

Predation of eggs and incubating females in willow ptarmigan *Lagopus l. lagopus*

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Nest predation is a major cause of reproductive loss in many ground-nesting birds. During 15 consecutive years the predation of nests and females throughout the incubation season were recorded in a willow ptarmigan *Lagopus l. lagopus* population in central Norway. The temporal predation patterns, factors affecting the predation probability and age-specific nesting patterns in this species were studied. There was a large annual variation in predation rate of both nests (0-50%) and incubating females (0-29%) in this area during the study period. The mean annual predation rate of nests (15%) was on average three times higher than the predation of incubating willow ptarmigan females (5%). Predation rate was not constant throughout the incubation season, and the nest predation rate increased with increasing number of available nests. The predation events started after the mean initiation day of incubation, and coincided with the highest number of available nests. None of the parameters we tested in a logistic regression analysis (physical condition, nest cover, experience and date for initiation of egg-laying) could predict the predation probability of nests and incubating females. However, "good" nest cover tended to have some predictive value on the predation probability. Yearling incubating females had significantly lower physical body condition than adults, and also there were differences in choice of nest site in relation to cover between the two age groups. Initiation of egg-laying in adult females tended to be distributed more evenly over the season, whereas yearling females had a more aggregated egg-laying pattern, compared to adults.

Key words: breeding, incubation, *Lagopus l. lagopus*, nest predation, willow ptarmigan

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INTRODUCTION

A major cause of reproductive loss in many ground-nesting birds is nest predation (Bergerud 1988, Wegge & Storaas 1990). In tetraonids such as the willow ptarmigan *Lagopus l. lagopus* nest predation can be an important factor causing the observed large variation in annual chick production (e.g. Myrberget 1984a, 1985, Steen & Erikstad 1996). Willow ptarmigan, like other grouse, rely on their cryptic eggs and plumage (Johnsgard 1983), low scent levels during incubation (Hudson 1986) and infrequent incubation recesses (Erikstad 1986) to avoid detection of their nest. Nevertheless, nest predation in willow ptarmigan can be substantial with large variation among years (Norway: 7 to 78%, Myrberget 1985; Canada: 14 to 80%, Hannon et al. 1988, O'Reilly & Hannon 1989).

Predation of the incubating female has a much more dramatic effect on the reproductive output than egg predation, which the female can compensate for by a new reproductive attempt. Females appear to be more susceptible to predation than males during the laying, incubation and brood rearing period, and predators killing females are e.g. raptors and red fox *Vulpes vulpes* (Hannon & Gruys 1987, Moss et al. 1990). Examination of prey remains in nests of golden eagle *Aquila chrysaetos*, have revealed that, before the brood-rearing period of the willow ptarmigan, the remains were mainly of females, whereas during the brood-rearing period the frequency of males and females were about equal (Lunde 1985). In an island population in northern Norway it was found that about 2% of the breeding females were killed

(Myrberget 1988), and in Newfoundland Bergerud (1988) reported 4% mortality of incubating females.

Different factors can affect the susceptibility of both nests and females, creating temporal or spatial predation patterns. Both previous breeding experience and physical body condition of the female can influence the reproductive performance (Myrberget 1986, Martin 1995, Wiebe & Martin 1998a). Female willow ptarmigan in poor condition have more and longer recesses from their nests (Erikstad 1986), which can make them more vulnerable to predation (but see Robb et al. 1992). Also, in some studies it has been found that yearling females tend to be in poorer body condition than adults during spring (Robb et al. 1992, Wiebe & Martin 1998a). This might influence the age dependent predation pattern and interact with the possible effect of former breeding experience.

Predation risk during egg-laying and incubation may change over time due to changes in the amount of vegetation for nest cover, number of active nests in the area, or availability of alternative prey species (e.g. Myrberget 1988). Such non-random predation with respect to timing of egg-laying can therefore create selection for temporal pattern of egg-laying in the population.

In this study we present data on the predation pattern of willow ptarmigan females and nests, from 15 consecutive breeding seasons, in a population in central Norway. We test for age-specific nesting patterns and examine how factors such as physical condition, nest cover, former breeding experience, and time of initiation of egg-laying affect the outcome of the reproduction event.

MATERIAL AND METHODS

Study area and field methods

This study was carried out in the Gåvålia and Kolla area, near Kongsvold Biological Station in Dovrefjell central Norway (62°17'N, 09°39'E) during 1978 to 1992. The study area used during 1978-1988 was about 10 km² and during 1989-1992 about 17 km². Pedersen et al. (1983) and Pedersen (1991, 1996) have earlier described the study area in detail. Potential predators observed on or near the study areas were in all years: hooded crow *Corvus c. cornix*, magpie *Pica pica*, raven *Corvus corax*, golden eagle, gyrfalcon *Falco rusticolus*, rough-legged buzzard *Buteo lagopus*, short-eared owl *Asio flammeus*, common gull *Larus canus*, hen harrier *Circus cyaneus*, red fox, stoat *Mustela erminea* and pine marten *Martes martes* (Pedersen et al. 1983, Pedersen 1996).

Each year spring territories were mapped (Pedersen et al. 1983) and nests were searched for from the beginning of June. Females were captured on the nest during the last week of incubation using a throw-net. Biometric measures were taken and birds were classified as yearlings in their second calendar year (hatched the pre-

vious year) or adults in their third calendar year or older (2+ years) according to the amount of pigmentation on the three outermost primaries (Bergerud et al. 1963). Captured females were ringed and most were equipped with radio transmitters. Prior to 1988, females were equipped with 12-15 g radio transmitters mounted as backpacks (Erikstad 1979). In a few cases we used 2.5-g radio transmitters attached to the tail feathers (H.C. Pedersen, unpubl. data). From 1988 to 1992 we used 12-g radio transmitters mounted as necklaces (e.g. Thirgood et al. 1995).

The date of initiation of egg-laying for each clutch was calculated by backdating from the hatching date assuming an incubation period of 21 days and a laying frequency of one egg per day (Myrberget 1984b) or by doing a floatation test of the eggs (Westerskov 1950). The incubation period was defined as the period between day 1 and day 21 of incubation for the individual female. The incubation season was defined as the period from the first female initiated incubation to the last incubating female had hatched her eggs.

A nest was classified as hatched if at least one egg hatched. If the eggs were robbed, the nest was classified as a depredated nest. In cases of partial egg predation where the female continued incubation to hatching (<2 % of nests), the nest was defined as hatched. When a female was found killed or remains with characteristic signs of predation were retrieved, we classified it as depredated female.

Nest cover and body condition

At each nest site horizontal nest cover was subjectively classified, giving scores from 0-5 by looking at the nest from directly above. Nests without any cover were given score 0, whereas nests which were completely concealed were given score 5. Scores 0-1 are later grouped and referred to as "poor" cover, scores 2-3 as "medium" cover, and scores 4-5 are referred to as "good" cover.

To assess physical body condition of the incubating female, we calculated the adjusted body mass and used the residual values of the regression relationship of body weight (measured to the nearest 5 g) on wing length (measured to the nearest mm) as a body condition index in the analyses (Robb et al. 1992).

Temporal predation risk

To compare predation risk of females starting egg-laying at different times during spring, we calculated adjusted date of initiation of egg-laying for all females. To allow comparison among years we had to control for "late" years and "early" years. This was done by expressing dates each year relative to the overall mean date for initiating egg-laying of all years. All dates are referred to as Julian dates, with 1 January as day 1.

Since predators are likely to respond to the overall density of nests in an area, re-nests were included in the material in order to estimate the number of available nests and daily predation risk throughout the incubation season. In all other analyses we only used first nests. Nests which hatched later than day 191 (10 July) and with 6 eggs or fewer were defined as re-nesting (Parker 1981). The Kaplan-Meyer product-limit method, modified for staggered entry of animals, was used to estimate the temporal risk of predation (Pollock et al. 1989). Daily estimate of risk of predation was averaged over 3-day intervals to reduce variance. The nests were defined as active nests from the day they were found to hatching or depredation. When the exact time of predation was unknown, we estimated date of predation by calculating one-half of the time from last date of contact with the intact nest to the date when the nest was found predated (Mayfield 1961, Musil et al. 1993, Cotter & Gratto 1995). Nests were checked at irregular intervals every 4-8 days.

Statistical analyses

Statistics were performed using SPSS for Windows, (Release 10.0.5, © 1999 SPSS Inc., Chicago, Illinois). Parametric tests were used for continuous data that were distributed normally and had homogenous variances. This was tested with the Kolmogorov-Smirnov test and the Levene's test, respectively. Nonparametric tests were used when data deviated from these conditions. Statistical tests are two-tailed if otherwise not stated. Logistic regression analysis was used to estimate the effect of different factors on the predation probability of nests and incubating females. Forward stepwise selection was applied to build the best predictive logistic model, with body condition, time for initiating of egg-laying, female age and nest cover as predictor variables.

Female age (yearling or adult) and nest cover (bad, medium or good) were entered as dummy-variables in the model. Sample sizes may differ among analyses because a complete set of information was not available for all nests or females.

RESULTS

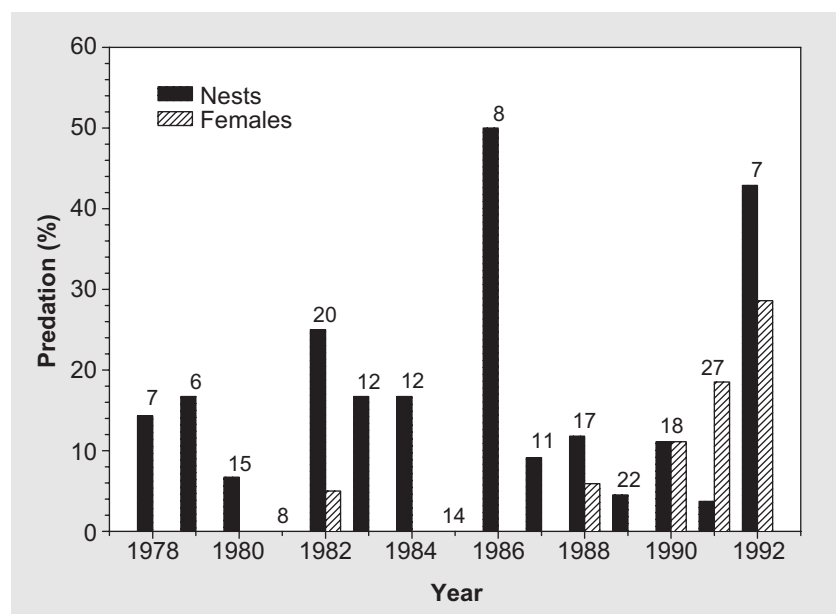
We found 270 willow ptarmigan nests in this study, of which we included 204 cases in the analysis of the predation pattern. The exclusion of 66 nests was due to possible field worker influence (28 cases), unknown fate of the nesting attempt (15 cases) and already predated when first found (23 cases). Data from Gåvålia and Kolla were pooled since there were no significant differences in any of the following parameters between the two areas: female physical condition ($t = 0.11$, $df = 99$, $P = 0.92$), nest cover ($\chi^2 = 1.90$, $df = 2$, $P = 0.39$), age distribution ($\chi^2 = 0.01$, $df = 1$, $P = 0.92$), or date for initiation of egg-laying ($t = 1.18$, $df = 192$, $P = 0.24$).

Predation risk

Among the 204 incubating females, 37 were exposed to predation. Twenty-six females had their nest predated (stoat, pine marten, red fox, hooded crow and raven) whereas 11 were killed by a predator (stoat, red fox, golden eagle and hen harrier). The total predation of nests and females showed large variation between years from 0 to 71% and averaged 20%. (Figure 1). Nest predation varied from 0 to 50% (mean 15%, $CV = 0.95$), whereas proportion of killed females varied from 0 to 29% (mean 5%, $CV = 1.86$). However, there was no significant relationship between proportion of nests predated and females killed ($r_s = 0.15$, $N = 15$, $P = 0.3$).

Figure 1

Annual variation in the proportion of nests and females depredated for the years 1978 to 1992 in a study area at Dovrefjell in central Norway. Numbers above the bars are annual sample size (N).



The incubation season started on day 147 (27 May) and terminated on day 189 (8 July), giving a total incubation season of 43 days. The risk of predation was estimated for the periods where the sample size allowed testing, i.e. from day 153 (2 June) to day 182 (1 July). Daily rates of predation were averaged over 3-day intervals to reduce variance. From day 153 to day 158 we did not find any predation (Figure 2). The predation events started after the mean day for initiating incubation, day 157 (6 June), and coincided with the highest number of available clutches. Total predation rate increased to 8.3% just before the first nest hatched (day 168; 17 June) and decreased to 2.9% in the end of the incubation season. Rate of nest predation varied from 0 to 6.7%, with the highest rate just before the first nest hatched (Figure 2). Nest predation rate increased with increasing number of available clutches, and this relationship was significant ($r_s = 0.76$, $N = 10$, $P = 0.01$). Rate of predation on females varied from 0 to 3.3% throughout the period (Figure 2), but we did not find any relationship between the number of active nests and female predation rate ($r_s = 0.39$, $N = 10$, $P = 0.26$).

None of the predictor variables (physical body condition, age, time of initiating egg-laying and nest cover) which we entered in the logistic regression analysis helped to predict the predation probability of nests and incubating females ($\chi^2 = 6.08$, $df = 6$, $P = 0.41$). However, "good" nest cover seemed to have some predictive value on the predation probability, although not significantly so ($\chi^2 = 5.48$, $df = 2$, $P = 0.065$, Table 1).

Age-related patterns

We tested for age-related differences in nesting females with body condition, date of initiating egg-laying, number of eggs, hatching

success and nest cover as variables. Body condition and nest cover was significantly different between the two age groups, whereas no such differences were found for any of the other factors (date of initiating egg-laying: Mann-Whitney $U = 3201$, $N_1 = 76$, $N_2 = 67$, $P = 0.32$; number of eggs: t-test, $t = 0.83$, $df = 141$, $P = 0.41$; hatching success: t-test, $t = 0.81$, $df = 128$, $P = 0.42$). Yearling females had significantly lower physical body condition than adults (t-test, $t = -3.86$, $df = 83$, $P < 0.001$, Figure 3), and there were age-related differences in choice of nest site in relation to cover (G-test, $G = 8.98$, $df = 2$, $P = 0.01$, Table 2). The initiation of egg-laying in adult females also tended to be distributed more evenly over the season, whereas yearling females had a more synchronous pattern, compared to adults (Levene's test, $F = 10.3$, $P = 0.002$, Figure 4).

Table 1. Status of willow ptarmigan followed during the incubation period in relation to horizontal nest cover.

	Nest cover		
	Poor (N = 16)	Medium (N = 91)	Good (N = 55)
Hatched %	62.5	79.1	85.5
Predated %	37.5	20.9	14.5

Table 2. Percentage distribution of horizontal nest cover in yearling and adult female willow ptarmigan.

	Nest cover			N
	% Poor	% Medium	% Good	
Yearling	2.3	69.8	27.9	43
Adult	20.0	42.9	37.1	35

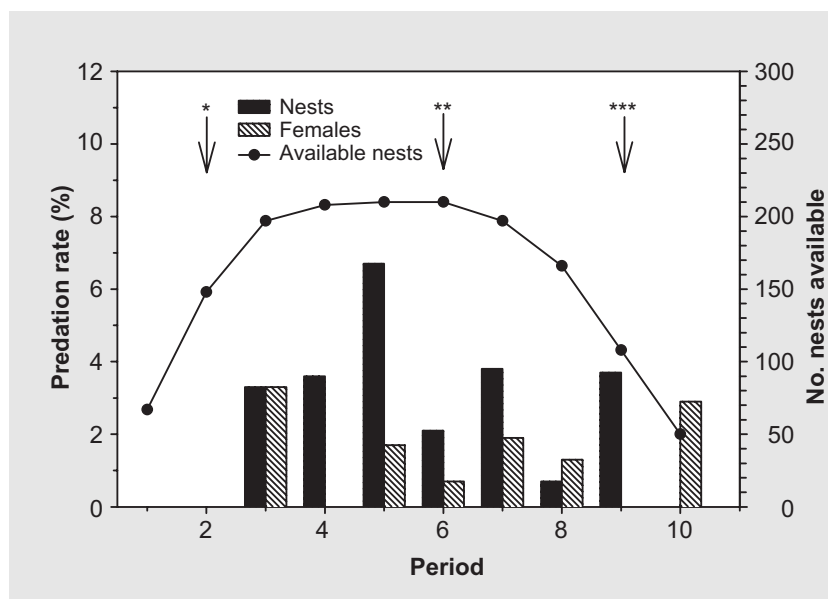
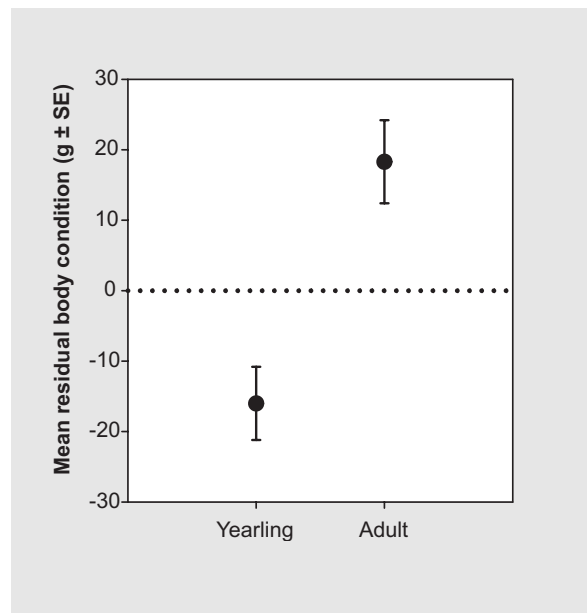


Figure 2

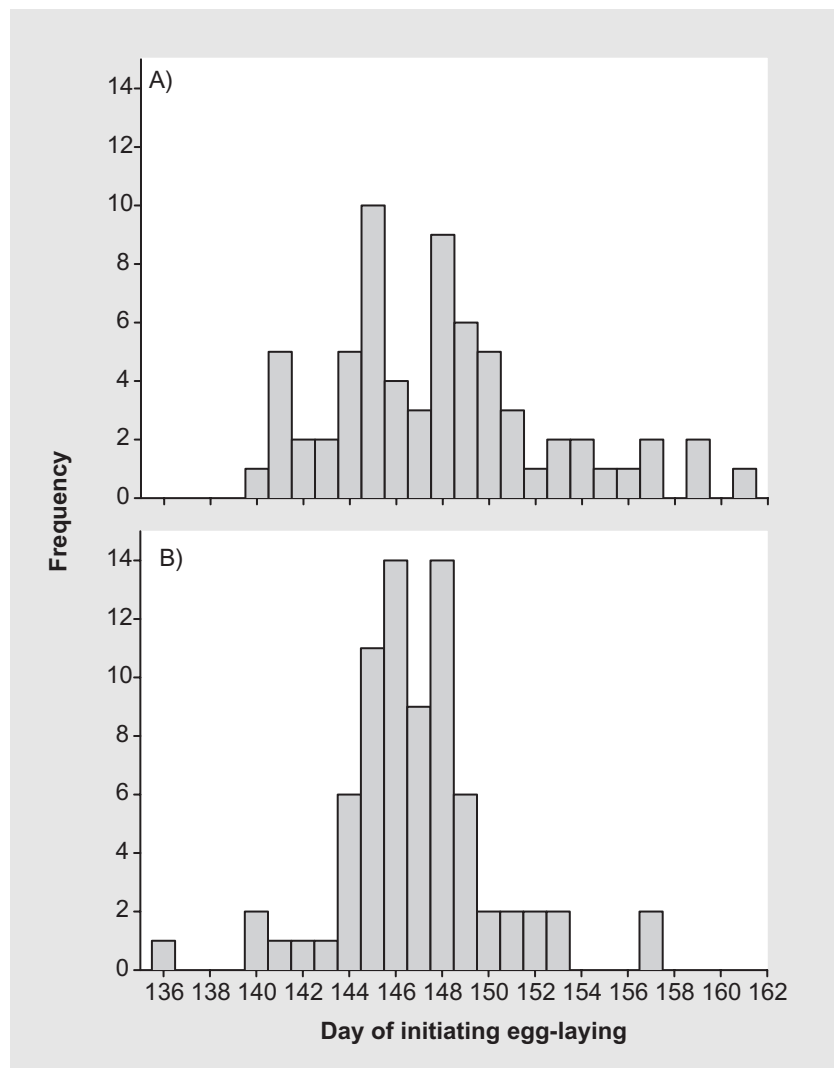
Predation rate during the incubation season for nests and females, and the number of available clutches for the corresponding period, aggregated over the study period. * Mean day for initiating incubation, ** first nest hatched and *** mean day for hatching. Period 1 = day 153-155, period 2 = day 156-158, period 3 = day 159-161, period 4 = day 162-164, period 5 = day 165-167, period 6 = day 168-170, period 7 = day 171-173, period 8 = day 174-176, period 9 = day 177-179 and period 10 = day 180-182. All dates are Julian dates, with 1 January as day 1 (1 June = day 152).

Figure 3

Age-related differences in body condition between yearlings and adults. Mean physical body condition index: unstandardised residuals (g) of regression of mean wing length (cm) on body weight (g), for yearling (N = 54) and adult females (N = 38).

**Figure 4**

Age-related differences in variation of initiation of egg-laying between A) adults and B) yearlings. Yearlings tend to aggregate in time, while adults are more variable and spread their egg-laying.



DISCUSSION

Annual variation in predation rate was large for both nests and incubating willow ptarmigan females during this 15 year study, with more variation in female than nest predation among years. In some years as much as half of the nests were robbed, while no predation was recorded in other years. The same pattern was also observed in incubating females where the predation rate ranged from zero to nearly one third of the females. Generally, the predation risk will vary among years according to predator density, alternative prey, and ptarmigan density (Hannon & Gruys 1987, Redpath 1991). The average predation rate on nests was three times higher than the average predation rate on incubating females. However, no correlation was found between the predation rate in nests and incubating females. This is probably an effect of variation in annual composition of the predator guild in the area and density variation of different predators.

The predation rate showed that predation risk varied throughout the incubation season. During the first 12 days of the incubation season no predation was observed. Predation started when the number of active nests approached a maximum, i.e. a few days after mean onset of incubation. Total predation rate increased to 8.3% just before the first nest hatched and remained relatively high despite the decreasing number of active nests. When we treated predated nests separately from predated females we found that predation risk of nests increased with number of active nests, but we did not find a similar pattern for female predation.

Presence of the female on the nest appears to be important for the predation risk (O'Reilly & Hannon 1989) and risk may be higher when the female is away from the nest foraging than when incubating (Dwernychuk & Boag 1972). Frequent incubation recesses to forage may therefore increase the predation risk. Studies of incubation behaviour in willow ptarmigan have shown that females in good physical condition take fewer incubation recesses than females in poorer condition, and that this is age dependent (Erikstad 1986). As shown in earlier studies (Robb et al. 1992, Wiebe & Martin 1998a), there were clear differences in body condition between young and adult females in this study. However, we found that neither physical body condition, former breeding experience (age), time of initiating egg-laying nor nest cover helped to predict the predation probability of nests and incubating females.

Willow ptarmigan have been shown to choose better cover than expected from a random selected nest site, though differences in nest cover seems to have no effect on nest predation probability in this species (Schieck & Hannon 1993). In contrast, in our analysis, although not significant at the 0.05 level, "good" nest cover tended to reduce the predation probability of nests and incubating females in the Dovrefjell area. The trade-off between reduced nest predation and increased female predation at more concealed sites that has been found in white-tailed ptarmigan *L. leucurus* (Wiebe

& Martin 1998b) might explain why the effect of nest cover seems to be somewhat blurred.

The willow ptarmigan population at Dovrefjell showed age-related differences regarding nest cover utilisation. Yearling females seemed to be more uniform in their choice of nest cover, compared to adult females that utilised the cover spectrum more heterogeneously than the yearlings. Uniform nest cover choice will increase the predictability for predators searching for nests, and therefore the less predictable nest cover choice by adults might be advantageous to reduce the predation risk.

In general, older birds with breeding experience outperform first time breeders (Curio 1983, Sæther 1990). Willow ptarmigan start breeding as yearlings, and therefore adult females have more breeding experience than yearlings. In the Dovrefjell population no age related differences were found between yearling and adult females as to mean date of initiating egg-laying, number of eggs and hatching success during this 15 years study (see also Hannon & Smith 1984). However, although no difference in mean date of initiating egg-laying was found between the two age groups, there was a clear difference in the temporal egg-laying pattern. In contrast to yearling females with an aggregated egg-laying in time, adult females were more variable in their time of initiating egg-laying (Figure 4). The observed egg-laying pattern in adults, with two peaks and a longer tail, might be caused by a higher frequency of renesting in this age group. This can be explained from the adults' greater willingness to take higher risks, because of their lower future reproductive value than yearlings. Synchronous egg-laying can be an effect of the limited time available for breeding at northern latitudes (Raveling 1978, Myrberget 1986). It can also be an anti-predator strategy; reproductive effort can be altered when the predation risk is high (Lima & Dill 1990), but if the predator is a generalist the wanted effect will not be obtained (Ims 1987). Risks taken during the present reproductive event can totally eliminate the possibility for future opportunities, and a trade-off between present and future (residual) reproduction arise (Magnhagen 1991). If initiation of egg-laying close to the population mean date is an anti-predator strategy and there is a trade-off between reproduction and predation, the risk taken by asynchronous egg-laying will affect future reproductive success. A higher risk taken by adult individuals is found in the marine fish *Gobius niger*, where young males refrained from reproducing when exposed to a predator, while older males reproduced under the same conditions (Magnhagen 1990). The older males took higher risks possibly because of their lower probability for future reproduction compared with the younger individuals. Whether older individuals necessarily take greater risks is a topic under discussion. They do not necessarily take greater risks, but they can have increased experiences and skills with increasing age (Reid 1988).

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SAMMENDRAG

Predasjon av egg og rugende høner hos lirype *Lagopus l. lagopus*

Reirpredasjon er en av de viktigste årsakene til mislykket reproduksjon hos mange bakkehekkende fugler. Gjennom en 15-års periode ble predasjon av egg og rugende høner undersøkt hos lirype *Lagopus l. lagopus* på Dovrefjell. Predasjonsmønsteret gjennom hekkesesongen, faktorer som påvirker sannsynligheten for at predasjon skjer og hekkeatferd i relasjon til alder ble undersøkt. Det var store forskjeller mellom år i andel reirpredasjon (0-50%) så vel som predasjon på rugende høner (0-29%). Gjennomsnittlig årlig reirpredasjon (15%) var tre ganger høyere enn predasjon på rugende høner. Frekvensen av predasjonstilfeller var ikke konstant gjennom hekkesesongen, men økte med økende antall tilgjengelige reir. Predasjonen startet etter gjennomsnittlig dato for rugestart, og samtidig som antall tilgjengelige reir var som høyest. Ingen av faktorene som ble benyttet i en logistisk regresjonsanalyse (kondisjon, reirskjul, hekkeerfaring og dato for start av egglegging) kunne predikere sannsynligheten for predasjon av egg eller rugende høner. Imidlertid syntes "godt" reirskjul å ha en viss betydning for sannsynligheten for predasjon. Ettårige rugende høner hadde signifikant dårligere kondisjon enn eldre høner, og det var dessuten forskjell i valg av reirskjul mellom de to aldersgruppene. Starttidspunkt for egglegging var fordelt jevnt over hele den aktuelle perioden hos voksne høner, sammenlignet med ettårige høner som hadde ett mer aggregert eggleggingsmønster.

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