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Nesting, clutch-size and breeding success of the Dunnock *Prunella modularis* in mountain birch forest in Swedish Lapland.

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Om boplats, kullstorlek och häckningsframgång hos järnsparv *Prunella modularis* i fjällbjörkskog i södra Lappland.

Anders Enemar

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The analysis is based on 332 Dunnock nests found during the bird census work of the LUVRE project in the Ammarnäs area, Swedish Lapland, from 1963—1983. Most nests were placed in juniper bushes and most clutches consisted of five eggs (mean clutch 5.2 ± 0.64 S. D., N = 155). Laying occurred from about 20 May to the first half of July with latest laying start observed on 10 July. Fifteen per cent of the eggs failed to hatch successfully and 70 per cent of the nests were lost during the nesting period of 27 days. The probability that an egg will give rise to a fledgling was 0.239 which means that the breeding success expressed as the mean number of fledged young per breeding attempt was 1.25. The rate of nest losses is among the highest found in small open-nesting passerine species. Genuine second clutches are probably needed to maintain the population size.

Denna studie är en analys av 332 häckningskort förda över bon funna i samband med fågelinventeringsarbete inom LUVRE-projektet i Ammarnäsområdets fjällbjörkskogar under åren 1963—1983. Inte mindre än 75% av de funna bona låg i enbuskar.

Värpningen börjar omkring 20 maj och nya äggkullar läggs ännu i första hälften av juli. Den senaste kullen började värpas den 10 juli. Den vanligaste kullstorleken var 5 ägg, därnäst 6 ägg. Medelkullen var 5,4 ägg i maj och 5.0 i senare hälften av juni. Den fallande trenden i kullstorleken är på gränsen till att vara säkerställd statistiskt. Medelkullen i hela materialet är 5,2 ± 0,64 S. D. Av äggen resulterade 85% i livskraftiga ungar. Nära nog 70% av häckningarna misslyckades av olika orsaker innan ungarna var flygga. Därtill försvann enstaka ägg och framförallt ungar under botiden. Tas hänsyn till alla former av förluster finner man att varje häckningsförsök genomsnittligt resulterade i endast 1,25 flygga ungar. Omfattningen av boförlusterna är bland de största som är kända för fribyggande tättingar. Den låga häckningsframgången antyder att andelen omlagda kullar måste vara hög. Beräkningar ger vid handen att äkta andrakullar sannolikt måste födas upp för att populationen skall vara självreproducerande.

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.ntroduction

The Dunnock is a regular breeder in the mountain birch forest of Swedish Lapland including the Ammarnäs area. Although it is a common species, the basic reproductive biology is poorly known (Glutz von Blotzheim *in litt.*) The aim of this study is to fil this gap, using data from the LUVRE project, which is an ornithological research program based on field work and run since 1963 in the Ammarnäs area (Enemar et al. 1984).

The nest record material

With few exceptions the breeding data refer to Dunnocks inhabiting the south-facing slopes of the mountains of Gaissatjåkke and Valle (65°58'—65°59'N; 15°58'—16°8'E) near Ammarnäs. The nests were mostly found by accident during bird census work. The analysis is based on 332 nest record cards from 21 seasons (1963—1983).

The number of nests found varies considerably between years (Fig. 1). There is an in-

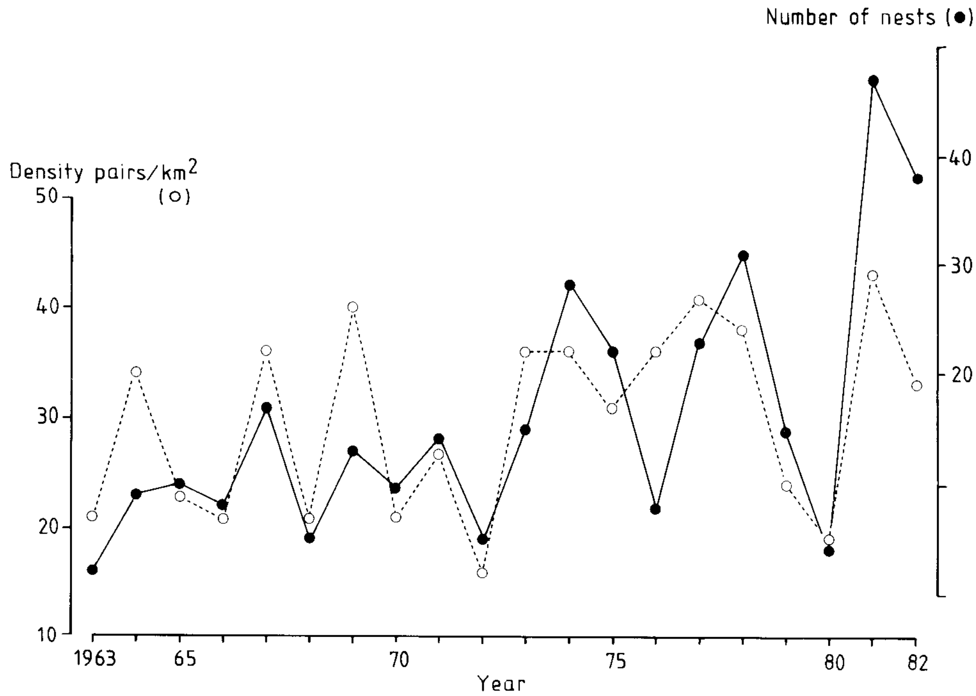

Fig. 1. Fluctuations in the Dunnock population density in the mountain birch forest at Ammarnäs (open circles; data from Enemar et al. 1984), and the number of nests found in the same area (filled circles) during 1963—1982.

creasing trend in the number of nests over the years which is probably due to improved skills of the field workers. The most informative cards were produced in connection with the mapping census which are based on repeated investigations of the same study plot, a procedure which enables the census-taker to revisit and examine a nest that has been found. It is evident in that the number of nests found fluctuates in parallel with the density of the Dunnock population in the study plots (Fig. 1). This means that the nest card information is biased in the sense that it more accurately reflects the conditions in the population peak years (many cards) than in the bottom years (few cards). Another bias is that nesting is not investigated with the same efficiency throughout the breeding season. Most observations were made during the bird census period, which begins in the first wee of June and lasts for about three weeks. The distribution of the observation periods of the nest record cards is shown in Tab. 1.

Tab. 1. The distribution of the nest record cards on 5-day periods of the breeding season. A. The distribution of cards according to date of discovery, or, if the nest was checked more than once, of the mean date of the observation period. B. Number of cards of nests containing eggs presented according to date of discovery.

	May	June						July			Total
Period No.	6	1	2	3	4	5	6	1	2	>3	
A	—	4	33	96	83	77	19	10	7	3	332
B	1	10	66	68	51	37	9	6	3	1	252

Tab. 2. Nest sites

	Number	Percentage
Juniper bush	240	74
Birch stump	50	15.5
Fork in birch or sallow	14	4.5
Between trunk and loosened bark, ·ithin roll of bark	11	3.5
Others	8	2.5
All	323	100.0

Results

ıest sites

Most nests were found in juniper bushes (Tab. 2). The proportion reported is probably too high because the juniper nests are easily discovered. The nests were also often placed in more or less excavated birch stumps or in the space between the trunk and loosened bark. This means that the nests are sometimes well concealed and that they are found in sites which are also used by other typical hole-nesting species such as the Redstart *Phoenicurus phoenicurus*. Most nests were found 0.5 to 1.5 m above ground, maximum height 4 m. Two nests were found on the ground, one under a piece of birch bark, and one under a root at the base of a birch trunk.

The breeding season

The first clutches were laid in the second half ı May, and we continued to find new clutches into the first half of July. It is evident that many pairs started laying about 20 May. The latest recorded breeding, a nest with 6 eggs, was found on 22 July and resulted in 4 ·stlings still in nest on 2 August. Thus, the Dunnock has a long breeding season compared to many other passerine species in the area. It should be noted, however, that knowledge of possibile breeding activities during the latter half of July is scanty for most species.

The nesting cycle

The length of the different phases of the nesting cycle has not been investigated especially and the information on the nest record cards on these matters is poor. To calculate breeding success it is necessary to estimate the length of the incubation and nestling periods. Five nest cards show that the incubation lasts for 11 or 12 days, and two cards reveal a period of 13 days. For calculations of breeding success an incubation period of 12 days was assumed. According to four nest cards the young leave the nest at an age of 10 days, but another card shows that they can remain in the nest for a further three days. A 10-day nestling period was chosen which together with the 12 days of incubation amounts to a 22 day nesting cycle. This probably means that the calculations of breeding success are based on the minimum number of days at risk in the nest for complete clutches and the broods.

It has been established repeatedly that the Dunnock normally lays one egg a day. The average clutch of the species is slightly more than five eggs (see below). This adds between four and five days to the nesting cycle if the incubation period is counted from the laying of the last egg. Thus, for successful breeding, the nestcup is occupied by eggs or nestlings for about 27 days.

The Dunnock can probably complete the nest-bound part of breeding within a period of five weeks. This estimate allows for a few days for the nest construction and a prolongation of the incubation and nestling periods of one or two days.

Clutch-size

A clutch was defined as completed when it was confirmed either by repeated eximination of the nest contents or by transillumination of the eggs (Arheimer & Enemar 1980). Complete clutches are known for 155 nests (Tab. 3). The mean clutch-size was 5.23 ± 0.643 (S.D.) eggs and clutches of five were the most frequent ones.

The date of start of laying could be traced for 95 nests, and the average clutch-size has been calculated for three separate periods of the breeding season (Tab. 3). A declining trend in clutch-size can be discerned from the second half of May to the last weeks of June. The difference between the beginning and

Tab. 3. Clutch-size

No. of eggs	Date of start of laying May 15—30	June 1—15	June 16—30	July 1—15	Before June 20 (date unknown)	Total no. of clutches
3	—	—	—	—	1	1
4	—	2	3	1	6	12
5	13	43	6	—	33	95
6	7	14	3	1	19	44
7	—	2	—	—	1	3
Totals	20	61	12	2	60	155
Mean ± S.D.	5.4±0.49	5.3±0.58	5.0±0.74	—	5.2±0.72	5.23±0.643

end of the breeding season, 0.4 eggs, is close to being statistically significant ($t = 1.99$, $p \approx 0.05$).

Hatching success

The number of newly hatched nestlings was often fewer than the number of eggs laid. This was due to hatching failures caused by unfertilized eggs or by death of the developing embryo. In the present context hatching failures also included weak young which died at hatching, or immediately after, and were removed by the parent birds before being observed. In 47 clutches which were known to be complete (5.23 ± 0.56 eggs) 37 out of 246 eggs (15%) failed to hatch successfully. In another 53 nests, where the clutches were probably complete, the failure rate was also 15% (40 out of 271 eggs). The two samples agree nicely indicating a hatching success of 85%. It follows that the mean clutch of the population produced only 4.45 hatchlings.

The hatching failures were distributed among 48% of the investigated nests. Single egg failures were characteristic (26 nests) but nests with two unsuccessful eggs were also common (17 nests). In four nests, three eggs failed to hatch and in one nests no less than five eggs out of six failed.

Rate of nest losses

No nests were inspected daily from the start of laying in order to measure the rate of nesting failures. The value of this can nevertheless be calculated by an application of Mayfield's (1961) method. Nest exposure time was available for 159 nests which were inspected at least twice. A nest loss during a visit interval of several days was arbitrarily assumed to have occurred on the day at the middle of the interval. The number of nest losses was 50 during a period of 1149 nest-days, which means a daily loss of 0.044 nests (corresponding to a survival rate of 0.96). Accordingly, this figure will be 0.70 (0.96^{27}) for the nesting period of 27 days. In other words, from the start of laying more than two of three breeding attempts will fail due to nest predation, nest destruction due to other reasons, nest desertion in connection with harsh weather, death of a parent bird, and so on.

Survival of eggs and nestlings

The main factor reducing egg and nestling survival is loss of the entire nest. But it happens that single eggs or nestlings also dissappear from or succumb in successful nests and these losses should be added to those of whole clutches and broods when the breeding success is calculated according to Mayfield. Available data are presented in Tab. 4, where the resulting daily survival rates of individual eggs and nestlings are given. The value is about the same throughout the nestings period. The differences in survival rates between laying, incubation, and nestling periods are not significant (chi-square test, $P > 0.1$).

Tab. 4. Survival rates of eggs and nestling, together with data from calculations according to Mayfield (1961).

	Eggs		Nestlings
	during laying	during incubation	
No. of nests	37	89	46
No. of egg/nestling days	259	2151	831
No. of losses	15	92[1)]	50[2)]
Daily survival rate	0.94	0.96	0.94

1) 3 records were single egg losses, the rest were loss of the whole clutch.
2) 14 were single nestling losses, the rest were loss of the whole brood.

The breeding success

The average probability of a newly laid egg giving rise to a fledgling can be calculated from the data presented above. The only missing information is the average number of days the egg is at risk before incubation. If incubation is arbitrarily considered to start when the last egg is laid this average number is 0.5 (n-1), where n is clutch-size. This gives 2.12 days at risk for the mean clutch-size of the population.

Following Mayfield (1961) and using information from Tab. 4 and the lengths of the incubation and nestling periods given above, the average expectation of life in the nest for an egg will be

$$0.94^{2.12} \times 0.96^{12} \times 0.94^{10} = 0.29$$

As shown above the hatching success of the eggs was 0.85. This reduces the probability of an egg reaching fledging to 0.24. In other words, slightly less than one egg out of four will give rise to a fledgling. Thus breeding success, expressed as the mean number of fledged young per breeding attempt, is 1.25.

Discussion

It is a drawback that the breeding season of the Dunnock has not been investigated with the same efficiency throughout, Most data are from the height of the season, June, which weakens the presented results.

Complete clutches usually contain 5 or 6 eggs which seems to be the same as elsewhere in Scandinavia (Svärdson & Durango 1959, von Haartman 1969, Haftorn 1971). There was a declining, although insignificant, trend in the clutch-size over the course of the breeding season. A larger sample may confirm such a trend. The many replacement clutches laid after the abundant nesting failures did not, apparently, contribute to a significant reduction in clutch-size. This indicates that the laying capacity of the females was good.

The annual mean clutch-size varied between 5.6 (n=12) and 4.9 (n=18) although no two seasons differed significantly. Clutch-size tended to decrease with increasing population density but this trend was not significant ($r=-0.33$, $n=12$, $P>0.20$). The clutch-size analyses are impeded by the fact that so few nest record cards are available from the years with low population density. But the general impression is that the clutch-size of the Dunnock is fairly stable.

As shown above nest losses were considerable, resulting in a low survival rate of eggs and nestlings. The forest in the study area is largely primeval, a condition which is generally associated with a high predation rate compared to man-made habitats impoverished in predators (Wesolowski 1985, with references). Wesolowski found a rate of nest losses of 0.7 for the mostly single-brooded Wood Warbler *Phylloscopus sibilarix* inhabiting a primeval forest in Poland. This is similar to the rate of losses in the Dunnock and represents one of the highest losses found in small open-nesting passerines.

The breeding success of the Dunnock can be compared to two other open-nesting small passerine species in northern habitats which have been analysed according to Mayfield's method. Nilsson (1983) calculated the survival rate of eggs and nestlings of the Reed Bunting *Emberiza schoeniclus* using nest record cards of the LUVRE project. The population densities of this species and the Dunnock have been about equal and have fluctuated in

Tab. 5. Calculated average production of fledged young per breeding pair when the rate of failure is 0.7 and the average production of fledglings per breeding attempt is 1.25. (For assumptions, see text.)
Strategy A. Clutches are re-laid after nest losses, no genuine second clutches.
Strategy B. Clutches are re-laid after nest losses, and early successful broods are followed by second clutches.

Strategy	Laying no.	Proportion of the population laying	Number of fledglings per pair	Accumulated number of fleglings per pair=a	Required adult survival rate to maintan population size = x[1)]
	1	1	1.25	1.25	0.76
A	2	0.7	0.88	2.13	0.65
	3	0.49	0.61	2.74	0.59
	1	1	1.25	1.25	0.76
B	2	1	1.25	2.50	0.62
	3	0.7	0.88	3.38	0.54

1) The adult survival x is solved from the equation $2(1-x) = x/2 \cdot a$, where (1-x) is the proportion of the two parent birds dying and x/2 is the survival rate of the number of offspring produced (a).

parallel over 20 years (Enemar et al. 1984). No less than 49% of completed clutches (not single fresh eggs) in the Reed Bunting will result in fledglings whereas the percentage for the Dunnock is 27, a substantial difference. Tiainen (1983), investigating the Willow Warbler *Phylloscopus trochilus* in Finland, found the survival rate of nests and of eggs/nestlings to be 0.399 and 0.342 respectively, calculated for the whole nest and egg/nestling periods. Corresponding Dunnock values are 0.30 and 0.28, again indicating the very limited breeding success of this species.

The low nesting success of the Dunnock raises the question of whether reproduction by the local population can replace the adult mortality. If so, then the reproductive capacity of the females must be considerable. Can the replacement of lost clutches be enough, or must genuine second clutches also be produced? These questions cannot be answered here unequivocally, but some light can be shed on them.

The adult survival rates required to maintain population size have been calculated for different levels of reproductive effort (average number of replacement clutches, with or without genuine second clutches) (Tab. 5). The calculations are based on the following assumptions: (1) all pairs start first laying between 15 and 20 May; (2) pairs relay whenever the clutch or brood happens to be lost during the nesting cycle; (3) only the length of the breeding season limits the production of replacement clutches; (4) new clutches are not started later than 15 July to secure enough time for the young become ready to migrate; (5) the nesting success is the same throughout the breeding season; (6) the survival rate of the fledglings (the first-year survival) is half that of the parent birds; (7) the beginning of each generation of replacement clutches is assumed to occur in the middle of a complete nesting cycle. The first nesting cycle is assumed to start on 15 May. This means that there will be time for three "average" breeding attempts within the breedi[illegible] season. However, pairs who lose their nests during the last week of the nesting cycle will probably not manage more than two attempts, whereas those who consistently lose clutches they have just completed can theoretically produce five or six clutches before [illegible] July.

The adult survival rates of small passerines varies between 0.4—0.7 (e.g. Cody 1971, Ricklefs 1973). Here I assume that the Dunnock survival rate is about 0.6 because it is a rather robust and medium-sized bird of this group. Table 5 shows that a considerable number of replacement clutches are required to account for an adult survival of 0.6. Apparently no less than half the population must produce, on average, three clutches when a single-brooded strategy is applied. As some pairs of this category may have lost two broods late in their nesting cycle with a low probability to relaying again, other pairs with early nest losses must compensate for this by laying even more than three clutches. It is far from certain that the female Dunnock can fullfil such a demand.

However, the population can be virtually self-maintaining if each pair has two breeding attempts and a double-brooded strategy is applied (Table 5). In order to reduce the adult survival from 0.62 to the required level of 0.60 probably only a small fraction of the population must accomplish three breeding attempts to compensate for those pairs who fail to produce two clutches. The two strategies do not differ much in reproductive output in comparison to the difference in the number of clutches produced. This is because of the low nesting success which results in only half the population being in a position to produce a genuine second clutch. Nevertheless, double-brooding considerably reduces the demand for a fraction of the females to produce three clutches or more. If we take into consideration the fact that all pairs probably do not manage to start breeding by the middle of May and that the extension of the nesting season into August is overestimated the probability of double-broodedness occurring increases substantially. The alternatives to the production of genuine second clutches are that the survival rate of the adult bird is higher than 0.6, that our data on the breeding success has been depressed by the influence of field workers, or that the population level is maintained by immigration.

The best support for the proposed double-brooded strategy of the Dunnock is Swanberg's (1955) observation of a Dunnock pair alternatively feeding fledged young and constructing a new nest in the mountain birch forest north of the arctic circle. The first egg was laid in the new nest on 4 July and the interval between the start of the two layings was estimated to about 33 days. Curry-Lindahl (1958) reports on a similar observation in the same habitat elsewhere in northern Lapland.

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