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Master thesis

**Scots pine (*Pinus sylvestris*)
phytochemistry predicts male
capercaillie (*Tetrao urogallus*)
browsing during winter**

Master in applied ecology

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Abstract

During winter, the capercaillie (*Tetrao urogallus*) faces harsh conditions with only heavily digestible food available. To cope with this, these birds consume large volumes to compensate for the low levels of digestible energy. During winter, capercaillies switch their diet to Scots pine (*Pinus sylvestris*), which is usually their main food source from November to March. Thus, capercaillies prefer mature Scots pine stands during winter and their body condition may actually improve on this winter diet.

I collected 19 male capercaillie, culled with rifles while feeding in pine trees, within Innlandet County, Norway, and Dalarna County, Sweden during the winter season of 2018-2019. I took samples of crop contents and body measurements from each culled bird; in addition, I took pine material from selected, control and random pine trees at each site. There were four levels of pine samples: 1) crop contents, 2) selected tree (plant), 3) control tree (patch) and 4) random tree (habitat). I identified two plant parts, 1) needles and 2) twigs with needles and cone(s), as dominating within the crops. I conducted analysis on all pine samples, which included measuring plant secondary metabolites (PSM) and nutrients.

In this study area, male capercaillies ate mostly Scots pine needles, but adults tended to eat more twigs with needles and cones than juveniles. The twigs with needles and cones had lower levels of PSM and were thicker than needles in diameter, which may explain increased selection from adults with more experience, bigger beaks and bodies. I found no difference in PSM or nutrient content between plant, patch and habitat. Nutrient levels were higher in crops than in the other three sample categories. Consequently, male capercaillies seemed to select pine material with higher crude protein content regardless of selected feeding tree. Further, browsing strategies seemed to differ between adult and juvenile males. For juveniles, PSM levels were lower at the habitat level and nutrient levels were higher at the patch level compared to adults. These results suggest that predicting selected feeding tree for male capercaillies on the basis of PSM and nutrient levels is not possible. Factors other than nutritional quality of pine will probably better explain the phenomena of male capercaillie flocking to certain areas during winter.

Sammendrag

Gjennom vintersesongen har storfuglen bare tungt fordøyelig mat tilgjengelig. For å løse dette spiser fuglene mer for å kompensere for det lave energiinnholdet i dietten. Når vinteren kommer bytter storfuglen diett til furu, og dette er som regel hovedkilden for mat fra november til mars. Eldre bestand av furu er foretrukket av storfugl gjennom vinteren og arten er så godt tilpasset at de i noen tilfeller kan legge på seg i løpet av en vintersesong.

Jeg samlet inn 19 tiurer skutt med rifle i furutrær i løpet av vinteren 2018-2019 i Innlandet, Norge og Dalarna, Sverige. Jeg registrerte kroppsmål og samlet prøver fra hver krope og tilfeldig furumateriale fra valgt, kontroll og tilfeldig tre. Med dette designet hadde studiet 4 nivåer av furumateriale med materiale fra krope, fra valgt tre (plante), fra kontroll tre (fleck) og fra tilfeldig tre (habitat). To plantedeler, 1) nåler og 2) kvist med nåler og skudd/kongler, var dominerende i kropose og videre analyser ble gjort på disse på alle nivåer inkludert ekstraherte verdier av motstandstoffer og næring.

I dette studieområdene spiste tiur for det meste furunåler, men voksne fugler spiste mer kvist med nåler og kongler enn de unge. Kvister med nåler og kongler hadde mindre nivå av motstandstoff samt at de var større enn nåler i diameter, som muligens kan forklare seleksjonen fra voksne fugler med mer erfaring, større nebb og kropp. Det var ingen forskjell mellom plante, flekk og habitat i motstandstoff- og næring. I kropose var bare næringsinnholdet forskjellig fra de andre 3 nivåene. Som følge av dette velger tiur det mest næringsrike furumateriale uavhengig av selektert beitetre. Videre ser det ut til at beitestrategien mellom gamle og unge er forskjellig. Det var lavere konsentrasjon av motstandstoffer på habitatnivå og høyere næringsinnhold på flekknivå brukt av unge enn av eldre tiurer. Resultatene tyder på at det ikke er mulig å forklare selektert beitetre på bakgrunn av motstandstoffer og næringsinnhold. Trolig er det andre faktorer enn næringskvalitet som spiller en større rolle når tiur flokker seg i bestemte områder på vinteren.

1. Introduction

Grouse (*Tetraoninae*) belong to the group of Holarctic birds adapted to cold climates, which inhabit arctic, alpine, boreal and temperate regions. They are resident species, and spend the winters in northern or mountainous habitats (Watson & Moss 2008). Their diets depend on the species adaptations to their respective habitats (Gonzalez *et al.* 2012), age of birds (Wegge & Kastdalen 2008), and food availability throughout the year (Pendergast & Boag 1970; Summers *et al.* 2004). In winter, most grouse are monophagous and the Nordic grouse species changes behavior (Marjakangas 1992) and they switch towards a stodgey diet (Bergerud & Gratson 1988; Saniga 1998; Bocca *et al.* 2014). After spring snowmelt, they rapidly switch back to more nutritious diets (Pulliainen & Tunkkari 1991; Odden *et al.* 2003). Because the winter diet contains lower levels of proteins and higher levels of fiber (Brittas 1988), dietary changes between seasons may influence individual energy levels and subsequently body conditions (Andreev 1991a; Andreev 1992; Andreev & Linden 1994).

Plants chemical characteristics such as nutrient quality (Pulliainen 1970b) and plant secondary metabolites (Spiteller, Jørgensen & Fath 2008) control the palatability of plants. Therefore, nutrient quality and secondary metabolites in plants may influence and drive browsing patterns and the selection of individual plants. On the other hand, Bryant and Kuropat (1980) showed that for some ptarmigan species (i.e. *Lagopus lagopus*, *L. muta*, *L. leucura*) energy, nutrient and fibre content of the food probably do not affect the palatability, digestibility or nutrient content during winter. Instead, the contents of secondary metabolites probably control palatability, digestibility and nutrient quality (Bryant & Kuropat 1980; Wang *et al.* 2012). During winter, certain grouse species (e.g. *Canachites Canadensis*, *Dendragapus obscurus* etc.) that browse on conifers (*Pinophyta*), tend to avoid high levels of plant secondary metabolites and also select needles with higher nutrient levels (Gurchinoff & Robinson 1972). Grouse may also avoid coniferous needles that have high plant secondary metabolite levels because coniferous needles have a high antimicrobial activity (Ellison 1976). Needle age may also affect the nutrient and secondary metabolite levels in coniferous needles (Lowry 1968), and subsequently the browsing by grouse (Remington & Hoffman 1996). As coniferous needles age, protein levels decrease and essential oils increase. The latter has an inhibitory effect upon rumen microbes in deer species (*Cervidae*), and may be apply to grouse species feeding on coniferous tree species (Oh *et al.* 1970). In addition to fluctuating plant secondary metabolite levels between trees

and time (Nerg *et al.* 1994; Thoss, O'Reilly-Wapstra & Iason 2007), coniferous needles generally have low levels of digestibility. To solve this, grouse eat large volumes to compensate for the low energy levels (Pendergast & Boag 1971).

The capercaillie (*Tetrao urogallus*) is probably the tetraonid species that is most resistant and best adapted to harsh winter conditions in the forest. Although capercaillie distribution is partially limited by winter conditions and human activity (Gjerde & Wegge 1987; Thiel *et al.* 2011), male capercaillies may increase body fat levels during winter (Hissa *et al.* 1990). As winter approaches, the capercaillie switch from a diverse diet to eating mainly Scots pine (*Pinus sylvestris*) (Pulliainen 1970a). During the winter months (November to March) pine dominates the diet with sporadic intake of other species (e.g. needles and berries from juniper (*Juniperus*)) (Seiskari 1962). Therefore, during the winter season the capercaillies prefer habitats containing coniferous forest stands dominated by Scots pine (Gjerde & Wegge 1989). The preferred forest structure may have lower overstory densities and relatively open surroundings (Gjerde 1991; Storch 1993).

During winter, capercaillies may be observed in flocks (Koskimies 1957), and they usually feed on the same trees year after year (Lindroth & Lindgren 1950). These trees are usually individuals that have been weakened in some way such as dying, decayed, malformed or mechanically injured. This phenomena may come from the capercaillie selectively feeding, as physiologically stressed conifers may produce less total plant secondary metabolites than healthy trees (Kozłowski 1971; Honkanen, Haukioja & Kitunen 1999). Andreev (Andreev 1991b) reported that the male black-billed capercaillies (*Tetrao urogalloides*) used older, open forests in winter because the trees and branches in denser younger forests (preferred by the female capercaillies) could not support their body weight. This may also be the case for the capercaillie in Scandinavia as the males tends to use sparse, older and probably taller and bigger trees than females during winter (Seiskari 1962; Gjerde 1991; Thiel *et al.* 2007).

Habitat selection by capercaillies during winter may be explained by predators, temperature or nutrients. Pulliainen (1970a) showed that selected pine material in the capercaillie's crop had higher nutrient values than non-selected pine material in feeding trees and control trees. Spidsø & Korsmo (1994), and Iason *et al.* (2011) showed that the selected feeding trees had lower plant secondary metabolite values than control trees. In this thesis, I provide a multi-scale study for male capercaillie feeding patterns and habitat selection during winter based on Scots pine phytochemistry. I hypothesize that nutrient and plant secondary metabolite

levels in Scots pine influences winter habitat selection and feeding patterns of male capercaillie on multiple scales. I evaluate potential effects of nutrients and plant secondary metabolites on male capercaillie selection at the following levels of scale; 1) crop, 2) plant, 3) patch and 4) habitat. I chose the male capercaillie as the study subject because they are easier to spot feeding during winter season compared to female capercaillie, and have a higher probability to be observed in flocks (Liukkonen, Bisi & Kurki 2007). I predict that plant material selected by male capercaillies would differ in nutrient quality and plant secondary metabolite values from other non-selected plant material at different scales, with the selected plant material having higher nutrient content and lower plant secondary metabolite values. I also predict that older and bigger males will have different feeding patterns and feed on plant material with different quality than the younger and smaller individuals. Up to 25% difference in body weight together with experience garnered over successive winters may reveal different foraging strategies between adults and juveniles.

2. Material and Methods

2.1 Study area

I collected samples during winter 2018-2019, in the municipalities of Rendalen, Stor-Elvdal and Åsnes in Innlandet County, Norway and within Älvdalen municipality of Dalarna County, Sweden. Lichen (*Lichenes*) – and bog forests with relatively open, old pine forests dominated the study sites. Landscapes consisted of open bogs, small valleys and single spruce (*Picea abies*) trees from all age classes. For the sampled birds and pine material (selected, control and random tree) elevations varied between 400 - 800 m. The temperature during the sampling averaged at -8 °C (SMHI 2019; Yr 2019). During days with successful sampling, the wind speed averaged at 1.5 meters/second. A deep layer of snow covered the ground in the entire study area the whole sampling season, and maximum snow depth observed during sampling was >1 m.

2.2 Fieldwork

I collected nineteen male capercaillie by culling with rifles. Seventeen of these were complete samples (crop and associated pine material from selected, control and random trees) while two samples contained only crop samples. The fieldwork lasted from 9 December 2018 to 26 February 2019 with a pause during 24 – 31 December 2018. The traditional hunting season closes on 23 December (Miljødirektoratet 2019). To be able to hunt capercaillie in Norway in January and February I successfully applied to the Norwegian Environment Agency for permit to harvest capercaillie after hunting season (see Appendix 1 for permit). Permits from landowners were also obtained and I notified municipalities and local police of my activities. In Sweden, the traditional hunting season for capercaillie starts 25th of August and ends 31th of January (Svenska-Jägareförbundet 2019), and I were able to collect samples during the regular hunting season in that country without needing to apply for an exemption, as I did not collect birds in February in Sweden. In total, sampling occurred over 32 different days during the three months December, January and February. During the sampling, capercaillies were collected 14 days. I observed a mean of 11.6 male capercaillies and shot 1.5 capercaillies per successful day. On unsuccessful days (n = 18), I observed 1.4 capercaillie males per day. Culling was most effective in December (n = 8) and I observed eight and shot one capercaillie per day of hunting during that month. In January, I

observed six and culled 0.4 per day ($n = 15$), and in February I observed 3.2 and culled 0.55 per day ($n = 9$).

2.2.1 Sampling of birds

The birds were sampled with rifles in the calibre 6.5x55 Swedish or 7.62x51mm with a scope with adjustable magnitude from 3 to 16 and with a 42 to 56 mm lens diameter. I searched old and relatively open mature pine forests during winter, and spotted feeding male capercaillies were stalked and shot. During good conditions, birds are relatively easy to spot at distances >500 m (dependent on forest density, terrain type etc.). When trees are covered in snow, male capercaillie are easy to spot while feeding in a pine trees because of their black plumage contrast with a white background, which makes them easier to hunt. Conversely, it is harder to spot a feeding capercaillies when trees are not covered in snow and they are usually first discovered at distances <200 m during these conditions, the normal range for shooting. Average successful shooting distance was 170 m (90 - 240 m).



Male capercaillies observed during “good conditions” in January. Photo: Jonas K G Hagen.

Before I extracted the crops from the birds, I made body measurements and estimated ages. Each bird was aged as either adult (older than one year) or juvenile (younger than one year). The beak height (mm) was measured with a calliper, and birds were weighed (kg) with a digital scale. I removed the skin over the breast muscles and then removed the exposed crop and placed it in a zip-lock bag and recorded the bird identification and location. The zip-lock bags were stored in a -20 degree C freezer.



Accessing the capercaillies crop (example from a black grouse). Photo: Marte Bakka Haugen.

2.2.2 Sampling of pine material

I used a shotgun to sample the associated pine material for each individual capercaillie. Pine material were sampled with 12-gauge shotgun with a 2-6 US shot dependent on what was available at the time. Starting with the tree the capercaillie was sampled from, I collected pine material from the approximate apparent height (the capercaillie was sitting) by shooting the sprigs down. Pine material was shot down and collected into zip-lock bags and marked appropriate. The same procedure was performed for the control and random trees. The control trees were chosen as the nearest tree to have (1) no evidence of browsing by capercaillie or presence of capercaillie (no pellets below tree, no discarded pine material below tree, no visible damage to branches, no snow removed from branches etc.), and (2) approximate same height (big enough to possibly be selected by capercaillie). The random trees were chosen as the closest tree from a point 200 m away in a random cardinal direction and that fulfilled the same requirements (as the control trees). In this design, the bird's crops served as the lowest level scale, selected pines served (i.e. plant) as the second lowest level of the scaling, the control trees (i.e. patch) served as the third level, and the random trees (i.e. habitat) served as the highest level in the scale. If present, pine material cut-offs left by the bird on the ground below the selected tree were also collected in order to investigate if the capercaillie selectively spits out initially selected pine material (this served as a fifth level, "discarded"). Coordinates of locations of the selected, non-selected and random trees were stored. When finished sampling pine material for the specific bird, the zip-lock bags containing pine material were stored together with the zip-lock bags containing crops in a -20 freezer.

2.3 Laboratory methods

2.3.1 Mapping crop content

The crops were thawed (around 15 minutes), and they then were turned inside out and the interior skin layer scraped to get 100% of the crop contents. Crop contents were grouped into different plant parts. There was no need to group the crop content into different plant species as 100% of all crop contents from 18 (1 crop was empty) crops were Scots pine. I found eight distinct different plant parts in the crop contents which were named; needles (hereafter N), twigs (hereafter T), yearling cones (hereafter C), old cones (>1 year old, hereafter OC), twigs with a small quantity of needles either bitten off or not fully grown (hereafter TNS), twigs <5 full grown needles (hereafter TN<5), twigs with a big quantity of needles (hereafter TNB) and twigs, needles and cones (hereafter TNC, pictures appendix 2). I grouped the plant parts by checking if anything was attached to the needles. If there was no other plant part attached (E.g. twig) it was determined as N. If the needle(s) had only a twig attached it was determined as either TNB, TN<5 or TNS dependent of the number of needles attached to the twig and the shape of those needles (bitten off by a capercaillie or not fully grown). If the needles were attached to a twig with a cone, they were determined into TNC. I also detected single yearling cones, old cones and twigs. These were determined as C, OC and T, respectively. For every T, TNS, TN<5, TNB, TNC detected and a subsample of N, I measured bite diameter (i.e. width). If there was more than five of each distinct plant part detected per crop, I measured five randomly selected. I also measured the total wet weight (g) for all T, TNS, TN<5, TNB and TNC detected in the crops. For N, C and OC I also measured total wet weight (g). See pictures of the distinct plant parts in Appendix 2.

2.3.2 Mimicking sampled pine material from crops

Sampled pine material from plant, patch and habitat trees had a diameter well beneath 1 cm in diameter, but still visually larger than the average bite diameter for selected material (in the crops) at around 0.35 cm. I cut the sprigs with a bent scissor (very similar to a capercaillie beak) to make the samples from the control and random trees as visually similar as possible to the actual selected plant parts from the crops. I only cut N and TNC as these plant parts were the dominant (highest percentage weight and proportions) in the crops of the birds. I cut 5 different TNC from each sample for each birds. I measured mimicked bite diameter, wet

weight for each mimicked TNC and total wet weight for the mimicked sample. For N, I only measured total wet weight.

2.3.3 Plant secondary metabolite and nutrient values

Plant secondary metabolites (hereafter, PSM) and crude protein (i.e. nutrients) from the pine samples were quantified to investigate winter diet selectivity of capercaillie. Most of the weight in crops consisted of N and TNC. These two plant parts were selected to analysis because simultaneously having the biggest proportions in the crop as well as having enough weight to perform analysis on. Each sampled plant part (N, TNC) per scale (crop, plant, patch, habitat and discarded) was divided into two subsamples for analysing PSM and nutrients respectively. The samples were coarsely ground (<2mm particle size) with a mortar and pestle in liquid nitrogen and weighted into their respective vials for analysis (stored in -20° C freezer).

The first subsample of 50 mg (wet weight) was used to assess total phenolic content using a colorimetric assay with a Folin-Ciocalteu reagent (Ainsworth & Gillespie 2007). The ground pine material was extracted in 1.0 ml of 100% methanol for 24 hours in a 2 ml microcentrifuge tube. The samples were then placed in a sonicating water bath and sonicated for two 3-min periods at 25°C, centrifuged at 13g for a period of 5 min and filtered through glass wool into an 1.5 mL micro-centrifuge tube. The extract was diluted using 20 µl of the extract with 30 µl of 100% methanol. Gallic acid (# 92-6-15, Acros Organics/Thermo Fisher Scientific; 2000 Park Lane Drive, Pittsburgh, PA 15275, USA) diluted in methanol was used as a standard (0 to 0.05 mg/mL). To detect phenolics in samples and standards, 200 µl of 10% Folin-Ciocalteu reagent to triplicate wells and 800 µl of 700 mM sodium Carbonate (Na₂CO₃ was added 0.02 ml of each extract and mixed by multi-channel pipettes. After allowing the solution to react for two hours at room temperature, the absorbance of each reaction at 765 nm was measured using a BioTek Synergy MX multi-mode plate reader. Total phenolic concentrations were quantified as mg gallic acid (3,4,5-trihydroxybenzoic acid) equivalents/g dry mass (Frye *et al.* 2013). The second subsample of 1.5-2.1 g was dried at 60 °C and sent to Dairy One Forage Laboratory (Ithaca, NY, USA) for analysis of nitrogen content using combustion methods. Nitrogen was converted into crude protein by multiplying the nitrogen content by 6.25. Proteins usually have 16% nitrogen content and therefore the nitrogen content multiplied by 6.25 (or 100/16) is termed crude protein (Robbins 1983). Crude protein was reported as percentage of dry mass.

I chose phenolics for the analysis because the compound cause negative energetic effects for herbivores browsing (Sorensen, McLister & Dearing 2005), and is used by the plant as a defence mechanism against herbivores (Spiteller, Jørgensen & Fath 2008; Hansen *et al.* 2016). Capercaillie are also known to avoid trees with high PSM values during winter season (Spidso & Korsmo 1994; Iason *et al.* 2011). Crude protein was chosen because the compound is a critical nutrient for wildlife and is converted into biomass for herbivores (Mattson 1980). Crude protein increase the probability of plant being selected by a free-ranging grouse species (Frye *et al.* 2013) including capercaillie (Pulliainen 1970a).

2.4 Data analysis

Out of the 19 male capercaillie sampled during the project, one was excluded due to an empty crop and the remaining 18 were included in the analysis. To investigate age/size of the bird and feeding preference I used beak height (mm) as a proxy. I used beak height because it is a more precise measurement than bodyweight. The latter can be affected by crop, gizzard and gut being empty or not. Age was not included as a variable in the analysis due to imprecision in age classification. Discarded pine material was also not included in any analysis due to small sample (n=6). One bird was excluded from analysis as beak height was not recorded. Total intake of phenolics (mg) and crude protein (gr) for N and TNC was calculated by multiplying wet weight of plant part in crop with dry/wet weight ratio to get dry weight. Then, dry weight of N/TNC content from crops was multiplied by concentration of phenolics (mg GA equivalent/gr dw) and crude protein (% of dry mass). This was done the same way for scales plant, patch and habitat to calculate potential intake. I mimicked potential intake using the same weights of plant parts from the crops.

To investigate possible differences in feeding pattern across beak heights, I fitted multiple models. To detect possible differences in total crop content (gr) I fitted a linear model with the explanatory variable beak height (mm). I also fitted beta regressions to investigate possible differences in N and TNC proportions of the crop, with the explanatory variable beak height. Beta regression models were used because these models better handles proportions (Douma & Weedon 2019). To examine possible selection of plant parts throughout the day I fitted a linear model with total crop content and a beta regression for N proportion and TNC proportion with time of day (sampled) as explanatory variable. The models were presented with predictions plots.

To compare total phenolic concentration (mg GA equivalent/gr dry-weight) and crude protein (% of dry-weight) for plant parts (N and TNC) at the different scales (crop, plant, patch and habitat) I used a two-way ANOVA presented in boxplots. To examine the relationship between beak height and the selectivity of browsing of phenolics in the different plant parts (N and TNC) I fitted linear models with total phenolic concentration for plant parts at each scale as the response variable and beak height as explanatory variables. In addition, for examining the relationship between beak height and browsing of crude protein in the different plant parts (N and TNC) I fitted beta regressions with Crude protein proportions for plant parts at each scale as the response variable and beak height as explanatory variable. Relationships were presented with predictions plots.

I used paired samples t-test or paired samples Wilcoxon test (if the assumption of normality violated for paired samples t-test) to compare total intake and possible intake of phenolics (mg) and crude protein (gr) between the scales crop-plant, crop-patch and crop-habitat. All statistical analysis were conducted in program R (R Development Core Team 2017).

3. Results

The 18 male capercaillie crops examined consisted of 100% Scots pine. The two dominant plant parts in the crop were N (needles) and TNC (twigs with needles and cones). N proportion averaged at 70%, ranging from 33 to 100%. TNC proportion averaged at 11%, ranging from 0 to 36%. Bite diameter for N averaged at 1.2 mm, ranging from 0.8 to 1.5 mm. Bite diameter for TNC averaged at 3.5 mm, ranging from 2.8 to 5.5 mm. Time of day sampled had a significant positive relationship with total crop content (gr) ($F_{23,4} = 1.16$, $p < 0.01$, $R^2 = 0.568$). Crop content increased by 0.17 gr for every hour into the day (Figure 1).



Figure 1. Predicted total crop content (wet weight, gr) with time into the day.

I found no relationship between beak height (mm) and total crop content (gr) ($p > 0.05$). However, there was a significant negative relationship between beak height and N proportion (Log-likelihood $_3 = 7.658$, $p = 0.021$, pseudo- $R^2 = 0.172$). For every mm beak height increased the odds for having more N decreased by 0.83 or 17% (Figure 2).

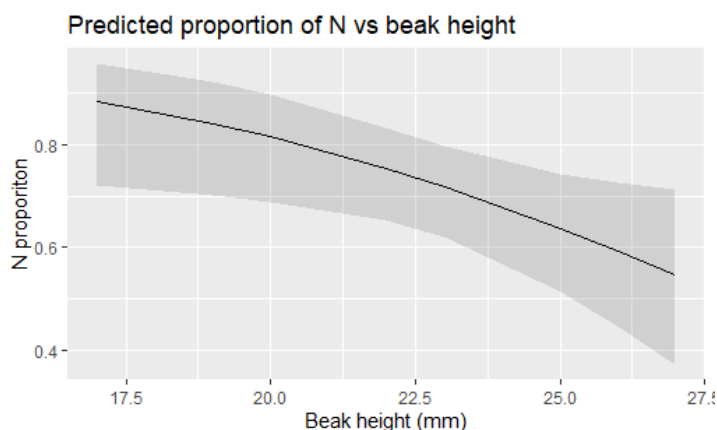


Figure 2. Predicted proportion of N with increasing beak height (mm).

There was a weak positive relationship between beak height and TNC proportion (Log-likelihood $\chi^2 = 56.36$, $p = 0.075$, pseudo- $R^2 = 0.080$). For every mm beak height increased the odds for having more TNC increased by 1.18 or 18% (Figure 3).

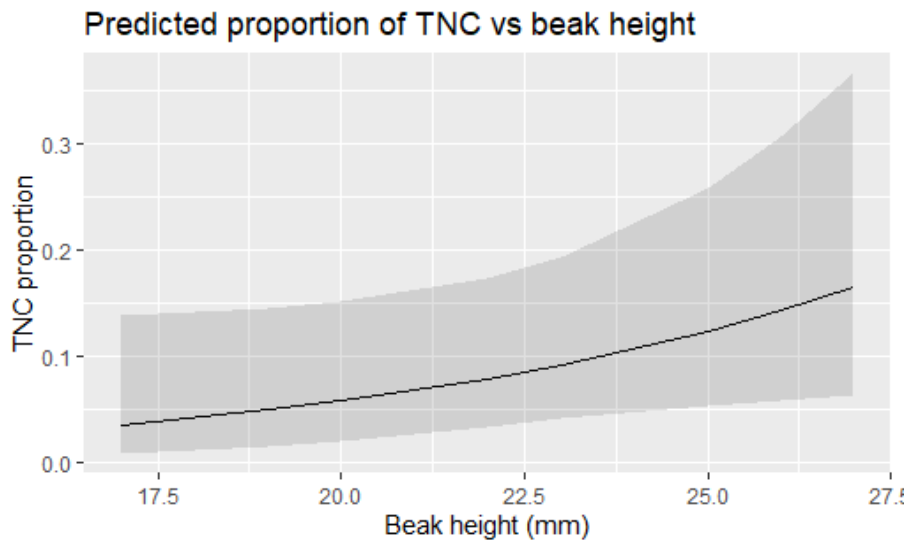


Figure 3. Predicted proportion of TNC with increasing beak height (mm).

Time of day showed no relationship with N proportion ($p = 0.51$), while TNC proportion (Log-likelihood $\chi^2 = 59.15$, $p = 0.019$, pseudo- $R^2 = 0.23$) showed a positive relationship. The odds of having more TNC increased by 1.003 or 0.3% (Figure 4).

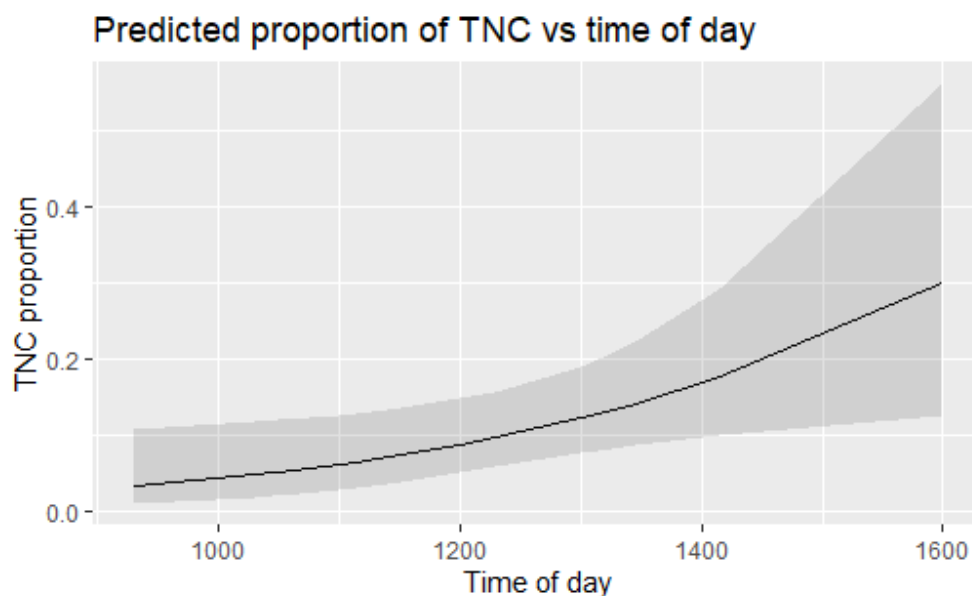


Figure 4. Predicted TNC proportion with time into the day.

Total phenolic concentration varied between the two plant parts ($F_{1,100} = 9.815$, $p = 0.002$), but not between scale ($F_{3,100} = 0.733$, $p = 0.534$) and the interaction between scale and plant part ($F_{3,100} = 0.159$, $p = 0.923$). The concentration of phenolics in TNC was 4.133 mg lower than in N (Figure 5).

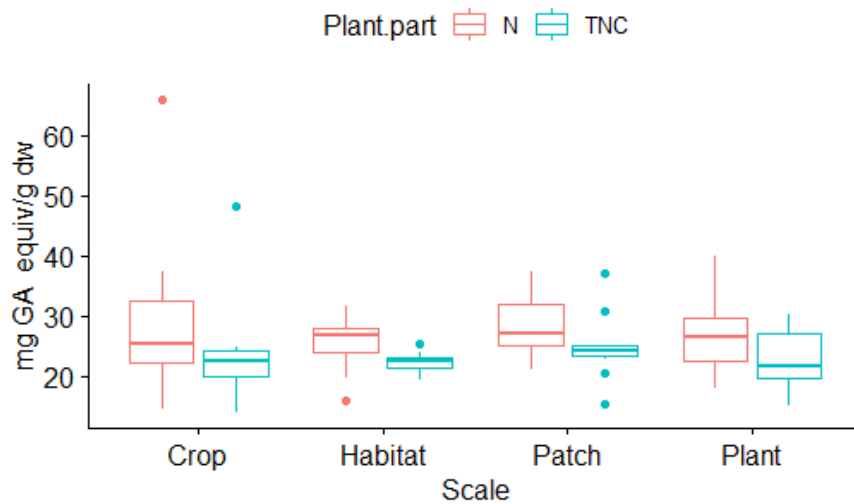


Figure 5. Average phenolic concentrations at the different scales (crop, plant, patch, habitat) for the different plant parts (N, TNC).

There was no relationship between beak height and Phenolic concentration for N and TNC at the scales crop, plant and patch ($p > 0.05$). However, phenolic concentration for N ($F_{1,13} = 6.336$, $p = 0.025$, $R^2 = 0.276$) had a significant positive relationships with beak height at habitat scale while TNC ($F_{1,9} = 4.601$, $p = 0.060$, $R^2 = 0.264$) showed a positive relationship with beak height at habitat scale. For every mm beak height increased phenolic concentration increased by 0.76 for N (figure 6) and 0.31 for TNC (figure 7).

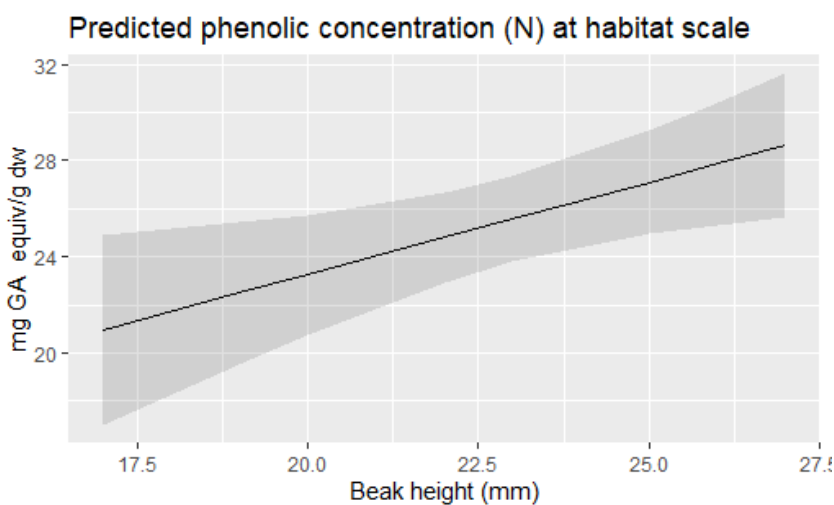


Figure 6. Predicted phenolic concentration (N) at habitat scale with beak height (mm).

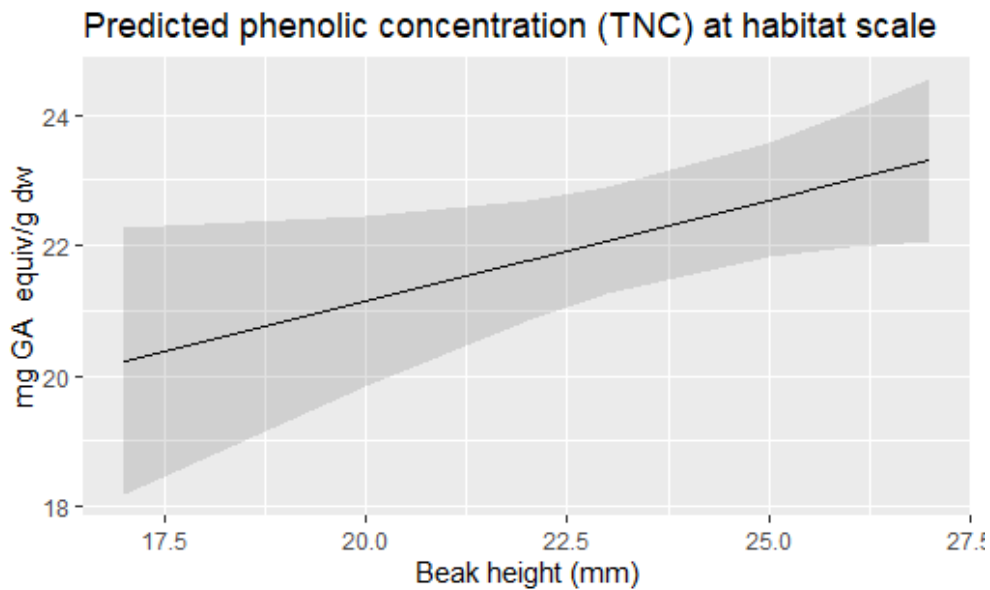


Figure 7. Predicted phenolic concentration (TNC) at habitat scale with beak height (mm).

Crude protein varied between the four scales ($F_{3,91} = 9.526$, $p < 0.001$), but not between plant part ($F_{1,91} = 0.567$, $p = 0.454$) and the interaction of scale and plant part ($F_{3,91} = 0.245$, $p = 0.865$). Crop had higher content of crude protein than plant ($p = 0.001$), patch ($p < 0.001$) and habitat ($p < 0.001$) (Figure 8).

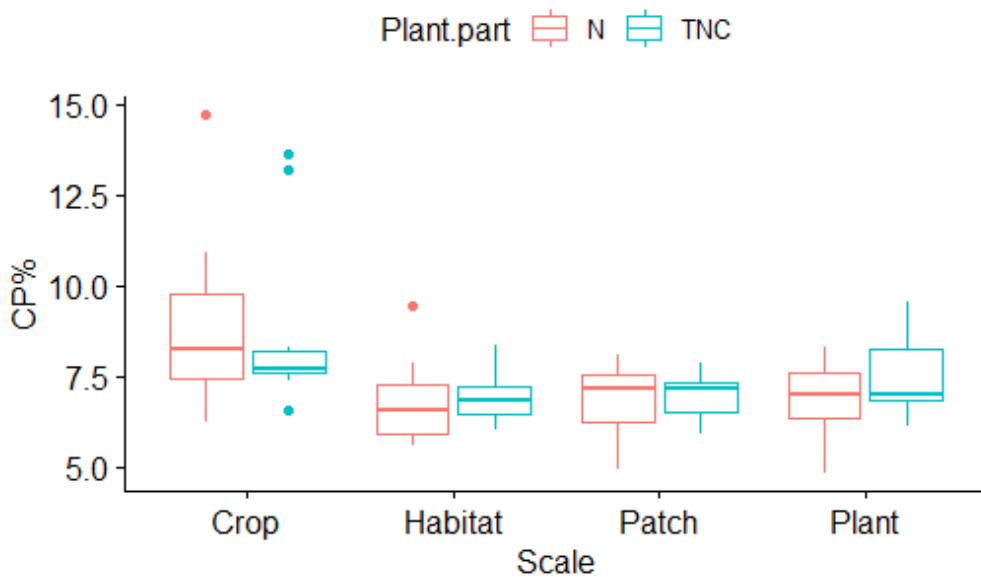


Figure 8. Average crude protein content at the different scales (crop, plant, patch, habitat) for the different plant parts (N, TNC).

There was no relationship between beak height and Crude protein content for N and TNC at the scales crop, plant and habitat ($p > 0.05$). However, crude protein content in N (Log-likelihood $_3 = 47.87$, $p = 0.041$, pseudo- $R^2 = 0.237$) and TNC (Log-likelihood $_3 = 42.36$, $p = 0.033$, pseudo- $R^2 = 0.293$) had significant negative relationships with beak height at patch scale. For every mm beak height increased the odds for having more crude protein in N at patch scale decreased by 0.97 or 3% (Figure 9) and the odds of having more crude protein in TNC at patch scale decreased by 0.98 or 2% (Figure 10).

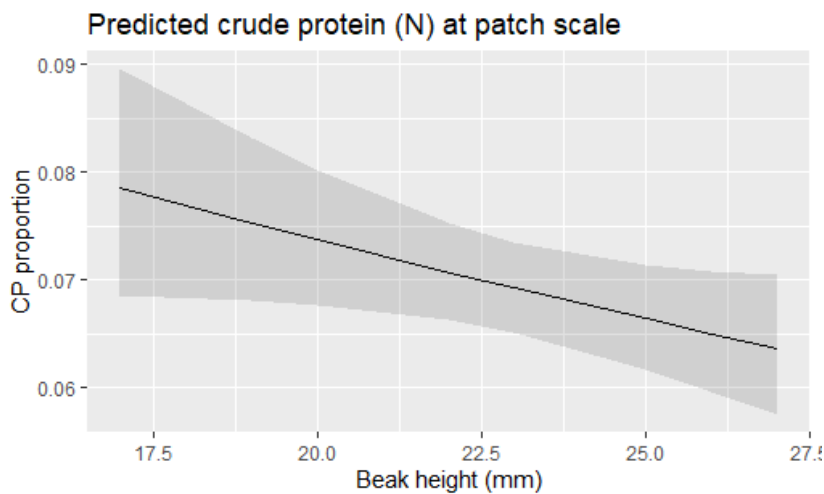


Figure 9. Predicted crude protein proportion (N) at patch scale with beak height (mm).

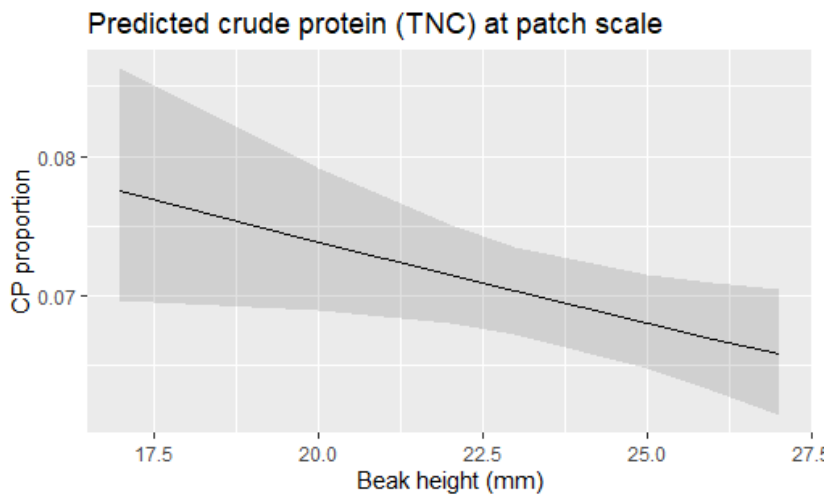


Figure 10. Predicted crude protein proportion (TNC) at patch scale with beak height (mm).

Total and potential intake of phenolics and crude protein did not differ between scales crop-plant ($p > 0.05$), crop-patch ($p > 0.05$) and crop-habitat ($p > 0.05$).

4. Discussion

In this study I show that male capercaillie select pine, mainly needles (N) and twigs with needles and cones (TNC), during winter. Total crop content (gr) and TNC proportion increased throughout the day. Total phenolic concentration varied only between the plant parts N and TNC. The total phenolic concentration was significantly lower in TNC than in N. Phenolic concentration in N and TNC was only related with beak height at habitat scale, and was positively correlated.

Crude protein content varied only between scales. Crude protein content did not differ between plant, patch and habitat. However, the birds had selected pine material with higher crude protein content as crop was significantly higher in crude protein content. Crude protein content for both N and TNC was only related to beak height at patch scale and was negatively correlated. Total intake and potential intake of phenolics (mg) and crude protein (gr) did not differ between crop and plant, patch and habitat scales.

This, and other studies (Pulliainen 1970a) confirms that the capercaillie have an evident preference for Scots pine during winter feeding season. Nevertheless, other food types can be consumed. Studies from Scotland reports that the capercaillie eats Sitka spruce (*Picea sitchensis*) during winter season (Picozzi, Moss & Catt 1996), and in northern Sweden studies show that some capercaillie eats Norway spruce in the mountainous regions where pine stands are lacking (Erik Ringaby personal communication, April 15th 2020). In Spain, the Cantabrian capercaillie (*Tetrao urogallus cantabricus*) have a strong preference for Pyrenean oak (*Quercus pyrenaica*) in addition to Scots pine during winter (Gonzalez *et al.* 2012). The capercaillie of the Jura mountains in Switzerland depends on fir (*Abies alba*) during winter (Sachot, Perrin & Neet 2003), and the black-billed capercaillie who lives north of 55 degrees in Russia feed exclusively on larch (*Larix*) for seven winter months or longer (Andreev 1991b). The evident variation in winter foods for capercaillie may tell us that their tolerance for PSM is high as they deal with a wide range of coniferous tree species together with oak, and further may indicate that browsing of nutrients is more important.

Increased proportions of TNC and decreased proportions of N in the adult crop may be because of increased physical requirements related to browsing and digesting contents with more fibre. Fibre can increase handling time (cropping, chewing, and rumination) for herbivores (e.g. cervids) feeding on coniferous species (Felton *et al.* 2018). This might also

be the case for capercaillie, and bigger birds with bigger gizzards may have an advantage digesting pine material with fibre. Larger size of all winter food parts have also been reported to be preferred by other bird species (Ramos 1996). When eating greater volumes of low-energy foods during winter (Pendergast & Boag 1971), birds may enlarge their gizzard to meet energy requirements on a heavier structured diet (van Gils *et al.* 2003). As a result, the gizzards probably have fewer but bigger gastroliths (Norris, Norris & Steen 1975), and adult grouse may adapt better to this (Gudmundson 2015) with increased average weight of grit stones inside the gizzard.

Selection of plant material from capercaillie during browsing may also come from a sense of smell and experience related to this. Birds have a well-developed olfactory system and are able to smell phenolics of each other (Conover 2007), and are therefore probably also able to smell and taste foods (Hamrum 1953). The adult capercaillie, whom have a bigger beak (appendix 3) than the juvenile will probably handle browsing of TNC better and may use this together with more experienced sense of smell to browse more effective. This can in turn benefit their daily activity budget and allow for more time being spent vigilant. The sense of smell may also explain the phenomena of discarded pine material below selected feeding trees.

Spidso and Korsmo (1994) reported that capercaillie selected pine trees with high nutrient levels below a certain limit of PSM. When levels of PSM increased, the selection shifted towards the trees with the lowest PSM levels. Similarly, Iason *et al.* (2011) reported that capercaillie avoided trees with higher PSM levels. However, in this study no difference in PSM levels between selected and control trees were detected. Nevertheless, selection towards PSM (phenolics) is evident between adults (increased beak height) and juveniles in this study, with adults having more plant parts with lower PSM. Predicted proportions of N and TNC showed apparent selection with the oldest/biggest birds having less of the worst and more of the best pine plant parts related to PSM concentration. On the other hand, juveniles had lower levels of PSM than adults at habitat level. Predicted TNC proportion also increased throughout the day, which may indicate that male capercaillie become more selective towards PSM throughout the day.

Selection against PSM may also be affected by location and site properties, and levels of two PSM groups (phenolics and monoterpenes) are reported decreasing with increasing elevation (Laracinepittet & Lebreton 1988; Ferrenberg *et al.* 2017). Sun exposure can also play an

important part, and the most exposed pine needles can have higher PSM levels than shaded material (Gleizes *et al.* 1980; Gref & Tenow 1987). There is individual variation in PSM levels between Scots pine trees (Thoss, O'Reilly-Wapstra & Iason 2007; Stolter *et al.* 2010) and levels of PSM might increase through the winter season (Nerg *et al.* 1994) or change with the changing climate (Ghimire *et al.* 2019). Old and fatigued trees have probably lower PSM levels than the younger trees (Kozlowski 1971; Honkanen, Haukioja & Kitunen 1999), this could also come from heavy browsing of the tree as young, as the plants may evolve strong defences during sapling stage only (Bryant, Chapin & Klein 1983).

Pulliainen (1970a) reported that pine material from capercaillie crops had higher nutrient levels than remaining pine material from selected tree and pine material from control trees. In this study, selection of nutrient from Scots pine material by capercaillie seems to be the same, as the crop had higher levels of crude protein than plant, patch and habitat trees, respectively. In addition, juveniles had higher levels of crude protein than adults at patch scale. Habitat and latitude may affect the nutrient levels in pine needles in general (Pensa, Jalkanen & Liblik 2007), but younger needles (first year needles vs second year needles) of Scots pine have proven to be more nutrient rich (Wyka, Zytowskiak & Oleksyn 2016). Since the younger needles contain more crude protein my results indicate that the capercaillie is able to select the most nutrient rich pine material, whom have higher nutrient levels than random controls.

The proportion of young pine material together with increased biomass could possibly be favourable for the capercaillie as nutrient levels in the canopy of the tree increases with higher proportion and amount of needle biomass (Blasko *et al.* 2020). Younger trees may also prove to be less nutrient rich for the capercaillie, and therefore commercialized, lowered age structured forests could therefore jeopardize the nutrient intake of capercaillie (Linden 1984). A skewed nutrient-PSM ratio may affect total consumption negatively (Sjoberg & Linden 1991) and too high ingestion of these compounds can lead to either death or severe physiological weakening in herbivores (Freeland & Janzen 1974). This may also be the reason for the evident selection of mature pine forest by male capercaillie, as these stands probably have higher quality food opportunities together with more snow for roosts (Linden 1981).

Tannin, which is a phenolic compound that binds to proteins, may also play a part in nutrient browsing as the compound can heavily decrease digestibility of nitrogen (DeGabriel *et al.*

2008) and affect fitness for herbivores (Degabriel *et al.* 2009). Nevertheless, Spidso and Korsmo (1994) reported that selected and non-selected pine trees during winter-feeding for capercaillie did not differ in tannin levels. One other factor that probably is favourable is acidification, and this have been reported to increase nutrient levels and decrease PSM levels in Scots pine (Spidso & Korsmo 1993). Ptarmigan winter foods are reported averaging around 10% crude protein (Giesen & Braun 1992), while this study averaging around 7%. This may tell us that capercaillie demand less nutrient rich winter diet than smaller grouse species. Moose-browsing studies have reported the same approximate values as this study of crude protein for Scots pine (Danell *et al.* 1991), and first browsing increases further browsing on the same Scots pine plants for moose (Mathisen, Milner & Skarpe 2017). This might also be the case for capercaillie feeding on the same species with the same crude protein levels.

My results suggest that selection of plant parts is mostly dependent on the individual bird and not time of day and further suggest that that juvenile birds have higher proportions of thinner (diameter) pine material containing more PSM than adults. There was no difference in PSM and nutrient content between crop, plant, patch and habitat except for the nutrient content in crops who were higher in nutrients than the other scales. Consequently, male capercaillie seem to selectively pick pine material with higher crude protein content regardless of selected feeding tree. Subsequently, predicting selected feeding tree on the basis of PSM and nutrient levels results from this study is not evident. Further, juvenile birds probably picks habitats lower in PSM levels than adults, and in addition juveniles probably also picks patches within a habitat with higher nutrient levels than adults. There seems to be different browsing strategies between adult and juvenile male capercaillie. The adults focused more on the plant parts, while the juveniles focused more on habitat and patch quality. The adults may select habitats and patches with more suitability towards vigilant behaviour, and in turn compensate for the worse habitats and patches with increasing and decreasing browsing of the best and worst plant parts in terms of PSM. This may be an adaption from the adult capercaillie feeding in “worse” habitats and patches than the juvenile.

Total and potential total intake of PSM and nutrients did not differ between the crop and the other three scales plant, patch and habitat. The idea of a conflict between forestry and winter habitat is evident, both because the capercaillie prefers mature trees that are favourable for forestry, and because capercaillie in some cases can do damage on the forest (Andersson

1970). In the context of the results of this study, removal of selected feeding trees at the time the specific birds was sampled would not have been harmful to the male capercaillie in terms of intake of PSM and nutrients as the potential intake from the random control samples was based on the same food quantity from each specific bird's crop. Also, this together with the other results from this study suggest that predicting selected feeding tree for male capercaillies on the basis of PSM and nutrient levels is not possible, and other factors than nutritional quality of pine will probably better explain the phenomena of male capercaillie flocking to certain areas during winter.

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Appendix 1



Høgskolen i Innlandet
Postboks 400
2418 ELVERUM

Trondheim, 03.01.2019

Deres ref.:
[Deres ref.]

Vår ref. (bes oppgitt ved svar):
2018/13803

Saksbehandler:
Ole Roar Davidsen

Tillatelse til innsamling av tiur og orrhane for forskning

Høgskolen i Innlandet (INN) gis tillatelse til innsamling av inntil 10 tiurer og 10 orrhane i Hedmark fylke i tilknytning til forskningsprosjekt.

Bakgrunn

Vi viser til søknad av 18. desember 2018 om tillatelse til å felle 10 tiurer og 10 orrhane i forbindelse med forskningsprosjekt som skal undersøke næringsvalget til tiur og orrhane.

Vurdering

Søknaden er behandlet etter forskrift 14. mars 2003 om Innfangning og Innsamling av villt for vitenskapelige eller andre særlige formål, jf. også lov 19. juni 2009 om forvaltning av naturens mangfold, § 18 f. Etter naturmangfoldloven § 7 skal prinsippene i loven §§ 8 til 12 legges til grunn som retningslinjer ved utøvelse av offentlig myndighet. Offentlige avgjørelser som kan få følger for naturmangfoldet skal så langt det er rimelig bygge på eksisterende og tilgjengelig kunnskap om arters bestands situasjon samt effekten av påvirkning, jf. naturmangfoldloven § 8.

Storfugl finnes over hele Norge, men er fåtallig i de nordligste delene da den foretrekker gammel barskog. Bestandsstørrelsen varierer fra år til år da storfugl har naturlige sykliske bestandsvariasjoner. Hekkebestanden i Norge er anslått til å være mellom 80 000 - 100 000 individer. I Norge ble det felt 9 760 storfugl i jaktåret 17/18, i Innlandet fylke ble det felt 4 290 samme jaktår.

Orrfugl finnes over hele Norge, men er fåtallig i de nordligste delene av landet. Bestandsstørrelsen varierer fra år til år da orrfugl har naturlige sykliske bestandsvariasjoner. Hekkebestanden i Norge er anslått til å være mellom 100 000 - 200 000 individer. I Norge ble det felt 19 660 orrfugl i jaktåret 17/18, i Innlandet fylke ble det felt 4 800 samme jaktår.

Uttak av 10 tiur og 10 orrhane vil ikke ha noen effekt på artens bestands situasjon eller overlevelse.

Direktoratet har vurdert og tatt hensyn til den samlede belastningen arten utsettes eller vil bli utsatt for, jf. naturmangfoldloven § 10.

Postadresse: Postboks 5672, Torshov, 7405 Trondheim | Telefon: 02400/73 58 05 00 | Faks: 73 58 05 01
E-post: post@miljodir.no | Internett: www.miljodirektoratet.no | Organisasjonsnummer: 999 601 391
Besøksadresser: Brattørkalla 15, 7010 Trondheim | Grensevingen 7, 0661 Oslo
Besøksadresser Statens naturopplysnings lokalkontorer: Se www.naturopplysn.no

**Tillatelse**

Med hjemmel i forskrift 14. mars 2003 om Innfangning og Innsamling av vilt for vitenskapelige eller andre særlige formål, gis INN ved Torstein Storaas tillatelse til å felle og samle Inn Inntil 10 tjur og 10 orrhøner i Hedmark fylke.

Følgende vilkår gjelder for tillatelsen:

- Tillatelsen gjelder felling og innsamling av Inntil 10 tjur og 10 orrhøner i Hedmark fylke i januar og februar 2019.
- Torstein Storaas bemyndiges til å la andre foreta innsamlingen på sine vegne. Bemyndigelsen skal være skriftlig med henvisning til denne tillatelsen, og skal medbringes under innsamling.
- Skal det innsamlingen foregå i et verneområde må rette vernemyndighet søkes.
- Berørte grunneiere, kommuner og stedlig politistasjon eller lensmannskontor skal varsles før virksomheten finner sted. Det skal opplyses om hva tillatelsen omfatter og tid og sted for aktiviteten, jf. forskrift om vitenskapelig fangst av vilt mv. § 5 varsling til grunneier, kommune og politimyndighet.
- Ved bruk av motorkjøretøy må nødvendige tillatelser være i orden, se rundskriv T-1/96 om lov om motorferdsel i utmark og vassdrag av 10. juni 1977 nr. 82.
- Den som skal utføre fellingen skal ha jegerprøven og det skal benyttes våpen og ammunisjon som er fastsatt for disse artene i forskrift 2. april 2002 om utøvelse av jakt, felling og fangst.
- Denne tillatelse og evt. bemyndigelse skal alltid medbringes under innsamling.
- En kortfattet oppsummering av resultatet fra innsamlingen, herunder antall fugler felt, skal rapporteres til Miljødirektoratet innen 31.mai 2019.

Klageadgang

Vedtaket kan påklages til Klima- og miljødepartementet innen 3 uker, jf. forvaltningsloven §§ 28 og 29. En eventuell klage skal fremsettes for direktoratet, jf. forvaltningsloven § 32.

Hilsen
Miljødirektoratet

Dette dokumentet er elektronisk godkjent



Knut Morten Vangen
seksjonsleder

Ole Roar Davidsen
rådgiver

Tenk miljø - velg digital postkasse fra e-Boks eller Digipost på www.norge.no.

Kopli til:

Fylkesmannen i Innlandet

Postboks 987

2604

LILLEHAMMER

Appendix 2



N. Photo: Jennifer Forbey.



TNC. Photo: Jennifer Forbey.



TNB. Photo: Jennifer Forbey.



TN<5. Photo: Jennifer Forbey.



TNS. Photo: Jennifer Forbey.



T. Photo: Jennifer Forbey.



C. Photo: Jennifer Forbey.



OC. Photo: Jonas K G Hagen.

Appendix 3



Picture of an adult (top) and a juvenile (bottom) male capercaillie. Photo: Jonas K G Hagen.