



## Original research article

## Assessing the effects of drainage and forest structure on presence and absence of fledglings of boreal grouse

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## ABSTRACT

Anthropogenic factors threaten biodiversity of natural habitats globally, including boreal forest habitats of culturally important game species, such as grouse. Forestry and intense draining of wetlands have resulted in landscape fragmentation of the peatlands and the forests in terms of their structure (a mosaic of differently managed small stands), and the loss and alteration of natural grouse habitats, which impacts on fitness parameters are still partly unexamined. We used grouse brood location data from the Finnish wildlife triangle censuses from 2017 to 2020 to study how forest structure and drainage affect breeding success of four grouse species. We calculated environmental characteristics (forest and landscape structure, peatlands and their drainage status) around individual brood observations with different buffer sizes and used them to explain brood size variation and the probability of complete failure (female with no brood). While the most important buffer zones differed by species, brood sizes were generally linked to habitats that offer shelter and food. Black grouse brood size increased when the proportions of deciduous trees and xeric heath forests increased. Hazel grouse broods were largest in spruce-dominated mires and herb-rich forests. Willow grouse brood size decreased with increasing proportion of poorer barren heath forest habitat. Capercaillie brood size decreased as a function of drainage ditch length. In Capercaillie and Black grouse, females without broods were overrepresented (zero-inflation), and the zero excess was related to habitats that differed from those of brooded females. These results suggest that forest management methods and peatland drainage can have a negative effect on offspring production of boreal grouse species. Restoration of natural peatlands and less invasive management such continuous cover forestry should enhance environmental conditions for grouse.

## 1. Introduction

Global biodiversity weakens as populations decline and disappear due to reduced demographic rates in their current environments that have been changed by anthropogenic factors (Jetz et al., 2007; Oliver and Morecroft, 2014; Ranta et al., 2006). These include

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exploitation of populations, fragmentation and loss of natural habitats, and climate change (Devictor et al., 2012; Jetz et al., 2007; Krauss et al., 2010). Anthropogenic land use is an important driver of biodiversity loss as it either completely destroys natural habitats or renders them unsuitable for the existing species (Jetz et al., 2007; Savilaakso et al., 2019; Sirkkiä et al., 2010; Titeux et al., 2016). One example is the intensive forestry that threatens biodiversity of boreal forests, one of the world's largest terrestrial ecosystems (Mörtberg et al., 2021; Tikkanen et al., 2006). The large-scale exploitation of boreal forest is a crucial conservation issue (Haila, 1994; Kurki et al., 2000; Sirkkiä et al., 2010), warranting studies on the effects of forestry activities on demographic rates of natural populations. At the landscape level, both habitat loss and fragmentation have negative effects on the viability of animal populations as they reduce demographic rates via a multitude of species-specific processes (Huhta et al., 2017; Kurki et al., 2000).

Around two-thirds of Finland's land area lies in the boreal forest zone (Sirkkiä, 2010) and is under intense forestry practises including harvesting, clear-cutting and management (thinning, planting, fertilizing), which has resulted in declines of many forest-dwelling organisms (Eyvindson et al., 2018; Jonsson et al., 2005). One of the largest changes in Finnish boreal forests took place between 1950s and early 1990s when peatlands and forests on wet mineral soils were drained throughout Finland and converted to forested peatlands or agricultural lands. In about 50 years, from 1950 to early 1980s ca. 6.5 million ha (55 %) of different types of peatlands were drained for forestry (Sikström and Hökkä, 2016; Turunen, 2007), which has resulted in major changes in peatland dwelling plant and animal communities (Vasander et al., 1997; Young et al., 2017). Today, ca. 53 % of all the peatlands are drained (Korhonen et al., 2021) and the landscape change from the past to the current has been radical for peatland dependent species (Fig. 1).

Grouse species have been affected by peatland drainage and forest management practises (Huhta et al., 2017; Kurki et al., 2000; Ludwig et al., 2008; Mikoláš et al., 2017). Boreal forests of Finland are natural habitats for four grouse species: the western capercaillie (*Tetrao urogallus*), the black grouse (*Lyrurus tetrix*), the hazel grouse (*Tetrastes bonasia*), and the willow grouse (*Lagopus lagopus*). Wetland drainage, deterioration of habitat quality and habitat fragmentation have reduced their breeding success and population sizes (Huhta et al., 2017; Kurki et al., 2000; Storch, 2000). These processes increase predation of nests and chicks by increasing predator densities and reduce chick survival by reducing shelter and arthropod communities, the most important food supply for grouse chicks in the first weeks of their life (Ludwig et al., 2008, 2010a Ludwig et al., 2010b; Miettinen et al., 2010). Potential drowning of chicks in ditches is also an immediate effect (Schekkerman et al., 2009). Ditches are usually present in the area in a labyrinth-like dense pattern, making it difficult for the animals to avoid them (Ludwig et al., 2008). So far, studies have not examined impacts of forestry and drainage in terms of grouse breeding success – nest success and brood survival – by considering the effects of different landscape and environmental factors at the local scale where individual movements take place. This is an important missing piece of information as grouse prefer certain types of habitats as their core living areas and brood survival is better in some habitats than others (Huhta et al., 2017).

Grouse apply multi-level habitat selection where breeding habitat is selected from a landscape that meets at least some of the most important requirements, such as minimum coverage (Melin et al., 2016). Habitat selection refers to a hierarchical process of behavioural responses that can lead to a disproportionate use of a given habitat to enhance survival and fitness (Rhim, 2013). For their summer habitats, the capercaillie, the black grouse and the hazel grouse require areas rich in bilberry and high tree density and canopy coverage (Broome et al., 2014). Small heather plants, especially bilberry (*Vaccinium myrtillus*), are an important source of food and shelter, as they protect not only from predators but also from changing weather conditions (Ludwig and Klaus, 2017; Melin et al., 2020; Miettinen et al., 2019; Schweiger et al., 2012). The capercaillie prefers mature, pine-dominant forests (Broome et al., 2014; Elvesveen et al., 2023; Miettinen et al., 2010), whereas the black grouse and the hazel grouse prefer more scrubby and patchy habitats where various bushes, small spruces, and deciduous trees grow, but the presence of open features, such as treeless mires, is important for the black grouse (Miettinen et al., 2019; Schweiger et al., 2012). The combination of heather plants and patches of grass is optimal for the black grouse broods, but for the hazel grouse it is not necessarily a good habitat (Ludwig and Klaus, 2017; Schweiger et al., 2012). The



**Fig. 1.** Maps showing typical development from part of our study area. Left: natural or near-natural peatland before drainage in 1950s and the current landscape in 2023. Scale 1:25000. Map centre location 64° 35' 57,896" N, 25° 22' 26,963" E. The old map digitized by Mr. Heikki Ala-aho, National Land Survey of Finland.

highest densities of the willow grouse are found in Northern Finland, but their range reaches the northern parts of central Finland (Miettinen et al., 2019). Typical willow grouse habitats are downy birch and willow thickets, but farther south they prefer the remaining peatland areas, edges of bogs and pine mires within the forested landscape as well as along bodies of water (Miettinen et al., 2019).

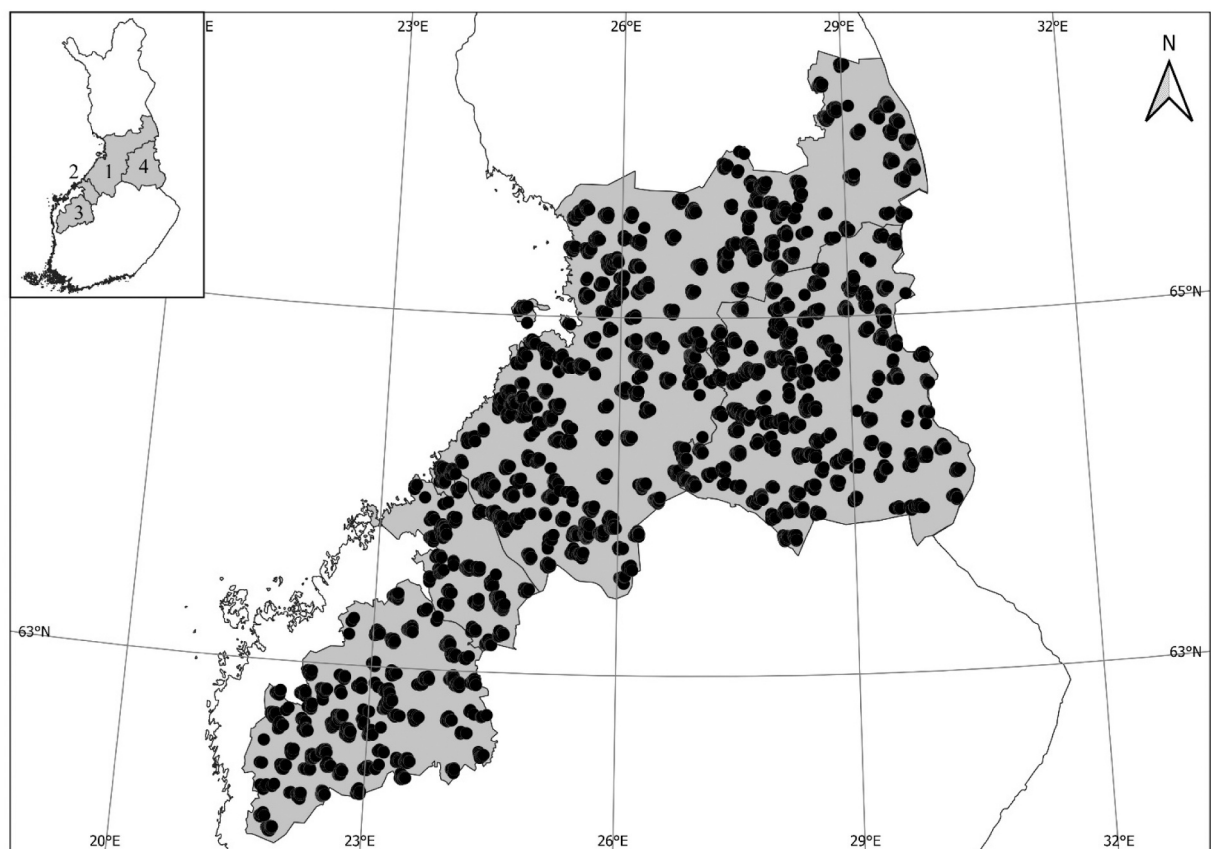
To make conservation plans for species that are affected by forest management, such as grouse, it is necessary to understand the factors that affect the habitat use of these species in different life stages (Rhim, 2013). Here, we examine the effect of forest and landscape structure on grouse brood size, which we use as proxy for breeding success encompassing both nest success and brood survival. In particular, our aim was to find out how presence of fledglings (breeding success) of different grouse species is related to the surrounding forest and landscape structure (including drainages). In addition, we study whether the possible excess of females without broods (zero-inflation) is related to same or different habitats as those related to brood size. We hypothesize that breeding success (brood size) is highest in the species-typical natural habitats, and that their success is reduced in human altered habitat and that breeding success declines as a function of increasing proportion of human altered habitat (here we mean especially the large-scale drainage, as majority of the forests in the study area have been under active forest management, but not necessarily drained).

## 2. Materials and methods

We chose Central-Northern part of Finland as the study area because of the high draining activity and the resulting length of ditches (Ludwig et al., 2008) (Fig. 1 and 2). The area is characterized by a mosaic of forested areas and peatlands/wetlands, with pine being the dominant tree (Table 1). The share of forest land out of total land area is 68 %, and of the forest lands, the share of peatland forests 42 % with ca. 65 % of the peatlands being drained (Vaahtera et al., 2023).

### 2.1. Grouse brood size and location data

We obtained grouse brood location data from the Finnish wildlife triangle census maintained by the Natural Resources Institute Finland. The wildlife triangle counting method was introduced in the 1980s (Helle et al., 2016). A wildlife triangle is an equilateral



**Fig. 2.** The study area ranged from Southwestern Ostrobothnia to North-eastern Finland. Locations of brood sightings in the wildlife triangle data in the study area are shown as black dots. The regions of Finland we used in the study have been numbered as follows: 1. North Ostrobothnia, 2. Central Ostrobothnia, 3. South Ostrobothnia and 4. Kainuu.

**Table 1**

Characteristics of the study area considering forests and peatlands (Vaahtera et al., 2021).

		Forest land (1000 ha)	Proportion (%) of different tree species out of total tree volume				Undrained mires (1000 ha)	Drained mires (1000 ha)	Drained mineral soils (1000 ha)
			<i>Pinus sylvestris</i>	<i>Picea abies</i>	<i>Betula</i> sp.	Other deciduous ( <i>Alnus</i> , <i>Populus</i> , <i>Salix</i> , <i>Sorbus</i> )			
1	North Ostrobothnia	2 503	61,7	19,7	16,7	1,9	658	1 070	224
2	Central Ostrobothnia	335	63,2	18,4	15,8	2,6	64	145	38
3	South Ostrobothnia	935	62,6	21,7	13,1	2,6	109	363	110
4	Kainuu	1623	59	22,8	16,4	1,8	310	513	82

triangle with a total route length of 12 kilometres, i.e., each side of the triangle is 4 kilometres. The locations of the triangles remain the same despite land use changes, such as logging, thinning, or other changes. Censusing is done by volunteers, mainly by local hunters in the late summer when grouse species have broods (during one day, between the end of July to early August). All observations of adult grouse and their brood sizes along with their exact locations (coordinates) are recorded. The detection rate of the census has been estimated to be ca. 60 % for adult birds, but closer to 100 % for chicks (Brittas and Karlbom, 1990). Naturally these rates may vary between regions, but most often the triangles in a given area are surveyed by hunters from that given region who are familiar with the territory and usually experienced with the census as well. For this study, we interpreted single females as failed nests or broods (meaning the number of chicks was zero), i.e., broods with no chicks. Therefore, our brood size variable encompasses breeding success from nest period until the late brooding stage in the autumn: the presence of fledglings (and their number) versus the complete absence of fledglings. In this study, we used census data collected during summer counts of 2017 – 2020. Altogether, there were 3917 brood observations in the final data (Table 2).

## 2.2. Environmental data

We derived the data on drainage and abundance of ditches from the topographic database of the National Land Survey of Finland (2023), data on forest structure and growth site type from the multisource National Forest Inventory Data (ms-NFI data) of Natural Resources Institute Finland (Luke, 2023), and data describing the mires (as polygons) from Finnish Environment Institute (SYKE, 2023). The datasets are freely available online as either GeoTiff raster- (ms-NFI data) or vector files (for mire polygons and ditches).

## 2.3. Spatial data analyses

We integrated the environmental data with the grouse location data via geospatial analyses in QGIS (QGIS.org, 2023). Here we created buffer zones with radii of 200 m, 500 m and 1000 m around each observed grouse location, and calculated statistics describing each of the environmental variables (Table 3) within these buffers with the zonal statistics tool. For non-continuous, categorical variables, we calculated the share of each class in the buffer zone. For data on the ditches (vector lines), we calculated the total length of the ditches in the buffer zone area, as well as the distance of the brood coordinate point from the nearest ditch vector. We calculated forest tree species composition using three categories, where the percentage represents the total proportion of the volume for each tree species. In the “single tree species composition” category one tree species dominates the buffer zone with at least 80 % of the total tree volume. In the “mixed forest composition” category any one of the tree species may occupy 20–80 % of the buffer zone total tree volume. Lastly, in the “fully mixed forest composition” category no single tree species will occupy more than 20 % of the buffer zone total tree volume.

The site type classification system in Finland is based on vegetation and on the premise that the presence of specific plants and understory community composition is related to the environmental conditions and fertility of the site. In the classification system (Cajander, 1949; Kalela, 1961), the focus is on the shrub-, field- and ground layer. The site types of Table 3 can be arranged from fertile to poor in the following order (and with the following dominant plant group): herb-rich forests (HR, *Oxalis-Mainathenum*), herb-rich heath forests (HRH, *Oxalis-V.myrtillus*), mesic heath forests (MH, *Myrtillus*), sub-xeric heath forests (SXH, *Vaccinium vitis-idaea*), xeric heath forests (XH, *Calluna*), and barren heath forests (BH, *Cladina*). A good overview of the system is given in Pohjanmies et al. (2021):

**Table 2**

Brood statistics for each species: total broods, failed broods, successful broods, and mean brood size.

Species	Total broods	No. of failed broods	Failed broods from total (%)	Smallest / largest brood (No. of chicks)	Mean brood size
Capercaillie	948	460	48.5	1 / 10	1.5
Black grouse	2083	751	36.0	1 / 10	2.3
Hazel grouse	797	83	10.4	1 / 10	2.9
Willow grouse	89	11	12.4	1 / 9	3.6



**Table 3**

Variables we used in the analyses. X = radius size of the buffer zone (200 m, 500 m and 1000 m) for which the variable is calculated.

Variable	Definition
OpenMireX	% of open mires (percentage within the buffer zone)
BHforestX	% of barren heath forest
SpruceMireX	% of spruce-dominated mire (spruce mire)
SXHforestX	% of sub-xeric heath forests
XHforestX	% of xeric heath forest
MHforestX	% of mesic heath forest
HRforestX	% of herb-rich forests
HRHforestX	% of herb-rich heath forest
PineBogX	% of pine bog
AgeX	Mean age of the forests
BirchX	% of birch (from total tree volume)
SpruceX	% of spruce (from total tree volume)
PineX	% of pine (from total tree volume)
OdtreesX	% of other deciduous trees (from total tree volume)
CanopyX	Canopy cover (%) of the forest
CanopyDTX	Canopy cover (%) of deciduous trees in the forest
SingleTreeX	% of single-tree forests ( $\geq 80$ %)
MixedX	% of mixed forests (20–80 %)
FullMixedX	% of fully mixed forests ( $\leq 20$ %)
TlditchesX	Total length of ditches (m) within the buffer
DBNditch	Distance (m) of the brood from the nearest ditch

*“Herb-rich forests are found on brown soils and heath forests mainly on podzol soils. Climatic variation from south to north unavoidably creates variation in vegetation within the site types, as do local topographic and soil conditions”* with Appendix S1 (in [Pohjanmies et al., 2021](#)) therein describing the system in more detail.

#### 2.4. Statistical analyses

We did statistical analyses using program R 4.2.0 and RStudio (2022.12.0+353 "Elsbeth Geranium") ([R Core Team, 2023](#)). First, we examined the relationships between the response variable (brood size) and the explanatory variables graphically (scatterplot matrix) to examine whether the relationships are linear and which explanatory variables might be significant factors for each bird species and buffer zone ([Zuur et al., 2010](#)). We analysed the effects of the environmental variables (the predictors) to variation in brood size (the response) using generalized linear mixed models (GLMM). We standardized the explanatory variables using zero as the mean and one as the standard deviation. Year was a random variable that explained possible differences between years in the brood size that cannot be accessed with the explanatory variables that we used. As the response variable is a count variable, we applied negative binomial and Poisson error distributions in modelling. Due to large proportions of zeros in response variables, we also applied zero-inflated (zi) models, which could reveal whether the brood size (count variable) and the possible excess of zeros were affected by the same or different environmental factors. We did R-analyses using either `glmer.nb` function of the `lme4` package ([Bates et al., 2015](#)) or the `glmmTMB`-function of the `glmmTMB` package ([Brooks et al., 2017](#)).

The species – zone analyses concerning buffer zones (200 – 1000 m) around the grouse observations first included all explanatory variables in the `glmer.nb` models, and we compared them using the AIC (Akaike information criterion) values of the models ([Burnham and Anderson, 2002](#)). We selected the buffer zone with the lowest AIC value for further analyses for each species. Then we eliminated the explanatory variables gradually if their `vif` (variance inflation factor) values exceeded two ([Zuur et al., 2010](#)). The `vif` values reflect the correlation among the explanatory variables. Large `vif` values can lead to multicollinearity problems ([Zuur et al., 2010](#)). Particularly, the capercaillie and black grouse data included a lot of observations of females without brood. The possible excess of zeros was considered as true or false zeros according to the guidelines given in [Martin et al. \(2005\)](#). We fitted the species-specific final set of explanatory variables with either negative binomial model (nb) or zero-inflated negative binomial model (zinb), and selected the species-specific full models (nb or zinb) according to the AIC-values and Likelihood Ratio Test (LRT-test), which could be applied in comparison of `glmmTMB` models. LRT-test was applied with the following script: `LRT <- anova(glmmTMBmodel1, glmmTMBmodel2, test = "Chisq")`. We first studied the full models by applying the `dredge` function of R's `MuMIn` package ([Barton, 2009](#)), which makes all possible combinations of the explanatory variables used in the analysis, thus revealing whether only one model or a set of models (i.e., several models within 2 AIC units) best explain the variation of the response variable ([Burnham and Anderson, 2002](#)). Here, we found no single best model for any species. Thus, we calculated average models (coefficients and their respective statistical significance) for each species with the `model.avg` function using models that received equal support (i.e., were within 2  $\Delta$ AIC units). We also calculated the sum of weights for the variables (indicating relative importance), and if it was close to 1, meaning in this case 0.8 or more, the variable was considered to be important. We used the sum of weights together with the number of models containing the adjacent variable (`Ncm`, shows the number of different models that contained the variable in question) and p-value to measure the importance of a variable ([Burnham and Anderson, 2002](#)). We drew the final figures from the models including these most important species-specific explanatory variables.

### 3. Results

The variable-sets that had the lowest AIC-values were variables from 1000-meter zone for capercaillie and black grouse, and variables from 500-meter zone for hazel grouse, and variables from 200-meter zone for the willow grouse.

#### 3.1. Capercaillie

The best model explaining capercaillie brood size was the zero-inflated negative binomial (zinb) model (full model AIC = 3098.318) instead of the simple nb-model (full model AIC = 3172.120). The LRT-test revealed very significant difference between the models (Chi-sq = 95.803, df = 11,  $p = 1.206 \times 10^{-15}$ ). The size of the capercaillie brood was negatively related to the total length of the ditches (Table 4; Fig. 3). In addition, the increased age of the forest as well as increased proportion of barren heath forest were associated to excess of zeros (Table 4).

#### 3.2. Black grouse

In black grouse, the best model explaining brood size variation was the zero-inflated negative binomial (zinb) model (full model AIC = 8001.713) instead of the simple nb-model (full model AIC = 8340.842). The LRT-test revealed very significant difference between the models (Chi-sq = 363.13, df = 12,  $p < 2.2 \times 10^{-16}$ ). The black grouse brood size was positively affected by the proportion of other deciduous trees (Table 5; Fig. 4a) and xeric heath forests (Table 5; Fig. 4b) and negatively affected by the proportion of barren heath forests (Table 5; Fig. 4c). The effect of total ditch length on black grouse brood size was negative, but insignificant. An increase in the proportion of open mires was significantly related to excess of zeros (Table 5).

#### 3.3. Hazel grouse

In hazel grouse the zinb-model (full model AIC = 3278.965) did not get support over the nb-model (full model AIC = 3269.818). The LRT-test did not find significant difference between the models (Chi-sq 12.853, df = 11,  $p = 0.303$ ). Thus, the results are based on the nb-analyses (without zi-component). The size of the hazel grouse brood was positively related to the proportion of spruce-dominated mires (Table 6, Fig. 5a) and herb-rich forests within the 500 m zone (Table 6, Fig. 5b).

#### 3.4. Willow grouse

In Willow grouse, the nb-model (full model AIC = 402.9775) was slightly better than the zinb-model (full model AIC = 405.4806), and the difference was not significant (LRT-test: Chi-sq 19.497, df = 11,  $p = 0.05274$ ). Thus, the results are based on the nb-analyses (without zi-component). The size of the willow grouse brood was positively related to the total length of the ditches and negatively related to proportion of barren heath forest within 200 m zone (Table 7, Fig. 6).

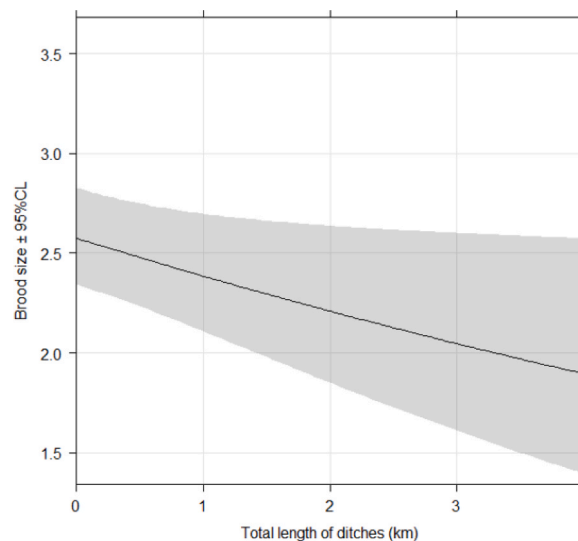
### 4. Discussion

We aimed to gain a more in-depth understanding of variation in offspring production of boreal grouse species as a function of forest and landscape characteristics (especially drainage) that could help in restoration and management of grouse habitats as well as in the implementation of grouse friendly forestry. Our results are mostly in line with existing knowledge on the effects of different forest and landscape variables (Huhta et al., 2017; Melin et al., 2016; Ministry of Agriculture and Forestry of Finland, 2014; Sirkiä et al., 2010). The total length of the ditches had a clear negative effect on the capercaillie brood size. The proportions of other deciduous trees (other than birch) and xeric heath forest were positively associated with black grouse brood size, while the proportions of spruce mire and

**Table 4**

Model-averaged results of the full zinb-model for capercaillie on 1000 m zone. The explanatory variables are listed on the left (cond = count model, zi = zero-inflated model), and the estimate, standard error (SE), z-value, and p-value are on the following columns as well as the sum of weights (SW) and number of models containing the adjacent variable (Ncm). Variables with a statistical significance and high sum of weights ( $>0.8$ ) are shown in bold.

Explanatory variable	Estimate	Adj. SE	z value	Pr(> z )	SW	Ncm
cond(Intercept)	0.9451	0.0485	19.469	$< 2 \times 10^{-16}$		
<b>cond(TLditches1000)</b>	<b>-0.0789</b>	<b>0.0364</b>	<b>2.167</b>	<b>0.030</b>	<b>1.00</b>	<b>14</b>
zi(Intercept)	-0.3153	0.0869	3.627	0.000		
<b>zi(Age1000)</b>	<b>0.1583</b>	<b>0.0815</b>	<b>1.942</b>	<b>0.052</b>	<b>0.95</b>	<b>13</b>
<b>zi(BHforest1000)</b>	<b>0.1272</b>	<b>0.0771</b>	<b>1.651</b>	<b>0.099</b>	<b>0.67</b>	<b>9</b>
zi(DBNditch)	0.0905	0.0763	1.186	0.236	0.32	5
zi(Mixed1000)	-0.0910	0.0779	1.168	0.243	0.22	3
zi(SpruceMire1000)	-0.0906	0.0813	1.115	0.265	0.21	3
zi(TLditches1000)	0.0549	0.0907	0.606	0.545	0.10	2
zi(HRforest1000)	-0.0346	0.0773	0.447	0.655	0.05	1



**Fig. 3.** The relationship between the total length of ditches and capercaillie brood size on the 1000-meter zone. The graph was created for the most important variable(s) based on the result of the average model (Table 4).

**Table 5**

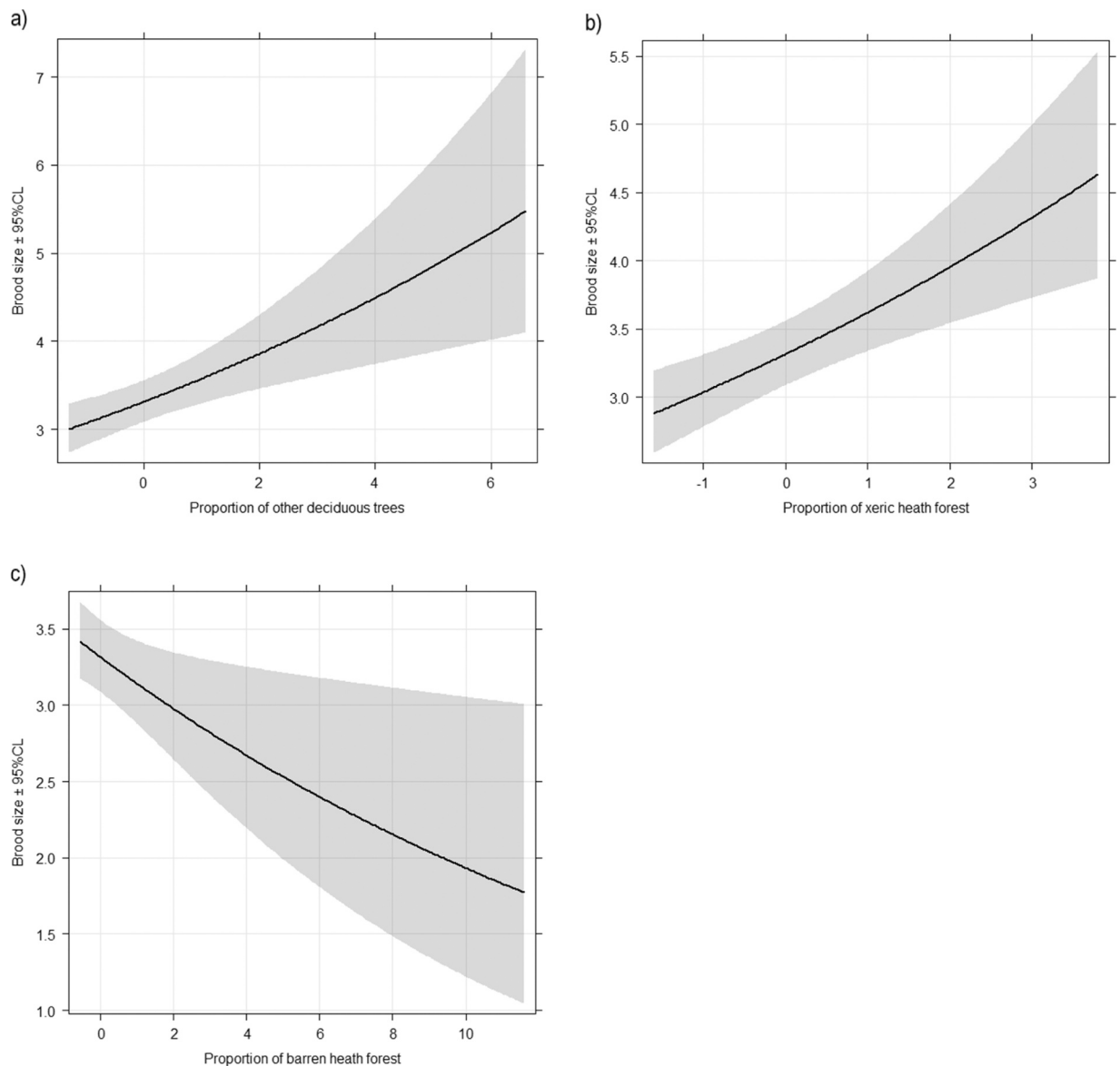
Model-averaged results of the full zinb-model for black grouse on 1000 m zone. The explanatory variables are listed on the left (cond = count model, zi = zero-inflated model), and the estimate, standard error (SE), z-value, and p-value are on the following columns as well as the sum of weights (SW) and number of models containing the adjacent variable (Ncm). Variables with a statistical significance and high sum of weights (>0.8) are shown in bold.

Average model						
Explanatory variable	Estimate	Adj. SE	z value	Pr(> z )	SW	Ncm
(Intercept)	1.1980	0.0362	33.091	< 2e-16		
<b>cond(BHforest1000)</b>	−0.0478	<b>0.0227</b>	<b>2.103</b>	<b>0.035</b>	<b>1.00</b>	<b>28</b>
<b>cond(XHforest1000)</b>	<b>0.0947</b>	<b>0.0224</b>	<b>4.229</b>	<b>0.000</b>	<b>1.00</b>	<b>28</b>
<b>cond(ODtrees1000)</b>	<b>0.0718</b>	<b>0.0205</b>	<b>3.508</b>	<b>0.000</b>	<b>1.00</b>	<b>28</b>
zi(Intercept)	−0.7500	0.0801	9.360	< 2e-16		
<b>zi(OpenMire1000)</b>	<b>0.0918</b>	<b>0.0529</b>	<b>1.735</b>	<b>0.083</b>	<b>0.94</b>	<b>26</b>
zi(SXHforest1000)	−0.1243	0.0579	2.147	0.032	0.70	19
cond(Age1000)	−0.0270	0.0197	1.373	0.170	0.49	14
zi(TLditches1000)	−0.0813	0.0559	1.454	0.146	0.48	14
zi(ODtrees1000)	−0.0838	0.0591	1.419	0.156	0.46	13
cond(SpruceMire1000)	−0.0218	0.0232	0.942	0.346	0.26	9
zi(XHforest1000)	−0.0406	0.0617	0.657	0.511	0.07	3

herb-rich forests correlated positively with hazel grouse brood size. The proportion of barren heath forest, however, had a negative correlation with black grouse brood size. The total length of the ditches seemed to have a positive effect on willow grouse brood size, but this could be a false positive due to the fact that most bogs have been drained (as we will discuss later in this article).

In the capercaillie and black grouse data, the proportion of zeros (no fledglings observed with the female) was related to habitats where observation efficiency should be relatively high. Increased forest age was related to excess of zeroes for capercaillie brood, and the increasing proportion of open mires increased the excess of zeroes for the black grouse. These findings suggest that the observed zeros were true zeros (females without brood), and thus, females without fledglings seemed to use slightly different environments than females with broods. Mazziotto et al. (2024) and Melin et al. (2016) have noted that regardless of the grouse species, the females with broods favour rather similar components of forest structure in terms of habitat selection. Whereas a female grouse without fledglings could be assumed to select habitats without any significant “brood” effect, thus creating the differences to the females with fledglings.

Our results suggest that grouse succeed the best in their favoured natural environments, and that land use changes driven by forestry practises, such as intense draining, can negatively impact grouse breeding success. However, it must be acknowledged that our analysis on the topic does not give a full picture as variables such as width or depth of the ditches is not available nor is the data on how old the drainage network is. Still, the species differed in terms of the most important spatial scale where the tested variables were explaining the observed brood size. The models compiled with variables from the largest buffer zone (1000 m) were the best for the capercaillie and the black grouse in terms of model AIC. This matches well with the results of Huhta et al. (2017) who found that the capercaillie and the black grouse broods were positively correlated with forest patch size. They prefer larger areas, and the structure of forest patches is key to the survival of grouse broods (Huhta et al., 2017). The most significant buffer zone for the hazel grouse was



**Fig. 4.** Relationships of the proportion of other deciduous trees, xeric heath forests and barren heath forests to the black grouse brood size on the 1000-meter zone. The graphs were created for the most important variables based on the results of the average model (Table 5).

500 m, which could reflect the hazel grouse's typically smaller territory size, which can vary between 20 and 70 ha in the spring (Matysek et al., 2018). Similarly, a willow grouse territory is comparably small, ca. 500  $\times$  700 m, and it is usually angular because it follows the edge of the bog (Osmala, 2012). This fits the most significant scale (200 m buffer zone) we observed for the species.

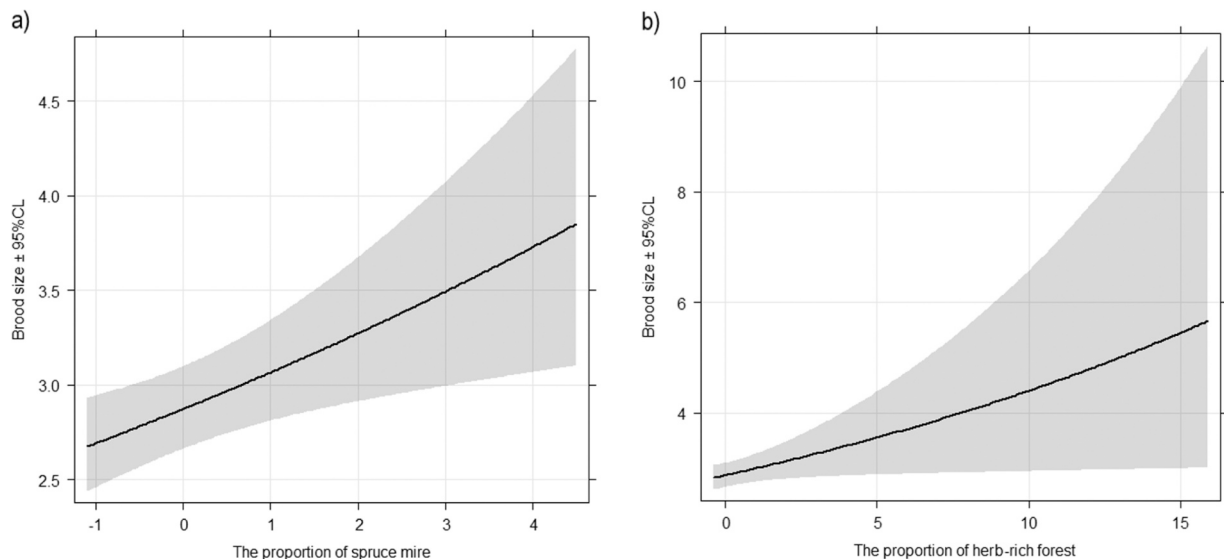
Black grouse brood size increased as the proportion of deciduous trees increased. This may reflect the importance of mixed forests formed by deciduous and conifer species. A diverse forest structure with a denser understorey and shrub layer may increase chick survival as it provides protection from harsh weather conditions (Huhta et al., 2017) and predators (Kurki et al., 2000; Wegge and Rolstad, 2011). Huhta et al. (2017) also estimated that the proportion of deciduous trees had a positive effect on black grouse brood size. As expected, the willow grouse did not have this effect, as it typically nests in more open areas. Regarding the capercaillie and the hazel grouse, canopy coverage or tree species proportions did not receive statistical support. It is possible the ms-NFI data does not describe the 3D structure of the forests where the presence of dense understorey has been found to be significant for grouse broods (Mazziotta et al., 2024; Melin et al., 2016). In hazel grouse, however, the proportion of herb-rich forests had a positive effect on the brood size, which could indicate the importance of a good forest cover, as herb-rich forests are typically richer in understorey vegetation. For the capercaillie, the age of the forest and the proportion of barren heath forest increased the probability of a failed brood. This could suggest that a good understorey coverage is needed, as such habitats tend to be sparser in older forests especially on a barren site type as these kinds of forests are mainly pine-dominated, and the understorey is dominated by lichens, whereas dwarf



**Table 6**

Model-averaged results of the hazel grouse full negative binomial model with all explanatory variables in the 500 m zone. The explanatory variables are listed on the left, and the estimate, standard error (SE), z-value, and p-value are on the following columns as well as the sum of weights (SW) and number of models containing the adjacent variable (Ncm). Variables with a statistical significance and high sum of weights (>0.8) are shown in bold.

Average model						
Explanatory variable	Estimate	Adj. SE	z value	Pr(> z )	SW	Ncm
(Intercept)	1.0552	0.0386	27.371	< 2e-16		
<b>SpruceMire500</b>	<b>0.0639</b>	<b>0.0241</b>	<b>2.651</b>	<b>0.008</b>	<b>1.00</b>	<b>10</b>
<b>HRforest500</b>	<b>0.0436</b>	<b>0.0204</b>	<b>2.141</b>	<b>0.032</b>	<b>0.92</b>	<b>9</b>
DBNditch	-0.0355	0.0272	1.306	0.192	0.32	3
BHforest500	-0.0213	0.0267	0.796	0.426	0.18	2
SingleTree500	0.0119	0.0277	0.430	0.667	0.08	1
Age500	-0.0104	0.0252	0.411	0.681	0.08	1
TLditches500	-0.0200	0.0284	0.707	0.480	0.08	1
OpenMire500	-0.0095	0.0257	0.371	0.710	0.08	1
Pine500	-0.0066	0.0250	0.264	0.792	0.07	1



**Fig. 5.** Relationships of the proportion of spruce mire and herb-rich forests to the hazel grouse brood size on the 500-meter zone. The graphs were created for the most important variables based on the results of the average model (Table 6).

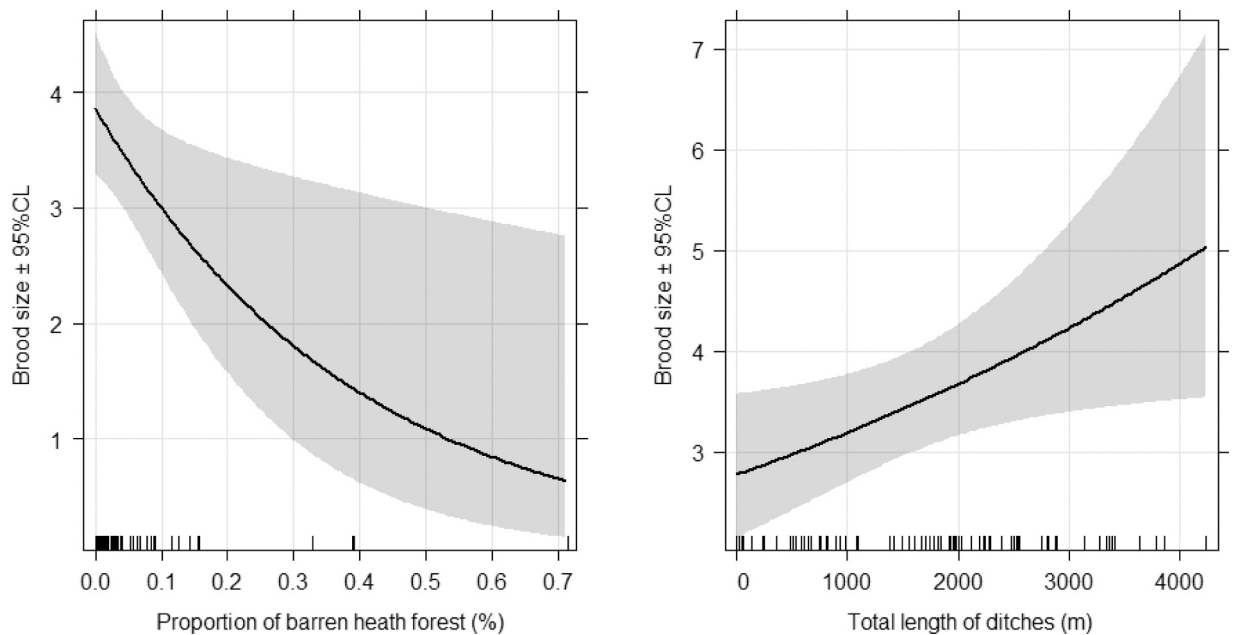
**Table 7**

Model-averaged results of the willow grouse negative binomial full model with all explanatory variables in the 200-meter zone. The explanatory variables are listed on the left, and the estimate, standard error (SE), z-value, and p-value are on the following columns as well as the sum of weights (SW) and number of models containing the adjacent variable (Ncm). Variables with a statistical significance and high sum of weights (>0.8) are shown in bold.

Average model						
Explanatory variable	Estimate	Adj. SE	z value	Pr(> z )	SW	Ncm
(Intercept)	1.23991	0.07947	2.160	< 2e-16		
<b>BHforest200</b>	-0.26940	0.11469	2.349	0.0188	<b>1.00</b>	<b>3</b>
<b>TLditches200</b>	0.17165	0.07947	2.160	0.0308	<b>1.00</b>	<b>3</b>
Pine200	-0.06877	0.07812	0.880	0.3786	0.25	1
DBNditch	0.06000	0.09988	0.601	0.5480	0.21	1

shrubs are mostly missing (Pohjanmies et al. 2021, Suppl. 1)), i.e. they do not represent mossy bilberry-rich forests that would offer grouse chicks the necessary food and shelter.

We found negative correlation between capercaillie brood size and the total length of the ditches, which is in line with previous studies (2008; Ministry of Agriculture and Forestry of Finland, 2014), but other species did not show similar response with the length of ditches. We also surprisingly found a positive relationship between willow grouse brood size and the total length of ditches. This is most likely due to the fact that almost all the best willow grouse bogs (spruce dominated bogs) have been drained in the study area, in



**Fig. 6.** Relationship of willow grouse brood size to the proportion of barren heath forest and the total length of the ditches on the 200-meter zone. The graphs were created for the most important variables based on the results of the average model (Table 7).

which case the number of ditches may simply correlate with the quality of the habitat (the presence of peatlands in general), which produces the contradictory result. It is generally known that willow grouse habitats from Southern Finland diminished during the large-scale drainage campaigns of the past (Auvinen et al., 2007; Lindén and Rajala, 1981; Ludwig et al., 2008). Finding a true effect of ditches for the willow grouse may require different kind of sampling and consideration of water levels (Ludwig et al., 2008, 2010a). An analysis focussing only on peatlands and considering the ages of the ditches might be able to show the true effect of drainage on willow grouse: whether e.g. 10-year-old, moss-covered ditches would have the same effect on grouse in general when compared to more recent ditches (Fig. 7). Unfortunately, data on year of draining is mostly unattainable and the question would require intensive field work focused on estimating the age- and condition of the ditch network.

The excess of females without broods (zero-inflation with true zeros) in the capercaillie and black grouse may indicate differential habitat use by single and brooded females. One explanation for this could be that single females and females with chicks differ in their habitat needs: the more vulnerable chicks need more shelter and vegetation cover for food, thermal shelter as well as against predation (Melin et al., 2016) while single females could better survive in a wider scale of habitats that are not tied to the needs of the fledglings.

There is an urgent need for forest management guidelines to take into account the needs of game species in forest management today. Firstly, we found that drainage is harmful for the capercaillie broods. Draining also reduces especially willow grouse habitats: bogs and mires at natural state. Secondly, as deciduous trees and herb-rich forests were important for grouse brood size, our results emphasize the importance of a sufficiently diverse forest structure in terms of tree species composition. In addition to this, recent studies have shown the importance of understorey vegetation for grouse broods (Melin et al., 2016), indicating that the complete removal of the undergrowth, bushes and deciduous trees should be avoided as the current, renewed guidelines on wildlife friendly forest management highlight as well (Lindén et al., 2014; Ministry of Agriculture and Forestry of Finland, 2014; Äijälä et al., 2019). Selectively logged forests (a method of continuous growth), for instance, can temporarily produce a fairly stable moderate canopy cover and understorey cover (Miettinen et al., 2010). Selective logging does not reduce the amount of food and shelter as clear-cutting does, and thus selective logging could provide a valuable alternative to even-aged forests and clear-cutting (Kvasnes and Storaas, 2007) especially in peatland forests, where it can also decrease the need for re-drainage (Juutinen et al., 2021).

Spatial planning over large areas is difficult in Finland, as forest ownership is fragmented. This results in mosaic of forest stands on average of 20–30 ha, where management decisions are made by different people and often independently of the neighbours. However, this is also beneficial to some extent, as it keeps the size of individual clear-cuts quite small and thus prevents major habitat modifications such as landscape-level clear cuttings. Yet, a variety of other techniques and method have been recommended to aid better consideration of wildlife species such as grouse in forest management. Here, the preservation and versatility of understorey vegetation should be emphasized in all stages of forest management (Melin et al., 2016). In today's forest management guidelines, emphasis is also placed on leaving small areas (0.005–0.02 ha) with denser vegetation (game thickets) completely outside of forestry operations, to the point that they should be left as retention tree groups also during the regeneration cuttings (the recommendations suggest 3–5 thickets per hectare) (Melin et al., 2016; Haara et al., 2021). The recovery of bilberry in areas where the land has been cultivated and the forest has been cut down could be promoted by better preservation of the areas still covered by bushes and shrubs (Ministry of Agriculture and Forestry of Finland, 2014). In addition, it is very important to take care of transition zones between different site or soil types and



**Fig. 7.** Two completely different ditches with different ages. Left: old ditch with moss layer already covering it. Right: old, but recently re-opened ditch with all the vegetation absent and with steep edges. While the two ditches can be assumed to have different effects on grouse broods, their types cannot be differentiated based on the available data, and the data on the age of the ditches is generally not attainable from any public source.

here the forested transition zones between peatland soils and mineral soils are especially important from the grouse brood point of view. Here too, the inclusion and maintenance of the right type of understory vegetation is important (Melin et al., 2016).

Our results support the idea that each grouse species needs its own kind of brood environments and anthropogenic habitat alteration has negative impact on their success. Drainage had a clear negative effect on the size of the capercaillie brood. The possible effects of forest management (e.g., felling, thinning) on brood size through canopy cover or age of the forests was not clear in the results for any other species besides the capercaillie (age of the forest increased the probability of a failed brood). This may suggest that grouse still find forested habitats in the managed landscape, and therefore, the brood environment data do not include the most intensely treated forests habitats. Our results support the recent guidelines in forestry and other environmental modification and restoration programs: restoration of peatlands and the presence of mixed forests should be nothing but positive for grouse broods. Similarly, the preservation of understory vegetation in all phases of forestry and a shift towards more mixed forests benefits boreal grouse species.

### Ethics statement

Not applicable: This manuscript does not include human or animal research. If this manuscript involves research on animals or humans, it is imperative to disclose all approval details.

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### Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

### Data availability

The authors do not have permission to share data.

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### References

Äijälä, O., Koistinen, A., Sved, J., Vanhatalo, K., & Väisänen, P. (2019). Metsänhoidon suosituksset. Tapion julkaisuja. (<https://www.metsanhoitosuosituksset.fi/taus>).

- Auvinen, A.-P., Hildén, M., Toivonen, H., Primmer, E., Niemelä, J., Aapala, K., Bäck, S., Härmä, P., Ikävalko, J., Järvenpää, E., Kaipainen, H., Korhonen, K.T., Kumela, H., Kärkkäinen, L., Lankoski, J., Laukkanen, M., Mannerkoski, I., Nuutinen, T., Nöjd, A., ... Virkkala, R. (2007). Evaluation of the Finnish National Biodiversity Action Plan 1997-2005 (29th ed.). Monographs of the Boreal Environment Research No. 29, Finnish Environmental Institute.
- Barton, K. (2009). Mu-Min: Multi-model inference. R Package Version 0.12.2/r18.
- Bates, D., Mächler, M., Bolker, B., Walker, S., 2015. Fitting linear mixed-effects models using lme4. *J. Stat. Softw.* 67 (1), 1–48. <https://doi.org/10.18637/jss.v067.i01>.
- Brittas, R., Karlsson, M., 1990. A field evaluation of the Finnish 3-man chain: a method for estimating forest grouse numbers and habitat use. *Ornis Fenn.* 67, 18–23.
- Brooks, M.E., Kristensen, K., van, Benthem, K.J., Magnusson, A., Berg, C.W., Nielsen, A., Skaug, H.J., Maechler, M., Bolker, B.M., 2017. glmmTMB balances speed and flexibility among packages for zero-inflated generalized linear mixed modeling. *R. J.* 9 (2), 378–400. <https://doi.org/10.32614/RJ-2017-066>.
- Broome, A., Connolly, T., Quine, C.P., 2014. An evaluation of thinning to improve habitat for capercaillie (*Tetrao urogallus*). *For. Ecol. Manag.* 314, 94–103. <https://doi.org/10.1016/j.foreco.2013.11.038>.
- Burnham, K.P., Anderson, D., 2002. *Model Sel. Multimodel Inference: A Pract. Inf. -Theor. Approach Vol. 2*.
- Cajander, A.K., 1949. Forest types and their significance. *Acta For. Fenn.* 56 (5) <https://doi.org/10.14214/aff.7396>.
- Devictor, V., Van Swaay, C., Brereton, T., Brotons, L., Chamberlain, D., Heliölä, J., Herrando, S., Julliard, R., Kuussaari, M., Lindström, Å., Reif, J., Roy, D.B., Schweiger, O., Settele, J., Stefanescu, C., Van Strien, A., Van Turnhout, C., Vermouzek, Z., WallisDeVries, M., Jiguet, F., 2012. Differences in the climatic debts of birds and butterflies at a continental scale. *Nat. Clim. Change* 2 (2), 121–124. <https://doi.org/10.1038/nclimate1347>.
- Elvesveen, J.E., Sørensen, O.J., Patten, M.A., 2023. Forest grouse response to forestry practices across four decades. *For. Ecol. Manag.* 538 <https://doi.org/10.1016/j.foreco.2023.121005>.
- Eyvindson, K., Repo, A., Mönkkönen, M., 2018. Mitigating forest biodiversity and ecosystem service losses in the era of bio-based economy. *For. Policy Econ.* 92, 119–127. <https://doi.org/10.1016/j.forpol.2018.04.009>.
- Haara, A., Matala, J., Melin, M., Miettinen, J., Korhonen, K.T., Packalen, T., Varjo, J., 2021. Economic effects of grouse-friendly forest management. *Silva Fennica* 55 (3). <https://doi.org/10.14214/sf.10468>.
- Haila, Y., 1994. Preserving ecological diversity in boreal forests: ecological background, research, and management. *Ann. Zool. Fenn.* 31 (1), 203–217. (<http://www.jstor.org/stable/23735511>).
- Helle, P., Ikonen, K., Kantola, A., 2016. Wildlife monitoring in Finland: online information for game administration, hunters, and the wider public. *Can. J. For. Res.* 46 (12), 1491–1496. <https://doi.org/10.1139/cjfr-2015-0454>.
- Huhta, E., Helle, P., Nivala, V., Nikula, A., 2017. The effect of human-modified landscape structure on forest grouse broods in two landscape types. *Ecosphere* 8 (9). <https://doi.org/10.1002/ecs2.1950>.
- Jetz, W., Wilcove, D.S., Dobson, A.P., 2007. Projected impacts of climate and land-use change on the global diversity of birds. *PLoS Biol.* 5 (6). (<https://doi.org/10.1371/journal.pbio.0050117>).
- Jonsson, B.G., Krüys, N., Ranius, T., 2005. Ecology of species living on dead wood – Lessons for dead wood management. *Silva Fennica* 39 (2), 289–309.
- Juutinen, A., Shanin, V., Ahtikoski, A., Rämö, J., Mäkipää, R., Laiho, R., Sarkkola, S., Laurén, A., Penttilä, T., Hökkä, H., Saarinen, M., 2021. Profitability of continuous-cover forestry in norway spruce dominated peatland forest and the role of water table. *Can. J. For. Res.* 51 (6), 859–870. <https://doi.org/10.1139/cjfr-2020-0305>.
- Kalela, A., 1961. Forest vegetation zones in Finland and their climatic parallel types (German). *Arch. Soc. Zool. -Bot. Fenn. 'Vanamo'* 16, 65–83.
- Korhonen, K.T., Ahola, A., Heikkinen, J., Henttonen, H.M., Hotanen, J.P., Ihalainen, A., Melin, M., Pitkänen, J., Rätty, M., Sirviö, M., Strandström, M., 2021. Forests of Finland 2014–2018 and their development 1921–2018. *Silva Fenn.* 55 (5) <https://doi.org/10.14214/sf.10662>.
- Krauss, J., Bommarco, R., Guardiola, M., Heikkinen, R.K., Helm, A., Kuussaari, M., Lindborg, R., Öckinger, E., Pärtel, M., Pino, J., Pöyry, J., Raatikainen, K.M., Sang, A., Stefanescu, C., Teder, T., Zobel, M., Steffan-Dewenter, I., 2010. Habitat fragmentation causes immediate and time-delayed biodiversity loss at different trophic levels. *Ecol. Lett.* 13 (5), 597–605. <https://doi.org/10.1111/j.1461-0248.2010.01457.x>.
- Kurki, S., Nikula, A., Helle, P., Lindé, H., 2000. Landscape fragmentation and forest composition effects on grouse breeding success in boreal forests. *Ecology* 81, 7. Kvasnes, M.A.J., Storaas, T., 2007. Effects of harvesting regime on food availability and cover from predators in capercaillie (*Tetrao urogallus*) brood habitats. *Scand. J. For. Res.* 22 (3), 241–247. <https://doi.org/10.1080/02827580701345884>.
- Lindén, M., Lilja-Rothsten, S., Saariisto, L., & Keto-Tokoi, P. (2014). Metsänhoidon suositukset riistametsänhoitoon, työopas. In Metsätalouden kehittämisskeskus Tapion julkaisuja. ([www.metsanhoitosuositukset.fi](http://www.metsanhoitosuositukset.fi)).
- Lindén, H., Rajala, P., 1981. Fluctuations and long-term trends in the relative densities of tetraonid populations in Finland, 1964-77. *Finnish Game Res.* 39, 13–34.
- Ludwig, G.X., Alatalo, R.V., Helle, P., Nissinen, K., Siitari, H., 2008. Large-scale drainage and breeding success in boreal forest grouse. *J. Appl. Ecol.* 45 (1), 325–333. <https://doi.org/10.1111/j.1365-2664.2007.01396.x>.
- Ludwig, G.X., Alatalo, R.V., Helle, P., Siitari, H., 2010a. Individual and environmental determinants of daily black grouse nest survival rates at variable predator densities. *Ann. Zool. Fenn.* 47 (6), 387–397. (<http://www.jstor.org/stable/23737059>).
- Ludwig, G.X., Alatalo, R.V., Helle, P., Siitari, H., 2010b. Individual and environmental determinants of early brood survival in black grouse *Tetrao tetrix*. *Wildl. Biol.* 16 (4), 367–378. <https://doi.org/10.2981/10-013>.
- Ludwig, T., Klaus, S., 2017. Habitat selection in the post-breeding period by Hazel Grouse *Tetrastes bonasia* in the Bohemian Forest. *J. Ornithol.* 158 (1), 101–112. <https://doi.org/10.1007/s10336-016-1365-z>.
- Luke (Natural Resources Institute Finland). (2023). File service for publicly available ms-NFI data. Available at: (<https://kartta.luke.fi/index-en.html>).
- Martin, T.G., Wintle, B.A., Rhodes, J.R., Kuhnert, P.M., Field, S.A., Low-Choy, S.J., Tyre, A.J., Possingham, H.P., 2005. Zero tolerance ecology: improving ecological inference by modelling the source of zero observations. *Ecol. Lett.* 8, 1235–1246.
- Matysek, M., Gwiazda, R., Bonczar, Z., 2018. Seasonal changes of the Hazel Grouse *Tetrastes bonasia* habitat requirements in managed mountain forests (Western Carpathians). *J. Ornithol.* 159 (1), 115–127. <https://doi.org/10.1007/s10336-017-1484-1>.
- Mazziotta, A., Lindén, A., Eyvindson, K., Bianchi, S., Kangas, A., Melin, M., Ruha, L., Forsman, J.T., 2024. Unraveling the characteristic spatial scale of species habitat selection for forest grouse in the boreal landscape. *Forest Ecology and Management* 563. <https://doi.org/10.1016/j.foreco.2024.122008>.
- Melin, M., Mehtätalo, L., Helle, P., Ikonen, K., Packalen, T., 2020. Decline of the boreal willow grouse (*Lagopus lagopus*) has been accelerated by more frequent snow-free springs. *Sci. Rep.* 10 (1) <https://doi.org/10.1038/s41598-020-63993-7>.
- Melin, M., Mehtätalo, L., Miettinen, J., Tossavainen, S., Packalen, P., 2016. Forest structure as a determinant of grouse brood occurrence – An analysis linking LiDAR data with presence/absence field data. *For. Ecol. Manag.* 380, 202–211. <https://doi.org/10.1016/j.foreco.2016.09.007>.
- Miettinen, J., Helle, P., Nikula, A., Niemelä, P., 2010. Capercaillie (*Tetrao urogallus*) habitat characteristics in north-boreal Finland. *Silva Fenn.* 44 (2), 235–254. (<http://www.metsä.fi/silvafennica/full/sf44/sf442235.pdf>).
- Miettinen, J., Rantala, M., & Svensberg, M. (2019). Riistametsänhoidon opas. ([https://riista.fi/wp-content/uploads/2019/02/riistametsanahidonopas\\_WEB\\_pakattu.pdf](https://riista.fi/wp-content/uploads/2019/02/riistametsanahidonopas_WEB_pakattu.pdf)).
- Mikoláš, M., Tejkal, M., Kuemmerle, T., Griffiths, P., Svoboda, M., Hlásny, T., Leitão, P.J., Morrissey, R.C., 2017. Forest management impacts on capercaillie (*Tetrao urogallus*) habitat distribution and connectivity in the Carpathians. *Landsc. Ecol.* 32 (1), 163–179. <https://doi.org/10.1007/s10980-016-0433-3>.
- Ministry of Agriculture and Forestry of Finland. (2014). Suomen metsäkanalintukantojen hoito-suunnitelma. (<https://mmm.fi/julkaisu?pubid=URN:ISBN:978-952-453-873-2>).
- Mörtberg, U., Pang, X.L., Treynis, R., Trubins, R., Mozgeris, G., 2021. Sustainability assessment of intensified forestry—forest bioenergy versus forest biodiversity targeting forest birds. *Sustain.* (Switz.) 13 (5), 1–20. <https://doi.org/10.3390/su13052789>.
- National Land Survey of Finland. (2023). Download service for pen data. Available at: (<https://asiointi.maanmittauslaitos.fi/karttapaiikka/tiedostopalvelu>).
- Oliver, T.H., Morecroft, M.D., 2014. Interactions between climate change and land use change on biodiversity: Attribution problems, risks, and opportunities. In: *Wiley Interdisciplinary Reviews: Climate Change*, Vol. 5. Wiley-Blackwell, pp. 317–335. <https://doi.org/10.1002/wcc.271>.
- Osmala, E. (2012). Riekon (*Lagopus l. lagopus*) reviiirin muodostus havumetsäalueella [Pro gradu-tutkielma]. Itä-Suomen yliopisto.



- Pohjanmies, T., Genikova, N., Hotanen, J.P., Ilvesniemi, H., Kryshen, A., Moshnikov, S., Oksanen, J., Salemaa, M., Tikhonova, E., Tonteri, T., Merilä, P., 2021. Site types revisited: comparison of traditional russian and finnish classification systems for European boreal forests. *Appl. Veg. Sci.* 24 (1) <https://doi.org/10.1111/avsc.12525>.
- QGIS.org. (2023). QGIS Geographic Information System. QGIS Association. (<http://www.qgis.org>).
- R Core Team. (2023). R: A language and environment for statistical computing. In R Foundation for Statistical Computing. (<https://www.r-project.org/>).
- Ranta, E., Lundberg, P., Kaitala, V., 2006. *Ecology of populations*. Cambridge University Press.
- Rhim, S.J., 2013. Hazel grouse winter habitat selection and conservation in temperate forest. *For. Ecol. Manag.* 295, 38–42. <https://doi.org/10.1016/j.foreco.2012.12.028>.
- Savilaakso, S., Häkkinen, M., Johansson, A., Uusitalo, A., Sandgren, T., Mönkkönen, M., Puttonen, P., 2019. What are the effects of even-aged and uneven-aged forest management on boreal forest biodiversity in Fennoscandia and European Russia? A systematic review protocol. In: *Environmental Evidence*, Vol. 8. BioMed Central Ltd. <https://doi.org/10.1186/s13750-019-0160-8>.
- Schekckerman, H., Teunissen, W., Oosterveld, E., 2009. Mortality of Black-tailed Godwit *Limosa limosa* and Northern Lapwing *Vanellus vanellus* chicks in wet grasslands: influence of predation and agriculture. *J. Ornithol.* 150 (1), 133–145. <https://doi.org/10.1007/s10336-008-0328-4>.
- Schweiger, A.K., Nopp-Mayr, U., Zohmann, M., 2012. Small-scale habitat use of black grouse (*Tetrao tetrix* L.) and rock ptarmigan (*Lagopus muta helvetica* Thienemann) in the Austrian Alps. *Eur. J. Wildl. Res.* 58 (1), 35–45. <https://doi.org/10.1007/s10344-011-0537-7>.
- Sikström, U., Hökkä, H., 2016. Interactions between soil water conditions and forest stands in boreal forests with implications for ditch network maintenance. *Silva Fenn.* 50 (1) <https://doi.org/10.14214/sf.1416>.
- Sirkä, S. (2010). Effects of large-scale human land use on Capercaillie (*Tetrao urogallus* L.) populations in Finland [Academic Dissertation, University of Helsinki]. (<http://ethesis.helsinki.fi>).
- Sirkä, S., Lindén, A., Helle, P., Nikula, A., Knape, J., Lindén, H., 2010. Are the declining trends in forest grouse populations due to changes in the forest age structure? A case study of Capercaillie in Finland. *Biol. Conserv.* 143 (6), 1540–1548. <https://doi.org/10.1016/j.biocon.2010.03.038>.
- Storch, I., 2000. Conservation status and threats to grouse worldwide: an overview. *Wildl. Biol.* 6 (4), 195–204. <https://doi.org/10.2981/wlb.2000.016>.
- SYKE (Finnish Environment Institute). (2023). Download service for open data. Available at: ([https://www.syke.fi/en-US/Open\\_information/Spatial\\_datasets](https://www.syke.fi/en-US/Open_information/Spatial_datasets)).
- Tikkanen, O.-P., Martikainen, P., Hyvärinen, E., Junninen, K., Kouki, J., 2006. Red-listed boreal forest species of Finland: associations with forest structure, tree species, and decaying wood. In: *Ann. Zool. Fenn.* Vol. 43.
- Titeux, N., Henle, K., Mihoub, J.B., Regos, A., Geijzendorffer, I.R., Cramer, W., Verburg, P.H., Brotons, L., 2016. Biodiversity scenarios neglect future land-use changes. *Glob. Change Biol.* 22 (7), 2505–2515. <https://doi.org/10.1111/gcb.13272>.
- Turunen, J., 2007. *Dev. Finn. Peatland Area Carbon Storage 1950–2000*.
- Vaahtera, E., Niinistö, T., Peltola, A., Rätty, M., Sauvula-Seppälä, T., Torvelainen, J. & Uotila, E. (2023). *Metsätalastollinen Vuosikirja 2022 - Finnish Statistical Yearbook of Forestry 2022*. Luonnonvarakeskus. (<http://urn.fi/URN:ISBN:978-952-380-584-2>).
- Vaahtera, E., Niinistö, T., Peltola, A., Rätty, M., Sauvula-Seppälä, T., Torvelainen, J., Uotila, E., Kulju, I. 2021. *Metsätalastollinen vuosikirja 2021 - Finnish Statistical Yearbook of Forestry 2021*. Luonnonvarakeskus, 204s. <http://urn.fi/URN:ISBN:978-952-380-325-1>.
- Vasander, H., Laiho, R., Laine, J., 1997. Changes in species diversity in peatlands drained for forestry. In: Trettin, C.C., Jurgensen, M.F., Grigal, D.F., Gale, M.R., Jeglum, J.K. (Eds.), *Northern Forested Wetlands: Ecology and Management*. CRC Press, Lewis Publishers, Boca Raton, Fla, USA, pp. 109–119.
- 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. *For. Ecol. Manag.* 261 (9), 1520–1529. <https://doi.org/10.1016/j.foreco.2011.01.041>.
- Young, D.M., Baird, A.J., Morris, P.J., Holden, J., 2017. Simulating the long-term impacts of drainage and restoration on the ecohydrology of peatlands. *Water Resour. Res.* 53 (8), 6510–6522. <https://doi.org/10.1002/2016WR019898>.
- Zuur, A.F., Ieno, E.N., Elphick, C.S., 2010. A protocol for data exploration to avoid common statistical problems. *Methods Ecol. Evol.* 1 (1), 3–14. <https://doi.org/10.1111/j.2041-210x.2009.00001.x>.