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Balancing the needs of capercaillie (*Tetrao urogallus*)
and moose (*Alces alces*) in large-scale human land use

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Abstract The capercaillie has been negatively affected by the loss of mature forests. However, forestry creates young plantations offering a superabundant food supply for moose. Using two spatial scales, we tested whether the landscape-level environmental requirements of the capercaillie and moose differ. We compared the spatial association between the abundances of the two species in 50- $\times$ 50-km grids and, using a set of regression models, analyzed how it was affected by various land use variables in five regions of Finland. Both species were generally most abundant in the same grid cells. Moreover, the association between abundance and several landscape variables was very similar for both species. Forest cover had a positive impact on both species in Eastern and South-Western Finland. Only in Western Finland was the capercaillie more positively associated with older forest than the moose. Human impact variables were negatively related to both capercaillie and moose abundance in Eastern and South-Western Finland, the effect being stronger for capercaillie. In Northern Finland, human impact turned positive. Our results highlight that, on broad landscape and regional

scales, we might not need to make trade-offs in management decisions concerning capercaillie and moose. While considering regional land use planning, the primary goal for both species seems to be to secure large areas of forest, preferably at a distance from human settlement.

Keywords Forestry · Game management · Landscape ecology · Macroecology · Wildlife triangle

Introduction

The capercaillie (*Tetrao urogallus*) and moose (*Alces alces*) are fundamentally important elements of the northern boreal forest fauna. The capercaillie is generally considered as a species of the wilderness, avoiding humans (e.g., Helle et al. 1994; Storch 2000b), while the moose exploits cultivations and forest plantations in an opportunistic manner (Haagenrud et al. 1987; however, see Nikula et al. 2004). The importance of young forest classes for moose (Cederlund and Okarma 1988) seems to be in contrast to the preference of mature stands by capercaillie (e.g., Seiskari 1958; Angelstam 2004). Both species have a long history of coexistence with people, as a desired target for hunters and also regarding social, cultural, and spiritual values (e.g., Taavitsainen 1980; Storch 2000a). However, their contrasting population development has created a situation where the moose, although still the most valuable species for hunters, is often regarded as a pest among the general public due to increased traffic collisions and damage to forestry and agriculture (Child and Stuart 1987; Haagenrud et al. 1987; Lavsund 1987), whereas the capercaillie is considered as a focal symbol of healthy forests with potential umbrella species characteristics (Lindén 2002a; Suter et al. 2002; Pakkala et al. 2003).

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In Finland, the winter populations of moose have increased from some hundred individuals in the 1920s to approximately 100,000 individuals in 1980, the most recent estimate being 86,000 individuals (Fig. 1; Nygrén 1987, 1996; Pusenius et al. 2008). The enormous increase in pine plantations, well-designed selective harvesting, and very small populations of large carnivores have been thought to be responsible for the increase (e.g., Nygrén 1987; Cederlund and Okarma 1988). In contrast, the abundant capercaillie populations in the first half of the twentieth century have seriously declined, and in Finland, only 20–60% of the earlier populations are left, depending on the region (Fig. 1; Lindén 2002b). This decrease is usually associated with the effects of forestry and other human land use, leading to habitat loss, forest fragmentation, and habitat deterioration (e.g., Bevanger 1995; Baines and Summers 1997; Storch 2000b; Ludwig et al. 2008).

Habitat suitability models created for both capercaillie and moose suggest that habitat variables may differ in importance according to the spatial scale (Dussault et al. 2005; Graf et al. 2005). Thus, analyses on many spatial scales are required to build a realistic model (e.g., Wiens 1989; Levin 1992). Habitat suitability models for moose combine information on food availability and cover, thus stressing the importance of deciduous trees and young pine plantations at the forest stand and home-range scales but mature (≥ 30 years old) coniferous forests at the landscape level (e.g., Allen et al. 1988; Heikkilä and Härkönen 1993; Dussault et al. 2005, 2006). For capercaillie, the total proportion of forest and bilberry cover have been found to be the most important predictors of species occurrence at home-range and landscape levels (Storch 1993a; Helle et al. 1994; Graf et al. 2005, 2007; Miettinen et al. 2008), but mature (> 50 years old) successional stages are usually preferred at the forest stand scale, especially by older males (e.g., Gjerde and Wegge 1989; Storch 1993b). However, young thinning forests (typically 30–55 years old) have more recently been found to be positively associated with

capercaillie density throughout Finland (Miettinen et al. 2008), and capercaillie males have formed new lekking sites in young (26–46 years old) forests both in Norway and in Finland (Rolstad et al. 2007; Valkeajärvi et al. 2007).

When broadening the scope from habitat and landscape levels (i.e., a mosaic of habitats, sensu Forman and Godron 1986) to a large-scale environment (i.e., mosaic of landscapes), different biological variables may become important. Macroecology aims to reveal the general mechanisms behind broadly occurring patterns and processes on organism, population, and ecosystem levels (Smith et al. 2008). From a species conservation perspective, it is especially important to examine the contribution of human activities to these patterns (Gaston 2004), such as how human influence is shaping the abundance and distribution of species and species richness (Pautasso 2007; Smith et al. 2008). In many cases, macroecological studies can provide tools for better informed land use planning and management decisions, not only considering spatial scale information (e.g., Whittingham et al. 2007; Fortin et al. 2008) but also temporal scales (e.g., Webb et al. 2007).

The suggested polarity in the habitat use of capercaillie and moose has led us to test whether these two species also differ in their responses towards large-scale human land use and forestry activities. In other words, we have sought to determine whether trade-offs are necessary in decisions concerning large-scale land use planning and the management of these two species (trade-off hypothesis). In this paper, we assess whether (and how) differences between the responses of the species exist on two spatial scales: in 50- $\times$ 50-km grids and in five regions that cover the whole of Finland.

Materials and methods

Species abundance data and spatial scales

The abundance of capercaillie and moose (Table 1) was examined using data from the wildlife triangle scheme (see Lindén et al. 1996). The wildlife triangle network consists of 1,650 triangles, from which 800–900 are counted twice a year, in winter (January–March) and in late summer, (August) mainly by volunteer hunters. The network covers Finland in a regionally representative way. These census routes are equilateral triangles with 4-km sides, thus forming a route of 12 km. Moose abundance is estimated in winter by counting snow tracks crossing the census line (tracks/10 km/day), whereas capercaillie abundance is based on grouse counts during August, using the same triangles (individuals per square kilometer of forest land). All grouse species are counted in a 60-m-wide census belt using a three-person chain (Rajala 1974).

Fig. 1 The abundance estimates of capercaillie and moose, attained from wildlife triangle data, from 1964 to 2008

Table 1 Variation in the variables used in modeling

	South-Western Finland (n=23)		South-Eastern Finland (n=14)		Western Finland (n=19)		Eastern Finland (n=24)		Northern Finland (n=49)	
	Range	Mean (SD)	Range	Mean (SD)	Range	Mean (SD)	Range	Mean (SD)	Range	Mean (SD)
t1.1										
t1.2										
t1.3										
t1.4	Caper	0.4–3.0	1.7 (0.7)	2.4 (0.6)	1.6–4.1	3.0 (0.7)	1.2–3.6	2.5 (0.6)	0.4–4.0	2.0 (0.7)
t1.5	Moose	2.0–11.3	6.5 (2.4)	5.0 (2.7)	1.5–12.9	5.7 (2.6)	0.6–10.8	4.3 (2.3)	0.1–10.3	2.6 (1.9)
t1.6	AVE	54.2–61.7	57.9 (1.7)	53.3 (2.0)	48.5–62.9	57.1 (3.6)	46.7–65.7	54.8 (4.0)	60.4–111.5	75.5 (13.7)
t1.7	<40	17.0–28.0	21.4 (3.0)	25.6 (2.0)	19.0–36.0	26.8 (4.8)	23.0–36.0	29.3 (3.7)	0.0–33.0	17.1 (6.9)
t1.8	<60	30.0–46.0	37.0 (3.9)	33.4 (3.7)	33.0–50.0	39.6 (4.4)	28.0–42.0	37.1 (4.0)	11.0–51.0	41.8 (6.2)
t1.9	SCA	7,309–25,321	15,108.7 (5,002.2)	9,152.8 (2,989.7)	5,539–18,093	11,193.4 (3,717.2)	1,803–14,673	7,369.8 (3,328.1)	2–10,734	2,372.6 (2,056.2)
t1.10	SET	11,225–879,315	111,569.7 (182,154.1)	36,151.1 (34,383.0)	8,451–128,338	31,980.1 (28,751.9)	4,968–99,294	22,307.8 (22,819.6)	2–143,177	8,815.7 (21,595.2)
t1.11	Fields	7.0–47.0	21.3 (10.5)	11.4 (6.6)	4.0–33.0	15.4 (8.3)	2.0–17.0	7.4 (3.7)	0.0–21.0	2.4 (3.9)
t1.12	TPF	48.0–69.0	58.7 (5.8)	59.6 (4.8)	56.0–77.0	66.9 (4.9)	50.0–77.0	67.3 (5.7)	11.0–73.0	58.9 (11.1)
t1.13	UFA	0.0–0.2	0.06 (0.05)	0.02 (0.02)	0.01–0.2	0.1 (0.06)	0.0–0.3	0.07 (0.07)	0.2–7.5	0.7 (1.1)
t1.14	Water	0.0–31.0	9.4 (8.1)	21.1 (9.8)	0.0–22.0	5.5 (5.9)	4.0–36.0	16.3 (9.3)	0.0–31.0	6.2 (5.9)

Caper capercaillie abundance among grid cells averaged over the years 1989–1996, Moose moose abundance among grid cells averaged over the years 1989–1997, AVE average age of the forest (estimated years), <40 proportion of forests under 40 years old (percent of grid cell area), >60 proportion of forests over 60 years old (percent of grid cell area), SCA scattered settlement (number of people), SET total settlement (number of people), Fields proportion of fields (% of grid cell area), TPF total proportion of forest land (percent of grid cell area), UFA unproductive forest area (percent of TPF in the grid cells), Water proportion of water bodies (percent of grid cell area)

Fig. 2 The wildlife triangle network in Finland, including the grid cell (50×50 km) system used in the analyses and the five regions: South-Western (SW; n=23), South-Eastern (SE; n=14), Western (W; n=19), Eastern (E; n=24) and Northern (N; n=51) Finland. Two grid cells in Northern Finland were excluded from the statistical analyses (total n=129) and one from correlation calculations (total n=130)

162	individual habitat selection, although some of the large-scale	the number of people living outside of population centers	213
163	phenomena we describe may be a result of processes	according to the community planning follow-up system of	214
164	operating at smaller scales (e.g., individual or local landscape	Finland's environmental administration in 1990.	215
165	scale; Johnson 1980).		
166	Second, we needed a scale that could offer a represen-	Statistical analyses	216
167	tative sample of observations (here, wildlife triangles).		
168	During the study period (1989–1996), there were on	First, we characterized the relationship between the abun-	217
169	average 51 wildlife triangle counts (range, 3–210, SD=	dance of capercaillie and moose by calculating correlation	218
170	28.8) in every grid cell; thus, more than 600 km per grid	coefficients separately for 130 grid cells throughout Finland.	219
171	cell was covered during that time, and almost 79,000 km	One grid cell had to be excluded from the calculations because	220
172	nationwide. The abundances within the grid cells are	of the lack of data. The correlations were calculated using the	221
173	therefore likely to be representative. Moreover, seasonal	species-specific average abundances in wildlife triangles over	222
174	movements of moose extend over areas within a maximum	the years 1989–2007 in order to emphasize the role of spatial	223
175	radius of about 30–40 km in Finland (Heikkinen 2000).	variation and minimize the roles of random variation and	224
176	Finally, we aimed to incorporate the assumed regional	temporal trends in our analyses. We used Spearman's rank	225
177	differences in Finland regarding the moose–capercaillie	correlation because the assumption of normality may not hold.	226
178	trade-off in linear regression models. Thus, as the second	The pattern of correlations does not consist of independent	227
179	spatial scale, we selected five study regions in Finland (Fig. 2;	values because of the spatial autocorrelation between grid	228
180	see details in “Statistical analyses”). South-Western Finland	cells. However, we present this correlative surface map as	229
181	is under the heaviest human impact, with large areas being	indicative evidence of the spatial contexts defining the	230
182	reserved for cultivated fields (mean=21% of the grid cell	relationships between the two species (Fig. 3).	231
183	area) and human settlement. In the eastern areas (Eastern	Secondly, in order to examine the differences in require-	232
184	and South-Eastern Finland), the area under cultivation is the	ments between capercaillie and moose, we continued our	233
185	smallest (7–11%) compared to other parts of the country,	analyses with a set of linear regression models using the	234
186	whereas the total area of water bodies is dramatically larger	compositional aspects of land use and the structural aspects	235
187	in the east compared to the west (Table 1). Northern Finland	of forestry as explanatory variables. This approach was	236
188	is probably the most distinctive region, with the lowest	based on elaboration, a technique that is widely used to	237
189	overall productivity, the oldest average age of the forest, and	analyze multivariate data in social sciences (Babbie 1987).	238
190	the lowest degree of human impact (see Table 1).	Elaboration has been applied in ecology by Penttilä et al.	239
191	Land use data	(2006), Pellikka et al. (2007) and recently by Kukkonen et	240
192	The land use data were compiled from multiple sources.	al. (2008). The main idea of these analyses was to explore	241
193	Forest variables were derived from the Finnish Forest	in which contexts and how strongly the assumed difference	242
194	Research Institute's 8th National Forest Survey 1986–1994	between species abundances was supported by the data, i.e.,	243
195	(Tomppo et al. 1998). The proportions of predominant tree	which aspects suppress or mask and which seem to promote	244
196	species and the age and development classes were	the contrast (if any). Following this idea, we analyzed how	245
197	calculated for each municipality and subsequently as	the association between the abundance of capercaillie and	246
198	averages for each 50×50-km grid cell using the relative	moose, represented by a regression slope, changed when	247
199	proportions of the municipalities as weights. The total	variables were included alone or as combinations in the	248
200	proportion of forest land (TPF) included all the forest with	regression model. The former enabled us to generally	249
201	an average growth of $\geq 1 \text{ m}^3 \text{ ha}^{-1} \text{ year}^{-1}$ (Table 1). Unpro-	examine the effects of independent and dependent varia-	250
202	ductive forest area included idle land and other forest areas	bles, whereas the latter reduced the role of indirect effects	251
203	with an average growth $< 1 \text{ m}^3 \text{ ha}^{-1} \text{ year}^{-1}$ and was	associated with the other included independent variables.	252
204	calculated as a proportion of TPF. The proportions of forest	In the analyses, the dependent variable was capercaillie	253
205	under 40 years and over 60 years, as well as the average	abundance averaged over the years 1989–1996 to tempo-	254
206	age of forest, were all calculated from the separate age	rally correspond as closely as possible with our land use	255
207	classes. The percentage cover of agricultural fields and	data. Moose abundance was included as the first explana-	256
208	water bodies, the amount of settlement (number of people),	tory variable in the model, and it was retained in the model	257
209	and the total length of roads were derived from digital maps	throughout the modeling procedure (see Table 2). We also	258
210	(sources: National Land Survey of Finland, Finnish Road	performed the same modeling, with moose abundance as the	259
211	Administration, and Finland's environmental administra-	dependent variable, but the interpretation of the results	260
212	tion). The amount of scattered settlement was calculated as	remained the same. Where the absolute value of the regression	261
		slope (describing the relationship between capercaillie and	262
		moose abundance) drastically decreases to near zero follow-	263

Fig. 3 A correlative surface map illustrating the relationship between the abundances of capercaillie and moose, averaged over the years 1989–2007. The values are Spearman’s rank correlation coefficients calculated for every 50-×50-km grid cell. Significant ($P\leq0.05$) correlations are marked with a *bold rim*

ing the inclusion of a variable, this may, regardless of the change in P values, indicate that the variable in question is connected with the difference in species abundances. Conversely, an increase in the absolute value of the slope may reveal variables possibly masking the contrast.

We then included those explanatory variables in the model that, according to the literature, should reveal a difference between the species abundances (Table 1). Both capercaillie and moose use forest as their primary habitat. However, the capercaillie has long been thought to be an old forest specialist (e.g., Rolstad and Wegge 1987a) or at least the species seems to prefer older forest classes whenever they are sufficiently abundant in the landscape (Angelstam 2004), while the moose favors young forests

Table 2 The modeling steps for the dependent variable “capercaillie abundance”

Step	Model	Condition
1	MOOSE	
2	MOOSE+AR stepwise selection	MOOSE forced into the model
3	MOOSE+AR+HI stepwise selection	MOOSE forced into the model
4	MOOSE+AR+HI+TPF+UFA stepwise selection	MOOSE forced into the model

The criterion for inclusion and exclusion of variables by stepwise selection was always $P=0.05$

MOOSE moose abundance, *AR* age-related variables (i.e., average age of the forest, proportion of forest under 40 years old, proportion of forest over 60 years old), *HI* human impact variables (i.e., the scattered and total settlement in 1990), *TPF* total proportion of forest land, *UFA* unproductive forest area

(Cederlund and Okarma 1988). Thus, we first included the factor AR (age-related variables) into the model, i.e., we performed a stepwise selection among the following variables: (1a) the average age of the forest (AVE), (1b) the proportion of forest under 40 years old (<40), and (1c) the proportion of forest over 60 years old (>60). In Norway, capercaillie habitat was classified as old forest when forests were aged 50 years and older (Gjerde and Wegge 1989). Lekking grounds were mainly found in forest patches older than 60–70 years (e.g., Rolstad and Wegge 1987a).

Secondly, we included the factor HI (human impact variables) in the model, i.e., the following variables were included in the stepwise selection: (2a) the number of people in scattered settlements in 1990 (SCA) and (2b) the total number of people in settlements in 1990 (SET). Here, we did not want to make any presuppositions about the order of factors AR and HI. Therefore, we tested whether our statistical reasoning was sensitive to the order of inclusion of AR and HI variables. We found that the variables were redundant with respect to the order of inclusion.

Finally, we included (3a) the TPF and (3b) unproductive forest area in the model using stepwise selection. This was because not only *forested areas* but also *the unproductive forest* may play an important role in determining the species abundances. A priori, these two variables should be considered as the least powerful ones explaining the proposed differences in the species responses because both capercaillie and moose are forest animals and probably benefit from high fertility, especially in the northern parts of the country (Pellikka et al. 2006). Thus, we included both the age-related forest variables and the human impact factor and examined whether the remaining variation could be explained by the more general forest landscape and soil fertility effects. The criterion of inclusion and exclusion of variables was always kept at $p=0.05$.

313 We conducted the analyses for five separate regions (Fig. 2;
 314 see also Pellikka et al. 2006), i.e., South-Western ($n=23$),
 315 South-Eastern ($n=14$), Western ($n=19$), Eastern ($n=24$), and
 316 Northern Finland ($n=49$), in order to take regional character-
 317 istics in the landscape into account. We excluded two zero
 318 moose abundance cells in Northern Finland from the
 319 statistical analyses. In all cases, the residuals of the models
 320 were normally distributed. Statistical analysis was performed
 321 with SPSS 15 and SAS 8.2 statistical packages.

322 Results

323 Correlation between abundances

324 When capercaillie and moose abundances were correlated,
 325 only 20 cells out of 130 had a Spearman correlation
 326 coefficient below -0.25 . The grid cells with a negative
 327 correlation showed no clear spatial pattern, as these cells
 328 were relatively evenly distributed throughout Finland. Only
 329 two cells close to the eastern border had significant ($P \leq$
 330 0.05) negative correlations between the abundances. In
 331 most of Finland (62% of the grid cells), the correlation
 332 coefficient was positive. Thus, there was a general tendency
 333 that both species reached their highest abundance in the
 334 same grid cells. Particularly in southern Finland, the cells
 335 with a strong positive correlation formed spatial clusters,
 336 indicating a phenomenon that is probably explained by
 337 factors operating on scales larger than our smallest unit of
 338 analysis (i.e., 50×50 km; Fig. 3).

339 In the regionally separated regression analyses, the slope
 340 describing the relationship between capercaillie and moose
 341 had a positive association in Northern as well as South-
 342 Eastern Finland (Appendix 1). In other regions, no clear
 343 pattern between the species abundances was observed.

344 Effect of age-related variables

345 In Western Finland, the average age of the forest had a
 346 positive impact on capercaillie abundance (significant at the
 347 level $P \leq 0.05$ assuming grid units to be independent
 348 samples). The effect was consistent during the whole
 349 modeling procedure, i.e., it was found when testing the
 350 variable independently ($B=0.123$, $t=3.19$, $P=0.005$) and
 351 during modeling steps 2–4 (see Appendix 1). The inclusion
 352 of age-related variables pushed the effect size between
 353 capercaillie and moose to virtually zero (Fig. 4).

354 In Eastern and South-Western Finland, the proportion of
 355 forest under 40 years old was included in the model at step
 356 2 with a positive association with capercaillie abundance. In
 357 Eastern Finland, the proportion of forest over 60 years old
 358 was also positively related to capercaillie abundance at
 359 step 2. However, in these regions, all the age-related

Fig. 4 The relationship between moose and capercaillie abundance at different modeling steps (see Tables 1 and 2 for total variable list and variable codes and Table 2 for modeling steps). The effect size is the coefficient of regression of moose abundance on capercaillie abundance (significant with $P \leq 0.05$ in Northern and South-Eastern Finland; for detailed numerical values, see Appendix 1). A decrease in the absolute value of the regression slope to near zero in conjunction with the inclusion of a variable indicates that, regardless of the change in P values, the variable in question is connected with the difference in species abundances. Conversely, an increase in the absolute value of the slope may reveal variables possibly masking the contrast. Models are regional linear regressions with stepwise selection of independent variables. The criterion of inclusion and exclusion of variables was always $P=0.05$

360	variables were dropped from the models in further	Effects of forest and unproductive forest cover	411
361	modeling steps. The interaction with the TPF appeared to		
362	be the main reason for these effects, and they were masked	The TPF had a positive effect on capercaillie abundance in	412
363	by the explanatory power of this variable. There was a	Eastern and South-Western Finland (Appendix 1). In both	413
364	significant positive correlation between the TPF and forest	regions, the effect size of moose abundance increased when	414
365	under 40 years old in both Eastern (Pearson $r=0.684$, $P<$	including the TPF in the model. In South-Western Finland,	415
366	0.0001) and South-Western Finland ($r=0.832$, $P<0.0001$)	the effect size again turned positive (Fig. 4).	416
367	and between the TPF and forest over 60 years (E Fin, $r=$	The effect of unproductive forest area was frequently	417
368	0.667 , $P=0.0001$; SW Fin, $r=0.839$, $P<0.0001$). In both	masked by other variables, namely, the TPF and age-related	418
369	Eastern and South-Western Finland, with the inclusion of	variables. There were strong correlations among all these	419
370	age-related variables, the effect size between capercaillie	variables, for example, among the unproductive forest area	420
371	and moose abundances increased (Fig. 4).	and the average age of the forest (Pearson r varied between	421
372	Age-related variables also had strong correlations with other	0.381 and 0.714 , and P values varied between 0.001 and	422
373	model variables in Northern Finland, where there was a strong	0.0646 in all other areas except South-Eastern Finland).	423
374	negative correlation between the average age of the forest and	Hence, for most regions, the variable was not included in the	424
375	the proportion of scattered settlement (Pearson $r=-0.621$,	models at all. When tested independently, the unproductive	425
376	$P<0.0001$). Although none of the age-related variables were	forest area had a positive impact on capercaillie abundance in	426
377	included in the models in Northern Finland, the average age	Eastern Finland ($B=3.697$, $t=2.35$, $P=0.028$) and a negative	427
378	of the forest had a negative impact on capercaillie abundance	trend in South-Eastern Finland ($B=-14.051$, $t=-1.87$, $P=$	428
379	when tested independently ($B=-0.018$, $t=-2.45$, $P=0.018$).	0.086). However, in South-Eastern Finland, the variable was	429
380	Effect of human impact variables	negatively associated with capercaillie abundance at step 4,	430
		after controlling for the effects of other variable groups.	431
381	The human impact (HI) variables were selected from a	When including the unproductive forest area in the model,	432
382	group of correlative variables that included the proportion	the effect size of moose abundance slightly increased in	433
383	of fields and the total length of roads [Pearson r varied	South-Eastern Finland (see Appendix 1), suggesting that the	434
384	between 0.425 and 0.920 , and the P values between 0.0001	negative relationship between unproductive forest area and	435
385	and 0.130 in all cases except the comparison of total	species abundance is similar for capercaillie and moose.	436
386	settlement (SET) versus fields]. There was a positive	To summarize, the relationship between capercaillie and	437
387	association between scattered settlement and capercaillie	moose abundance, i.e., the effect size in Fig. 4, remained	438
388	abundance in Northern Finland (see Appendix 1). The	mainly positive, irrespective of the region or model step.	439
389	amount of scattered settlement had more explanatory power	The downward swing in the effect size curve (Fig. 4), i.e.,	440
390	than correlated age-related variables, namely, the average	support for the trade-off hypothesis, was in three out of five	441
391	age of the forest (see above). With the inclusion of human	regions connected with the effect of human impact	442
392	impact variables in the regression model, the effect size of	variables and in one case connected with forest age.	443
393	moose abundance was reduced but remained significantly		
394	positive (Fig. 4).	Discussion	444
395	The effect of scattered settlement turned negative in		
396	Eastern and South-Western Finland when the variable	The relationship between the abundances of capercaillie and	445
397	was tested independently (E Fin, $B=-0.000$, $t=-2.28$,	moose was not significantly negative in any of the five regions.	446
398	$P=0.033$; SW Fin, $B=-0.000$, $t=-2.10$, $P=0.048$). How-	This provides indicative evidence against the trade-off	447
399	ever, during the modeling steps, the variable was not	hypothesis. Unexpectedly, in two of the regions, a significant	448
400	included in the models, but it was masked by the amount of	positive relationship was detected, indicating that the require-	449
401	total (scattered and non-scattered) settlement. The amount of	ments or conditions that determine the large-scale abundance	450
402	total settlement had a negative effect on capercaillie	of these two species are shared more than they are divergent.	451
403	abundance in Eastern and South-Western Finland at step 3		
404	(see Appendix 1). In both Eastern and South-Western	Effect of age-related variables	452
405	Finland, the relationship between moose and capercaillie		
406	abundance was reduced with the inclusion of total settlement	In Western Finland, the trade-off hypothesis was partially	453
407	in the regression model (Fig. 4). In Eastern Finland, the	supported in the sense that capercaillie abundance seems to	454
408	effect size decreased close to that at step 1 but remained	be more positively associated with older forest than moose	455
409	positive. In contrast, in South-Western Finland the effect size	abundance. Traditionally, the capercaillie has been thought	456
410	turned negative.	to be dependent on older forest stages (e.g., Rolstad and	457
		Wegge 1987a; Helle et al. 1989). Some more recent studies	458

459 similarly indicate that capercaillie seem to prefer older forest
 460 whenever it is sufficiently available in the landscape (Helle et
 461 al. 1994; Sjöberg 1996; Angelstam 2004). On the contrary,
 462 younger forest age classes and plantations are considered as
 463 a continuous food supply for moose (Cederlund and
 464 Markgren 1987), and clear cuts and young pine stands are
 465 often particularly highly used (Cederlund and Okarma 1988).

466 The average age of the forest was negatively associated
 467 with capercaillie abundance in Northern Finland. This result is
 468 consistent with other recent studies, suggesting that young and
 469 middle-aged forest classes are common in the vicinity of high
 470 capercaillie abundances in Northern Finland (Miettinen et al.
 471 2005). The capercaillie is also capable of forming new
 472 lekking sites in young forests (26–46 years old, Rolstad et al.
 473 2007; Valkeajärvi et al. 2007). This is somewhat surprising
 474 when considering the traditional viewpoint that lists the
 475 capercaillie as an “old forest specialist” (e.g., Rolstad and
 476 Wegge 1987a). One explanation can be found in the
 477 extensive forest management practices (e.g., clear cuttings
 478 and forest regeneration by plantations) introduced after
 479 World War II and started in Northern Finland (Lindén et al.
 480 2000). The total area of clear-cuts and plantations of different
 481 ages has grown enormously, nowadays comprising most of
 482 the forested area. Hence, forest age might no longer act as a
 483 factor distinguishing different quality capercaillie landscapes
 484 in Finland, especially in the north (see also Miettinen et al.
 485 2008). However, it is important to note that Northern Finland
 486 is the largest region of all those considered here and thus
 487 contains the greatest variability. The large spatial scale in our
 488 study may mask some connections between capercaillie
 489 abundance and smaller scale habitat selection.

490 Effect of human impact variables

491 The main reason for the positive association between
 492 scattered settlement and the abundance of both species in
 493 Northern Finland might be connected to overall soil
 494 fertility: Human settlements are generally situated on more
 495 fertile grounds (see also Pautasso 2007). Studies conducted
 496 in northern Alberta and Alaska (Schneider and Wasel 2000;
 497 Maier et al. 2005) reported higher moose densities close to
 498 towns due to high-quality food in the surroundings of towns,
 499 habituation to people as well as avoidance of predators (i.e.,
 500 wolves and bears, which do not tolerate humans; see also
 501 Stephens and Peterson 1984). In Northern Finland, moose
 502 predation by large carnivores is largely hindered by man.
 503 Wolves, in particular, are usually shot whenever dispersing
 504 into the reindeer husbandry regions in North Finland (Kojola
 505 et al. 2006), and the same practice has been reported in
 506 Sweden and Norway (Wabakken et al. 2001). For capercail-
 507 lie, predator avoidance is probably not the cause of the positive
 508 human impact because small and middle-sized carnivores
 509 usually reach higher densities close to fields and scattered

settlements (Kurki et al. 1997). Some of the settlements in the
 north have followed the locations of good hunting grounds,
 which may also explain the positive relationship between
 scattered settlement and capercaillie abundance.

The human impact on both of the species turned negative in
 Southern Finland (Lindén et al. 2000; Lindén 2002a; Miettinen
 et al. 2008), showing how important it is to account for
 geographical gradients in the analyses (Fortin et al. 2008). In
 South-Western Finland the trade-off hypothesis was sup-
 ported when first controlling for forest age and then including
 the effect of total settlement in the model (the negative effect
 size in Fig. 4). It therefore seems that the capercaillie is, to
 some extent, more affected by the negative aspects of human
 settlement than the moose. It has been suggested that winter
 home ranges of moose may have a more distant location from
 man-made landscapes compared to summer ranges (Nikula et
 al. 2004). Although roads and moose fences make the
 approach toward cities difficult for ungulates in Scandinavia
 (Nellemann et al. 2001), fences may also increase moose
 densities near roads (Ball and Dahlgren 2002). The caper-
 caillie, on the other hand, is among the grouse species that
 clearly avoid areas with a heavy human impact (e.g., Helle et
 al. 1994; Kurki et al. 2000; Storch 2000b, 2007).

Effect of forest cover

The TPF had a positive impact on capercaillie abundance in
 Eastern and South-Western Finland. In South-Western
 Finland, in particular, intensive agriculture and other human
 land use negatively affects capercaillie. It has been
 reported, for example, that in Southern Finland, the amount
 of forest is an important variable in predicting the
 occurrence of capercaillie lekking sites compared to the
 average landscape (Lindén and Pasanen 1987; Helle et al.
 1994). The positive effect of total forest land is important
 for the lekking sites up to 1.5 km distance from the lekking
 center (Lindén and Pasanen 1987; Helle et al. 1994).
 Because the minimum size for a lekking area is 300 ha
 (Wegge and Larsen 1987), capercaillie males seem to have
 difficulties in forming lekking sites in Southern Finland,
 probably due to forest loss and fragmentation. In this study,
 the need for vast forested areas for capercaillie in South-
 Western Finland was clear, even after controlling for forest
 age and human impact. Several other studies have also
 reported negative effects of forest loss on capercaillie on
 different scales (e.g., Rolstad and Wegge 1987b; Kurki et
 al. 2000; Storch 2000b; Mikusiński and Angelstam 2004).

Overall forest cover was positively related to the
 abundance of both capercaillie and moose, as expected.
 Indeed, on the European scale, the moose is also negatively
 affected by forest loss (Mikusiński and Angelstam 2004).
 Some studies have suggested that not only forest cover but
 also soil fertility plays an important role in determining moose

abundance. In winter, moose habitat and home ranges include significantly more pine-dominated forest on peatland or shrub land (Heikkilä and Härkönen 1993; Nikula et al. 2004; Cassing et al. 2006). In Finland, the moose is generally more controlled by hunting than the capercaillie. The management of moose aims at a population level that is widely accepted by agriculture, forestry, and road traffic (Haagenrud et al. 1987; Nygrén and Pesonen 1993). In this sense, moose abundance in Finland is first and foremost regulated by humans (Lehtonen 1998). However, to have an effect on our results, the capacity of hunting to regulate abundances should be correlated with our land use variables. In other words, hunting should be more efficient in grid cells with a large proportion of certain land use class(es). According to our knowledge, no clear evidence of such a correlation exists (other than the fact that more animals are hunted in areas with higher population levels). In addition, the use of long-term average abundance values reduces the potential hunting effects in our models. Furthermore, the abundance estimates for moose were collected in winter, while the hunting season is in autumn. Thus, even if moose abundance is lowered to an acceptable level by hunting each autumn, the remaining wintering population may be assumed to seek out and settle in areas with desirable land use characteristics. Nonetheless, it would be of interest to include the effect of hunting in future studies. Regarding the capercaillie, not even the relatively high shooting yields seem to be correlated with grouse population trends in Finland (Lindén 1991).

Conclusion

To address regional problems in game management, it is important to study large-scale landscape characteristics (for example see Angelstam et al. 2004; Mikusiński and Angelstam 2004). Landscape patterns on large spatial scales may be informative in predicting phenomena on smaller scales (Gaston 2004; Cassing et al. 2006). However, we cannot simply assume that the patterns and processes at the landscape level or on broader scales are only reflections of habitat-level phenomena (see also Whittingham et al. 2007). Therefore, it is especially important to incorporate several spatial and temporal scales when examining the relationship between species and their environment (Wiens 1989; Levin 1992). Overall, regional game management should be based on data covering both large areas and multiple species requirements.

We observed a general trend that rejects the trade-off hypothesis: The capercaillie and moose do not appear to have dissimilar responses to large-scale land use, despite their divergent habitat requirements. We can reject the hypothesis based on the twofold evidence. First, the correlation between the abundance of capercaillie and moose was mainly positive, indicating that the species are abundant

in the same broad areas. Second, further support was given by the regression models, which provided no clear evidence of any examined factor revealing a difference between the species on large spatial scales. Instead, the species responses to landscape variables were in general very similar.

We acknowledge that our explanatory variables, and the scales that we chose, were somewhat coarse. For moose, for example, earlier studies have found evidence of responses on multiple scales, including scales below the level of the habitat patch (Bowyer and Kie 2006). However, we did not intend to create another habitat suitability or habitat use model for these species because this has already been done in several papers (e.g., Allen et al. 1988; Gjerde and Wegge 1989; Dussault et al. 2006; Graf et al. 2005). Many of the studies concerning moose habitat choice have operated either within home ranges or on the landscape level (e.g., Nikula et al. 2004; Dussault et al. 2005; Cassing et al. 2006), and broad landscape-level variables are usually strong predictors of capercaillie occurrence (e.g., Mikusiński and Angelstam 2004; Graf et al. 2007; Miettinen et al. 2008). Our selection of large spatial scales also appeared appropriate in the light of the results obtained in the sense that the grid cells with a strong positive correlation formed spatial clusters (Fig. 3). In addition, the extent of the study scale (2,500 km² per grid cell) and our use of long-term average abundance values gives reason to believe that the seasonal differences in species abundances (capercaillie data collected in summer and moose data in winter) are not an important source of error in our analyses. Nonetheless, we stress that our study provides only a preliminary and general overview of the responses of these species to large-scale land use.

It is clear that the existing differences between the species are due to mechanisms mostly operating on finer scales than the ones studied here. On a more local scale, such as the home range and/or a forest stand, the species probably occupy different habitats. This may be one reason for the observed contrasting population trends of capercaillie and moose (Fig. 1). However, it seems to be too strong to argue that capercaillie and moose have completely opposite environmental requirements. While considering regional land use planning, the primary goal for both species seems to be to secure large enough areas of forest, preferably at a distance from human settlement (e.g., Storch 2000b; Mikusiński and Angelstam 2004).

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Integrity of research and reporting All research presented complies with the current laws of the country. The authors declare that they have no conflicts of interest.

Appendix 1

Table 3 Effect size estimates (B) for the model parameters, test values (t/F), and significance values (P) for regional linear regressions

	South-Western Finland ($n=23$)				Eastern Finland ($n=24$)				South-Eastern Finland ($n=14$)				Western Finland ($n=19$)				Northern Finland ($n=49$)			
	Model step				Model step				Model step				Model step				Model step			
	1	2	3	4	1	2	3	4	1	2	3	4	1	2	3	4	1	2	3	4
t3.1																				
t3.2																				
t3.3																				
t3.4																				
t3.5	B M	0.024	0.050	-0.050	0.032	0.031	0.061	0.034	0.061											
t3.6	t/F M	0.38	0.82	0.72	0.41	0.59	1.97	0.66	2.14											
t3.7	OP M	0.708	0.376	0.407	0.529	0.562	0.176	0.425	0.158											
t3.8	$B <40$		0.133				0.077													
t3.9	$F <40$		9.27				7.83													
t3.10	$P <40$		0.006				0.011													
t3.11	$B >60$						0.072													
t3.12	$F >60$						8.33													
t3.13	$P >60$						0.009													
t3.14	B SET			-0.000				-0.000												
t3.15	F SET			9.57				14.18												
t3.16	P SET			0.006				0.001												
t3.17	B TPF				0.077				0.069											
t3.18	F TPF				14.16				16.08											
t3.19	P TPF				0.001				0.001											
t3.20	B M									0.127	0.127	0.127	0.131	0.033	0.002	0.002	0.172	0.172	0.124	0.124
t3.21	t/F M									2.57	6.58	6.58	10.36	0.5	0	0	3.49	12.17	5.54	5.54
t3.22	P M									0.025	0.025	0.025	0.008	0.622	0.968	0.968	0.001	0.001	0.023	0.023
t3.23	B AVE																			
t3.24	F AVE																			
t3.25	P AVE																			
t3.26	B SCA																			
t3.27	F SCA																			
t3.28	P SCA																			
t3.29	B UFA																			
t3.30	F UFA																			
t3.31	P UFA																			

The dependent variable is the average capercaillie abundance in 1989–1996. Model steps are described in Table 2. The criterion for inclusion and exclusion of variables is $P=0.05$

M moose abundance, AVE average age of the forest, <40 proportion of forests under 40 years old, >60 proportion of forests over 60 years old, SCA scattered settlement, SET total settlement, TPF total proportion of forest land, UFA unproductive forest area

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