Estimation of nesting success and frequency of re-laying in Willow Grouse *Lagopus lagopus*

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In a comparison of the observed and estimated egg loss values, Mayfield's (1961) method was found to yield reliable estimates of nesting success for a population of Willow Grouse *Lagopus lagopus* in northern Norway. A method has been evolved for calculating the frequency of re-laying from the Mayfield estimates of nesting success. The data indicate that about 60 % of the hens that lost their initial nests started replacement clutches. However, the hatching success of these re-nesting attempts was sufficient to compensate for only about 20 % of the eggs initially lost.

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Introduction

Loss of eggs, mainly due to predation, represents a major factor in the population dynamics of many tetraonid species, such as the Willow Grouse *Lagopus lagopus* (e.g. Myrberget 1972, 1975a). Tetraonids do not build very visible nests, so that in studies of egg losses many nests are located only late in the incubation period. The recorded losses do not therefore include possible losses earlier in the nesting period, nor do they show to what degree egg losses are being compensated for by re-laying.

Mayfield (1961, 1975) proposed a method for calculating the rate of nesting success which allows for this bias due to nest age at discovery. The rate of egg loss is estimated from information collected during the period in which the nests have been kept under observation, viz. the *exposure* period. The method assumes (i) that the egg loss rate remains the same throughout the nesting period (however, see Klett & Johnson 1982), and (ii) that the nests which are found are representative of those of the population as a whole (see Green 1977, Willis 1981).

We here present data on the nesting success of a population of Willow Grouse in northern Norway during the years 1974–80. For this population the fate of most nesting attempts is known, irrespective of whether or not all the nests were found. The aim has been to examine whether the Mayfield method yields a reliable estimate of the rate of nesting success. Such estimates, however, ought also to take into consideration the frequency of re-laying after loss of the initial nest, as well as the success rate of such re-nesting. We have therefore developed a method for calculating the frequency of re-laying based on the estimates of nesting success obtained by the Mayfield method.

Material and method

The field work was done on the coastal island of Tranøy (69°09'N, 17°25'E) and on three islets lying nearby (total area of 137 ha.). The vegetation and soils have been described previously by Myrberget (1975b).

A census of the breeding population was carried out in May and/or early June, using the 'pointing dog' mapping method (Myrberget 1976). The census data and the distributions of the breeding territories in most years have been presented previously (Myrberget 1976, 1983, Myrberget et al. 1977, Blom & Myrberget 1978, and Erikstad et al. 1982).

The recorded numbers of breeding females refer to the situation in mid-May, i.e. just before egg-laying had started. Five hens that disappeared around May 15, probably before they had laid any eggs, have been excluded from the calculations (2 in 1975 and 1977, 1 in 1973).

The date on which egg-laying started in any given nest was calculated from the nest's hatching date, assuming that the eggs were laid at intervals of 1.1 days and that the incubation period was 21 days (e.g. Westerskov 1956). Each nest was then assigned a *relative* egg-laying date, i.e. the number of days before or after the median egg-laying date for each year (defined as the middle date of the 5 successive dates on which the highest number of hens had started to lay).

Broods were located by using pointing dogs. The chicks were aged from the curves for total body weight, plotted in relation to age, made for chicks of known age in the same years (known to be just as accurate as ageing from the wing length, see Myrberget 1975c).

The material comprises 96 complete egg clutches, for which the total length of the exposure periods was 985 nest-days, i.e. the mean exposure period per nest was 10 days. The standard errors (SE) of some of the

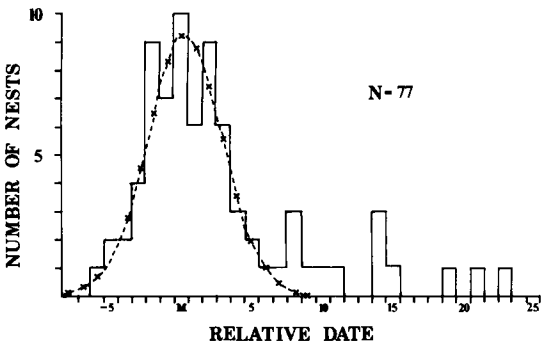

Fig. 1. Distribution of the dates for the start of egg-laying in the nests observed in 1974–80, expressed as their relative dates (see text). M = the median date. The curve shows the normal distribution, representing the early nests, with relative dates up to +7 (mean=+0.25, SD=±1.75).

Mayfield estimates have been calculated in the way described by Johnson (1979). The 95 % confidence limit (95% CL) is 2 SE.

In calculating the frequency of re-laying, the annual Mayfield nesting success rates were first calculated for all types of nests combined. These rates and the observed total numbers of hatched replacement clutches (nests and broods combined) were then used to calculate the number of replacement clutches started.

Results

Characteristics of early and late nests. Most of the hens started to lay their eggs within 2–3 days of the median date for the particular year in question (Fig. 1). The slope of the curve in Fig. 1 indicates a normal distribution up to the relative date of +7 days. Those nests that had been started up to a time of +7 days are hereafter referred to as *early* nests, which we assume mainly represent first clutches. Nests that were started at a later relative date (*late* nests), are assumed primarily to represent re-laying consequent upon the loss of the initial nests. The mean (± standard deviation) clutch size value for the early nests was 10.6 ± 3.1 eggs, and that for the late nests 7.1 ± 1.8 eggs.

Egg loss rates. Of the 96 nests observed (78 early and 18 late nests), in 19 (19.8 %) suffered loss of all the eggs (see Table 1). The observed nests contained altogether 936 eggs, of which 191 (20.4 %) were later lost. Thus, most of the egg loss rate originates from loss of entire clutches.

On average, 41 % of the hens in the population were observed to have lost their first clutch, and the mean value given by the Mayfield estimates for the loss of entire early clutches was 42 % (Table 2). The Mayfield method would thus seem to yield a reliable estimate for the rate of egg loss for the present material taken as a whole.

The Mayfield estimate for the loss rate for entire early clutches, for all years combined, was 43% (95%CL: 22–78%), and that for late clutches 53% (25–86%). Thus, the hatching success values for early and late clutches seem to be of the same magnitude.

Re-laying frequency. For all the years together, some 67 (3+64) hens probably lost their first clutches (Table 1). Twenty-eight cases of late nests and late-hatched broods were observed (Table 1),

Table 1. The observed breeding success in different years.

	1974	1975	1976	1977	1978	1979	1980	Total
Hens present	34	35	26	22	17	16	15	165
Early nests								
Nests deserted during the egg-laying period	0	1	1	1	0	0	0	3
Nests examined[1)]	10	18	14	12	8	6	10	78
Nests robbed[1)]	1	3	2	1	1	4	1	13
Other hens with chicks	13	5	5	3	4	1	2	33
Successful hens[2)]	22	20[4)]	17[4)]	14[4)]	11	3	11	98
Nesting losses observed[3)]	12	14	8	7	6	13	4	64
Late nests								
Nests examined[1)]	4	4	1	3	2	3	1	18
Nests robbed[1)]	2	1	1	2	0	0	0	6
Other hens with chicks	1	3	1	3	0	1	1	10
Total re-nestings observed	5	7	2	6	2	4	2	28
Successful re-nestings	3	6	1	4	2	4	2[4)]	22
Total exposure nest-days	112	268	134	169	108	83	111	985

1) Only completed clutches.
2) Nests examined, minus nests robbed, plus other hens with chicks.
3) Hens present, minus nests deserted during the egg-laying period and successful hens.
4) Includes one nest destroyed by us just before hatching should have occurred.
5) Nests examined, plus hens with chicks.

Table 2. The estimated loss rates (%), of entire initial clutches of eggs, given by two different methods. Based on the data given in Table 1.

	1974	1975	1976	1977	1978	1979	1980	Mean
Observed loss[1)]	35	41	32	33	35	81	27	41
Mayfield's method								
Exposure nest-days	65	224	119	130	74	53	96	—
Estimated loss	38	33	41	23	36	96	30	42

1) Total nesting losses expressed as a percentage of the hens present minus the number of deserted nests.

which indicates that at least 41% of the hens had re-nested. The Mayfield estimates, however, indicated that, on average, 62% of the hens had re-nested (Table 3).

Discussion

Both the test of the reliability of the Mayfield method for estimating nesting success, and the calculation of the frequency of re-laying from the Mayfield estimates are based on the assumption that all the early nests were initial nests and that all the late clutches represented re-nesting. This may not be entirely correct, but the error involved is probably only a small one, because (a) most of the early nests were started within a period of 6 days, (b) the difference between the mean numbers of eggs laid in the early and in the late nests (3.5 eggs) is similar to that found by Parker (1981) in an experimental study in another part of northern Norway, and (c) no difference has been found in the egg-laying dates between yearling and older hens (unpubl. data).

The following facts may also have led to some minor errors in our results: (i) the estimates of the Willow Grouse breeding numbers are subjected to an error of ± 1 pair (e.g. Myrberget 1983); (ii) a few hens may have lost all their chicks so soon after the eggs hatched that this led us to assume that they had lost all their eggs late in the incubation period; (iii) possible attempts to re-nest more than once were not taken into consideration; and (iv) our work in the area may have helped predators to discover some nests (however, see Erikstad et al. 1982).

For the studied population as a whole, our results indicate that the Mayfield method does yield a reliable estimate of the rate of egg loss throughout the nesting period, even though most of the observations were derived from the latter part of the incubation period. However, the wide range of the 95% confidence limits indicates that one must be very cautious when comparing values for egg loss rates for different years, areas or bird species (see also Hensler & Nichols 1981). To increase the sample size when calculating the frequency of re-laying, the data for early and late clutches could be combined, because the rates for both groups seem to be similar, as was also found by Parker (1981).

In Parker's study, at least 26% of the Willow Grouse that had lost their initial nests re-nested. Most of the hens that he studied had lost their eggs during the incubation period. In the present study, however, all losses which occurred in the nesting period were included in the estimates, and the results indicate that about 60% of these hens probably re-nested. Since some of the recorded egg losses occured late in the incubation period, a circumstance which makes re-nesting unlikely (unpubl. data), this means that probably most of the hens that lost their eggs during the egg-laying period, or very early in the incubation period, had tried to re-nest.

However, since the clutches laid in the late nests contain only 2/3 of the eggs in early clutches, re-nesting replaces only about 40% of the initial

Table 3. Estimates of the frequency of re-nesting in different years. Based on the data given in Table 1.

	1974	1975	1976	1977	1978	1979	1980	Mean
Observed freqency[1)]	42	47	22	75	33	31	50	43
Mayfield estimate								
numbers	6	9	2	6	3	(13)[2)]	3	—
freqency	50	60	22	75	50	(100)	75	62

1) Total number of observed re-nestings expressed as a percentage of the hens present minus the number of successful hens.
2) Actual value 16, but this is higher than the observed loss of 13 nests (Table 1).

eggs. If half of the late nests are robbed, second clutches will compensate for only 20% of the initial loss.

Egg predation seems to be an important factor affecting the population dynamics of those tetraonid species which exhibit cyclic fluctuations in numbers (e.g. Hagen 1952, Myrberget 1972, 1975a, Weeden & Theberge 1972, Lindén 1981, Storaas et al. 1982, Angelstam 1983). In our study the observed rate of egg loss was only about half as great as the estimated total loss. This stresses the need, in any discussions of the egg loss rates of tetraonids, for using only estimates obtained by methods, such as the Mayfield one, that take into account egg losses occurring before the nests were located. Possible compensation for the losses of initial clutches by re-nesting must also be considered.

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Selostus: **Pesimätuloksen arviointi ja uusintapesinnän yleisyys riekolla**

Riekolla kuten muillakin kanalinnuilla munapesyeiden tuhoutuminen on keskeinen populaatiodynaaminen tekijä, jonka arvioimista vaikeuttaa se, että osa pesistä löydetään vasta haudontavaiheessa. Myöskään uusintapesyeiden pesimätulosta ei useinkaan tunneta.

Kirjoituksessa tarkastellaan, miten luotettavia arvoja pesimätuloksen arvioimiseksi kehitetty Mayfieldin menetelmä antoi riekkopopulaatiossa, jonka pesimätulosta ja uusintapesintää tutkittiin tarkoin Pohjois-Norjassa kesinä 1974–80.

Populaation naaraista 41 % menetti ensimmäisen pesänsä ja Mayfieldin menetelmällä laskettuna löydetyistä ilmeisistä ensipesinnöistä (muninta aloitettu viikon kuluessa mediaanipäivästä, kuva 1) munapesätuhoja oli keskimäärin 42 % (taul. 2). Mayfieldin menetelmä antoi siten kaikkien vuosien yhdistetyssä aineistossa luotettavan arvion pesimätuloksesta, joka oli samansuuruinen sekä ensi- että uusintapesinnöiksi tulkituissa pesyeissä. Mayfieldin menetelmällä laskettuna 62 % naaraista, joiden ensipesye tuhoutui, muni uusintapesyeen (taul. 3), mutta niiden pesimätulos korvasi vain 20 % ensipesintöjen tuhoista.

Vertailu osoitti, että Mayfieldin menetelmä antaa luotettavan arvion riekon pesimätuloksesta, vaikka suurin osa pesistä löytyisi vasta haudonnan loppuvaiheessa.

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