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Bachelor thesis 2018

The Norwegian grouse-nest survival lottery

Det norske skogshøns-reiroverlevelse lotteriet

Bachelor thesis Inland University

2018

Samtykker til tilgjengeliggjøring i digitalt arkiv Brage JA NEI

Forord

Som lidenskapelig skogsfugl og rypejeger har skolegangen på Evenstad gitt meg et helt annet syn på disse fantastiske fuglene, samt naturen generelt. Gjennom denne oppgaven som har fokusert på reirpredasjon har jeg lært mye nytt om skogsfugl og rype, samt at det videre har skapt mer interesse for videre jobbing innenfor dette fagfeltet. Med dette sagt gleder jeg meg til 2 år til hvor jeg forhåpentligvis skal lære mye mer om disse fuglene.

En stor takk til Torstein Storaas og Torfinn Jahren. Uten dere hadde dette ikke vært mulig, med stor og ikke minst nødvendig hjelp i alt fra statistikk og skriving. Jeg vil også takke familie, venner og medstudenter med støtte underveis i disse 3 årene.

Evenstad, April 2018

Jonas K G Hagen

Abstract

During incubation, hens in gallinaceous species are faced with trade-offs between self-maintenance and metabolic requirements of the eggs. The hen also has to minimize the probability of detection by predators, by nest site selection and nesting behaviour.

I survived daily number and length of recesses, incubation constancy and the timing of recesses of 70 capercaillie (*Tetrao urogallus*), 11 black grouse (*Lyrurus tetrix*) and 18 willow ptarmigan (*Lagopus lagopus*) hens by the use of camera traps during 2009-2015. The differences in nesting behaviour between species were small. Capercaillie, black grouse and willow ptarmigan took 1.84, 2.06 and 2.25 daily recesses averaging 29.10, 25.90 and 26.64 minutes, resulting in incubation constancies of 0.96, 0.96 and 0.95, respectively. Predators detected nests only when the female was sitting on the nest. 31 of 69 (31%) nests were robbed the 2 hours after midnight when the incubation constancy was 0.97. During 04:00 – 06:00 capercaillie took most recesses, but was still sitting 95% of the time on the nest. The difference in nest predation between species cannot be attributed to differences in the observed nesting behaviour.

Julian date, number or length of the recess, incubation constancy or interactions between the factors did not explain differences in nest survival of capercaillie hens. I suggest that variation within females normal incubation behaviour does not affect the probability of nest predation, and that predators generally detect grouse nests when the hen reveal her nest when escaping the approaching predator. The survival of a grouse nest is a lottery where the hen usually has little influence on the outcome.

Sammendrag

Hunfugler hos hønsfuglarter må gjennom rugetiden avveie om de skal investere i seg selv eller sine egg. Hunfugler må også minimere risken for å bli oppdaget fra predatorer gjennom habitatvalg og rugeoppførsel.

Jeg registrerte jeg daglig antall og lengde på rugepauser, rugekonstans og tidspunkt for pauser for 70 storfugl (*Tetrao urogallus*), 11 orrfugl (*Tetrao tetrix*) og 18 lirypehøner (*Lagopus lagopus*) som var overvålet ved hjelp digitale viltkameraer i perioden fra 2009 til 2015. Forskjellene i rugeoppførsel var små. Storfugl, orrfugl og lirype hadde 1.84, 2.06 og 2.25 daglige pauser med en gjennomsnittlig lengde på 29.10, 25.90 og 26.64 minutter. Dette resulterte henholdsvis i en rugekonstans på 0.96, 0.96 og 0.95. Predatorer fant reiret bare når høna var på reiret. 31 av 69 (31%) av reirene ble røvet i de to timene etter midnatt når også rugekonstansen var 0.97. Mellom 04:00 og 06:00 røyer hadde flest pauser, men satt fortsatt på reiret 95% av tiden. Forskjellene i reirpredasjon mellom artene kan ikke kobles mot forskjeller i observert reiroppførsel.

Juliansk dato, antall og lengde på pauser, rugekonstans eller interaksjoner mellom disse faktorene kunne ikke forklare reiroverlevelse hos storfugl. Jeg foreslår at variasjon mellom røyenes normale rugeoppførsel ikke har noen effekt på sjansen for reirpredasjon, samt at predatorer stort sett finner reir da fuglen avslører hvor reir er da hun rømmer. Overlevelsen av hønsfuglreir er et lotteri hvor stort hunfuglen har liten påvirkning på hvordan utfallet blir.

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Introduction

In Gallinaceous (*Galliformes*) birds, the hens nest and incubate on the ground and leave the nest with the chicks after hatching. Ground-nesting bird species are highly vulnerable to predation on incubating female and eggs. The nesting bird need both to avoid being killed and protect the eggs (Conover 2007).

Fennoscandian forest grouse (*Tetraoninae*) are today highly valued game species. Capercaillie (*Tetrao urogallus*) and black grouse (*Lyrurus tetrrix*) are lekking species, while willow ptarmigan (*Lagopus lagopus*) live in pairs. Population size and reproductive output in capercaillie and black grouse have decreased over time (Jahren *et al.* 2016) and willow ptarmigan has been listed as near threatened on the Norwegian red list (Kålås 2015). Increased predation by red fox and pine marten on eggs and chicks are probably an important reason for declining capercaillie and black grouse populations (Jahren 2017). Between 1930 and 2012, crude nest success has dropped down from 89% and 90% to 35% and 55% for capercaillie and black grouse, respectively (Jahren *et al.* 2016).

The probability of nest predation may be affected by 1) Density of predators near nest, 2) Nesting habitat selection, and 3) Behaviour of incubating hen. Predator abundance and activity inside the nesting home range increase probability of predation (Conover 2007). Jahren *et al.* (2017) showed this also in capercaillie and black grouse as density indexes of red fox (*Vulpes vulpes*) and pine marten (*Martes martes*) in winter were the most important factors predicting probability for predation.

Nesting habitat characteristics may affect the probability for predation of nests (Anich, Worland & Martin 2013; Dinkins *et al.* 2014). The visibility of nests may determine probability of predation and which predators that are able to find the nests (Coates & Delehanty 2008; Kolada, Casazza & Sedinger 2009; Fogarty *et al.* 2017). Predation pressure from generalist predators may be higher in heavily fragmented human influenced forests (Andren *et al.* 1985; Kurki *et al.* 2000; Soe *et al.* 2017). Hens selecting nesting habitat in less fragmented forests may increase nest survival. Storaas and Wegge (1987) did however not find any difference in nest losses between habitats in Norwegian capercaillie and black grouse, and proposed the importance of unpredictability in nest choice.

Scents from nests may affect the probability for predators to find nests, dependent on several physically and visual nest factors (Conover 2007). Size of the bird, female body condition and incubation behaviour may affect the production of odours and may possibly influence nesting success (Wiebe & Martin 1997). Incubation behaviour may be measured as number of daily nesting recesses, recess length and incubation constancy (percentage of day incubating), and may be related to hen weight. The food quality during spring affected the weight of the nesting female (Watson & Moss 2008), and the incubation constancy was positively correlated to the females weight (Storaas, Wegge & Kastdalen 2000). Heavy hens probably also reproduce more chicks (Wiebe & Martin 1998; Caizergues & Ellison 2000). As well-nourished females have high incubation constancy, I predicted a positive correlation between incubation constancy and nest survival.

Storaas and Wegge (1997) found that the black grouse hens took more and shorter recesses than the capercaillie hens. I expect the smaller willow ptarmigan hen to take more and shorter recesses. Wilson, Martin and Hannon (2007) suggested that ecological factors such as predation probably influenced nest survival more than nesting behaviour. However, nesting behaviour may directly influence nest predation. As well-nourished hens take few recesses and have high incubation constancy I predict that that nest survival and the indexes of nesting behaviour is correlated, between and within species. I also expect that most nests are robbed at times when the hens take most recesses. In this study I assess the importance of incubation behaviour to nest predation by relating number and length of recesses and incubation constancy of capercaillie, black grouse and willow ptarmigan to the probability of nest predation.

Material and methods

Study area

Incubation data and nest fates come from nests detected in Hedmark and Nord-Trøndelag counties in Norway from 2009 to 2015. The two counties are Norway's biggest measured in forest production. Both counties are situated in the boreal zone and the forests are commercially managed except for some smaller patches with protected areas. The main tree species are Scots pine (*Pinus Sylvestris*) and Norway spruce (*Picea abies*). Deciduous tree species are also regular with birch (*Betula Betula*) the most frequent, but also alder (*Alnus Incana*), rowan (*Sorbus Aucuparia*) and aspen (*Populus Tremula*). Capercaillie, black grouse and willow ptarmigan are common and highly valued game species in the study area.

Searching nests

Nests were located in three ways. 1) Active search for nests using well trained pointing dogs (only Hedmark County with permission from landowner and municipality). 2) Advertisement through media and niche magazines. Media outlets on local, regional and national level were used in early May to invite people to report nest locations. 3) Look up and establish contact with forestry workers who was working in the forest during the spring, and invite them to report nest locations. Additionally, to ensure most of the egg-laying was finished before nests were located, organized searching for nests did not start before 10 of May each year and lasted to the end of June. Nests detected by chance were reported all summer. Camera traps were deployed as soon as possible after nest detection (Jahren 2012).

Digital camera photographs and data work

The digital game cameras used to monitor nests were three different types (Moultrie I-45, 4 MP (Moultrie 2018)) and Bushnell Trophy Cam, 8 MP (Bushnell-corporation 2018) and Wingcam 2 (Winge våpen 2018). All models had infrared motion detectors, an infrared flash and a SD memory card slot. Series of photographs from each nest were scanned for hen behaviour. I registered if the nesting hen was on or off the nest. I used a binary variable, 1 for on, and 0 for off. I used the program Xnview (Xn View 2018) to make the review of the nest pictures more efficient, more like a film. Poor camera mounting (length from camera to nest, vegetation etc.) and concealed hens made it difficult to observe behaviour at every nest. I included 70 capercaillie, 11 black grouse and 18 willow ptarmigan nests in the analysis. The

photographs from these nests were of high enough frequency to detect incubation behaviour. Nests that were excluded from analysis were due to low frequency of photographs (e.g. < 1 per hour) or the hen was concealed by vegetation. Finally, from 70 capercaillie, 11 black grouse and 18 willow ptarmigan nests, I extracted metadata from 909, 161 and 342 photos depicting recess behavior. Metadata included time of day and date. All statistical analysis were conducted in program R (R Development Core Team 2017).

Table 1. *List of nests and number of pictures and number of off/on events related to recesses.*

	Number of nests	Number of pictures used for analysis
Capercaillie	70	909
Black grouse	11	161
Willow Ptarmigan	18	342

To compare the capercaillie, black grouse and willow ptarmigan nesting behaviour (number of daily recesses, recess length and incubation constancy (percentage of day incubating)) I used a one-way anova, with box plots to display it. To display predation peaks (frequency per hour of day), nesting activity peaks (recess frequency per hour of day) and mean incubation constancy per hour of day I used histograms. To measure when the predation peaked I gathered all the data I had for predation events (including nests that had poor camera mounting etc), therefore there are additional nests included to measure predation peaks than nests analysed for incubation behaviour. To examine the relationships between nesting behaviour and nesting success for capercaillie I used a generalized linear model with the explanatory variables number of daily recesses, length of recesses and incubation constancy. I also fitted a model with julian date to investigate potential effects of time on incubation behaviour and fate. Finally, I fitted the interactions between Julian date and number of daily recesses, length of recesses and incubation constancy.

Results

Table 2. *Summary of nesting behaviour for capercaillie, black grouse and willow ptarmigan.*

Species	Number of nests (hatched/predated)	Mean number of recesses per day	Mean length of recess (min)	Mean incubation constancy
Capercaillie	70(44/26)	1.84	29.10	0.96
Black grouse	11(9/2)	2.06	25.90	0.96
Willow ptarmigan	18(16/2)	2.25	26.64	0.95

I found a significant difference in mean number of recesses between the species capercaillie, black grouse and willow ptarmigan ($F_{2,720} = 8.244$, $p < 0.001$). The mean number of recesses was significantly different between capercaillie (1.84) and willow ptarmigan (2.25, $p < 0.001$), but there was no difference between capercaillie and black grouse (2.06, $p = 0.23$) and black grouse and willow ptarmigan ($p = 0.45$; Figure 1).

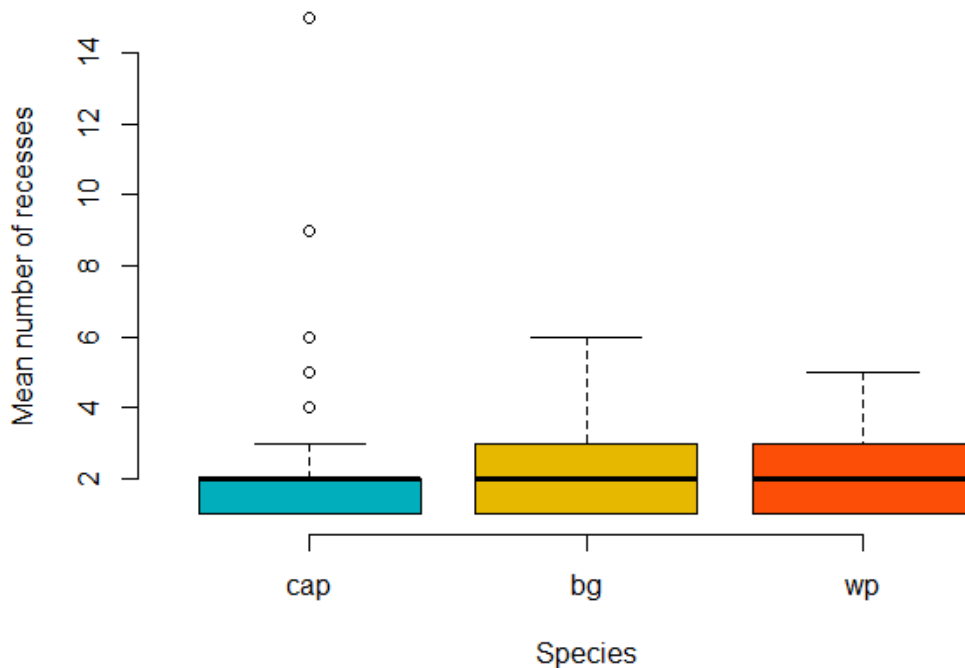


Figure 1. Mean number of recesses for capercaillie (*cap*), black grouse (*bg*) and willow ptarmigan (*wp*).

I found no significant difference in mean length of recesses between the species capercaillie, black grouse and willow ptarmigan ($F_{2,720} = 2.171$, $p=0.115$).

I found a significant difference in mean incubation constancy between the species capercaillie, black grouse and willow ptarmigan ($F_{2,720} = 4.203$, $p=0.015$). The mean incubation constancy was significantly different between capercaillie (0.96) and willow ptarmigan (0.95, $p=0.01$), but there was no difference between capercaillie and black grouse (0.96, $p=0.75$) and black grouse and willow ptarmigan ($p=0.39$; Figure 2).

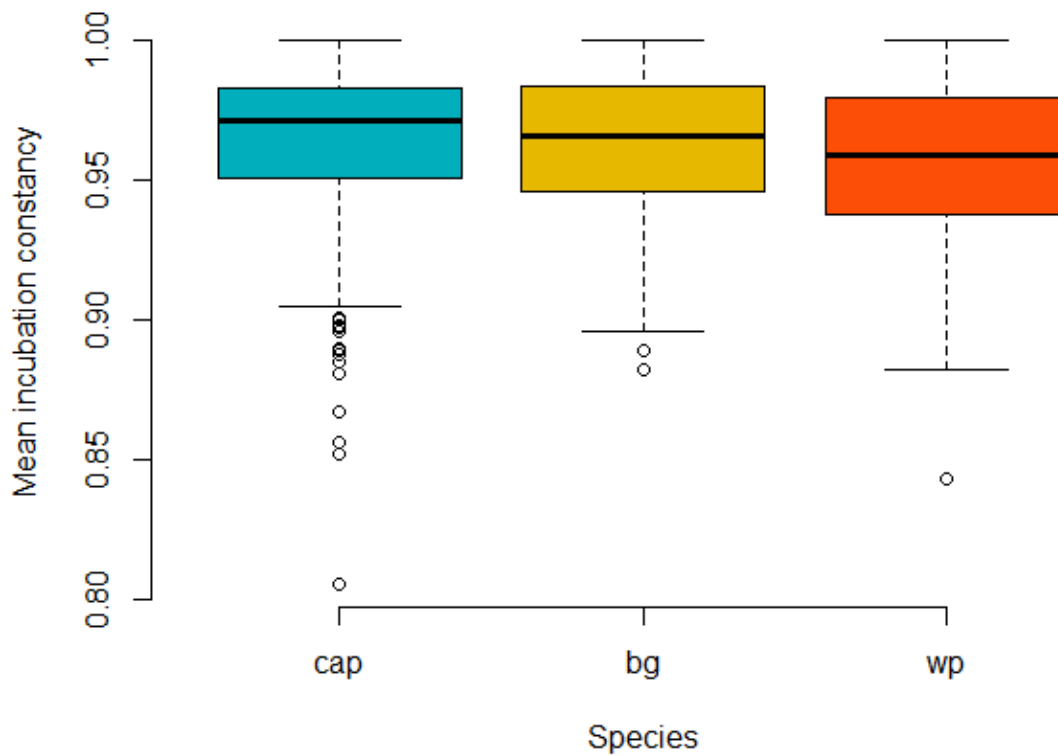


Figure 2. Mean incubation constancy for capercaillie (cap), black grouse (bg) and willow ptarmigan (wp).

There was no relationship between the chance of hatching (nesting success) for capercaillie and the number of recesses, recess length, incubation constancy, Julian date or the interaction between Julian date and number of recesses, recess length and incubation constancy ($p=0,446$).

Predation events peaked the first two hours of the day when 31% of the predation events happened (Figure 3).

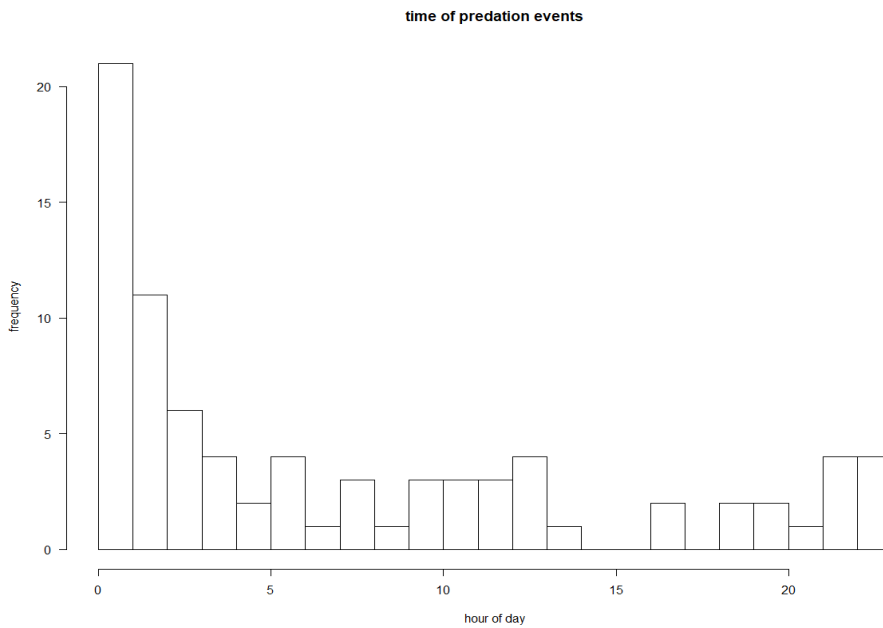


Figure 3. Histogram over predation frequency distributed for each hour of the day.

Recess frequency for capercaillie peaked between 04:00 and 06:00 in the morning and 20:00-22:00 in the evening (Figure 4).

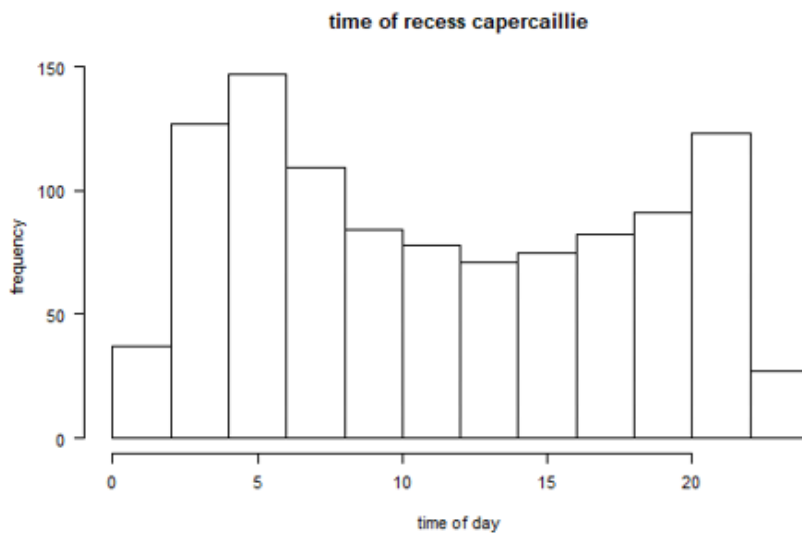


Figure 4. Histogram over recess frequency for capercaillie distributed for each hour of the day.

Incubation constancy for capercaillie was relatively high during the whole day with 0,95 at the lowest level around 5 in the morning (Figure 5).

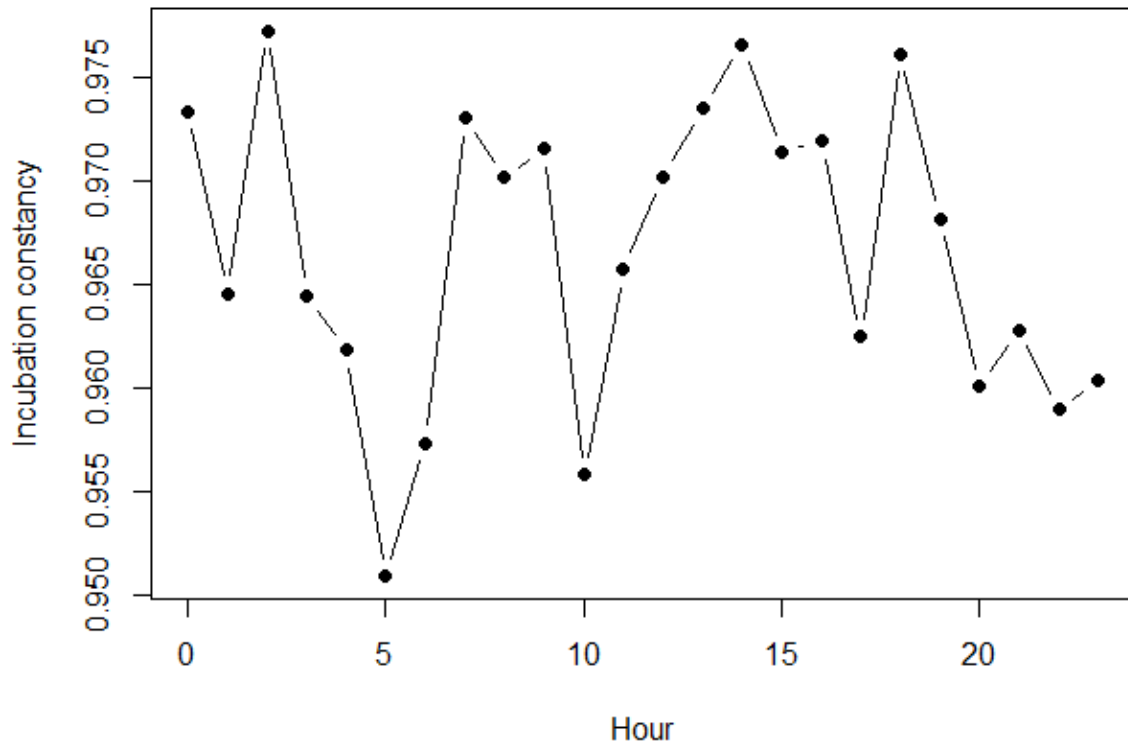


Figure 5. Plot for incubation constancy for capercaillie distributed for each hour of the day.

Discussion

Here I show that differences in incubation behaviour between the species were only minor, and there were only differences between capercaillie and willow ptarmigan in number of recesses and incubation constancy. Capercaillie had a lower number of recesses and higher incubation constancy than willow ptarmigan. Incubation behaviour did not relate to the nesting success for capercaillie hens. The best-fitted model could not reveal any relationship between incubation behaviour and nesting success. Because of this, normal variation in capercaillie hens normal incubation behaviour probably does not affect the probability of nest predation.

Body weight of nesting hens is an important factor for the nesting hens body condition during the nesting period. The nutrition the nesting hen is able to absorb before the egg-laying period is probably one of the main drivers of her physical abilities. The amount of nutrition the hen is able to absorb during the winter is important, and if the winter is unusually cold, grouse have to return to their snow-holes before they have eaten enough (Watson & Moss 2008).

Consequently, capercaillie, black grouse and willow ptarmigan hens may lose weight during the winter, and have worse body condition than normal when the spring starts. Watson and Moss (2008) also writes that high-quality spring diets are crucial for the nesting females body condition. Most of the energy and protein required for egg laying must come from food digested a couple of weeks before egg-laying time. When feeding before egg-laying, early growing plants in the spring are preferable and higher in nutrition (Watson & Moss 2008). Therefore, the arrival of spring and spring phenology may indirectly affect nesting behaviour via nutritional content in plants. The ability to endure high intensive incubation may therefore be limited by weather conditions during both winter and spring (Wiebe & Martin 1997; Wilson & Martin 2010).

Incubation is probably more demanding for lighter hens. To obtain high incubation constancy black grouse hens take more and shorter recesses than capercaillie hens (Storaas & Wegge 1997). With the findings of Storaas and Wegge (1997) that black grouse females take more and shorter recesses and, due to the differences in size of grouse-hens, I expected the lighter willow ptarmigan hen to have even more and shorter recesses than both capercaillie and black grouse. Simultaneously, the body condition would be worse with lower weight, and the incubation constancy may be decreasing with smaller size of nesting hen. Renesting is

physically demanding, and probably decreases body condition. Storaas, Wegge and Kastdalen (2000) detected that only the heavier adult capercaillie hens were re-nesting. Same trends are probably for black grouse (Willebrand 1992). Changed incubation behaviour with more and longer recesses and probably decreasing incubation constancy, is a result of decreased body condition. As the adult hen grouse probably are heavier than the yearling (Erikstad, Pedersen & Steen 1985), the ability to carry out high intensive incubation throughout the nesting period and possibly extended incubation time seems weight and age related (Wiebe & Martin 1998; Caizergues & Ellison 2000). The normal weight of a capercaillie, black grouse and willow ptarmigan female in Norway is 1,7-2.5, 0.8-1 and 0.5 kilograms, respectively. High intensive incubation seems weight related, both within and between the species. Due to this and the aspects discussed, the idea of differences in incubation behaviour between the species emerged.

Differences in nesting behaviour between the species were only minor, and there were only differences between capercaillie and willow ptarmigan in number of recesses and incubation constancy. Capercaillie had fewer recesses and higher incubation constancy than willow ptarmigan. The methods used in this thesis are different from earlier similar studies. With the use of digital game cameras we were able to intimately monitor every movement of the nesting hen, sometimes (dependent on camera mounting) including turning of eggs, movement on the nest while incubating such as feeding and turning, and sometimes flying off the nest at a start of a recess. Even the shortest recesses was registered, and at some points the recesses could be as short as a few seconds. Sometimes I may have lost detection of short recesses because sometimes the intervals between each picture taken was for example 10 or 20 minutes. Those 10 minutes without any picture taken could contain 1 or 2 short recesses. Still the same method was used for all the three species and further similarities or differences may occur if more precise monitoring methods emerge in the future. As the indexes of incubation behaviour were surprisingly similar between species and probably not sufficient to explain the differences in nest success between capercaillie and black grouse (Jahren 2017) or the willow ptarmigan (Munkebye *et al.* 2003).

Predation rate could instead be more related to the size of the incubating female. Even though the average capercaillie hen are bigger, heavier and have better body condition than the average black grouse and willow ptarmigan hen, their nests get depredated more. With

increased activity around the nest, olfactory outcome would increase. Bigger sized birds emit more scent molecules (Conover 2007). As the capercaillie hens are bigger, the increased olfactory outcome may help the predators searching for nests. The predators probably detects the nests only when the hen is on the nest (Coates, Connelly & Delehanty 2008). Even though the probability of predation is higher when hens are on the nest. Even though the nesting hen probably needs to be sitting on the nest in order to be depredated, the mammalian (red fox and pine marten) predators which are the common forest grouse nest predator in Norway (Jahren 2017) need to get extremely close in order to detect the nest. Storaas, Kastdalen and Wegge (1999) used hunting dogs to calculate that mammalian predators would detect capercaillie and black grouse nests if the bird were flushed from the nest closer than 1.6m and 1.1m, respectively. Therefore, the detection distance between the predator and the nest given by flush behaviour is probably more important than recess behaviour in relation to nest predation.

The nesting female faces trade-offs between self-maintenance and metabolic requirement for the eggs (Coates & Delehanty 2008; Jia, Sun & Swenson 2010; Fu *et al.* 2017). Annual survival for adult grouse females may also affect the decisions in the trade-offs. Capercaillie hens have higher annual survival than black grouse (Wegge & Rolstad 2011; Ahlen *et al.* 2013) and willow ptarmigan (Heier 2016). The decision between remaining on the nest or escape when a predator approaches could be explained by annual survival rates. The birds with higher annual survival may invest more in their own life and escape the nest earlier than the birds with lower annual survival that invest more in reproduction.

Differences in nesting behaviour could not explain the probability of nest predation for capercaillie. Other ecological mechanisms may be more important in explaining predation patterns of capercaillie nests. For capercaillie, my study confirms the conclusion of Storaas and Wegges (1997) analysing of a smaller sample. Nest losses were not associated with the time or frequency of departures from the nest. The effect of age and experience of nesting hen could also influence nesting success. The ability to produce more eggs and chicks (Willebrand 1992; Wiebe & Martin 1998; Caizergues & Ellison 2000; Storaas, Wegge & Kastdalen 2000; Davis, Phillips & Doherty 2015) seems to be greater for older grouse hens. Nests that are initiated earlier may cause higher nest success, and adult hens could initiate nesting period earlier (Davis, Phillips & Doherty 2015). The females with lowest body condition probably

invested more in reproduction than the ones in good body condition (Robb, Martin & Hannon 1992), and subsequently probably have less energy available towards anti-predator behaviour during brood rearing. Anti-predation adaption may be better for older experienced hens. Grouse hens that are nesting need to adopt best possible incubation strategy in order to maintain a high incubation constancy, saving herself and her eggs from predation.

Conclusion

Differences in nesting behaviour between capercaillie, black grouse and willow ptarmigan were small. The differences in nest predation between species cannot be attributed to variation between the species incubation behaviour. When the nesting hen is sitting on the nest, the predator need to be extremely close to flush and find it. There are a small chance for the predator to actually find the nest after approaching it. The idea of a nesting lotteri is also supported with the predation peaking the hour after midnight. If the nesting hen unluckily sits on the nest exactly when a predator approach that special hour, the chance of predation increases. With predators generally detecting nest while grouse hens is on, the hen reveal her nest while escaping. Norwegian grouse predation is a lotteri where hens have little influence on the outcome.

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