model (F = 33.18,	Intercept			-0.51 ± 0.14
$R^2 = 0.59$, $p < 0.0001$;	Old bilberry forest	93.39	<0.0001	0.07 ± 0.01
N = 73)	Other old forest	0.17	0.69	0.001 ± 0.004
	Observer	0.36	0.55	0.04 ± 0.07

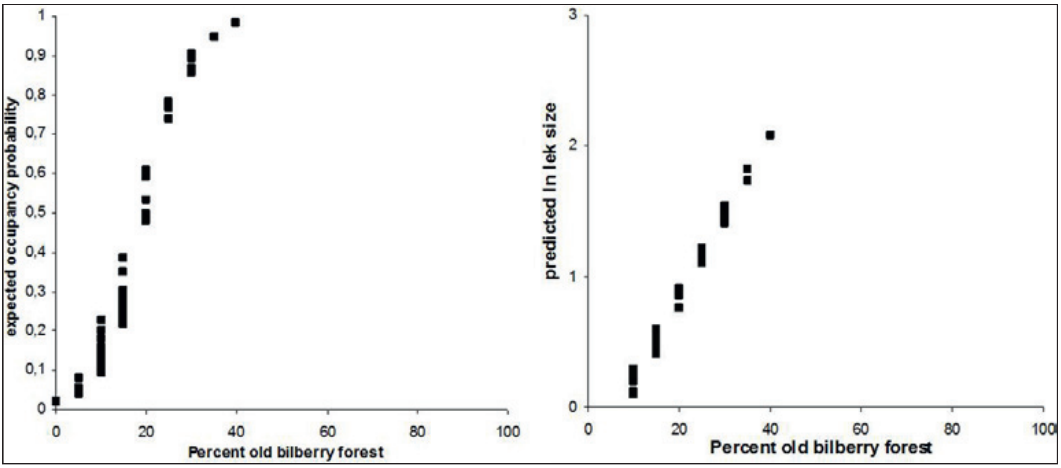

Figure 4. Expected and predicted values for the effects of old bilberry forest from the logistic (left) and the linear (right) model (see Table 2). The values in the linear model are natural log-transformed.

forest, lek occupancy was virtually assured. For instance, when old bilberry forest constitutes 20% of an area, the Capercaillie likelihood of lek occupancy is approximately 3.5 times higher than for 10%.

The linear model revealed much the same results as the logistic model where old bilberry forest was the sole predictor of lek size (Table 2, Fig. 4). Lek size increased by 2.1 Capercaillie with an increase in old bilberry forest from 20 to 30%.

DISCUSSION

This study documents a significant and positive association between Capercaillie lek occupancy and size, and both general old forest and old bilberry forest. At a given proportion of these forest types, old bilberry forest had larger effects on lek occupancy and size. When analysed in the same model, only old bilberry forest had significant effects on lek occupancy and size. We propose that this reveals the positive effects of bilberry as a key dietary component, and as a proxy of a richer environment for Capercaillie, thereby increasing the probability of lek formation and further increasing the number of territorial males.

Capercaillie lek occupancy and size correlated positively with our two measures of forest type. Capercaillies prefer old forests (Rolstad & Wegge 1987, Swenson & Angelstam 1993, Kurki *et al.* 2000, Baines *et al.* 2004), and especially bilberry forests, where they forage on bilberry or insects living in this vegetation (Spidsø & Stuen 1988, Storch 1993, Picozzi *et al.* 1999, Proctor & Summers 2002, Baines *et al.* 2004, Summers *et al.* 2004, Wegge *et al.* 2005). Our study further indicates that it is the bilberry-component in the old forest habitat that most likely increases lek formation and size. This habitat obviously produces more preferred food and has more structural diversity as protection against predators (Kastdalen & Wegge 1991; Picossi *et al.* 1996), which are probably the factors that lead to higher production, survival and population density (see Baines *et al.* 2004). Hence, this will finally increase the likelihood of establishment of male territories and displaying grounds. However, it is also likely that other components in the bilberry-rich forest attract Capercaillies, because it is a moist and productive environment (Fremstad 1997).

Other old forest types, including more marginal pine forests, did not influence Capercaillie lek occupancy or size. In many areas, including our study area, these constituents are often in surplus. That lek occupancy correlated with the proportion of general old forests was apparently because these forests also included old bilberry forests.

Larger probability of lek occupancy with increasing forest productivity, and with area, may be a response to minimum required home-range size of individuals in a productivity gradient (see predictive model in Rolstad & Wegge 1987). A Capercaillie home-range is approximately 50 ha depending on patch size, patch quality and isolation corresponding to an old bilberry forest proportion of roughly 17% (within 1 km radius). In a bilberry forest the home-range size is less than in a more marginal old forest, thus increasing likelihood of lek occupancy and size for a given patch size (see also Wegge & Rolstad 1986). Our study shows that increased proportion of old bilberry forest increases the likelihood of lek occupancy and size, indicating that this forest type holds a higher home-range quality compared to old forest. When the old forest increases in quality, i.e. increased bilberry, the probability curve shifts to higher values (Fig. 3). Similar spatial effects are also found in other studies (Storch 1993, Andren 1994, Angelstam 2004, Baines *et al.* 2004, Hanski & Walsh 2004).

In field biology there is a trade-off between sample size, observer effort and precision at different levels (Legendre & Legendre 1998). For a given economic budget, sampling more leks will reduce the effort per lek, and vice versa, introducing a trade between less precise knowledge of leks in general to good knowledge of some leks. Our «expert opinion» methodology (see Johnson & Gillingham 2004, Seoane *et al*. 2005) is effective in revealing broad qualitative trends concerning ecological questions such as Capercaillie habitat requirements, which need large, representative samples to give robust answers. This would have been very costly, with more effort invested per lek giving more precision in individual estimates. We have chosen to have less quantitative precision but more replicates, to obtain enough data to test our hypothesis. Our method may not be as accurate in determining lek occupancy or exact lek sizes compared to more resource-demanding inventories done in other studies, but instead enabled us to get a large data set. We also note that our results did not depend on observer identity, suggesting that our method was relatively precise.

Our study, along with other studies, revealed that bilberry is important to Capercaillie populations, and we suggest that modern forestry reduces the proportion of bilberry vegetation. Modern forestry has thereby a negative influence on Capercaillie abundance through the clear-cut and planting practice which suppresses bilberry vegetation, favouring other vegetation such as grass and heather and suppressing the field layer in general. In open landscapes, as on clear-cuts, a shift in field vegetation towards grass and heather occurs because bilberry needs darker, more stable and humid conditions found in old forest environments (Ritchie 1956). Dense plantations suppress the field layer further, and timber harvest drains the nutrients out of the ecosystem. Hence, stable and productive old forest environments which are needed for rich bilberry cover to develop are shrinking today (Hanski & Hammond 1995, Löfman & Kouki 2001). As Capercaillie is a flagship species and also an umbrella species for other old-growth species (Suter *et al*. 2002, Jansson & Andren 2003, Pakkala *et al*. 2003), our results should be implemented in forest management plans to sustain bird species dependent on old-growth forest.

In conclusion, Capercaillie lek occupancy is positively related to old bilberry forest. As this forest type has declined over the last decades, this link may provide an explanation for the simultaneous population declines of Capercaillie. We document critical qualities necessary to be conserved by forestry practices for Capercaillie to be able to thrive and maintain viable populations. Due to the steep increase in likelihood of lek occupancy at low proportions of old bilberry forest it will pay off to increase this proportion. The ultimate key to sustain viable Capercaillie populations is by conserving reasonable amounts of old bilberry forest.

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SAMMENDRAG

Gammel blåbærskog øker sannsynligheten for tilstedeværelse av storfuglleik i Sør-Norge

Storfugl *Tetrao urogallus* foretrekker gammelskog og blåbærplanten *Vaccinium myrtillus* er vist å være meget betydningsfull ved habitatbruk og i dietten. Basert på disse kjensgjerningene ønsket dette studiet å se nærmere på om gammel blåbærskog er spesielt viktig også for leik- tilstedeværelse. I perioden 2003-5 undersøkte vi 246 tiurleiker, hvorav 217 var tidligere undersøkt på 1980-tallet, i 8 kommuner fordelt på 3 fylker i Sør-Norge. Ved befaringen av tiurleikene anslo vi gammelskogsandelen, inkludert blåbærskog, i en kilometers radius og tilstedeværelsen av territoriell tiur i 300 m radius rundt leiksentrumet. Våre resultater viste at leik- tilstedeværelse og -størrelse avhenger sterkt av andelen gammel blåbærskog. Fattigere, mindre næringsrik, gammelskog

hadde ingen effekt på leik-tilstedeværelse eller leik-størrelse. Disse resultatene bør bli implementert i skogforvaltningen for å ivareta storfuglens leikområder og for å øke storfuglbestanden.

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