

## Contemporary mature forest cover does not explain the persistence of Capercaillie (*Tetrao urogallus*) lekking areas in Finland

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Capercaillie (*Tetrao urogallus*) has traditionally been considered an old forest-dependent species. The lekking sites especially, were thought to be located in older forests. We studied the persistence of Capercaillie lekking areas in relation to mature forest cover at three study areas in Finland (southwestern, SW; central, CE; and northern, NO). A total of 381 leks were inspected twice at intervals of 10–30 years and were classified as either persisting or vacated. We defined mature forest as forest with  $> 152 \text{ m}^3 \text{ ha}^{-1}$  of timber (SW and CE Finland) or  $> 68 \text{ m}^3 \text{ ha}^{-1}$  of timber (NO Finland). We measured mature-forest cover within two radii around the leks (1,000 and 3,000 m) using satellite image-based forest inventories, and performed logistic regression analyses on these data. We did not find significant trends between mature-forest cover and lekking-area persistence in any of the study areas. However, the proportion of mature forests may have already been too low to detect the significance of this factor. The only significant factor affecting the lekking-site persistence was time lag between surveys. The positive relationship between the time lag and lekking-site persistence in CE and NO Finland may be due to the partial recovery of the landscapes in terms of forest regrowth, from extensive clear-cut harvesting in the 1950s and 1960s. In SW Finland, the relationship was negative, possibly indicating more permanent changes in the landscape that is currently characterized by human settlements and agricultural areas. We conclude that in present-day Finland, the area covered by mature forest is most likely too scarce to explain the lekking-area persistence of Capercaillie. An alternative explanation is that some important structural characteristics are missing from the current mature forests.



## 1. Introduction

Large-scale loss and fragmentation of old-growth forests have been generally acknowledged as driving forces behind the declines of many boreal-forest bird species (e.g., Virkkala 1990, Hansson 1992, Schmiegelow *et al.* 1997). Also, for Capercaillie (*Tetrao urogallus*), changes in forested habitats have been among the most important causes of its population decline in Finland and elsewhere (e.g., Lindén & Rajala 1981, Lakka & Kouki 2009, Storch 2000; but see Sirkiä *et al.* 2010a).

Capercaillie has long been considered a species associated with old forests (e.g., Valkeajärvi & Ijäs 1986, Storch 1993, Swenson & Angelstam 1993; but see Seiskari 1962). Males especially have been reported to prefer large forested areas with average tree age older than 60–70 years for their traditional lekking sites (Rolstad & Wegge 1987a, 1989a). In 1985 in Northern Finland, nearly 70 Capercaillie lekking sites were inventoried, and these leks were located in forests on average older than 120 years (Helle *et al.* 1989). However, since then, new lekking sites have been found in relatively young forests (Miettinen *et al.* 2005, Rolstad *et al.* 2007, Valkeajärvi *et al.* 2007), suggesting that fairly young forest stands (age at least 30–40 years) can be suitable habitat for Capercaillie and its lekking sites in managed boreal forests (see also Miettinen *et al.* 2008, 2010).

Capercaillie lekking areas consist of a lekking site and the surrounding daytime home ranges (daily territories) of males (Wegge & Larsen 1987). The minimum size for a lekking area, including the daily territory, is 300 hectares (Wegge & Larsen 1987). Landscape-level investigation is required to study phenomena affecting lekking areas because larger-scale landscape structure affects Capercaillie leks (e.g., Lindén & Pasanen 1987, Helle *et al.* 1994, Miettinen *et al.* 2005).

In addition to forest cover, grain size of the landscape mosaic is one of the major determinants of the viability of Capercaillie lekking population (Rolstad & Wegge 1987b, Rolstad & Wegge 1989a). Grain size is defined here as the average size of mosaic patches relative to home ranges or movement patterns of organisms (Rolstad & Wegge 1989b and references therein). In the present study, we aimed to discover the effects of mature forest cover and fragmentation on the persistence

of Capercaillie lekking areas (for a definition, see above). We assumed mosaic-like, positive effects of fragmentation, mainly because a landscape that consists of many small patches can satisfy the year-round habitat requirements of a species more readily than a more homogeneous landscape (e.g., Helle *et al.* 1994). Management-wise, it is important to know exactly which forest-age or development classes are the most important for the lekking areas of Capercaillie, and whether the configuration of the focal habitat, in addition to the amount, should also be considered. As species responses to landscape-level phenomena depend on the spatial scale (e.g., Fuhlendorf *et al.* 2002), we studied the relationship between lekking-area persistence and mature forests at two spatial scales: 1,000 and 3,000 m radii.

## 2. Material and methods

All material and methods are described in detail in Sirkiä *et al.* (2011).

### 2.1. Lekking-area occupancy data

Altogether 381 lekking sites were surveyed in three study areas situated in (1) South-western (SW, N = 55), (2) Central (CE, N = 238) and (3) Northern Finland (NO, N = 88; see Sirkiä *et al.* 2011 for a map). Leks were inspected twice, first during 1970–1992, and again during 2000–2005 (Sirkiä *et al.* 2011). The minimum time lag between the surveys varied from 10 to 32 years (Table 1). In both surveys, the sites were visited during the lekking season in March–May, and seen/heard Capercaillie individuals, snow tracks or fresh excrements were all interpreted as an occupied lekking area. We classified the occupancy data according to the distance between the leks of the old and new survey. We classified the old and new leks that were  $\leq 1,000$  m apart as persisting leks (see Rolstad & Wegge 1989a), whereas sites with old leks  $> 1000$  m apart from new leks were considered vacated. The remaining group of leks (new leks  $> 1,000$  m away from the old ones) could contain leks that were already in use in 1970–1992 but were missed by the surveyors. Thus, we omitted this category of leks from statistical analyses. The proportion of vacated leks was 29, 84 and

Table 1. Variation in structural variables of forests at the landscape scale (3,000 m) surrounding the studied lekking areas (both persisting and vacated) in three study areas (SW, CE and NO Finland; see text). The variation in time lag between the two lekking-site surveys is also indicated. Variables marked with an asterisk are calculated for the mature forest (see text) versus other patches. IQR = inter-quartile range, MFC = mature forest cover (% of forest > 152 m<sup>3</sup>ha<sup>-1</sup> for SW and CE Finland, > 68 m<sup>3</sup>ha<sup>-1</sup> for NO Finland), PD = patch density (# per 100 ha), MPS = mean patch size (ha), TE = total edge (km), TIME = the minimum estimated time interval between the two lekking site surveys (years).

	SW Finland (N = 55)		CE Finland (N = 238)		NO Finland (N = 88)	
	Range	Median (IQR)	Range	Median (IQR)	Range	Median (IQR)
MFC	15.8–45.0	27.0 (6.8)	6.9–44.2	21.2 (11.0)	5.5–54.2	22.8 (12.1)
PD*	7.5–34.1	19.6 (7.2)	7.7–48.6	25.1 (15.2)	9.9–43.9	24.4 (8.0)
MPS*	0.5–3.8	1.3 (0.8)	0.2–3.2	0.9 (0.8)	0.3–5.5	0.9 (0.7)
TE*	168–591	412 (96.0)	154–542	358 (94.2)	130–654	359 (128.9)
TIME	10–32	14 (5.0)	22–30	27 (0.0)	10–17	14 (2.5)

22% in SW, CE and NO Finland, respectively, in total being 62% (236 out of 381 leks).

## 2.2. Landscape data

The landscape data were derived from multi-source national forest inventories (MS–NFI, Tomppo *et al.* 2008). MS–NFI exploits Landsat TM 5 satellite images and ground reference plots to yield geographically explicit information of forest resources. The satellite images from SW, CE and NO Finland originate from 1998, 1996 and 2002–2003, respectively. Following the procedure described in Sirkiä *et al.* (2011), we classified the landscape data simply as “habitat” and “matrix”, so that the former included all the forest pixels (size of 25 m × 25 m) having volume of timber above a specific threshold (see next paragraph), and the latter included all the other areas, such as roads, inhabited areas, fields, and water, as well as forests with timber volume below the threshold.

In SW and CE Finland, forested areas with timber volume > 152 m<sup>3</sup>ha<sup>-1</sup> were classified as habitat, whereas forested areas with timber volume ≤ 152 m<sup>3</sup>ha<sup>-1</sup> were classified, along with non-forested areas, as matrix habitat. In NO Finland, however, the timber-volume threshold was 68 m<sup>3</sup>ha<sup>-1</sup>, reflecting the lower soil productivity in NO Finland and the consequent slower yearly increment in timber volume. These criteria fall in the middle of the average timber volumes of young and advanced thinning forests, defining the threshold to-

wards older forest stands (Tomppo *et al.* 1998). “Habitat” thus always included advanced thinning stands and older, i.e., forests older than 51–70 years (hereafter referred to as “mature forest”, i.e., closed-canopy forests with some timber-sized trees; diameter at 1.3 m height > 17 cm; Peltola 2003).

We calculated landscape predictors around Carcaillie leks separately for two spatial scales with FRAGSTATS (McGarical & Marks 1995). The first spatial scale, a circle with a radius of 1,000 m from the central point of a lek, covered the whole lekking area (314 ha; e.g., Wegge & Larsen 1987). The second spatial scale, a circle with a radius of 3,000 m, represented the landscape context in which the lekking areas were embedded (covering 2,827 ha). Using large spatial scales (hundreds of hectares) decreases the standard error of the selected timber-volume estimates to approx. 10–20% (Tokola & Heikkilä 1997). We calculated the following indices: mature-forest cover (proportion of forest > 152 m<sup>3</sup>ha<sup>-1</sup> or > 68 m<sup>3</sup>ha<sup>-1</sup> within the total area); mean patch size (ha; MPS); patch density (number of patches per 100 ha; PD); and total length of edge between mature forest and other patches (m; TE) (Table 1).

## 2.3. Fragmentation index and statistical models

We used a correlation-based Principal Component Analysis (Proc PRINCOMP, SAS 9.2) for both

Table 2. Principal component loadings for the indices representing mature-forest fragmentation, at 1,000 and 3,000 m radius surrounding lekking sites of Capercaillie ( $N = 381$ ).

Radius (m)	Indices	PC1	PC2
1,000	Mean patch size	0.71	-0.01
	Patch density	-0.63	0.46
	Total edge	0.33	0.89
	% of variation explained	61	33
3,000	Mean patch size	0.72	0.06
	Patch density	-0.65	0.42
	Total edge	0.25	0.90
	% of variation explained	61	35

spatial scales separately to obtain a fragmentation index from MPS, PD and TE (Trzcinski *et al.* 1999, Sirkiä *et al.* 2011). All correlations between MPS, PD and TE were significant at  $P < 0.0001$ , except for the correlation between PD and TE, which was non-significant ( $P > 0.05$ ) at both spatial scales. The first two components explained over 90% of variation at both spatial scales. However, PC 1 reflected mostly MPS, accompanied with increasing TE and decreasing PD (Table 2). In contrast, as PC 2 increased, PD and TE increased whereas MPS remained near zero, being slightly negative at 1,000-m spatial scale and slightly positive at 3,000-m spatial scale (Table 2). Thus, neither PC 1 nor PC 2 ultimately embodied the simultaneous effects of fragmentation, i.e., decreasing MPS together with increasing PD and TE

(Trzcinski *et al.* 1999, Sirkiä *et al.* 2011). Moreover, the relationship between PC 2 and mature-forest cover was significantly positive at both spatial scales (Fig. 1.; compare to figure 2 in Sirkiä *et al.* 2011). We thus concluded that a reliable measure of fragmentation using MPS, PD and TE in the PC analysis could not be created with our data. Hence, these variables were not used in further modelling.

To analyze the relationship between mature-forest cover and lekking-area persistence, we used logistic regression models (Proc GENMOD, SAS 9.2) with the dependent variable, lek, modelled binomially as persisting or vacated using a logit link function and forest cover (COVER) and the estimated minimum time lag between the lekking-site surveys (TIME) treated as independent variables. The modelling was conducted for each study area ( $N = 55, 238$  and  $88$  for SW, CE and NO Finland, respectively) and for both spatial scales (1,000 and 3,000 m) separately.

### 3. Results

We found no significant effects of mature ( $> 152 \text{ m}^3 \text{ ha}^{-1}$  of timber for SW and CE Finland, and  $> 68 \text{ m}^3 \text{ ha}^{-1}$  of timber for NO Finland) forest cover on the persistence of Capercaillie lekking areas in any of the study areas, regardless of spatial scale (Table 3). Only the variable TIME, i.e., the minimum time interval between the lekking-site surveys, was significantly related to the persistence of lekking

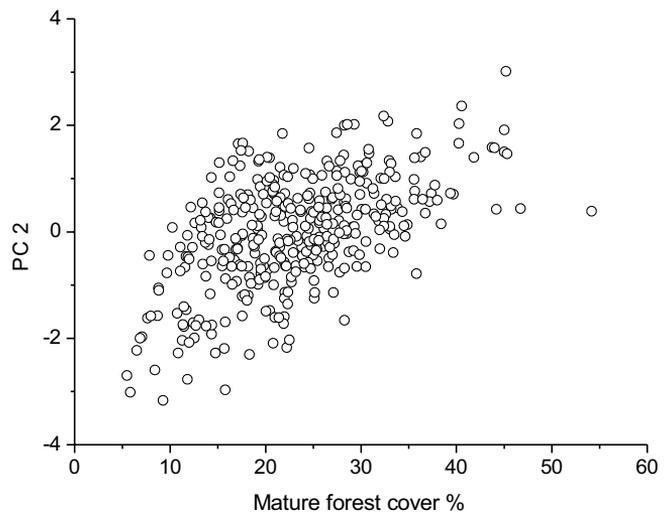


Fig. 1. The relationship between the second principal component (PC 2) and the percentage of mature forest cover ( $> 152 \text{ m}^3 \text{ ha}^{-1}$  of timber for SW and CE Finland, and  $> 68 \text{ m}^3 \text{ ha}^{-1}$  of timber for NO Finland) at 3,000 m spatial scale surrounding the lekking sites ( $N = 381$ ,  $r = 0.55$ ,  $P < 0.0001$ ).

Table 3. Logistic-regression-based likelihoods of the persistence of Capercaillie leks in relation to mature-forest cover for  $r = 1,000$  m and  $r = 3,000$  m ( $N = 55, 238$  and  $88$  for SW, CE and NO Finland, respectively).

Area	Radius (m)	Variable	Estimate	SE	$\chi^2$	$P$	Dev/DF
SW	1,000	Intercept	5.741	2.225	6.66	0.010	1.07
		COVER	-0.027	0.033	0.65	0.420	
		TIME	-0.269	0.107	10.73	0.001	
	3,000	Intercept	2.744	2.239	1.50	0.220	1.06
		COVER	0.058	0.060	1.02	0.313	
		TIME	-0.234	0.098	8.87	0.003	
CE	1,000	Intercept	-43.399	7.095	37.42	<.0001	0.64
		COVER	-0.009	0.022	0.18	0.670	
		TIME	1.529	0.258	60.29	<.0001	
	3,000	Intercept	-43.809	7.103	38.04	<.0001	0.63
		COVER	0.002	0.030	0.00	0.954	
		TIME	1.534	0.257	61.00	<.0001	
NO	1,000	Intercept	-5.962	2.449	5.93	0.015	0.96
		COVER	0.001	0.021	0.00	0.973	
		TIME	0.534	0.176	10.56	0.001	
	3,000	Intercept	-5.981	2.435	6.04	0.014	0.96
		COVER	0.002	0.029	0.00	0.948	
		TIME	0.533	0.176	10.60	0.001	

areas, with a positive relationship in CE and NO Finland, and a negative one in SW Finland (Table 3). We evaluated the goodness-of-fit of the models first by examining at the mean deviance, i.e., the ratio of deviance to its degrees of freedom (approx. 1 in a satisfactory model; Collett 2003). We found that the goodness-of-fit peaked for the models of SW and NO Finland (Table 3). In the model for CE Finland there seemed to be underdispersion, probably at least partly caused by the large proportion of zeros in CE Finland data (82%). Secondly, we calculated the Hosmer-Lemeshow statistics for each model (a measure goodness-of-fit of a model for ungrouped binary data; Collett 2003, Agresti 2007) and found that according to these statistics all the fitted models were satisfactory. Finally, we also tested if modelling all the study areas together ( $N = 381$ ; the proportion of vacated leks was 62%) with study area as a categorical variable would change the results, but did not detect significant effects of mature-forest cover (results not shown; see also Sirkiä *et al.* 2011). When examining descriptive statistics for the surroundings of lekking sites, we found that mature-forest cover was low in all study areas (median between 21–27%; Table 1) and also variation in mean patch size (MPS) was only some tens of pixels (one pixel =  $25 \text{ m} \times 25 \text{ m}$ , i.e.,  $0.0625 \text{ ha}$ ; Table 1). Thus, mature-forest areas

tended to be small and scattered in the studied landscapes.

## 4. Discussion

### 4.1. Effect of mature-forest area

The area of mature forests was not among the major determinants of Capercaillie lekking-site persistence in managed boreal forests in Finland, at least in the three studied landscapes (see also Sirkiä *et al.* 2010a). Our results match those of Miettinen *et al.* (2008), who found that the amount of mature forest was either not significantly associated with Capercaillie density, or the relationship was negative. However, their study was conducted in a grid of  $50 \text{ km} \times 50 \text{ km}$ , which probably affected variation in the amount of mature and other forest stands. Miettinen *et al.* (2005) concluded earlier that mature forests ( $> 100 \text{ m}^3 \text{ ha}^{-1}$ ) were actually more abundant near lekking sites in eastern Finland, compared to “average” landscapes. Their main conclusion, however, was that lek size (number of males) was mostly affected by the area of thinning stands ( $36\text{--}100 \text{ m}^3 \text{ ha}^{-1}$ , age typically 30–90 years).

In managed boreal forests of present-day Fin-

land, the overall forest cover seems to explain Capercaillie presence better than older forest classes (e.g., Miettinen *et al.* 2008, Sirkiä *et al.* 2011). By referring to “overall forest cover” we mean all timber-volume classes from young thinning forest upwards, that is, roughly  $> 60 \text{ m}^3 \text{ ha}^{-1}$  of timber in the southern half of Finland, and  $> 30 \text{ m}^3 \text{ ha}^{-1}$  of timber in the northern half of Finland (age approximately  $> 30\text{--}40$  years). As suggested by Rolstad *et al.* (2007), leks observed in present mature forests might have been established decades ago when these stands were younger, but stands regenerated in the era of modern forestry (starting around 1940s) have until now been too young for Capercaillie. Comparison of the habitat use of Capercaillie in the 1980s and 1990s with that in the beginning of 2000s confirm this kind of change in Capercaillie habitat use during a relatively short period (Miettinen *et al.* 2009). Miettinen *et al.* (2009) concluded that Capercaillie habitats in northern Finland (at 800-m spatial scale) were still rich in mature forest (diameter at 1.3 m height 24–40 cm) in 1989–1992, but not in 2000–2003. Younger forests might not be optimal for Capercaillie, but rather the best available in the modern landscape, because older forest areas have become too small, especially for Capercaillie leks (Mykrä *et al.* 2000, Miettinen *et al.* 2005). For instance, Mykrä *et al.* (2000) concluded that in northeast Finland, only 8% of randomly-located 1,257-ha landscapes included enough mature ( $> 100 \text{ m}^3 \text{ ha}^{-1}$ ) forest for a viable Capercaillie lek (defined as an area of 300 ha). Thus, the overall size of a given forest area might be more important than forest age or tree-species composition, especially when considering the spatial requirements of the lekking sites (Lindén & Pasanen 1987, Helle *et al.* 1994, Sirkiä *et al.* 2011).

Habitat selection of a species is scale-dependent (e.g., Fuhlendorf *et al.* 2002). Therefore, we may not have been able to detect a significant connection between the mature-forest proportion and lekking-site persistence, because our analyses may have operated at spatial scales not relevant to Capercaillie leks. For instance, Virkkala and Rajasärkkä (2006) found that Capercaillie densities in northern Finland were nearly an order of magnitude higher in old-forest areas (size 40–120 km<sup>2</sup>, forest age  $> 100$  years, timber volume 150–195 m<sup>3</sup>ha<sup>-1</sup>) compared to the surrounding managed fo-

rest. Thus, by including an even larger radius than 3,000 m (covering 28 km<sup>2</sup>) our results may have changed. Similarly, it is possible (albeit unlikely) that searching for a relationship between mature forests and lekking-site persistence at a forest-stand scale, a radius of a few hundred meters, would have yielded different results. However, several recent studies suggest a weak or non-existing relationship between mature forests and Capercaillie response (occurrence of a lekking site or density; e.g., Rolstad *et al.* 2007, Miettinen *et al.* 2008, 2010, Sirkiä *et al.* 2010a, 2010b, Wegge & Rolstad 2011). All these papers studied the phenomenon using different spatial (and temporal) scales, some covering areas up to several thousands of square kilometers (e.g., Sirkiä *et al.* 2010b).

There is seemingly something more general behind the weak relationship between mature or old forests and Capercaillie occurrence. Besides the overall size of the forest area, found to be important by Virkkala and Rajasärkkä (2006), one explanation could be connected to the structural variability inside mature-forest stands. Modern-day mature forests may not resemble natural-like old forests, because some important structural characteristics are missing (Miettinen *et al.* 2009, 2010). From the satellite-image-based data it is impossible to account for the amount of horizontal cover, the quality and quantity of food (see also Lakka & Kouki 2009) or other stand characteristics that may be important for the species. Thus, although the growing-stock volume of Finnish forests has continuously increased in Finland since the 1960s (e.g., Peltola 2003), we cannot be certain if the quality of the current mature forest stands corresponds to that needed for the long-term viability of Capercaillie and their lekking sites.

#### 4.2. Effect of time lag between surveys

Capercaillie males spend a large proportion of their year near lekking sites (Wegge & Larsen 1987). The males are also faithful to the same lekking site year after year, and according to a forest-cutting experiment, lek populations are relatively tolerant to disturbances (Rolstad & Wegge 1989c). Moving the lekking centre from a forest patch to another may be regarded as an adaptation

to disturbances, natural or human-caused (Rolstad & Wegge 1989c, Rolstad *et al.* 2007, Valkeajärvi *et al.* 2007). These aspects make it probable that there is a time lag between the diminishing amount of mature forests (caused by logging) and lekking-site extinction (e.g., Wiens & Rotenberry 1985, Ewers & Didham 2006). Indeed, with separate models for the three study areas we found significant effects of the estimated minimum time period between the surveys, both negative (for SW Finland) and positive (for CE and NO Finland).

Although significant, the factor describing time lag contains many uncertainties and must therefore be interpreted with caution. To quantify the precise duration of lekking-site persistence it would have been necessary to survey the leks more frequently, i.e., each year. However, acknowledging constraints in the interpretation of our results, we can still hypothesize that there are major differences between the landscapes of southernmost Finland and those in central and northern Finland. The positive relationship between the time lag and lekking-site persistence in CE and NO Finland might be due to the partial recovery of the landscapes in terms of forest regrowth to the vast areas that had been clear-cut harvested in the 1950s and 1960s (Miettinen *et al.* 2008). In SW Finland, however, human land-use is dominated by settlements and agricultural areas, making these parts of the landscape more or less permanently unavailable for lekking Capercaillie (Lindén & Pasanen 1987, Helle *et al.* 1994, Lindén *et al.* 2000). Thus, the longer the time period between the surveys, the more likely it is to find a lekking site to have become vacated in SW Finland.

### 4.3. Effect of fragmentation?

Technical reasons for us not being able to establish a reliable measure of fragmentation might partially depend on the landscape data used. Firstly, forest estimates derived from satellite images are not accurate at the level of a single pixel (25 m × 25 m in our data; Tokola & Heikkilä 1997), which causes adjacent pixels to be erroneously classified as different habitat. Secondly, the division of pixels according to some threshold (e.g., > 152 m<sup>3</sup>ha<sup>-1</sup> and ≤ 152 m<sup>3</sup>ha<sup>-1</sup>) yields a similar effect: gradients of forest age are artificially defined as separate habi-

tat patches, despite not being perceived as such by Capercaillie (Miettinen *et al.* 2005, Sirkiä *et al.* 2011). Distortion caused by either one or both of these factors leads to an increasing amount of edge along with increasing mean patch size (as with the PC 1 in our analyses; Table 2). Hence, we could not obtain a fragmentation index independent of forest cover as described in Trzcinski *et al.* (1999). This problem suggests that the means whereby habitat quality is quantified should be considered carefully in future studies of habitat cover and fragmentation.

Moreover, if it had been possible to include a whole range of landscapes, i.e., also those with more than 54% of mature (> 68 m<sup>3</sup>ha<sup>-1</sup>) forest cover into the analysis (see NO Finland in Table 1), a more reliable fragmentation index could probably have been calculated (e.g., Sirkiä *et al.* 2011). Cooper and Walters (2002) experienced similar problems in using PC analysis to create a fragmentation index, and concluded that the degree to which fragmentation could be separated from the effects of habitat cover depended on the amount of cover at a particular scale. But also the resolution of landscape data, in relation to grain size perceived by species, should be considered to avoid misinterpretations caused merely by technical or qualitative properties of the data. Thus, the extent of the focal habitat, the grain size of fragmentation in relation to spatial requirements of the focal species, and the resolution of the landscape data probably all influenced our results. It is important to note that we cannot exclude the possibility that the fragmentation of mature forests affects Capercaillie lekking-site persistence, and that there are several other options for measuring fragmentation that are not dealt with here.

### 4.4. Conclusions

Modern forestry has apparently caused major changes both in the small-scale structure of forests (e.g., cover and food provided by the multi-layered forest structure) and in the large-scale availability of forest habitats and their configuration (e.g., Hansson 1992, Mykrä *et al.* 2000, Miettinen *et al.* 2009). How well the Capercaillie really is adapted to younger forests is a question that in our opinion still needs to be resolved, both by taking

into consideration lekking-site viability and by examining life-history stages (see also Sirkiä *et al.* 2010a). In present-day Finland, however, the task is challenging, because the overall amount of mature forest (particularly natural-like mature forest) is so small. Management-wise, the overall forest cover (young thinning forest and older) should be maintained at high level especially within the larger landscape surrounding known lekking sites (e.g., Helle *et al.* 1994, Sirkiä *et al.* 2011). Another priority would be to enhance the structural variability of forest stands within large forested areas (Miettinen *et al.* 2010, Sirkiä *et al.* 2011).

### **Vanhan metsän määrä ei selitä metson soidinalueiden säilymistä nyky-Suomessa**

Metso (*Tetrao urogallus*) on perinteisesti tunnettu vanhasta metsästä riippuvaisena lajina; lajin soidinpaikat sijaitsevat pääosin vanhoissa metsissä. Selvitimme, miten vanhan (kuutiotilavuus > 68 m<sup>3</sup>ha<sup>-1</sup> Pohjois-Suomessa ja > 152 m<sup>3</sup>ha<sup>-1</sup> Varsinais- ja Keski-Suomessa) metsän määrä on yhteydessä metson soidinalueiden säilymiseen Suomessa.

Yhteensä 381 soidinpaikkaa tarkastettiin kahteen otteeseen 10–32 vuoden välein, ja luokiteltiin tarkastusten perusteella säilyneiksi tai hylätyiksi. Vanhan metsän osuus mitattiin satelliittihavaintoihin perustuvaa metsien inventointiaineistoa käyttäen 1 000 ja 3 000 m säteeltä soidinten ympäriltä. Aineisto analysoitiin logistisella regressioanalyysillä. Vanhan metsän määrän ja soidinalueiden säilymisen väliltä ei löytynyt merkitsevää yhteyttä yhdelläkään kolmesta tutkimusalueesta. Vanhan metsän osuus maisemassa oli kuitenkin alhainen, mikä saattoi hankaloittaa yhteyden havaitsemista. Myös muut tekijät, joita ei mitattu (kuten metsän sisärakenne), saattoivat vaikuttaa tuloksiin.

Ainoastaan soidintarkastusten aikavälillä oli merkitsevä yhteys soidinalueiden säilymiseen. Pohjois- ja Keski-Suomessa soidin säilyi sitä todennäköisemmin, mitä kauemmin aikaa tarkastusten välillä oli kulunut. Varsinais-Suomessa puolestaan soidin oli sitä todennäköisemmin hylätty, mitä pidempi tarkastusten aikaväli oli. On mahdollista, että soidinmaisema on metsäisemmällä alueilla Pohjois- ja Keski-Suomessa ennättänyt palautua laajempien avohakkuiden ajoista, kun taas

eteläisimmässä Suomessa maiseman muutokset ovat pysyvämpiä, mm. ihmisasutuksen ja peltoisuuden aiheuttamia.

### **References**

- Agresti, A. 2007: An introduction to categorical data analysis (2<sup>nd</sup> ed.). — John Wiley & Sons, Inc., Hoboken, New Jersey.
- Collett, D. 2003: Modelling binary data (2<sup>nd</sup> ed.). — Chapman & Hall/CRC (Texts in statistical science series).
- Cooper, C.B. & Walters, J.R. 2002: Independent effects of woodland loss and fragmentation in brown treecreeper distribution. — *Biological Conservation* 105: 1–10.
- Ewers, R.M. & Didham, R.K. 2006: Confounding factors in the detection of species responses to habitat fragmentation. — *Biological Review* 81: 117–142.
- Fuhlendorf, S.D., Woodward, A.J.W., Leslie Jr, D.M. & Shackford, J.S. 2002: Multi-scale effects of habitat loss and fragmentation on lesser prairie-chicken populations of the US Southern Great Plains. — *Landscape Ecology* 17: 617–628.
- Hansson, L. 1992: Landscape ecology of boreal forests. — *Trends in Ecology and Evolution* 7: 299–302.
- Helle, P., Helle, T. & Lindén, H. 1994: Capercaillie (*Tetrao urogallus*) lekking sites in fragmented Finnish forest landscape. — *Scandinavian Journal of Forest Research* 9: 386–396.
- Helle, T., Helle, P., Lindén, H. & Kilpelä, S.-S. 1989: Stand characteristics of capercaillie lekking sites in northern Finland. — *Suomen Riista* 35: 26–35. (In Finnish with English summary)
- Lakka, J. & Kouki, J. 2009: Patterns of field layer invertebrates in successional stages of managed boreal forests: Implications for the declining Capercaillie *Tetrao urogallus* L. population. — *Forest Ecology and Management* 257: 600–607.
- Lindén, H., Danilov, P.I., Gromtsev, A.N., Helle, P., Ivantsev, E.V. & Kurhinen, J. 2000: Large-scale forest corridors to connect the taiga fauna to Fennoscandia. — *Wildlife Biology* 6: 179–188.
- Lindén, H. & Pasanen, J. 1987: Capercaillie leks are threatened by forest fragmentation. — *Suomen Riista* 34: 66–76. (In Finnish with English summary)
- Lindén, H. & Rajala, P. 1981: Fluctuations and long-term trends in the relative densities of tetraonid populations in Finland, 1964–77. — *Finnish Game Research* 39: 13–34.
- McGarigal, K. & Marks, B.J. 1995: FRAGSTATS: spatial pattern analysis for quantifying landscape structure. — General Technical Report PNW-GTR-351, Portland.
- Miettinen, J., Helle, P. & Nikula, A. 2005: Lek area characteristics of capercaillie (*Tetrao urogallus*) in eastern Finland as analysed from satellite-based forest inven-

- tory data. — *Scandinavian Journal of Forest Research* 20: 358–369.
- Miettinen, J., Helle, P., Nikula, A. & Niemelä, P. 2008: Large-scale landscape composition and capercaillie (*Tetrao urogallus*) density in Finland. — *Annales Zoologici Fennici* 45: 161–173.
- Miettinen, J., Helle, P., Nikula, A. & Niemelä, P. 2009: Changes in landscape-scale habitat selection of capercaillie (*Tetrao urogallus*) in managed north-boreal forest. — *Silva Fennica* 43: 595–608.
- Miettinen, J., Helle, P., Nikula, A. & Niemelä, P. 2010: Capercaillie (*Tetrao urogallus*) habitat characteristics in north-boreal Finland. — *Silva Fennica* 44: 235–254.
- Mykrä, S., Kurki, S. & Nikula, A. 2000: The spacing of mature forest habitat in relation to species-specific scales in managed boreal forests in NE Finland. — *Annales Zoologici Fennici* 37: 79–91.
- Peltola, A. 2003: Forest Resources. — In *Finnish Statistical Yearbook of Forestry 2003* (ed. Peltola, A.): 31–69. Finnish Forest Research Institute, Helsinki.
- Rolstad, J., Rolstad, E. & Wegge, P. 2007: Capercaillie *Tetrao urogallus* lek formation in young forest. — *Wildlife Biology* 13 (Suppl. 1): 59–67.
- Rolstad, J. & Wegge, P. 1987a: Habitat characteristics of Capercaillie *Tetrao urogallus* display grounds in southeastern Norway. — *Holarctic Ecology* 10: 219–229.
- Rolstad, J. & Wegge, P. 1987b: Distribution and size of capercaillie leks in relation to old forest fragmentation. — *Oecologia* 72: 389–394.
- Rolstad, J. & Wegge, P. 1989a: Effects of logging on capercaillie *Tetrao urogallus* leks. III. Extinction and recolonization on lek populations in relation to clearfelling and fragmentation of old forest. — *Scandinavian Journal of Forest Research* 4: 129–135.
- Rolstad, J. & Wegge, P. 1989b: Capercaillie *Tetrao urogallus* populations and modern forestry – a case for landscape ecological studies. — *Finnish Game Research* 46: 43–52.
- Rolstad, J. & Wegge, P. 1989c: Effects of logging on capercaillie *Tetrao urogallus* leks. II. Cutting experiments in Southeastern Norway. — *Scandinavian Journal of Forest Research* 4: 111–127.
- Schmiegelow, F.K.A., Machtans, C.S. & Hannon, S.J. 1997: Are boreal birds resilient to forest fragmentation? An experimental study of short-term community responses. — *Ecology* 78: 1914–1932.
- Seiskari, P. 1962: On the winter ecology of capercaillie, *Tetrao urogallus*, and the black grouse, *Lyrurus tetrix*, in Finland. — *Papers on Game Research* 22: 1–119.
- Sirkiä, S., Helle, P., Lindén, H., Nikula, A., Norrdahl, K., Suorsa, P. & Valkeajärvi, P. 2011: Persistence of Capercaillie (*Tetrao urogallus*) lekking areas depends on forest cover and fine-grain fragmentation of boreal forest landscapes. — *Ornis Fennica* 88: 15–29.
- Sirkiä, S., Lindén, H., Helle, P., Nikula, A., Knape, J. & Lindén, H. 2010a: Are the declining trends in forest grouse populations due to changes in the forest age structure? A case study of Capercaillie in Finland. — *Biological Conservation* 143: 1540–1548.
- Sirkiä, S., Pellikka, J. & Lindén, H. 2010b: Balancing the needs of capercaillie (*Tetrao urogallus*) and moose (*Alces alces*) in large-scale human land use. — *European Journal of Wildlife Research* 56: 249–260.
- Storch, I. 1993: Patterns and strategies of winter habitat selection in alpine capercaillie. — *Ecography* 16: 351–359.
- Storch, I. 2000: Conservation status and threats to grouse worldwide: an overview. — *Wildlife Biology* 6: 195–204.
- Swenson, J.E. & Angelstam, P. 1993: Habitat separation by sympatric forest grouse in Fennoscandia in relation to boreal forest succession. — *Canadian Journal of Zoology* 71: 1303–1310.
- Tokola, T. & Heikkilä, J. 1997: Improving satellite image based forest inventory by using a priori site quality information. — *Silva Fennica* 31: 67–78.
- Tomppo, E., Katila, M., Moilanen, J., Mäkelä, H. & Peräsaari, J. 1998: Kunnittaiset metsävaratiedot 1990–94. — *Folia Forestalia* 4B: 619–839. (In Finnish)
- Tomppo, E., Olsson, H., Ståhl, G., Nilsson, M., Hagner, O. & Katila, M. 2008: Combining national forest inventory field plots and remote sensing data for forest databases. — *Remote Sensing of Environment* 112: 1982–1999.
- Trzcinski, M.K., Fahrig, L. & Merriam, G. 1999: Independent effects of forest cover and fragmentation on the distribution of forest breeding birds. — *Ecological Applications* 9: 586–593.
- Valkeajärvi, P. & Ijäs, L. 1986: On the display requirements of capercaillie in Central Finland. — *Suomen Riista* 33: 5–18. (In Finnish with English summary)
- Valkeajärvi, P., Ijäs, L. & Lamberg, T. 2007: Capercaillie display grounds move – short and long term observations. — *Suomen Riista* 53: 104–120. (In Finnish with English summary)
- Virkkala, R. 1990: Ecology of the Siberian Tit *Parus cinctus* in relation to habitat quality: effects of forest management. — *Ornis Scandinavica* 21: 139–146.
- Virkkala, R. & Rajasärkkä, A. 2006: Spatial variation of bird species in landscapes dominated by old-growth forests in northern boreal Finland. — *Biodiversity and Conservation* 15: 2143–2162.
- Wegge, P. & Larsen, B.B. 1987: Spacing of adult and subadult male common capercaillie during the breeding season. — *Auk* 104: 481–490.
- Wegge, P. & Rolstad, J. 2011: Clearcutting forestry and Eurasian boreal forest grouse: Long term monitoring of sympatric capercaillie *Tetrao urogallus* and black grouse *T. tetrix* reveals unexpected effects on their population performances. — *Forest Ecology and Management* 261: 1520–1529.
- Wiens, J.A. & Rotenberry, J.T. 1985: Response of breeding passerine birds to rangeland alteration in a North American shrubsteppe locality. — *Journal of Applied Ecology* 22: 655–668.