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## Forest grouse response to forestry practices across four decades

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### A B S T R A C T

Fennoscandian boreal forests have been logged for centuries, yet only since the second world war has management shifted from selective logging to clear-cutting. In general, this shift equates to fewer stands of uneven age and higher vertical complexity and more stands of even age and lower complexity. Ecological responses to this shift in forestry practice are expected and could be especially significant for umbrella species, those species whose protection affords a sort of trickle-down protection for a host of other species. Two putative umbrella species are the Black Grouse (*Lyrurus tetrix*) and Western Capercaillie (*Tetrao urogallus*), large galliform birds of forested habitats of northern Eurasia. We used a 45-year dataset from southeastern Norway to assess how closely each of these species tracked changes in forest cutting class, age, stand density, and in the proportion of deciduous trees. We found that occupancy was hierarchical. The Black Grouse tended to occupy primarily younger (<40 y) forests and secondarily forests with higher cover of deciduous trees (>48%) and, at the understorey level, a dominance of bilberry (*Vaccinium myrtillus*), whereas the capercaillie tended to occupy primarily forest that had not been logged in many years (cutting class IV or V) and secondarily an understorey layer of bilberry and lower stand density. In general, the Black Grouse tracked change in stand density more closely, whereas the capercaillie restricted occupancy to older forest (>100 y) dominated by conifers. Both species were detected most often when stand density was intermediate, with the densest forest typically avoided. In sum, the Western Capercaillie is likely to be a good umbrella species for old-growth boreal forest, particularly coniferous forest, but the Black Grouse, with its more malleable response to forestry practices, would not, as it occurs in mixed forests that are neither too old nor too young. We conclude that management for healthy Black Grouse populations may require little change from current practice as long as sufficient deciduous cover is retained. By contrast, protection of old-growth or mature forests ultimately will be crucial to persistence of Western Capercaillie populations—the species will occupy cut forest, but it is found in such forests much less often. Such protection may necessitate a shift away from clear-cutting as well as a broader perspective to ensure sufficient old growth is retained across the landscape.

### 1. Introduction

Boreal forests of Fennoscandia have been logged persistently for nearly five centuries (Rautio et al., 2016), with felling accelerating in the 1940s after clear-cutting was adopted (Esseen et al., 1992), an adoption that necessarily dictated a transition from selective logging to even-aged forest management (Kuuluvainen et al., 2012). Prior to a system of even-aged forests, one could not speak of seral stages or cutting classes; instead, individual trees were targeted for removal such that regeneration cycles are staggered across space and time. These uneven-aged forests better retain characteristics of mature forests and, hence, better support species and communities that depend on boreal forests (Kuuluvainen et al., 2012; Gauthier, et al., 2015). Fennoscandia's altered forest landscape has led to general concerns about loss of boreal forest biodiversity and associated ecosystem services (Gauthier et al., 2015; Thom and Seidl, 2015; Pohjanmies et al., 2017; Ram et al., 2017).

Of particular concern, both ecologically and culturally, are reported declines of large gamebirds such as forest grouse (Storch, 2000). In general populations of the two largest grouse species, the Black Grouse

(*Lyrurus tetrix*) and the Western Capercaillie (*Tetrao urogallus*), decreased sharply across Europe after 1900 to stabilize at much lower levels in recent decades (Jahren et al., 2016). Each species is a bellwether for boreal forests, in that each has been classified as an umbrella species (Suter et al., 2002; Mikoláš et al., 2017; Andesner et al., 2021), a kind of surrogate species that provides protection, indirectly, for habitat or ecosystems used by many other species (Caro, 2010). Conservation of umbrella species is thus essential to conserve biodiversity more broadly, making it essential to understand thoroughly landscape-scale determinants of their occupancy patterns.

Population sizes of the Black Grouse and the Western Capercaillie often fluctuate synchronously (Lindström et al., 1996), yet there is evidence that the species occupy different seral stages of boreal forest, with the former associated with early stand development, 10–30 years old, and the latter associated with stands 50–90+ years old (Seiskari, 1962; Sørensen, 1979; Swenson and Angelstam, 1993; Angelstam, 2004; Rolstad et al., 2009). It thus has been hypothesized that “When converting old forest to clearcuts and plantations, commercial forestry ... [will] affect capercaillie negatively and ... be favourable to black grouse”

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(Wegge and Rolstad 2011:1520). Putative seral associations aside, the two species can be found in the same forests—habitat diverges on average, but there is considerable overlap (Anglestam, 2004:Table 2), especially in snow-free months (diets diverge in winter; Seiskari, 1962; Hjeljord et al., 1994). Overlap in occupancy means that population size data may not support hypotheses about higher numbers of the Black Grouse but smaller numbers of the Western Capercaillie when amount of mature forest declines (Wegge and Rolstad, 2011). Moreover, population density of both species correlates positively with the proportion of old-growth forest in the landscape (Lande et al., 2014), reproductive success of both species correlates negatively with fragmentation, patch size, and loss of mature forest from clear-cutting (Kurki et al., 2000), and although broods of both species occur more often in mature, natural forest (Rolstad et al., 1988; Wegge and Kastdalen, 2008), chick production itself may correlate negatively with proportion of old forest (Lande et al., 2014).

It may be, then, the forest age alone is an insufficient metric to explain putative species-level differences in occupancy of different seral stages; alternative explanations, such as variation in vegetation and plant composition, must be sought. Furthermore, it has been suggested that forest age is important but only after taking into account other factors (e.g., Wegge and Rolstad, 2011), such that forest-related attributes that affect occupancy are hierarchical. We used data from long-term (1976–2019) censuses of grouse and grouse sign in southeastern Norway to assess how forest age class, forest management, and vegetation classification separately or together account for occurrence patterns of the Black Grouse and Western Capercaillie. Our aim was to further test hypotheses about the capercaillie's putative propensity to avoid young forest stands intruded by deciduous trees and the Black Grouse's preference for these same young stands (Lindén and Helle, 2003; Sirkkiä et al., 2010). We tested predictions with hierarchical approaches, multivariate techniques, and Bayesian models. If hypotheses held, then forest management must strike a balance between needs of species that prefer older versus younger stands. In this sense, we assume that an umbrella species is tied to a specific habitat (see Breckheimer et al., 2014); hence, if we cannot link a species to a specific habitat, then it cannot, by definition, be an umbrella. If the umbrella hypothesis holds, then the extent to which the two species together may be used under a sort of shared umbrella will simplify management and conservation plans for boreal forests.

## 2. Materials and methods

### 2.1. Study area

The surveyed area in southeastern Norway encompasses ~103 km<sup>2</sup> in the municipalities of Hurdal, Gran, Nannestad, and Ostre Toten (a polygon with corners roughly at 60°29'26"N, 10°42'52"E; 60°28'36"N, 10°56'45"E; 60°20'17"N, 10°52'38"E; and 60°21'22"N, 10°58'40"E). Skrukkelia Valley runs centrally from east to northwest, dividing surrounding hills in the south and north, hills that rise abruptly from the valley floor to >800 m in the north and >700 m in the south. The lowest point is Skrukkelisjøen, at 329 m a.s.l. Average annual precipitation is 1031 mm, and winters are characterized by deep snow cover. Forest is dominated by *Picea abies* (Norway Spruce), with only scattered patches of *Pinus sylvestris* (Scots Pine) on poorer soils or on the edge of mires and bogs. As a result of intensive timber extraction since the 1950s, few large deciduous trees, chiefly *Betula pubescens* (Downy Birch), *Alnus incana* (Grey Alder), and *Populus tremula* (Common Aspen), can be found, and early successional species such as *Sorbus aucuparia* (Rowan) and *Salix* spp. (willow, which often forms a dense, Moose *Alces alces*-browsed shrub layer in clearcuts).

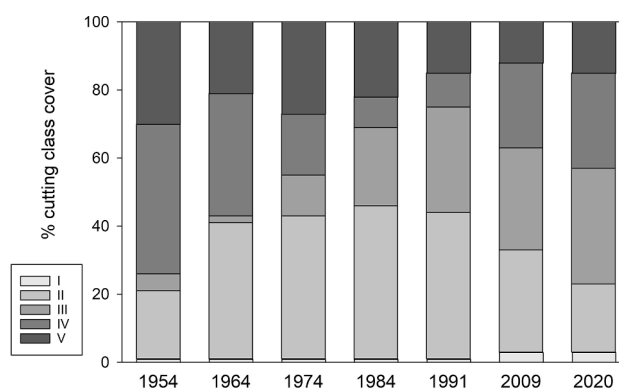
Most of the forest in the study area, as well as in the greater area surrounding it—a total of 350 km<sup>2</sup>—is owned and managed by the forestry company Mathiesen-Eidsvold Værks (MEV), which has had ISO (International Standardization Organisation) 14,001 certification since

2000 and FSC (Forest Stewardship Council) certification since 2014. Approximately 295 km<sup>2</sup> of this area is productive forest, with annual felling of 76,000 m<sup>3</sup>, of which 12,000 m<sup>3</sup> is thinning and 64,000 m<sup>3</sup> timber. MEV maintains an extensive network of forest roads, totalling some 360 km in extent (<https://www.mev.no>). Beginning in the mid-1930s, forestry shifted to a more intensive practices (Fig. 1), and since the 1940s clear-cutting has been the main tool for timber harvest. Since, timber harvest has been planned to provide a regular and predictable outcome, chiefly via creation of spruce monocultures by (a) planting of saplings after clearcut, (b) thinning of young, cutting class II (see below) stands (i.e., removal of sprouting birch and other broadleaf trees), and (c) application of herbicides in cutting classes I and III to avert dominance of broadleaves (mainly alder and birch). In the 1960s and 1970s, bogs and mires were drained to increase area for forest production and stands in cutting classes IV and V were fertilized. Alternative felling methods constitutes 10% of the annual the felling area since 1984 (Fig. 1). As a result of intensive management from clear-cutting, thinning, and replanting, forests on site were a mosaic of even-aged, spruce-dominated stands of different age classes, with some old forest, almost exclusively at the highest elevations.

### 2.2. Field data

Twelve looped transects were established on MEV land, averaging 12 km in length. Grouse censuses were conducted with a two-man line modelled on the Finnish 3-man chain (Rajala 1974; Helle and Lindström, 1991). Walking side by side 20-m apart, each participant covered 10 m laterally, yielding a 40-m wide belt survey. (A 3-man chain was used initially, but after the first two years it was abandoned in favour of a 2-man system to minimize difficulties to hold to a tight line in dense woods and on difficult terrain.) Before the 2010s, transects were surveyed with paper map and compass; later transects were navigated with GPS units. Even so, roughly the same transect routes were surveyed each year. Censuses were conducted in mid-August of 1976–1980, 1991–1993, 2012, 2015, and 2019 with an array of participants, from students to MEV employees; one constant is that OJS took part in or oversaw all data collection. Surveys lacked systematic bias and followed a consistent protocol throughout.

A standardized field form was developed to ensure data consistency across years. Surveyors paused only to record an occurrence (bird, feathers, or dust bath) of either focal species. We excluded sign that could not be identified conclusively to a focal species. Stand density (scale of 1–10, with 10 densest; corresponds roughly to % tree cover),



**Fig. 1.** Percentages of the five cutting classes (Table 1) on Mathiesen-Eidsvold Værks land, the bulk of the study area near Hurdal, Norway. Note the transition, after 1991, from high levels of class II (young forest or early reforestation) and low levels of classes IV (old production forest) and V (mature forest) to lower levels of class II, an increase in class III (young production forest), and concomitant increases in classes III in the 1980 s and classes IV and V since 2000, although now class IV is mainly a monoculture of spruce rather stands of naturally regrown forest.

vegetation type, and forest age were recorded in a 10-m radius at all occurrence points, as was evidence of timber cutting class (Table 1), chiefly to ensure consistent estimates of forest age.

Forest age was available on maps through the 1990s, but later surveyors had to judge it on the basis of tree height and of site quality ranked from high to low productivity (Table 2).

We recorded, in a 10-m radius, percentage of deciduous trees, most of which was the Downy Birch, a species hypothesized to be a driver of Black Grouse abundance (Lindén and Helle, 2003). Vegetation type was judged by key plant species and impression in the 10-m circle surrounding an occurrence (Table 3). For analysis, vegetation types were grouped into habitat types deemed to have similar properties, designed to prevent classification errors caused by personnel interpreting vegetation differently. Habitat was ‘available’ for a species for any sampled point at which that species was not detected. In 1993 and 2019 additional availability surveys on vegetation composition and forest structure were conducted at 500 non-grouse points, selected on the basis of where a surveyor walking a transect stood at 30-min intervals.

### 2.3. Statistical analyses

We explored change over time in Black Grouse and Western Capercaillie populations with a profile analysis, a modification of multivariate analysis of variance to accommodate repeated measures. At its core, a profile analysis can be thought of as a multivariate paired *t*-test. Three tests are built into a profile analysis: flatness (whether the response changes over sampling periods, in our cases surveys;  $H_0$ : profiles flat), levels (differences among groups of interest, in our cases species;  $H_0$ : profile levels same), and parallelism (whether there is a group  $\times$  sample interaction;  $H_0$ : profiles parallel). Our response variable was annual sum of all encounters, whether birds, feathers (counted as one individual), or dust baths (counted as one individual). The analysis was run using R package ‘profileR’ (Bulut and Desjardins, 2018).

We assessed habitat use by the two focal species by means of classification trees, which are able to handle higher-order interactions, nonlinear relationships, and missing values. Furthermore, the technique has no distributional assumptions, and data may be a mix of continuous and discrete (De’ath and Fabricius, 2000). Beyond these advantages, it produces easily interpretable graphical results. Trees are built via recursive partitioning of the data, such that the most homogeneous grouping of the response is obtained at each hierarchical step. Trees were constructed using R package ‘rpart’ (Therneau and Atkinson, 2019), with the complexity parameter (*cp*) set to 0.0125, ensuring fine resolution, and a response variable of present (1)/absent (0). Results were visualized with R package ‘rpart.plot’ (Milborrow, 2021).

We built a custom Bayesian multinomial model to investigate habitat use. Such a model allowed us both to incorporate uncertainty and to estimate probability of encounter under different cutting classes (Table 2), forest densities, deciduous tree cover, and vegetation classes (Table 3). We ran models with data pooled. Models were written in JAGS code and run via R package ‘rjags’ (Plummer, 2022). The response variable was presence (bird, feather, or dust bath). We also wrote JAGS code for a Bayesian Poisson regression, with the intercept,  $\beta_0$ , constrained to be positive. For both models, priors were weakly informative.

**Table 1**

Forest cutting classification system (Svensson et al., 2021), the industry standard in Norwegian forestry.

Class	Definition	Equivalent age class (Table 2)
I	Forest during reforestation	I <sub>0</sub>
II	Established reforestation and young forest	I <sub>1</sub> , I <sub>2</sub>
III	Young production forest	II <sub>3</sub> , II <sub>4</sub>
IV	Older production forest	III
V	Mature forest	IV

**Table 2**

Forest age classification system (Sørensen, 1979).

Age class	Tree height	Inferred age (site quality A–F)
I <sub>0</sub>	<1 m	<40 years
I <sub>1</sub>	1–3 m	<40 years
I <sub>2</sub>	3–7 m	<40 years
II <sub>3</sub>	7–14 m	30–70 years
II <sub>4</sub>	14–17 m	30–70 years
III	>17 m	50–110 years
IV	>20 m	70–110 + years

**Table 3**

Vegetation classification scheme (Fremstad, 1997). Vegetation type names have been translated to English. “Vegetation class” refers to natural groups of vegetation types to reduce the number of types for subsequent analyses.

Vegetation type	Code	Vegetation class
Bilberry spruce forest	A4(a)	Bilberry
Cowberry-bilberry forest	A2a	Cowberry
Heather bog-bilberry pine forest	A3a	Heather
Small-fern spruce forest	A5a	Fern
Low-herb spruce forest	B1a	Herb
Tall-fern spruce forest	C1a	Tall
Tall-herb spruce forest	C2b	Tall
Poor swamp spruce forest	E1(a)–2	Swamp
Rich swamp spruce forest	E4	Swamp
Ombrotrophic bog	J1–4	Fen
Poor fen	K1–4	Fen
Intermediate fen	L1–4	Fen
Rich fen	M1–4	Fen

### 3. Results

Profiles of presence (birds seen + feather detections + dust baths found) of the Black Grouse and Western Capercaillie were not synchronous, in that the  $H_0$  of parallelism was rejected (Wilks’  $\Lambda_{10,13} = 0.16, p < 0.001$ ). Because profiles are not parallel, at least one cannot be flat, obviating a need to test the flatness  $H_0$ . Levels also differed ( $F_{1,22} = 5.46, p < 0.03$ ), with incidence of the Black Grouse higher, on average (Fig. 2). Incidence of that species tracked stand density across years—with  $p > 0.97$ , the true and underlying slope of the relationship was positive—but capercaillie incidence did not (Fig. 2; posterior  $p = 0.49$ , meaning slope direction was, in effect, a coin flip).

Viewed as presence/absence, the probability of a Black Grouse detection was highest in young forest with bilberry (*Vaccinium myrtillus*), fen, or other species that comprise lower herbaceous layers and a modest proportion of deciduous tree cover, although in older forest the species was detected more often when deciduous cover was high (Fig. 3A). Western Capercaillie detection was highest in uncut, old forest (age class IV, cutting class V) with low (10% or less) deciduous tree cover but other similar herbaceous layer to that for the Black Grouse (Fig. 3B). In no instance, here or below, was there a difference between the sexes in habitat use.

The Western Capercaillie was encountered with highest probability ( $P_{Tetrao} = 0.69$ ; i.e., estimated from summing the independent means of the posterior distributions) in forests with high (IV–V; Table 1) cutting class, meaning older forests less routinely disturbed, in years past, by selective logging (Fig. 4).

That species was found most often when stand density was moderate. Neither species was encountered often when stand density was very high or very low (Fig. 5).

For both cutting class and stand density, the Black Grouse tended to track forest conditions more closely, but in general probability of encounter of the two species differed more for cutting class than for stand density (Figs. 4 and 5). Both species broadly tracked the percentage of deciduous trees in the forest and were most likely to be found if deciduous cover was < 15% ( $P_{Lyrus} = 0.49, P_{Tetrao} = 0.79$ ), but the

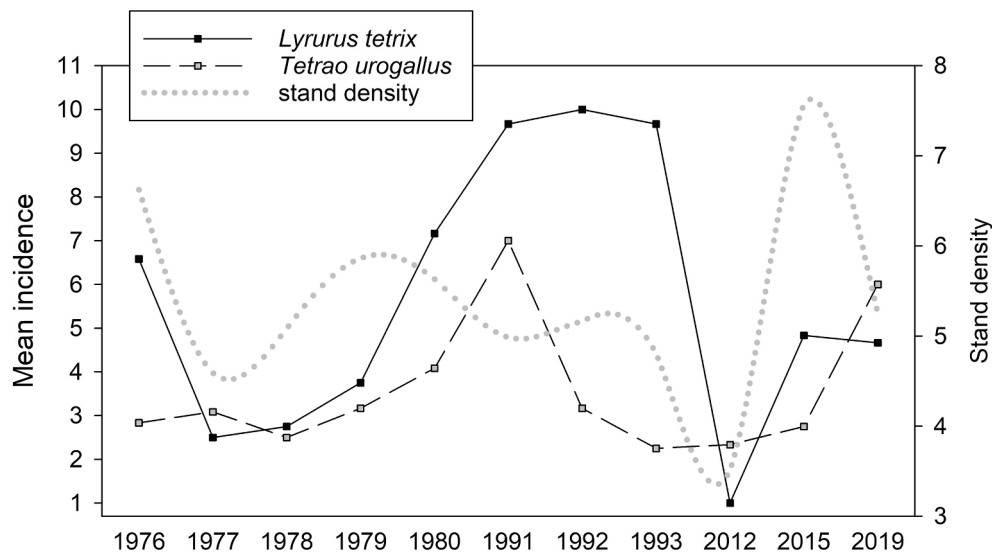


Fig. 2. Profiles for counts of the Black Grouse (*Lyrurus tetrrix*) and Western Capercaillie (*Tetrao urogallus*) near Hurdal, Norway, plotted against mean stand density. Note both the non-consecutive years, the only rough synchronicity between the species, and the tendency for the Black Grouse to more closely track stand density.

Black Grouse was, overall, more tolerant of lower proportion of conifers (Fig. 6).

Vegetation class (“habitat”) had a similar pattern (not shown), with both species overwhelming found where bilberry formed the ground cover ( $p_{Lyrurus} = 0.65$  [0.61, 0.69],  $p_{Tetrao} = 0.73$  [0.69, 0.78]), roughly matching that class’s availability (0.71).

#### 4. Discussion

Our main predictions, generated from some, but not all, previous research, were supported. The Western Capercaillie was found with highest probability in older, less disturbed forests, cutting classes IV and V (Figs. 3 and 4) with low deciduous cover, which corroborates previous findings (Børset & Krafft, 1973; Rolstad et al., 1988; Swenson & Angelstam, 1993; Angelstam, 2004). Our findings therefore both support and contradict a hypothesis that the capercaillie is tied to coniferous cover itself independent of forest age (Sirkiä et al., 2010). The Black Grouse was found chiefly in cutting classes II and III (Fig. 4) and forests of young to moderate age (<50 years; Fig. 3), corroborating results from some prior studies (Børset and Krafft, 1973; Swenson and Angelstam, 1993; Angelstam, 2004). We moreover showed that Black Grouse occupancy was associated hierarchically after habitat selection (*sensu* Patten et al., 2021) for forest of moderate age with an elevated percentage of deciduous trees, which tend to be pioneer species after disturbance such as logging or fire (Archambault et al., 1998; Peterson et al., 2009). Deciduous cover in our study area was contributed principally by the Downy Birch, suggesting our findings may support a hypothesis that birch cover specifically relates to Black Grouse abundance (Lindén and Helle, 2003).

We failed to corroborate any difference between the Black Grouse and the Western Capercaillie with regard to stand density: both species were encountered most often when density was neither especially high nor especially low (Fig. 5), a finding that matched those of Wegge and Rolstad (2011). By itself stand density tells us only about forest cover, not about forest composition. We suggest that this result is the result of differences in what type of forests the species preferred and used, the Western Capercaillie in old forest dominated by conifers, the Black Grouse in younger forest dominated by the Downy Birch and other deciduous trees. Moreover, as stand density varied over the 44-yr study period, the frequency of Black Grouse encounters varied roughly in concert (Fig. 2). We conclude that that species does not select forests of moderate stand density so much as its selection is facultative, largely

responsive to what is available. The Western Capercaillie may have responded favourably, at least recently, to changes in forest management that led to increased proportions of cutting classes IV and V, the older, less disturbed forests and even the moderately affected class III forests, which the species will occupy (Fig. 1). Capercaillie encounters in the study area were flat excepting a peak in the early 1990s that we cannot explain and an upsurge after the mid-2000s (Fig. 2), which perhaps not coincidentally matches the upsurge in classes IV and V.

The two species frequent the same understorey vegetation, too: each had the highest encounter probability where bilberry dominated, although bilberry-dominated understorey is typical of the study area, and use did not differ from availability, being roughly two-thirds for either. A study in Finland (Lakka and Kouki, 2009) reported that bilberry abundance (and associated arthropods) were highest in mature and young forest stands, a pattern that could be interpreted to match disparate forest age preferences of the Western Capercaillie and Black Grouse, yet in our study the proportion of bilberry understorey varied only slightly across cutting classes, from a low of 0.66 for class I to highs of 0.75 for class II and 0.74 for class IV. Still, it may be that such subtle differences among cutting classes align with results from Lakka and Kouki’s (2009), who classified forest as ‘young’ (class I–II?), ‘middle-aged’ (class III?), or ‘mature’ (class IV–V?). Bilberry flourishes when forests offer at least some shade (Eldegard et al., 2019), decreases following clear-cutting (Atlegrim and Sjöberg, 1996), and reaches high productivity in uncut forests (Rodríguez and Kouki, 2015), conditions that imply high stand density and high cutting class (although not so high as to shade-out the species). In our study, though, each species was encountered with low probability when stand density was high, and only capercaillie encounters peaked when cutting class was high, suggesting that bilberries were being shaded out to some unknown extent. Nonetheless, an important role for bilberry has been claimed for both species (Storch, 1993; Beeston et al., 2005; Wegge and Kastdalen, 2008), and it may be that population size tracks bilberry productivity (and associated insect productivity), allowing for at least a one-year lag (Selås, 2019).

Three classes of hypotheses attempt to explain declines in forest grouse in Europe: intensified land use, climate change, and increased predation (Jahren et al., 2016). Our results bolster land use arguments, at least as they relate to forestry practices. Intensive logging is detrimental to the Western Capercaillie population, and maintenance of at least moderate stand density is likely to favour both the Black Grouse and bilberry-dominated understorey, a potentially important source of nutrition (perhaps especially for broods; Wegge et al., 2022). Passerine

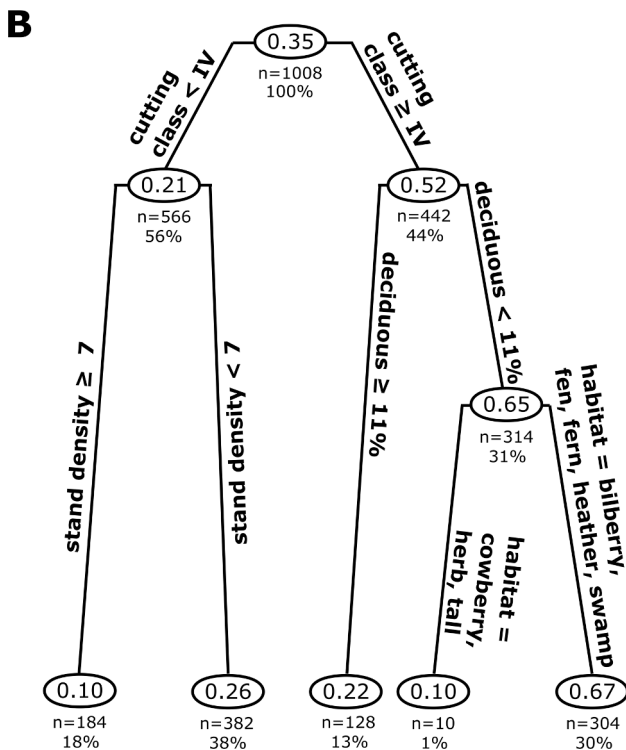
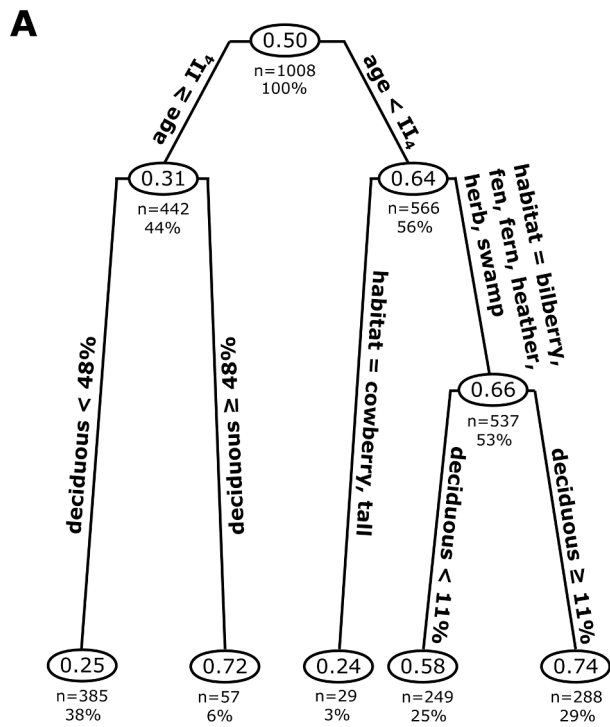


Fig. 3. Classification trees for presence of the A) Black Grouse (*Lyrurus tetrix*) and B) Western Capercaillie (*Tetrao urogallus*) near Hurdal, Norway. The root node indicates the probability the species was encountered. Black Grouse presence was highest in younger forest with a low herbaceous layer and modest proportion of deciduous trees. Western Capercaillie presence was highest in uncut forest with a similar herbaceous layer but few deciduous trees.

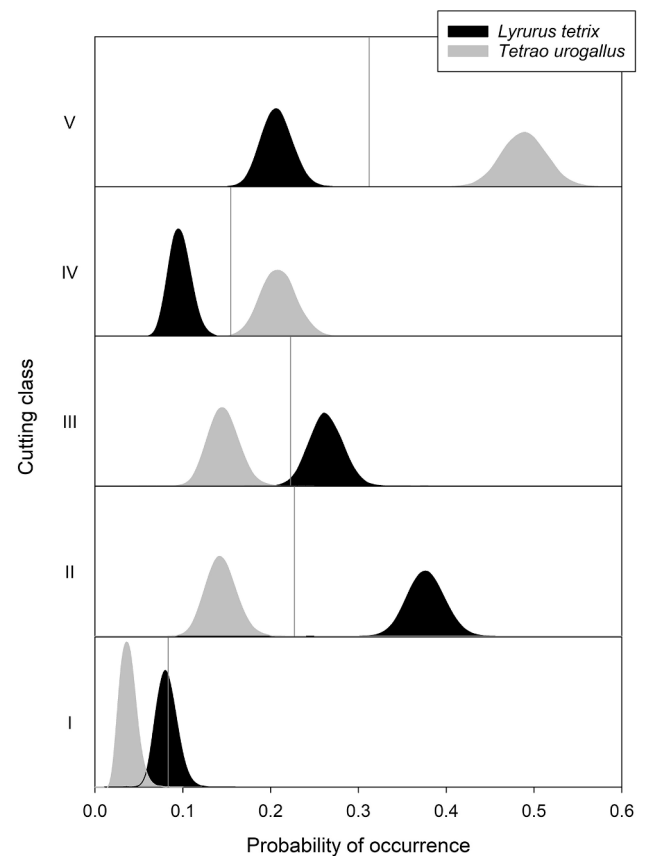
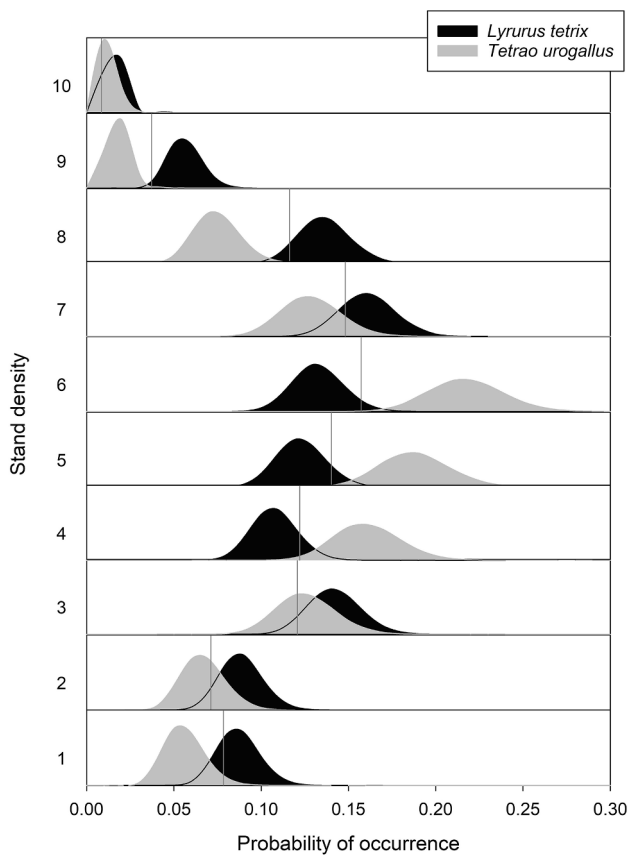


Fig. 4. Posterior probability distributions for multinomial estimates by cutting class for Black Grouse (*Lyrurus tetrix*) and Western Capercaillie (*Tetrao urogallus*) occurrence near Hurdal, Norway. Vertical lines mark the proportion of data points in a cutting class. Distributions that do not overlap considerably, whether for species or class, imply encounter probabilities differ. Note that the Black Grouse tracks cutting class proportion, whereas the capercaillie occurs disproportionately in classes IV and V (i.e., older and less disturbed forest; Table 1).

birds play an important role in dispersing bilberry seeds (Arnberg et al. 2023), and it may be that forest grouse do as well, suggesting the possibility of feedback loops wherein a forest that sustains healthy bird populations will sustain healthy bilberry populations, which in turn attracts birds.

Effects of ongoing climate change are difficult to ascertain and may not be apparent until decades in the future. We have hints, though, in that mortality of capercaillie chicks is highest “during and immediately after heavy rainfalls” (Wegge and Kastdalen, 2007), conditions that are forecast to increase in northern Europe (Christensen et al., 2019). There is evidence, too, that breeding success is lower when summers are warmer (Moss et al., 2001; Selås et al., 2011), although such reports were perhaps not supported by findings that warmer weather immediately after hatch was associated with higher success (Wegge et al., 2022).

Predation adds a wrinkle to perceptions of or conclusions about how land use affects habitat suitability. Predation has been claimed as the main limiting factor of forest grouse reproduction (Kurki et al., 1997; Storaas and Wegge, 1987; Wegge and Kastdalen, 2007). Because predation rates do not necessarily vary by habitat alteration (Storaas and Wegge, 1987), it has been argued that forestry practices alone are an insufficient explanation for population declines for forest grouse (Sirkiä et al., 2010; Wegge and Rolstad, 2011). Nonetheless, predation may interact with anthropogenic habitat alteration. For example, it has been suggested that clearing of forest may facilitate predator abundance and hunter efficiency in boreal systems (Kurki et al., 1998), although



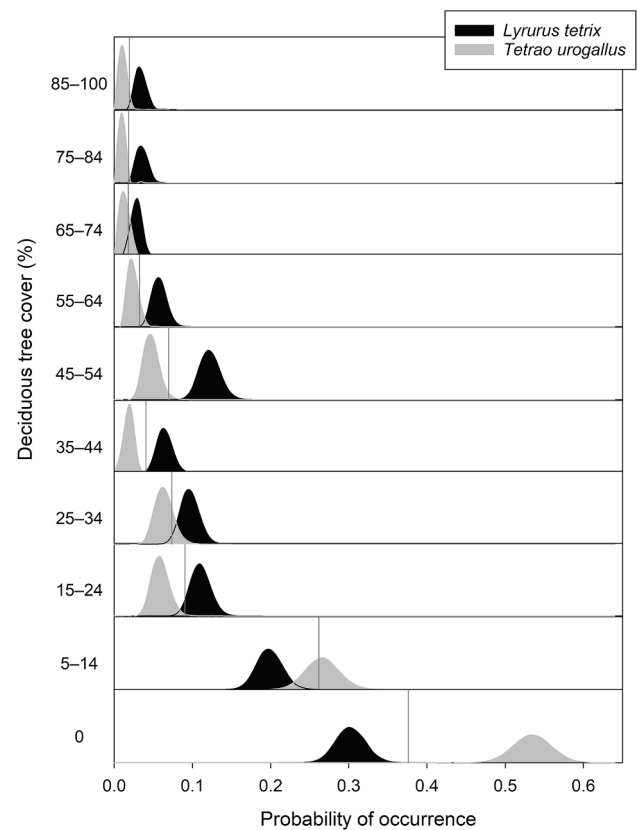
**Fig. 5.** Posterior probability distributions for multinomial estimates by stand density for Black Grouse (*Lyrurus tetrix*) and Western Capercaillie (*Tetrao urogallus*) occurrence near Hurdal, Norway. Vertical lines mark the proportion of data points in that density band. Distributions that do not overlap considerably, whether for species or density, mean encounter probabilities differ markedly. Note that the Black Grouse roughly tracks density, whereas the capercaillie is encountered most often at intermediate stand density.

predation appears not to play the predominant role in breeding success of forest grouse (Wegge et al., 2022). The interplay between land use practices and rates of predation needs further investigation.

### 5. Conclusions

Ecological surrogates are a means to reduce dimensionality (Wiens et al., 2008) or, bluntly, a shortcut “whereby attention is focused on one or a few species” (Simberloff, 1998:248), the idea being that conservation of one or few species will have a trickle-down effect such that many other species are conserved as well. It is now common to see papers that speak of surrogate species for this or that ecosystem or habitat. Were we to accept that both the Black Grouse and the Western Capercaillie are umbrella species then we would need to specify for what they are umbrellas. We interpret our results to mean that only the Western Capercaillie can be reasonably considered an umbrella species: it is the species that strongly prefers unlogged or lightly logged coniferous forest (cutting classes IV and V), with an emphasis on forest age rather than stand density (Figs. 3–6). The Black Grouse, by contrast, more closely tracks the forest’s fortunes (Fig. 2), with encounters up at intermediate cutting classes (II and III) and when forests includes more deciduous cover (Figs. 3 and 6). It appears to be too plastic to qualify as an umbrella. Further, its populations do not fluctuate in close synchrony to those of the capercaillie, so it cannot be used as a surrogate for it.

Old-growth forest support many specialized and sometimes endemic species across the animal, plant, and fungal kingdoms (Frank et al., 2009). Any species that could act as an umbrella would be a boon both to



**Fig. 6.** Posterior probability distributions for multinomial estimates by deciduous tree cover (%) for Black Grouse (*Lyrurus tetrix*) and Western Capercaillie (*Tetrao urogallus*) occurrence near Hurdal, Norway. Vertical lines mark the proportion of data points in that percentage band. Distributions that do not overlap considerably, whether for species or percentage, mean encounter probabilities differ markedly. Note that both species were encountered with highest probability when cover of deciduous trees was <15% and that the capercaillie was particularly tied to coniferous forest.

management and to biodiversity conservation. Delayed timber harvest is the most cost-effective means to conserve biodiversity in old-growth boreal forests (Juutinen, 2008) and is most likely to provide proper conditions for the Western Capercaillie. Forest management geared toward persistence of a minimum viable population of the capercaillie—the threshold in one study was ~470 individuals (Grimm and Storch, 2000)—is, we posit, likely to protect numerous old-growth species. The rotational system used at our study area provides a clue in that for a century the area has been managed extensively using ‘modern’ forestry principles yet retains a reduced but apparently viable population of the Western Capercaillie (as well as the Black Grouse), adding some support to conclusions elsewhere (e.g., Wegge and Rolstad, 2011) that grouse populations are at least somewhat tolerant of forest management. Even so, apparent unreported or unappreciated conversion of old forest to plantations (Ahlström et al., 2022) may prove, in the long run, especially detrimental to Scandinavian populations of the capercaillie.

### Author contributions

The kernel of this paper was JEE’s M.Sc. thesis. OJS and MAP together advised JEE through successful defence of his thesis. MAP used that thesis as the basis to write the paper and helped with or conducted statistical analyses, as well as created associated graphics (based on JEE’s originals) included herein. OJS oversaw field work dating back to the project’s inception and provided key data and insight. All authors approved the final manuscript.

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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.

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