

MASTER THESIS

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Does Weather Affect Brooding Behaviour?

Modelling quantified behaviour of brooding willow ptarmigan
Lagopus lagopus hens in relation to weather conditions

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Preface

As a humble student at the master's programme in Terrestrial Ecology and Nature Management at Nord University, this thesis marks the end of my time in the programme. The thesis has been conducted as a part of a project called "*Willow ptarmigan in a changing climate*", led by The Norwegian Institute of Nature Research (NINA) and Nord University and financed by The Norwegian Environmental Agency. My separate thesis has also been funded by I.K. Lykkes fund, managed by The Royal Norwegian Society of Sciences and Letters (DKNVS). I would like to give a huge thank you to my first main supervisor Pål F. Moa (former Associate Professor, Nord University) and to my second main supervisor Erlend B. Nilsen (Senior Research Scientist, NINA, and Professor, Nord University) for indescribable guidance, help, and support throughout the last 2,5 years. I would also like to give a big thank you to my co-supervisors; Lasse Frost Eriksen (PhD-student, NINA) and Jan Eivind Østnes (Associate Professor, Nord University) for guidance, feedback and support through the process. A big high-five goes to Markus Israelsen (Department engineer, NINA) for guidance in the use of methods in the field, good conversations and great help with data distribution. I would like to thank the Faculty of Biosciences at Nord University for their willingness to facilitate when time where an issue. Also, a big thank you to my fellow students; Henry, Christopher, Jonas, Oddbjørn, Silje, Chris, Jon Erling and Andreas, for a wonderful time together. Last, but far from least, I would like to give the biggest thank you to my family, for supporting me and giving me the opportunity to pursue my goals and fulfil my dreams.



Steinkjer, November 23rd, 2020

Fredrik Droigk Vaadal

Abstract

Birds breeding in alpine and arctic regions have less opportunities to adjust their time of reproduction due to the short time window available. That is why highly adaptable species have a greater chance of successfully outlive those lesser suited for change, both in short- and long term. However, former research on the brooding behaviour of willow ptarmigan have only partially concluded that age, phenology, time of the year and climatic conditions are effects which leads to behavioural disorders and trade-offs.

In this study two hypotheses were developed to explain the brooding behaviour based on an ON-frequency approach using camera trap data. I used data from 21 radio-tagged female willow ptarmigans *Lagopus lagopus* in an alpine area in Central Norway to test if a number of covariates could explain observed brooding behaviour. Specifically, I tested 1) if weather variables such as temperature and precipitation were affecting the brooding behaviour of individual hens, and 2) if age and/or biometric measures (weight and wing length) were individual variables that affected the brooding behaviour of individual hens. I found no significant effects of climatic conditions or biometric factors on brooding behaviour. However, tendencies showed that some of the variations in ON-frequency might be explained by unknown factors if more detailed data were available. I also found that repeatable tests of ON-frequency for individual willow ptarmigan hens could be explained by a variance of 12%, however not what caused the variance.

The results of this study indicate that future investigations of the brooding behaviour of willow ptarmigans needs more detailed, and additional measurements to fully be able to explain what factors are affecting behaviour. Further development of methods used in this study may help answer questions of various behavioural ques, but also enhance results showcased in this thesis. However, this study implies that it is important to investigate brooding behaviour of willow ptarmigans in the future, in addition that it provides important knowledge to be used in predicting the future of the willow ptarmigan in a changing climate.

Keywords: Brooding behaviour, weather, biometric measurements, age, camera traps, quantified behaviour, *Lagopus lagopus*, willow ptarmigan.

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1. Introduction

Climate change have become a daily topic worldwide over the past decades (Brodie et al., 2012). In the same time span science has provided accumulating evidence that the environments that surrounds us are changing (Brodie et al., 2012). The fact that the climate on our planet is changing is nothing unique to our time (Le Treut et al., 2007). Our planet as we know it have changed numerous times in the past and will most definitely continue to do so in the future (Brodie et al., 2012; Le Treut et al., 2007). The ominous fact, however, is that the climate today changes faster than what is possible for nature to follow (Brodie et al., 2012). Although all of the worlds million odd species are equipped with various capabilities to adapt to change, the time spans for adaption varies largely (Clark & Ehlinger, 1987). This means that some species are coping better than others regarding change, even between congeners, in the context of adapting to a changing climate (Nagy & Grabherr, 2009).

Birds worldwide have developed and adapted strategies to survive in a range of different environments. On the northern hemisphere, arctic and alpine birds are known for their adaptations to tolerate harsh conditions throughout the year (Andreev, 1999; Martin & Wiebe, 2004). Metabolic and energetic adaptations of resident species found in alpine and arctic environments help these species to survive in surroundings where temperatures fluctuate between freezing temperatures during the winter months, to warm temperatures in the summer (Andreev, 1999; Martin & Wiebe, 2004; West & Norton, 1975). Birds living in alpine and arctic areas often face stochastic weather conditions, and they must be adapted to tolerate such unanticipated events (Martin & Wiebe, 2004). Stochastic events might be particularly prominent in the breeding season, which in northern latitudes and high altitudes already is limited to a short time window (Martin & Wiebe, 2004; Sandercock et al., 2005). According to Saalfield et al. (2019), long-term climatic change that results in earlier snowmelt have the potential to greatly affect arctic-breeding birds, especially if birds are unable to advance nest initiation to keep up with seasonal advancement of prey.

Climatic conditions are considered to be among the major environmental factors that have been studied to identify ecological correlations of life history variation in species (Sandercock et al., 2005). Wingfield & Ramenofsky (2011), found that organisms may time their breeding to a period when the conditions for reproductive success is optimal. This also applies to species living in arctic and alpine environments. However, these species have less opportunities to adjust their time of reproduction due to the short time window available (Sandercock et al., 2005). With that in mind, abnormal weather conditions occurring for a given time of the year

(i.e. in the breeding season), may result in allostatic overload and stress for the species affected (Wingfield & Ramenofsky, 2011), and thereby influence the breeding success negatively. Breeding may also be affected by predation, food limitation and the duration of breeding (Sandercock et al., 2005). Breeding is of course, as we know, vital for passing the genes on to the next generation. As a consequence, highly adaptable species have a greater chance of successfully outlive those lesser suited for change, both in short- and long term.

Due to climate change, the weather has become more unpredictable (Brodie et al., 2012). Changes in temperatures and annual precipitation levels are affecting natural systems and animal populations on a global scale (Boyer, 2019). Studies have shown that animal populations and ecosystems are being affected by abnormal weather events worldwide (Lu et al., 2020; Saalfeld et al., 2019; Underwood & Bertazzon, 2019). Temperature and precipitation are common variables used to assess whether birds are affected by climate change. Temperature and precipitation as negative effects on nestling mass and survivability has been detected in several bird populations (Marques-Santos & Dingemanse, 2020; Saalfeld et al., 2019). To this date, most research to date have focused on temperature effects on nestling development and parental effort during reproduction to assess how the weather impacts the breeding success of birds (Andreasson et al., 2020). Furthermore, an increasing amount of evidence indicates that temperature change also significantly affects birds that breed in cooler temperate areas (Andreasson et al., 2020). Animal populations living at high elevations are often assumed to be in peril of extinctions or local extirpations due to elevational-dispersal limitations and thermoregulatory constraints as habitats change and get warmer (Wann et al., 2016).

Studies on species resident to alpine and arctic regions show that effects from inclement weather, in combination with other variables, may have a significant impact on brooding behaviour and success. In Colorado (North America), a study on the white-tailed ptarmigan *Lagopus leucura* questioned the general assumption that alpine animal populations are highly sensitive to warming temperatures (Wann et al., 2016). Wann et al. (2016) analysed reproductive data for two populations over a period of 45 years, and showed that the median hatch date had advanced by 3.7 and 1.9 days per decade for northern and southern sites respectively. However, the hatch date was remarkably invariant to fluctuations in seasonal weather with respect to reproductive success. The results also indicated a positive correlation between warm and dry conditions and number of chicks per hen (Wann et al., 2016). Studies of passerines and waders in a mountain area in southern Norway showed that changes in breeding ground vegetation probably was an effect of climate change, resulting in a declining

number of breeding pairs (Byrkjedal & Kålås, 2012). Martin and Wiebe (2004) found that older white-tailed ptarmigan females laid their eggs earlier than two-year olds and yearlings, and also that the clutch sizes increased with female age. Their study also showed that this age-related pattern was valid in years with harsh weather conditions. However, the same study also showed that age-specific variation in body condition and fecundity of willow ptarmigan *Lagopus lagopus* was not evident, although lacking data presumably may have influenced the results. Therefore, age-specific variations could either be confirmed or ruled out as a possible effect on brooding willow ptarmigan. In addition, willow ptarmigans rely on their body reserves throughout the winter, and has to pass through a nutritional bottleneck that keeps narrowing until snow starts to melt (Andreev, 1999). This means that when brooding commences by the time snow melt begins (Martin & Wiebe, 2004), the willow ptarmigan hens are at a low point of body mass percentage and are therefore also highly vulnerable to stress (Andreev, 1999). Furthermore, the willow ptarmigan hen may also be forced to leave the nest periodically to feed (Pedersen & Karlsen, 2007), hence the hen is the only parent brooding even though the species is characterized as monogamic (Andreev, 1999; Pedersen & Karlsen, 2007). This forced behaviour places additional energy costs on the hen, and has raised the question on how much energy the willow ptarmigan hen has to invest in developing embryos (Andreev, 1999), furthermore how this may affect the behaviour when brooding.

The aim of the present study is to investigate possible variables that may affect the behaviour in brooding hens in a willow ptarmigan population in Central Norway. The willow ptarmigan is a circumpolar species that can be found in alpine tundra habitats in the northern hemisphere (Kvasnes et al., 2015). The Norwegian populations inhabit alpine to subalpine regions throughout Norway (Pedersen & Karlsen, 2007). Temperature, precipitation, age and biometric measures will be analysed and compared to behavioural observations on brooding hens collected over a 3-year period. My hypotheses are 1) weather variables such as temperature and precipitation affects the brooding behaviour of individual hens, 2) age and/or biometric measures (weight and wing length) are individual variables that affects the brooding behaviour of individual hens. Regardless of the outcome of my hypotheses, wildlife management and future research could benefit from the results of this study. The study may contribute with important knowledge to help management address obstacles for the studied population in a future where weather conditions are modelled to become more unpredictable and stochastic (Brodie et al., 2012).

Earlier studies have shown that brooding initiation of the willow ptarmigan can be delayed because of unfavourable weather conditions (Erikstad & Andersen, 1983). However, there seems to be little or no evidence of weather affecting willow ptarmigan hens during brooding to the extent that the hens behaviour is expressed abnormally (Martin & Wiebe, 2004; Wann et al., 2016). Although, adverse weather (e.g. events of snow fall) could prolong the brooding period, resulting in less available time to forage during brooding, when looking at number of times the hen uses off the nest per day (Pedersen & Karlsen, 2007). However, this is not critical for the hens (Andreev, 1999), hence they can lay on the nest for longer periods. On the basis that the willow ptarmigan hens' behaviour when brooding is proven affected by how good their body reserves are (Erikstad, 1986), it may be possible that the hens are forced to use longer and/or more periods off the nest searching for food when the conditions are right, simply to get the required amount of energy needed (Andreev, 1999). This could also lead to forced time off the nest in periods that normally is not suitable. On that basis, using too much time off the nest could result in severe cooling of eggs (Pedersen & Karlsen, 2007). Cooling of the eggs however, cannot be seen as a singular effect regarding the survivability of eggs, considering that eggs can withstand to be cooled for shorter periods (Andreev, 1999; Pedersen & Karlsen, 2007; Pedersen & Steen, 1979).

2. Materials and method

2.1 Study species

The willow ptarmigan is a ground nesting, medium sized grouse species with a body weight around 400-600 grams. In May or June the female lay her eggs in a shallow nest and the normal clutch size is 8-12 eggs. The eggs have a light brown colour with red-brown spots, which give them a perfect camouflage in the mountainous terrain. The brooding period is around three weeks, and normally all eggs hatch during one day (Pedersen & Karlsen, 2007). The reason for this simultaneous hatching is that the hen rearranges the eggs in the nest during the brooding period, and thereby make sure that all the eggs are ready to hatch at the same time (Pedersen & Karlsen, 2007).

2.2 Study area

This study is based on data collected during field studies in two locations in Lierne municipality in Central Norway; Lifjellet (64°25'–64°30'N, 13°11'–13°24'E) and Gusvatnet (64°15'–64°18'N, 13°25'–13°37'E), respectively (Heier, 2018; Israelsen et al., 2020) (Figure 1). Due to movement within the studied population, the dataset also includes relocations in neighbouring municipalities (Heier, 2018; Israelsen et al., 2020). The study areas are situated in the subalpine

to alpine bioclimatic zone. The lower parts of the study area are mostly dominated by willow *Salix spp.* L., with scattered patches of mountain birch *Betula pubescens* Ehrh. forests. In the midsection the vegetation is dominated by sedges, grasses, patches of dwarf birch *Betula nana* L. and snowbeds. At the highest elevations, the surroundings lack a continuous vegetation cover (Nilsen et al., 2020). For a more detailed description of the bioclimatic zones in the study area, see Israelsen et al. (2020). Normal precipitation in the area is approx. 675 mm per year. Mean annual temperatures span from -10 °C in January to 12 °C in July. In winter, snow dept is 1-3 meters, and snow cover seems to persist from early October to late May. Typical predators on eggs, juvenile and adult ptarmigans in the area is gyrfalcon *Falco rusticolus* and golden eagle *Aquila chrysaetos*, raven *Corvus corax*, red foxes *Vulpes vulpes* and to a limited extent arctic foxes *Vulpes lagopus* and wolverine *Gulo gulo* (Nilsen et al., 2020).

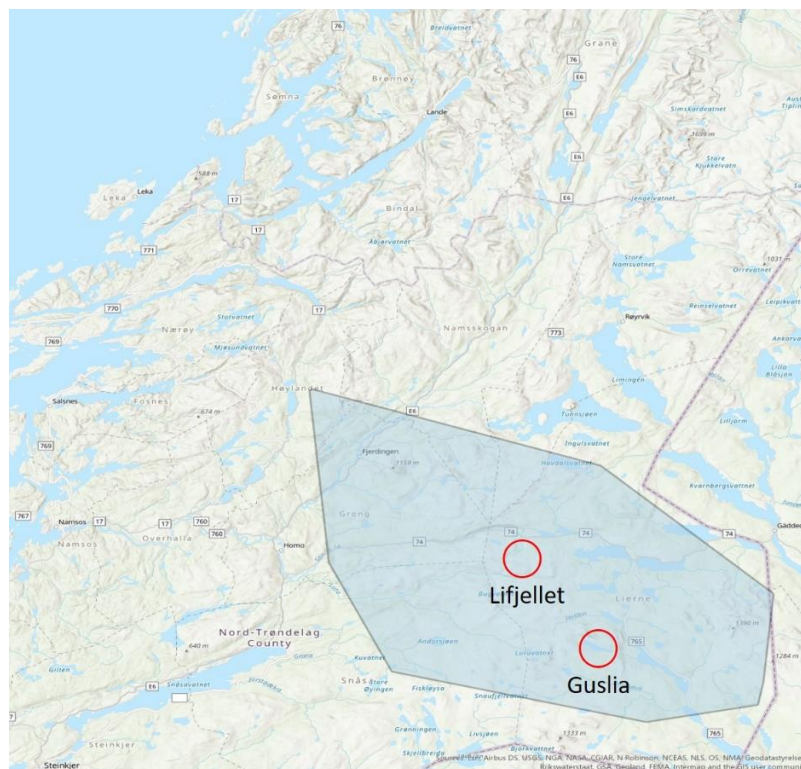


Figure 1: Overview of the total study area for all camera traps established during the project period 2015-2019. The perimeter is outlined by the outer camera trap locations. Red circles denote the two locations Lifjellet and Guslia where the capture and tagging of willow ptarmigan took place in March 2015-2019.

2.3 Field methods

By using snowmobiles, long-handled dip nets and high-powered head lamps, willow ptarmigans were captured at night-time (Israelsen et al., 2020; Nilsen et al., 2020). The captures were carried out in 2015-2019, mainly in March. After capture, the birds were placed in an opaque, cotton bag, to reduce stress while they were aged, sexed, weighed, and the chest

and wing length were measured. Sex determination was carried out based on plumage coloration, wing length and patterns of pigmentation of the three outermost primaries (Bergerud et al., 1963). The birds were aged either as juveniles (birds that were ≤ 1 year old) or adults (birds that were > 1 year old). In addition, feathers were sampled for DNA analysis to confirm the field sex determination. Before the birds were released, they were fitted with a metal ring on the leg ($\sim 2,4$ g, Museum Stavanger) and a Holohil RI-2BM or Holohil RI-2DM radio transmitter ($\sim 14,1$ g). The combined weight of the leg ring and radio transmitter did not exceed 3,5% of the body weight for any of the tagged birds. Of the total sample of birds tagged with VHF radio collars ($n=188$), a total of 182 individuals were possible to relocate. The last six individuals were excluded because they were never recovered. Of these 182 individuals, 91 individuals were female.

During triangulation of the marked birds from helicopter (aerial triangulation) in May (only in 2016-2019) it was possible to detect the locations of the individual birds in the breeding season. Based on triangulation from the ground, the accurate location of the nests were found.

After the nests were located, camera traps were installed to monitor each nest. To back-calculate the egg-laying date, we did a float-test on two of the eggs in the clutch to determine the age of the eggs (Westerskov, 1950). Camera traps were only mounted on active nests (i.e. nests with eggs). Across the study period, the camera traps were programmed following two schedules, because of the use of different camera types: 1) programmed to take one picture every half hour defined by the time (at xx:00 or at xx:30), in addition to take a “three picture sequence” (TPS) in a time lapse of 3-5 seconds whenever the motion sensor was triggered, 2) programmed to take a TPS in a time lapse of 3-5 seconds every half-an hour after the previous TPS were taken (regardless of whether the previous pictures were time triggered or motion sensor triggered), in addition to take a TPS whenever the motion sensor was triggered. The camera traps were placed between 1-3 meters from the nest, and at a height not exceeding 1 meter. If no natural support for the camera trap was present, we used materials found close to the nests (intentionally to not draw unnatural attention from potential predators). No vegetation was removed when camera traps were mounted. The camera traps were uninstalled in mid-July, i.e. after the end of hatching period.

2.4 Data extraction from camera traps

The total dataset based on monitoring of 91 nests (91 radio-collared hens) from 2015 to 2019 consisted of 433 990 pictures. Of these, 23 camera traps were excluded due to camera failure

(the time-lapse sequence or the motion sensor was set different from the scheduled above) or errors in camera installation (i.e. the camera was not monitoring the nest because they were mounted in a wrong direction). For this thesis, only nests from 2017-2019 were included. After rejecting failure camera traps (n=23), discarding 2015-2016 camera traps (n=35), and nests that either were predated by mammalian or avian predators or in other ways abandoned by the hen (n=12; mostly because of the data from these cameras could be of abnormal behaviour due to i.e. disturbance or stress from predators, or starvation) the number of camera traps included in the study landed on 21 (n=21).

In order to quantify the behaviour based on the camera trap pictures a list of parameters was prepared to list down observational ‘values’ while manually reviewing the pictures (Appendix A). To describe behaviour, the parameters ON_NEST and OFF_NEST was used. By doing so it was possible to count the number of times the hen was ON or OFF the nest per day (24h). The response variable used for further analysis was the number of times the hen was ON the nest (hereafter ON-frequency) per day. If the ON or OFF period overlapped midnight (00:00) I selected the day where the time-period was predominant (if no predominant time-period could be defined, the ON or OFF time was registered on the following day).

To substantiate the behaviour of the hens in case of ON-frequency on the nest, it was desirable to use as many “optimal camera trap setups” as possible (optimal camera trap setup = able to detect “every time” and duration (hh:mm) the hen moved off or came on the nest) to assess if the use of an ON-frequency approach gave the proper impression of the hens’ behaviour whilst brooding.

Because I was interested in testing to which extent weather variables affected the brooding, weather data had to be obtained for the study period. Therefore, weather data (temperature and precipitation) were obtained by using data measured by the weather station Holand (Nordli, 433 MASL), which is located approx. 24 kilometres east/north-east of both study areas. Data for the respective time periods for all years (2017-2019) was obtained from The Norwegian Meteorological Institute’s free access weather- and climate database; eKlima (Meterologisk Institutt, 2020). Average daily temperature and average daily precipitation for the respective days were used to represent the variation in daily weather conditions.

2.5 Statistical analysis

To quantify the individual reliability (R; Appendix D) of brooding behaviour, I used a mixed effects model with ON-frequency as a response variable and individual ID as random effect,

implemented with the rpt function in R-package rptR (Schielzeth et al., 2019). The number of parametric bootstraps were set to 5000. Because the response variable represent the number of occasions per day, it was modelled assuming a poisson error structure (Schielzeth et al., 2019).

I performed two separate analysis for modelling behaviour in my dataset because biometric measures weight and wing length was only available for hens captured previously the same year as the monitoring. Because of this, in addition to one hen (ID=4281483) that did not have data to calculate day of brooding (DoB), 20 hens were included in the first analysis (age, weather and timing) and only 14 in the following analysis (biometrics and age).

To test if the behaviour of the brooding hens were affected by Year, Age, Precipitation, Temperature, Days before Hatching (DbH), Day of the Year (DoY) and/or Day of Brooding (DoB) I used generalized linear mixed models using template model builder (glmmTMB function in R package glmmTMB; Magnusson et al. (2020)) with ON-frequency as a response variable. I tested both the main effects of Year, Age, Precipitation, Temperature, DbH, DoY, DoB, as well as the interaction effects of Age \times Temperature, Age \times Precipitation, DbH \times Age, DbH \times Precipitation, DbH \times Temperature, DoY \times Age, DoY \times Precipitation, DoY \times Temperature and DoY \times DbH as fixed explanatory terms. Because the response variable represent the number of occasions per day, it was modelled assuming a poisson error structure and log-link function. Bird identity (ID) was included as a random intercept to account for repeated observations for individual birds (Zuur et al., 2009).

To test if the behaviour of brooding hens were affected by Age, Weight and/or Symmetry ($\frac{\text{Left wing (length)}}{\text{Right wing (length)}}$), I fitted generalized linear mixed models using template model builder (glmmTMB function in glmmTMB) with ON-frequency as response variable and Weight and Symmetry, and Age \times Weight, Weight \times Symmetry and Weight + Symmetry \times Age interactions as fixed explanatory terms. Because the response variable represent the number of occasions per day, it was modelled assuming a poisson error structure and log-link function. Bird identity (ID) was included as a random intercept to account for repeated observations for individual birds (Zuur et al., 2009).

To emphasize the fitted models I used Akaike's information criterion (AIC) to perform model selection (Burnham & Anderson, 2002). The reason why I used AIC is because it provides a measure of strength of evidence for each model that represents a plausible biological hypothesis relative to the entire set of models considered (Mazerolle, 2006).

The statistical analysis was carried out in RStudio (R Development Core Team, 2020) for Windows (Team 2017). I used Microsoft Excel (2007) to make schematic presentations and the R package ‘ggplot2’ (Wickham, 2017) in RStudio for other graphic presentations. For model building I used the R package ‘glmmTMB’ (Magnusson et al., 2020). For weighting the AIC in all analysis I used the R package ‘AICcmodavg’ (Mazerolle, 2016). To look at repeatability between individual behaviour I used the R package ‘rptR’ (Schielzeth et al., 2019).

3. Results

3.1 Dataset summary – differences between years

The number of camera traps (= nests) included in the analyses were 5 for 2017, 8 for 2018 and 8 for 2019, i.e. a total 21. The brooding periods were between 15 June - 6 July in 2017, 18 May - 4 July in 2018 and 30 May - 5 July in 2019. The total number of days when hens were brooding (the total time window of brooding hens) was determined as the timeframe between the earliest calculated day of egg laying, and the latest hatching date observed on camera. Thus the total number of days when hens where brooding was 28 days in 2017, 58 days in 2018 and 37 in 2019, respectively.

The mean number of times the hen was on the nest (i.e. ON-frequency) per day across all years was 3.7 ± 1.46 (SD). The yearly mean daily ON-frequency varied between 3.3 ± 1.40 to 4.0 ± 1.35 (Table 1). The mean number of days of brooding from back-calculated egg laying date to hatch date for all years had a mean of 21.1 ± 2.68 . The mean number of days of brooding within years varied between 19.8 ± 3.54 to 22.3 ± 1.65 (Table 1).

Table 1: Overview of yearly mean daily ON-frequency, mean days of brooding, number of nests (N) and total number of days hens where brooding.

Year	Mean daily ON-frequency	Mean days of brooding	Nests (N)	Number of days hens where brooding
2017	3.3 ± 1.40	19.8 ± 3.54	5	28
2018	3.9 ± 1.54	$21.1 \pm 1.86^*$	8	58
2019	4.0 ± 1.35	22.3 ± 1.65	8	37
Total	3.7 ± 1.46	21.1 ± 2.68	21	123

*Calculated from 7 nests. One hen did not have data from water test, hence no data to back-calculate egg laying (ID=4281483)

3.2 Reference camera traps

Only two camera traps fitted the “optimal camera trap setup” criteria. These camera traps are hereby called “reference camera traps”. The reference camera traps showed an interesting

resemblance when looking into the length of time used in periods on the nest (Figure 2). There was a similar activity in terms of length in time for on-periods when hatching approached for both reference camera traps. Just before hatching took place, the hens spent a relatively long time (09h 57min and 10h 48min hours, respectively) ON the nest. Then the hens continued to spend medium long periods (approx. 4h to 8h hours) ON the nest, with short periods OFF (approx. 8min to 1h 30min). Furthermore, in the time after hatching, the hens spent yet again a relatively long time (11h 59min and 12h 58min, respectively) ON the nest. After this, both the ON and OFF periods were similarly short (ranging from 2min to 2h 18min), before the hens eventually left with the chicks. Therefore, the observed similarity in ON and OFF time when the willow ptarmigan hen were brooding was a well suited approach to quantify the behaviour of the hen during the brooding period with the use of an ON-frequency approach.

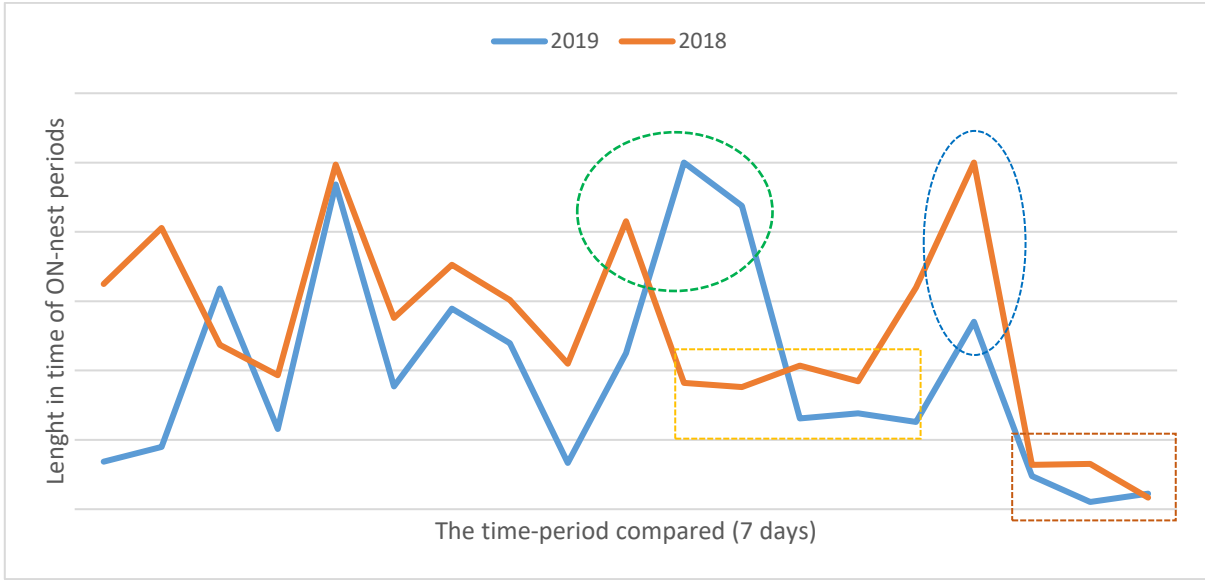


Figure 2: On-time comparison from reference cameras (2018 and 2019). **Green circle** shows how a longer period on the nest occur just before hatching commences. **Yellow square** shows shorter how periods distinguish the time when hatching. **Blue circle** shows how a longer period on the nest occurs just after hatching. **Red square** shows how the time before leaving is spend on shorter on periods before leaving the nest with the chicks.

3.3 On-frequency tendencies during the brooding period

Looking at the ON-frequencies of willow ptarmigan hens during the brooding periods, I discovered that there may have been tendencies in amount of times on the nest in relation to DoY (day of the year; Figure 3). In 2017, there were similarities in the data in terms of a continuous pattern of days with high number of times on the nest, followed by days with low numbers of times on the nest. For 2018, the pattern of number of times on the nest were less variable, and there were also less change in number of times spent on the nest throughout

observation periods. In 2019, the number of times on the nest seemed to fluctuate between highs and lows, but were somewhat more stable in number of times on the nest throughout observation periods (similar to 2018).



Figure 3: Daily ON-frequency for individual hens in relation to day of the year during brooding periods in a three-year period (2017-2019) Tendencies of similar behaviour is observed within years.

3.4 On-frequency tendencies during days before hatching (DbH)

When looking at the ON-frequencies of willow ptarmigan hens during the brooding periods I also discovered that there were similar behavioural tendencies in different stages of the brooding compared to days before hatching (DbH; Figure 4). The DbH back-calculate the hatching date, thus showing how ON-frequency varies for different individual hens towards hatching without taking to account the different hatching dates. For 2017, the hens were relatively few number of times on the nest the last five days before hatching. The number of times on the nest during the last five days before hatching were also relatively similar between individual hens. In 2018, the hens had a relatively high number of times on the nest in the last five days before hatching. However, the number of times on the nest last five days were not as similar as in 2017. In 2019, the tendencies match 2017, having relatively high numbers on the

nest the last five days of brooding. The number of times on the nest were also relatively similar between individual hens, although not as evident as they were in 2018.



Figure 4: Daily ON-frequency for individual hens in relation to days before hatching during brooding periods in a three-year period (2017-2019) Tendencies of similar behaviour is observed within years.

3.5 Quantifying the reliability of measurements

When quantifying the individual reliability (repeatability) of measurements using ON-frequency as response variable, I found that repeatability for ON-frequency within all years (2017-2019) was 0.12 (SE=0.051) on the link-scale approximation with a confidence interval of repeatability derived from parametric bootstrapping being [0.012, 0.213] (Figure 5). In other words, the repeatability indicate that only 12% of the variance ON-frequency can be explained by ID.

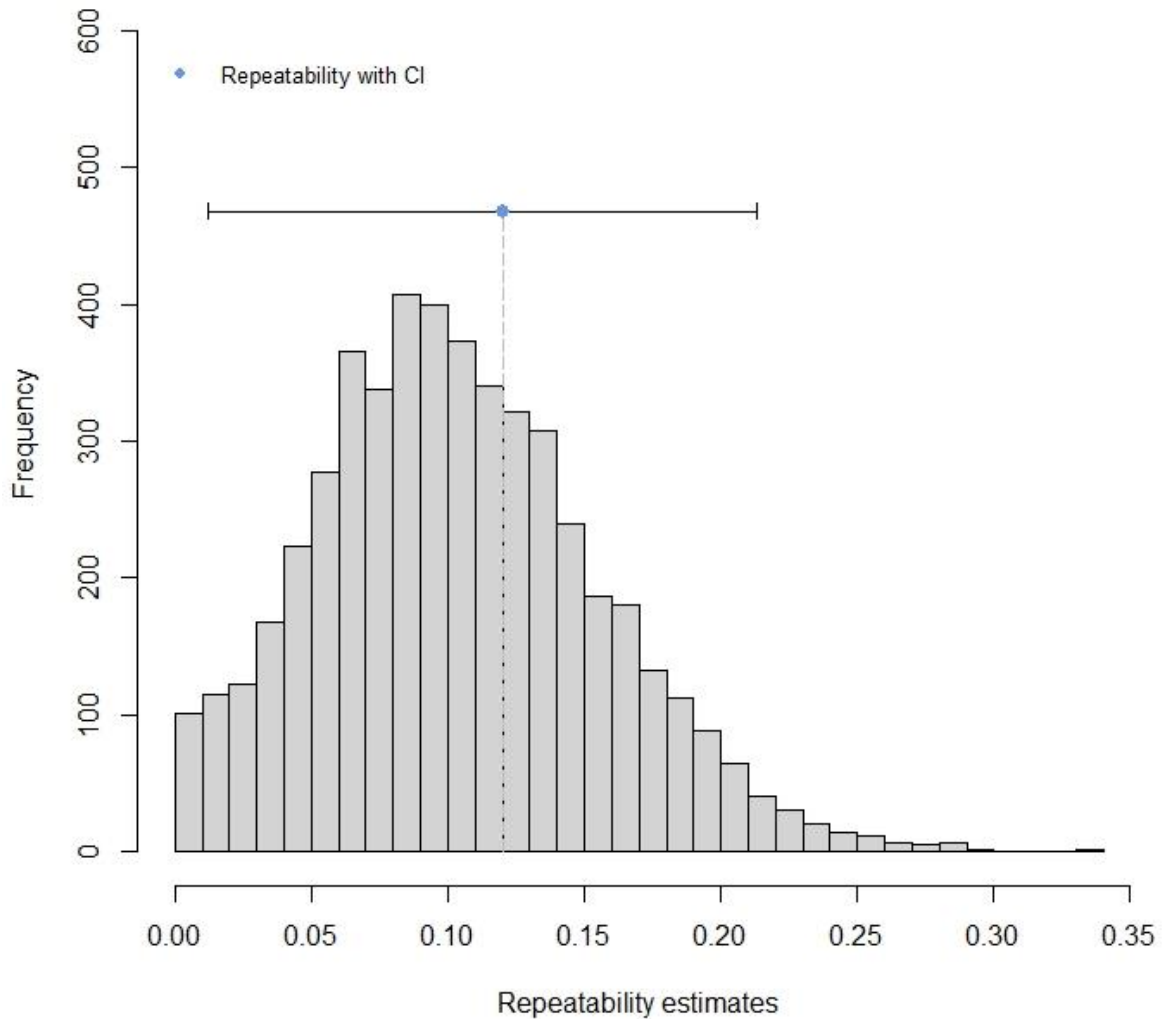


Figure 5: Repeatability estimations of ON-frequency as response to ID as random effect and grouping factor, and 5000 as number of parametric bootstraps. The figure shows a link-scale approximations repeatability of 0.12 (12%).

3.6 Weather-, Timing and Age effects on brooding behaviour

When modelling ON-frequency as a function of individual covariates age, phenology (DbH, DoB), time of the year (DoY) and climate parameters (Temperature and Precipitation), I found no substantial support for any of the main effects nor their interaction (Table 2, Appendix B). Among all evaluated models, the intercept only model had the lower AIC_c , and a weigh (w_i) of 0.24. The second and third model (main effects of Temperature and Age, respectively) also received some support ($\Delta AIC_c < 2$), but parsimony suggest the effects have very limited support. The more complex models including 2-way interactions between the terms had little or no support compared.

Table 2: Candidate models and model statistics for modelling ON-frequency as a function of respected variables for 20 willow ptarmigan females in 2017, 2018 and 2019, respectively. Results from a generalized linear mixed model using template model builder (glmmTMB) (DoB = day of brooding, DbH = day before hatching, DoY = day of the year).

Response	Model	K	AIC _c	ΔAIC _c	AIC _c Wt(w _i)	CumWt
ON-Frequency	Intercept	2	1180.44	0.00	0.24	0.24
	Temperature	3	1182.20	1.75	0.10	0.34
	Age	3	1182.41	1.97	0.09	0.43
	DbH	3	1182.44	2.00	0.09	0.52
	DoB	3	1182.45	2.01	0.09	0.61
	Precipitation	3	1182.45	2.01	0.09	0.69
	Year	4	1182.46	2.02	0.09	0.78
	DoY	3	1182.48	2.03	0.09	0.87

3.7 Biometric- and Age effects on brooding behaviour

Weight and biometric measures were obtained for 14 individual hens in the same year as the brooding period was monitored and only these hens were part of the Age, Weight and Symmetry analysis and modelling. When modelling ON-frequency as a function of covariates age and biometric measures (Weight and Symmetry), I found no substantial support for any of the main effects nor their interaction (Table 3, Appendix C). Among all evaluated models, the intercept only model had the lower AIC_c, and weigh (w_i) of 0.36. The second to fourth models (the 2-way interaction of Age × Symmetry and main effects of Symmetry and Weight, respectively) also received some support (ΔAIC_c < 2), but parsimony suggest the effects have very limited support. The more complex models including 2-way and 3-way interactions between terms had little or no support compared.

Table 3: Candidate models and model statistics for modelling ON-frequency as a function of Age (juvenile or adult), Weight and Symmetry for 13 willow ptarmigan females in 2017, 2018 and 2019, respectively. Results from a generalized linear mixed model using template model builder (glmmTMB).

Response	Model	K	AIC _c	ΔAIC _c	AIC _c Wt(w _i)	CumWt
ON-Frequency	Intercept	2	783.66	0.00	0.36	0.36
	Age × Symmetry	5	785.06	1.40	0.18	0.53
	Symmetry	3	785.10	1.44	0.17	0.71
	Weight	3	785.25	1.59	0.16	0.87

4. Discussion

In this study, I have investigated the factors that contribute to variation in nesting behaviour in willow ptarmigan. I focused my analyses around covariates (Age), phenology (DbH, DoB), time of the year (DoY) and climate parameters (Temperature and Precipitation) to see if any of these factors have significant effects on brooding behaviour of the willow ptarmigan hen (ON-frequency). Based on my model selection routines based on AIC, I did not find any considerable effect of neither age, phenology, time of the year nor climatic parameters on the response variable. However, when assessing the repeatability of the behaviour within females, I found a significant yet limited degree of repeatability. In the following, I discuss my results in the light of previous research.

The results when looking at age as an effect on brooding behaviour are to some extent coherent with previous studies looking at similar effects in terms of breeding success for other ptarmigan species (Martin & Wiebe, 2004; Wann et al., 2016), which concluded that there are little or no difference between adults (>1) and juveniles (≤ 1) in case of breeding success (Hannon & Smith, 1984). Furthermore, in case of egg-laying date, older females have been proven to lay eggs earlier than yearlings (Martin & Wiebe, 2004), which may affect the brooding in case of different weather conditions between early and late spring. However, I did not detect any linear change in brooding behaviour as the season progressed in my study. Likewise, temperature and precipitation did not have significant effects on the ON-frequency. This does not necessarily contrast with previous studies documenting effects of spring conditions on breeding success (Pedersen & Karlsen, 2007; Wann et al., 2016). However, this was not assessed in this study. Likewise, if a postponed spring with predominance of snow cover as late as June was evident, this could possibly result in reduced breeding success if weather conditions, in case of colder temperatures and more precipitation, was to be severe enough (Pedersen & Karlsen, 2007). Although this could possibly be affecting breeding success, such weather conditions within the normal brooding-period (late May to early July) seems to have little effect on eggs in terms of cooling, hence eggs of willow ptarmigan can survive even if buried in snow for shorter periods (Pedersen & Karlsen, 2007). The effects of weather on brooding behaviour and trade-offs by the hen, however, is little studied.

Contrary to what I expected, I found no effect of body weight on brooding behaviour. The results were somewhat surprising, hence body weight of the willow ptarmigan hen is thought to be linked to behaviour in case of number of times taken ON and OFF the nest per day (Pedersen & Karlsen, 2007). It was however not so surprising that the age + weight model did

not express significance to ON-frequency, hence Wiebe and Martin (1998a) found in their study evidence for strong age-specific variation in body condition in willow ptarmigans, meaning that age not necessarily is linked to weight, and the results in this study expresses similar findings. Furthermore, it is known that hens in good condition (read; body mass) are better suited for brooding, and individual hens can lose over 20% of body mass during brooding (Pedersen & Karlsen, 2007). This means that individuals with higher body mass have more reserves to rely on when the environmental conditions are unfavourable, likewise are individuals with lower body mass less suited for unfavourable conditions (Pedersen & Karlsen, 2007). Therefore, hens in bad condition (read; low body mass) needs to spend more times off the nest, simply because they need to forage more often to maintain relative body mass to continue brooding (Pedersen & Karlsen, 2007; Wiebe & Martin, 1997). Furthermore, my study did not test whether vegetation cover was influencing the condition of the hens, although Wiebe and Martin (1998b) found that the features of the nest sites were associated with physical characteristics. Their study showed that hens in poor spring condition used nests with more overhead cover than those in better condition, which could have supported or changed the results in this study if included. Another consideration is that these analysis did not use data from all 21 individual hens (N = 14), which may have been a too small dataset to assess the true relationships between the explanatory variable(s) and the response variable (Bissonette, 1999).

None of the covariates I investigated had any direct effects on brooding behaviour, as assessed by ON-frequency. However, still there were some differences between females in the frequency, and 12% of the variance ON-frequency was explained by ID within the study-period implying some consistency within females. Although the results show a small significance, it is considered unlikely that data similar to the ON-frequency approach used in this study is a good measurement of behaviour, hence similar approaches have been characterized equally (Rudeck et al., 2020). The results from the analysis could not characterize ON-frequency to be the single most likely measurement to describe individual variance. However, the results may be considered valuable on the basis that behaviour when brooding is not singularly affected by what is measured using an ON-frequency, but most definitely is affecting the behaviour in combination with other, unknown factors. In addition, because the variance cannot be explained by a single known factor, the remaining 88% of variance (which is considered random noise), could be explained by other, unknown factors, i.e. stress and anxiety-related behaviour (Rudeck et al., 2020). If the dataset would have had more than one measurement of behaviour (ON-frequency), it may have been possible to look at different types of behaviour, i.e. flexibility or

canalization (Bell et al., 2009), in order to explain more than 12% of variance. Because the ON-frequency is calculated by using observations on repeatedly measured behaviour over a given time (brooding-period), the repeatability might be more significant within years because the data is sampled in similar environmental conditions (i.e. similar weather conditions and/or similar spring initiation) (Bell et al., 2009). On the other hand, repeatability over the total study-period (2017-2019) might decrease consistency because the interval of data sampling between individuals are obtained over a longer period of time (Dingemanse et al., 2002). In addition, a factor which is difficult to assess in the case of repeatability, is phenotypic plasticity. In this study, this is linked to an underlying uncertainty whether plasticity is considered as a part of the ON-frequency approach, hence the ON-frequency is quantified data of behaviour based on singular observations, which may contain additional unknown information (the on and off times are only measured when observing the hen either on or off the nest, not for how long or for what reason). Furthermore, this may have resulted in a low variance in this study, simply because the ON-frequency approach did not have the proper details to define individual differences, i.e. expressions in phenotypic plasticity and/or other unknown cues affecting behaviour.

Relatively large differences were found between years in the same time for onset of brooding. This was somewhat expected, although earlier spring initiation tendencies due to i.e. climate change has been looked into and showcased in recent decades (Dunn & Winkler, 2010; Hopkin, 2007; Wann et al., 2016). In addition, the differences showcased in this study may also indicate high level of plasticity in order to start brooding regarding spring initiation due to other, unknown reasons. Whether the willow ptarmigan hens when brooding was affected by earlier spring initiation in relation to breeding success was not an object of this study. Clarke and Johnson (1992) found that earlier spring (hence earlier brooding-period) did not affect the white-tailed ptarmigan *Lagopus leucurus altipetenes*, a species comparable to the willow ptarmigan. On that note, earlier spring initiation in case of snowmelt in 2018 (Eriksen, 2019) is believed to may have had an effect on brooding behaviour, in case of brooding initiation, and number of brooding days, even though it was found insignificant. This assumption is supported by the results of Hannon et al. (1988) and Martin and Wiebe (2004) which studied willow ptarmigans in Canada. Both studies found positive correlations between hatch date and snow melt date. Furthermore, distribution of nests in relation to snow cover and elevation were not assessed in my study, although this could have strengthened the assumptions above (Byrkjedal & Kålås, 2012; Wiebe & Martin, 1998b). It was not assessed if some of the nests were cases of

re-nesting, however it is plausible that cases of re-nesting may have affected the dataset of this study, in relation to that brooding-initiation date for some of the hens were seemingly later than for others (Pedersen & Karlsen, 2007).

Because my statistical results were overall insignificant, I looked at the overall ON-frequency in relation to day of the year (DoY) to see whether there were any clear tendencies in ON-frequency between individual hens and years. I found that the ON-frequency tendencies that may be a result of varying brooding conditions, meaning that the hens may have been forced to stay on the nest some whole days, and other days they may have been able to take times off. This tendency seems to be relatively even throughout some periods. I also found tendencies which may be a result from more favourable brooding conditions. If the brooding conditions are somewhat favourable for the hens, it means that they can chose themselves when to take times on and off the nest. Although, it may be that the behaviour observed could be explained by individual freedom of choice, in relation to individual preference of times off per day. However, in the case the tendency observed were from when the brooding conditions were unfavourable, it could mean that the tendency shows minimum times needed off the nest in order to survive/continue brooding (Pedersen & Karlsen, 2007). It is however possible that the tendency is too individually linked to be significant based on the ON-frequency approach.

I also looked at the overall ON-frequencies in relation to days before hatching (DbH) to see whether there were any clear tendencies in ON-frequency between individual hens and years. I found tendencies that may be a result of limited possibilities to take time off the nest when hatching commence. This could either be a result of weather conditions being too challenging for the eggs (in case of cooling) or the hen (in case of not being able to forage efficiently) (Pedersen & Karlsen, 2007). I also found tendencies which may come from hens which obtained a suboptimal body mass before brooding initiation, hence some nests was monitored earlier than normal due to an early spring initiation (Eriksen, 2019). This assumption is only based on plausibility, hence the early spring initiation may only be a plausible effect because little of such effects are mentioned in literature. Other tendencies observed may also come from a case of age-specific differences and/or differences in body condition of the hens observed (Pedersen & Karlsen, 2007; Wiebe & Martin, 1998a), however this was found insignificant in statistical analysis. Some nests were additionally assumed to be re-nestings, which may have hidden significance in the analysis, hence this was not assessed in the statistics. Other tendencies that

were found may also be a result of continuous unfavourable weather for a longer period, possibly in combination with low body condition from various reasons (Martin & Wiebe, 2004).

In this study, I used several field methods and public available data which could have been improved and/or obtained differently to fit my study better. One of these methods was using camera traps to monitor nests, hence camera traps are a widely used method in animal observational studies, i.e. monitor individual behaviour in combination with other methods of sampling (Odden, 2015; Trolliet et al., 2014). Although the method used in the present study was well standardized and used to monitor the hens on the nest, it did not meet the criteria of monitoring movement on and off the nest in detail (i.e. detect every time the hen went on or off the nest). This made the approach to a detailed behavioural study on the brooding willow ptarmigan hen impossible, although two cameras met the criteria for detailed observations well (the reference cameras). This forced me to use an ON-frequency approach, which meant looking at daily number of times on and off the nest in significance to various variables. The reference camera traps amplified the assumption that an ON-frequency approach was possible to use in order to detect behaviour, based on the comparability in the reference camera traps' ON-frequency in relation to their detailed overview of the observed time spent on and off the nest. The use of an ON-frequency approach was not optimal in analysing possible effects on behaviour of brooding willow ptarmigans. However, there are several reasons why this approach was selected; field methods regarding camera trap setup did not fit the study approach fully (behaviour); the available weather data (temperature and precipitation) was better suited for an overall analysis (data from only one weather station); the risk of including vast amounts of bias data was minimized due to not using uncertain detailed observations (mostly because camera trap mountings and settings did not meet criteria to observe behaviour in detail).

Weather data was obtained only from one single weather station (Holand), therefore data used were equal for all camera trap locations within the same dates and periods. This meant that detecting possible effects from various weather conditions on brooding behaviour on the same dates was excluded. However, in combination with day of brooding (DoB), day of the year (DoY) and days before hatching (DbH) it was possible to analyse if effects on brooding behaviour in case of how weather conditions affected different stages of brooding, also between years and individual hens. To further assess if weather conditions may affect additional brooding behaviour, it could be possible to either 1) use surrounding weather stations in adjacent locations to interpolate weather data (Lussana, 2017). However, there are only a small number of weather stations close to the study area (Meteorologisk Institutt, 2020), which could result in

inaccurate predictions, hence number and density of weather stations is coherent with accuracy of the resulting predictions (Hasenauer et al., 2003). Or 2) use small weather stations on each nest to detect local variations (Kedia, 2016). However, such technology would not apply to already completed field work and data.

5. Conclusion

The results did not give proper support to my hypotheses. However, the results is somewhat coherent with previous studies which aid in defining the willow ptarmigan as a unique species regarding influences from weather conditions in alpine and arctic environments in relation to age, time of the year, length of brooding, brooding initiation and biometric measures. Trying to explain behaviour with a sequential ON-frequency approach was somewhat challenging, hence behavioural studies have expressed the necessity of using detailed and combined methods to observe real-time changes in behavioural patterns of animal species (Hughey et al., 2018). Nevertheless, using the ON-frequency approach I was able to detect various tendencies in willow ptarmigan hens' behaviour when brooding. Although it was not possible to determine what effects caused the tendencies found, the study amplifies the perceptions that the willow ptarmigan is non-affected by the studied variables to the degree that plausible effects are too small to detect using an ON-frequency approach. Whether the observed tendencies could be a result from phenotypic plasticity is not rendered in the discussion as a possible theory of approach (Brodie et al., 2012), but future studies might be served by looking into this theory. I recommend future studies on behaviour of brooding willow ptarmigan hens to improve the method described to fit the purpose of detecting behavioural cues more precise. In addition, I hope the approach used in this study inspires to look further into the plausible effects on brooding willow ptarmigan hens in order to help wildlife management understand and detect when stochastic effects may danger vulnerable willow ptarmigan populations in the future.

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Appendix Appendix A

Table A: table of content: observational parameters used in manual review of picture-dataset.

ID	Kolonnetittel	Beskrivelse	Generate d from file	Generated from other than file	Observa tion in picture
A	FILE_NAME	Filename generated from file generated by NINA		X	
B	HEN_ID	Leg-ring ID		X	
C	YEAR	Year of camera trap setup		X	
D	CAMERA	Camera number		X	
E	CAMERA_BRAND	Camera brand		X	
F	CAMERA_MODEL	Camera model - i.e.: SC522	NA		
G	TEMP	Temperature	NA		
H	DATE	Date when picture was taken		X	
I	TIME	Time of the day picture was taken		X	
J	PIC_TYPE	Picture type - 1=timelapse 2=motion sensor			X
K	EMPTY	Empty picture - 0=empty, 1=not empty (animals in picture)			X
L	FAILURE	Picture state - 0=NO FAILURE 1=Lens covered by ice or fog 2=Picture is black or damaged 3=Nest outside of picture 4=Camera fallen down or turned			X
M	VEG_COVER	Vegetation covering the nest - 0=NO 1=YES			X
N	RAIN	0=No rain, 1=damp rain 2=mildly rain 3=heavy rain, 4=insecure			X
O	SNOW	0=no snow, 1=little 2=medium 3=heavy 4=insecure (snowfall)			X
P	GR_COVER_SNOW	Ground covered by snow - 0=NO 1=YES 2=PARTLY			X
Q	VIS_NEST	Nest visibility - 1=Nest visible 2=Nest not visible (i.e. brush blocking the view)			X
R	ON/OFF_NEST	Hen on or off the nest - 1=ON, 2=OFF			X
S	MALE	Willow ptarmigan male visible? 0=NO 1=YES			X
T	CHICK_OBS	Chicks observed? - 0=NO 1=YES			X
U	CHICK_SEEN	Number of chicks seen - NUMBER (1=1, 2=2, 3=3...)			X
V	OTHER_SP.	Other species visible? 0=NO OTHER SPECIES 1=OTHER SPECIES			X
W	OTHER_SP_NAME	Other species name - Name (i.e. red fox, moose or marten... unknown)			X
X	OTHER_SP_NU	Number of predators: NUMBER (1=1 2=2 3=3...)			X
Y	PREDATION	Predation on 1=EGGS, 2=CHICKS, 3=HEN			X
Z	COMMENT	COMMENT ON OBSERVATION OR OTHER PARTICULARLY INTERESTING PICTURE -			X
AA	P.I.	1=YES			X

Appendix B

Table B: Extended candidate models and model statistics for modelling ON-frequency as a function of Age (juvenile or adult), Weight and Symmetry for 20 willow ptarmigan females in 2017, 2018 and 2019, respectively. Results from a generalized linear mixed model using template model builder (glmmTMB).

Response	Model	K	AIC _c	ΔAIC _c	AIC _c Wt(w _i)	CumWt
ON-Frequency	Intercept	2	1180.44	0.00	0.24	0.24
	Temperature	3	1182.20	1.75	0.10	0.34
	Age	3	1182.41	1.97	0.09	0.43
	DbH	3	1182.44	2.00	0.09	0.52
	DoB	3	1182.45	2.01	0.09	0.61
	Precipitation	3	1182.45	2.01	0.09	0.69
	Year	4	1182.46	2.02	0.09	0.78
	DoY	3	1182.48	2.03	0.09	0.87
	DoY × Temperature	5	1185.92	5.47	0.02	0.87
	Temp. × Precipitation	5	1186.12	5.67	0.01	0.88
	DoY × DbH	5	1186.15	5.71	0.01	0.90
	Age × Temperature	5	1186.24	5.80	0.01	0.01
	DbH × Temperature	5	1186.24	5.80	0.01	0.94
	Age × Precipitation	5	1186.29	5.84	0.01	0.95
	DoY × Precipitation	5	1186.30	5.86	0.01	0.96
	DbH × Precipitation	5	1186.39	5.95	0.01	0.98
	DbH × Age	5	1186.48	6.04	0.01	0.99
	DoY × Age	5	1186.52	6.07	0.01	1.00

Appendix C

Table C: Extended candidate models and model statistics for modelling ON-frequency as a function of Age (juvenile or adult), Weight and Symmetry for 14 willow ptarmigan females in 2017, 2018 and 2019, respectively. Results from a generalized linear mixed model using template model builder (glmmTMB).

Response	Model	K	AIC _c	ΔAIC _c	AIC _c Wt(w _i)	CumWt
ON-Frequency	Intercept	2	783.66	0.00	0.36	0.36
	Age × Symmetry	5	785.06	1.40	0.18	0.53
	Symmetry	3	785.10	1.44	0.17	0.71
	Weight	3	785.25	1.59	0.16	0.87
	Weight + Symmetry × Age	6	787.17	3.51	0.06	0.93
	Age × Weight	5	787.93	4.27	0.04	0.97
	Weight × Symmetry	5	788.64	4.98	0.03	1.00

Appendix D

Overview of statistical formulas and explanations.

Repeatability:

The repeatability describes the relative partitioning of variance into within-group and between-group sources of variance and is more generally referred to as the intra-class correlation (ICC) (M A Stoffel et al., 2019). In additions, the ICC is the most widely used statistics to estimate behavioural consistency of quantified consistent individual differences by measuring the behaviour of individuals on more than one occasion (Bell et al., 2009). Simplified, the repeatability (R) is calculated as the variance among group means (VG) over the sum of variance among means (VG) and group mean residuals (VR):

$$R = \frac{VG}{(VG + VR)}$$

For further explanations, see i.e. Nakagawa and Schielzeth (2010) or M A Stoffel et al. (2017).

Delta AIC_c (ΔAIC_c):

The ΔAIC_c is a measure of each model relative to the best model, and is calculated as:

$$\Delta AIC_i = \text{Delta } AIC_i = AIC_i - \text{min}AIC$$

When ΔAIC_c is < 2 it suggests substantial evidence for the model, values between 3 and 7 indicate that the model has considerably less support, and $\Delta AIC_c > 10$ indicates that the model is very unlikely (Mazerolle, 2006)

Akaike weights (w_i):

Akaike weights (w_i) provide a measurement of strength of evidence for each model, and represent the ratio of ΔAIC_c of a given model relative to the whole set of candidate models:

$$w_i = \frac{\exp(-\frac{\Delta_i}{2})}{\sum_{r=1}^R \exp(-\frac{\Delta_r}{2})}$$

The Akaike weights indicate the probability that one model is the best among the whole set of candidate models. For instance, An Akaike weight of 0.14 for a model, indicates that given the data, it has 14% chance of being the best model among those considered in the set of candidate models (Mazerolle, 2006)

Evidence ratio:

Evidence ratio is given by comparing Akaike weights of the best model and competing models to determine to what extent it is better than the other (Mazerolle, 2006):

$$Evidence\ ratio = \frac{w_i}{w_j}$$