

# Population increase and the breeding biology of the Dunnock *Prunella modularis* in southern Finland

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The breeding biology of the Dunnock (*Prunella modularis*) was studied on the basis of 517 nest cards gathered mainly from southern Finland during 1954–87. The habitats used included several kinds of forests, spruce and mixed forests being the most common. Most nests were located in spruce bushes (62.5% of nests) or in juniper bushes (15.3%).

Laying of the first clutches started on average on 16 May (SD=7.0 days, n=151); there was no difference between habitats, but northwards the laying was delayed. Due to the second and the replacement clutches, the laying period continued until late July; the latest clutches were commenced on 23 July. Mean clutch size was 5.44 (SD=0.69, n=97) in June, but significantly lower in May (5.11, SD=0.61, n=151) and July (4.14, SD=0.62, n=21). Clutch size did not vary significantly between habitats, latitudinal zones, or cool and warm years. The probability of an egg giving rise to a fledgling was 0.37. The daily survival probability of nestlings was significantly higher than that of eggs. The breeding success increased with advancement of season. The overall survival probability was lower in cool (0.20) than in warm (0.46) Mays. The low survival of eggs during cool weather was attributed to increased predation of conspicuously coloured eggs. There was no difference in survival probability between habitats during the egg stage.

The results are briefly discussed with respect to the recent population increase of the Dunnock in Finland.

## 1. Introduction

The Dunnock (*Prunella modularis*) has been a very successful bird species in Finland during the last few decades. The number of breeding pairs was fewer than 10 000 during the 1940s, but in the mid-1970s the population had reached the level of 240 000 pairs (Merikallio 1958, Järvinen & Väisänen 1977, 1978).

Despite this amazing increase in population size, hardly any information has been published on the population ecology of the species in Finland. Excluding general handbooks (most notably v. Haartman et al. 1963–72) only two studies

exist. Holmquist (1939) described very briefly breeding observations on six territories in the Helsinki area. Later v. Haartman (1969), analysing Finnish nest card data on passerine birds, considered briefly the breeding biology of the Dunnock. In England, however, the behavioural ecology of the Dunnock has recently been under intensive study (Birkhead 1981, Snow & Snow 1982, Davies & Lundberg 1984, 1985, Davies 1985, 1986, Davies & Houston 1986, Burke & al. 1989); and three papers on the breeding biology have also been recently published (Sweden: Ene-mar 1987, West Germany: Weitz 1987, Poland: Tomek 1988).

In this paper I analyse the Finnish nest card data accumulated before 1988 to find out whether this material can provide some explanations for the recent population increase. From this perspective, I will consider several factors of breeding biology, but I will concentrate on clutch size, commencement of egg laying, and breeding success. Clutch size and commencement of laying are compared across different habitats and four latitudinal zones; the clutch size is also compared between years with a warm or a cool May. Breeding success is compared between first and replacement clutches, as well as between warm and cool years, and different habitats. In another paper (Tuomenpuro 1989) I have quantitatively analysed the habitat preferences of the Dunnock in southern Finland during the breeding season.

## 2. Material and methods

### 2.1. Material

The basic nest card material has been gathered by The Finnish Society of Sciences and Letters, since 1986 in cooperation with the Zoological Museum of the University of Helsinki. The material here considered amounts to 517 cards dating from 1954 to 1987. As cards are mainly compiled by amateur ornithologists, only a subset of the cards can be used for detailed analysis. The number of cards where both the clutch size and the commencement of egg laying could be determined was 269 cards (Table 1). Of these 151 were

considered genuine first clutches (i.e. clutches started in May, see below), and 118 replacement clutches.

Almost all the cards come from southern Finland. Table 2 presents the latitudinal distribution of the cards based on 100 km-wide zones of the Finnish national grid. The three southernmost zones cover 81% of the material, and the next zone another 16% of the cards. The remaining eight zones comprise only 4% of the material.

### 2.2. Methods

Three criteria were used to determine the date of commencement of laying. Firstly (*Known* in Table 1), if the nest was visited during the laying period, the date was known exactly. Secondly (*Calculated*), if the hatching or fledging date was known, the commencement of laying could be calculated. In this case both the incubation and nestling periods were rounded off to twelve days. Thirdly (*Estimated*), if the nest was visited at least twice during the incubation and/or nestling period, the commencement of laying could be estimated, and was set at the median of the possible dates. The clutch was defined as completed using the criteria applied by v. Haartman (1969).

As nest cards do not contain any information on the number of clutches laid by a particular female during one season, the true first clutches could not be precisely distinguished from the replacement and second clutches. In southern Finland almost all females start their first clutch in

Table 1. Nest cards accumulated from 1954 to 1987 grouped according to the commencement of laying. Informative cards are those with sufficiently detailed data for determining clutch size and date of the commencement of laying (for details, see text).

	May	June	July	Total
Informative cards	151	97	21	269
Known	49	37	5	91
Calculated	24	18	6	48
Estimated	78	42	10	130
Other cards				248
Total				517

Table 2. Distribution of nest cards in the different geographic zones. Zone 66 refers to the 100 km-wide zone at a distance of 6600–6700 km from the equator at 27°E, and so forth. Other explanations as in Table 1.

Zone	All cards	Informative cards
66	70	35
67	185	111
68	158	71
69	80	34
70–77	18	13
Not known	6	5
Total	517	269

May (Tuomenpuro, unpubl.), and thus the clutches started before 1 June were classified as genuine first clutches. All other clutches, including second clutches laid after a successful first clutch and replacement clutches laid after unsuccessful breeding attempts, were classified as replacement clutches. This classification may yield some error, as it in fact excludes some true first clutches and includes some replacement clutches among the first clutches (Tuomenpuro, unpubl.).

To study the differences in several parameters between habitats, the habitats were classified into three broad classes:

- 1) spruce-dominated,
- 2) other coniferous, and
- 3) mixed forests.

Using the method presented by Mayfield (1961, 1975) and further developed by Johnson (1979) and Hensler & Nichols (1981), it is possible to use all nests visited at least twice for calculations of breeding success. When applying this method, the exact date of nest failure, or losses of single eggs or nestlings were seldom known. The failures were estimated to have taken place on the median date of possible dates unless otherwise stated on the nest card.

Instead of calculating separately daily survival rates for nests and for eggs/nestlings in successful nests, and subsequently multiplying these two rates to obtain the overall survival probability, I will calculate the overall daily survival rates for all eggs and nestlings. This calculation directly takes into account the losses of entire clutches/broods, and losses of single eggs/nestlings from otherwise successful clutches/broods; but the calculation excludes hatching failures. The probability of hatching failure was estimated as a proportion of unhatched eggs of all eggs ready to hatch. In the calculations of the survival over different nesting stages the following lengths of risk for median eggs/nestlings were applied:

- 1) laying period 2.0 days,
- 2) incubation period 12.1 days and
- 3) nestling period 11.8 days (both based on unpublished nest card data).

The statistical significance between the daily survival rates of different nesting stages was tested

with t-tests (see Johnson 1979, Sokal & Rohlf 1981). The degrees of freedom for the tests were derived from the number of nests under observation.

Using the mean ambient temperature for May each of the years 1954–87 was classified as having a warm or a cool spring. The climatic data from Heinola (61°12'N, 26°03'E) was obtained from the reports of the Meteorological Institute of Finland. After calculating the median for mean temperature, each year was assigned to one of the two groups by comparing the value of the year to the median. Each group thus contains nest cards from 17 years. The mean temperature was 11.2°C (SD=1.16) in warm, and 8.5°C (SD=0.98) in cool, years.

### 3. Results

#### 3.1. Breeding habitat and nest sites

The breeding habitat was indicated on 490 cards (Table 3). Almost all nests were found in different forests, only 13 (2.7%) being situated in other habitats, for example gardens. The nest site was given on 515 cards (Table 4). The great majority of nests (322, 62.5%) were located in a spruce bush. The second most common site was a juniper (*Juniperus communis*) bush (79 nests, 15.3%).

A comparison of nest site distribution between 149 first and 118 replacement clutches revealed a significant difference in the frequency of spruce bushes (Table 4). In May the nests were located more often in spruce bushes than later in the season ( $\chi^2=14.9$ ,  $df=1$ ,  $P<0.001$ ). The difference

Table 3. Distribution of the 490 Dunnock nests in different habitats.

Habitat	Nests	%
Sapling stand of spruces	57	11.6
Spruce forest	161	32.9
Scots pine forest	27	5.5
Coniferous forest	33	6.7
Mixed forest	147	30.0
Deciduous forest	52	10.6
Other	13	2.7

Table 4. Sites of nests; all 515 cards, and 267 informative cards (see Table 1) grouped according to commencement of laying.

Site	All cards		Informative cards			
	Nests	%	May	%	June/July	%
Spruce bush	322	63	111	75	61	52
Juniper bush	79	15	16	11	25	21
Other bush	8	2	—	—	3	3
Between two bushes	28	6	7	5	3	3
Spruce (tree)	29	6	5	3	7	6
Other tree	3	1	—	—	—	—
Fallen tree	12	2	4	3	1	1
Heap of twigs	20	4	4	3	9	8
Other (incl. on ground)	14	3	2	1	9	8

may, however, be artificial as there were more spruce-dominated and other coniferous forests and fewer mixed or deciduous forests among cards compiled in May compared with cards on replacement clutches ( $\chi^2=10.4$ ,  $df=2$ ,  $P<0.01$ ).

### 3.2. Timing of breeding

The laying of first clutches started, on average, on 16 May ( $SD=7.0$  days, Table 5), the median date being 15 May. The earliest date for commencement of laying was 2 May (Fig. 1). However, in one clutch, not included in Fig. 1 due to failure during the early laying period, laying commenced on 29

April 1974. The bulk (58.9%) of the first clutches were started between 9 and 18 May.

The commencement of laying of the first clutches in four geographic zones is given in Table 5. In the southernmost zone the laying starts, on average, on 14 May ( $SD=5.6$  days) and in central Finland (the northernmost zone) on 19 May ( $SD=6.5$  days). The delay in laying between central and southern Finland is thus five days. The difference is significant (Table 5).

In spruce-dominated forests laying started, on average, on 15 May; in other habitats on 16 May; the difference being non-significant (Table 6).

As clutches laid in June and July include both the second and replacement clutches, it is not

Table 5. Commencement of laying and size of clutch in first clutches in four latitudinal zones, means  $\pm$  standard deviations. Day 1 = 1 May, other explanations as in Table 2. There is a significant difference in the commencement of laying between the zones (ANOVA,  $P<0.05$ ); laying starts significantly earlier in zones 66–67 than in zones 69–77 (t-test,  $P<0.05$ ).

Zone	N	Laying	Clutch size
66	17	14.4 $\pm$ 5.56	4.82 $\pm$ 0.63
67	72	14.8 $\pm$ 7.20	5.22 $\pm$ 0.51
68	37	16.3 $\pm$ 6.96	5.03 $\pm$ 0.76
69–77	24	19.3 $\pm$ 6.48	5.04 $\pm$ 0.55
Total	150	15.9 $\pm$ 6.97	5.11 $\pm$ 0.61
		F=2.83, $P<0.05$	F=2.44, $P<0.10$

Table 6. Commencement of laying (Day 1 = 1 May) and size of clutch in first clutches in different forest habitats, means  $\pm$  standard deviations. ANOVA revealed no significant differences between the means.

Habitat	N	Laying	Clutch size
Spruce	68	15.0 $\pm$ 7.18	5.06 $\pm$ 0.64
Coniferous or Scots pine	27	16.4 $\pm$ 6.77	5.00 $\pm$ 0.55
Mixed or deciduous	49	16.2 $\pm$ 6.77	5.22 $\pm$ 0.62
		F=0.69, $P>0.10$	F=1.48, $P>0.10$

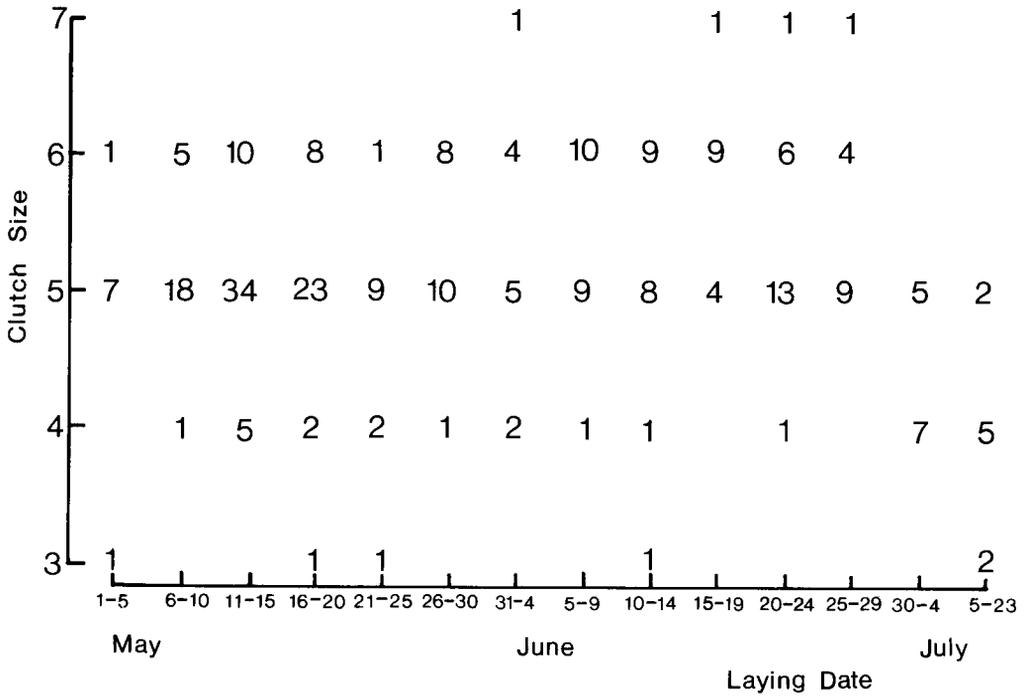


Fig. 1. Clutch size of the Dunnock in relation to commencement of laying in southern Finland. There is no significant linear dependence between clutch size and laying date ( $y=-0.0017x+5.21$ ,  $r=0.05$ ,  $P>0.10$ ).

reasonable to give mean values for the commencement of laying of these clutches. However, there are two slight peaks in the commencement of laying, one of 20 clutches between 5 and 9 June (Fig. 1) and another peak of 21 clutches between 20 and 24 June. In all, the laying of 53 (45%) replacement clutches commenced during the first half of June, and the last 21 clutches (18%) were started in July. In the two latest nests laying was not started until 23 July.

**3.3. Clutch size**

The clutch size varied between 3 and 6 eggs for first broods, and between 3 and 7 eggs for replacement broods (Table 7). The most common size was 5 eggs; this class included 67.5% of first, and 45.8% of replacement, clutches. Another common clutch size was 6 eggs, including 22.5% of first, and 34.7% of replacement, clutches. Only

six clutches had three, and four clutches seven, eggs.

The mean clutch size of all 269 clutches was 5.16 eggs (SD=0.71). Clutch size showed no linear dependence on the date of commencement of laying (Fig. 1). However, clutch size was signifi-

Table 7. Clutch size distribution of clutches started in May (i.e. first clutches), and June/July (i.e. replacement clutches). The mean clutch size is significantly higher in June than in May or July (ANOVA,  $P<0.05$ ).

	Clutch size					Mean	SD	N
	3	4	5	6	7			
May	3	12	102	34	-	5.11	0.61	151
June	1	4	47	41	4	5.44	0.69	97
July	2	12	7	-	-	4.24	0.62	21
Total	6	28	156	75	4	5.16	0.71	269

cantly greater in June (mean 5.44, SD=0.69) than in May (mean 5.11, SD=0.61) or July (mean 4.24, SD=0.62; Table 7). Thus clutch size increases, on average, by 0.33 eggs from May to June, and then declines by 1.20 eggs to July.

Comparison across all the latitudinal zones did not reveal a significant difference ( $P < 0.10$ ) in the clutch size of first broods (Table 5). Although the mean clutch size in mixed forests seemed to be slightly greater than in other habitats (Table 6), there was no significant difference between the habitats.

The mean clutch size was the same in warm (5.11, SD=0.62,  $n=92$ ) and cool Mays (5.10, SD=0.61,  $n=59$ ). When studying the dependence of clutch size on laying date separately in warm and cool Mays, no linear trend was found in either group.

### 3.4. Breeding success

*Losses of eggs and nestlings.* Altogether 629 eggs were lost during laying and incubation. Moreover, 147 nestlings were lost during the nestling period (Table 8). These figures include both the losses of whole clutches and partial losses of one or more eggs/nestlings.

One third (33.5%, 211 eggs) of egg losses were attributable to predation. Normally the whole clutch was destroyed, but from three clutches only one, from two clutches two and from one clutch

three, eggs were taken. The predator was seldom identified, but seven clutches containing a total of 32 eggs were probably taken by corvids (*Corvus corone*, *Pica pica* or *Garrulus glandarius*). The other predators included a cat (*Felis domestica*), a squirrel (*Sciurus vulgaris*) and people.

The disappearance of 57 eggs was almost certainly due to predation. Of the disappearances, 15 were due to partial loss of six clutches, and the rest were due to the loss of whole clutches. Losses of unknown cause (198 eggs) were probably mostly due to predation. Altogether 115 eggs failed to hatch, and 54 were failures of a single egg per clutch. Twenty clutches contained two, and seven clutches three, unhatched eggs. Nearly 8% (48 eggs) of losses were attributable to the desertion of the clutch; the reasons for desertion were not known.

Almost two-thirds (65.3%, 96 nestlings) of the losses of nestlings were due to unknown reasons (Table 8). However, most of these are probably attributable to predation. Predation caused the loss of at least 35 nestlings, and most probably also 10 nestlings which disappeared from two nests. Five nestlings starved, and one fell from the nest.

*Overall breeding success.* Based on the pooled data of all nests (Table 9), the daily survival rate of an egg during the laying period was 0.943 (SD=0.0077), and during incubation 0.956 (SD=0.0020), the difference of 0.013 is not statistically significant ( $t=1.62$ ,  $df=421$ , ns). As the difference is not significant and the material from the laying period is scanty, these two periods are combined in all further calculations and the term 'egg period' is used to refer to the combined stage.

Combining the laying and incubation periods, the daily survival rate of eggs is 0.955 (SD=0.0019), which is significantly lower than the daily survival rate of nestlings (0.980, SD=0.0016,  $t=9.74$ ,  $df=555$ ,  $P < 0.001$ ). Using the above daily survival rates gives a probability of 0.52 for an egg surviving until hatching, and a probability of 0.79 for a newly hatched nestling surviving until the fledgling stage. Taking the hatchability of eggs, 0.90 (Table 10), into account the overall probability for an egg of producing a fledgling is thus 0.37.

To examine possible changes in the survival probability with the advancement of the breeding

Table 8. Causes of egg and nestling losses (N=eggs/nestlings).

	N	%
Egg stage	629	100.0
Predation	211	33.5
Desertion	48	7.6
Disappearance	57	9.1
Unhatched	115	18.3
Unknown	198	31.5
Nestling stage	147	100.0
Predation	35	23.8
Starvation	5	3.4
Disappearance	10	6.8
Other	1	0.7
Unknown	96	65.3

Table 9. Survival rates of Dunnock eggs and nestlings in different nesting stages; daily survival rates and standard deviations (in parentheses), and survival probability over each nesting stage. N gives the number of nests under observation. Losses refer to number of eggs and nestlings lost during egg and nestling stages. In calculations of survival over a stage, the following lengths for nesting stages were assumed: laying stage 2.0, incubation stage 12.1 and nestling stage 11.8 days.

Stage	N	Egg+nestling days	Losses	Daily survival (SD)	Survival over a stage
Laying	128	900	51	0.9433 (0.00771)	0.89
Incubation	295	10579	463	0.9562 (0.00199)	0.58
Nestling	238	7313	147	0.9799 (0.00164)	0.79

season, the survival rates of first clutches were compared with those of replacement clutches (Table 11). The analysis revealed that the daily survival rate of eggs is significantly better in June/July (0.962) than in May (0.950,  $t=3.10$ ,  $df=317$ ,  $P<0.01$ ). The survival probability of nestlings does not change from May to June/July. The difference in survival rates between eggs and nestlings is thus greater early (0.028) compared to late in the season (0.020). The hatching probability is slightly higher in May (0.916) than in June/July (0.881, Table 10). The overall probability of an egg producing a fledgling is 0.34 in clutches started in May, and 0.41 in clutches started in June/July.

*Impact of temperature in May on survival.* Only clutches started in May were considered when

Table 10. Hatchability of eggs grouped according to laying date (first v. replacement clutches), weather conditions in May, and habitat.

	Eggs	% hatched
All	1158	90.1
First clutches	654	91.6
Replacements	504	88.1
Warm May	430	92.1
Cool May	224	90.6
Spruce forest	278	91.7
Coniferous forest	112	93.8
Mixed forest	264	90.5

studying the impact of temperature conditions in May on breeding success. In years with a warm May, the daily survival rate of eggs was 0.044 higher than in years with a cool May, the difference being significant ( $t=7.16$ ,  $df=181$ ,  $P<0.001$ ; Table 11). The hatchability of eggs (Table 10) was practically equal in both year-groups, but the survival of nestlings was 0.012 higher in warm Mays ( $t=2.39$ ,  $df=134$ ,  $P<0.05$ , Table 11). However, the average weather conditions in May may be a poor predictor of nestling survival, as many of the clutches laid in May do not reach the fledgling stage until June. The difference in the overall survival probability of an egg to produce a fledgling between these two groups is marked; the survival probability is 0.46 in warm Mays but only 0.20 in cool Mays.

*Breeding success in different habitats.* Only clutches laid in May were considered when analysing differences in survival probability between habitats. The analysis revealed no differences during the egg stage (Table 11). However, nestlings survived better in coniferous than in spruce forests ( $t=4.39$ ,  $df=72$ ,  $P<0.001$ ), or mixed forests ( $t=5.38$ ,  $df=82$ ,  $P<0.001$ ).

## 4. Discussion

### 4.1. Habitat and nest site

In Finland Dunnocks inhabit almost exclusively forest habitats (Table 3); spruce forests or mixed forests with spruce, Scots pine and birch formed the great majority of the observations. Of the 490

nests only 13 (2.7%) were situated in other habitats. In a recent quantitative analysis (Tuomenpuro 1989), it was concluded that the shrub layer of junipers or young spruces is the most essential feature of the habitat for the Dunnock, and the species composition of the upper tree layer is of little importance. According to v. Haartman et al. (1963–72), the most preferred habitat of the Dunnock is birch-dominated forest with spruce undergrowth. However, Haila et al. (1980) found that on the Åland Islands, SW Finland, the density of Dunningtons was the highest (8.2 pairs/km<sup>2</sup>) in luxuriant spruce-dominated forest. In Finnish Lapland Dunningtons inhabit mountain birch forests (v. Haartman et al. 1963–72, Rajasärkkä 1988).

Almost two-thirds of the nests were in spruce bushes (Table 4). In another sample gathered at Heinola, southern Finland, spruce bushes comprised only 29% of the 75 nest sites. The nest was as often located between two spruce bushes. Fallen trees (mainly spruces) and heaps of twigs were

also important nest sites, containing 18% and 15% of the nests, respectively (Tuomenpuro, unpubl.). The number of nests in spruce bush was significantly higher in nest card data than at Heinola ( $\chi^2=29.6$ ,  $df=1$ ,  $P<0.001$ ). This difference may be partly real but is presumably partially due to observation biases in nest card data. Nests in heaps of twigs and between two spruce bushes are more difficult to find than nests in small spruces (own obs.). Thus, nests of the former class may escape detection when nests are not searched for systematically. This problem often affects nest card data.

#### 4.2. Breeding season

The earliest clutches are laid at the beginning of May, and the last clutches in late July. The length of the breeding season thus exceeds 2.5 months. In the pooled data from 34 years (Fig. 1) there seems

Table 11. Survival rates of Dunnock eggs and nestlings grouped according to laying date (first v. replacement clutches), weather conditions in May, and habitat. Other explanations as in Table 9.

Stage	N	Egg+nestling days	Losses	Daily survival (SD)	Survival over a stage
Egg stage:					
First clutches	183	6580	328	0.9502 (0.00268)	0.486
Replacements	136	4899	186	0.9620 (0.00273)	0.579
Warm May	106	4153	140	0.9663 (0.00280)	0.617
Cool May	77	2427	188	0.9225 (0.00543)	0.321
Spruce forest	81	2909	154	0.9471 (0.00415)	0.464
Coniferous forest	31	1017	46	0.9548 (0.00652)	0.521
Mixed forest	71	2654	128	0.9518 (0.00416)	0.498
Nestling stage:					
First clutches	136	4195	90	0.9785 (0.00224)	0.774
Replacements	102	3118	57	0.9817 (0.00240)	0.804
Warm May	81	2820	49	0.9826 (0.00246)	0.813
Cool May	55	1375	41	0.9702 (0.00459)	0.700
Spruce forest	52	1554	36	0.9768 (0.00382)	0.758
Coniferous forest	22	783	3	0.9962 (0.00221)	0.956
Mixed forest	62	1858	51	0.9726 (0.00379)	0.720

to be a slight peak for the laying of first clutches in mid-May, but the laying season continues without major interruptions until early July. If the female starts to lay the first clutch on 16 May (the mean date, Table 6), and the laying period is four, the incubation period about 12, and the nestling period 11–12 days, then the nestlings of the first brood will leave the nest on about 12 June. If the female begins to construct her second nest immediately, she can start to lay the second clutch on about 17–20 June. However, there is no pronounced peak around these dates (Fig. 1). This is probably due to many replacement clutches laid during the first half of June. Furthermore, at least some females may start to construct their second nest before the nestlings of the first brood have reached the fledgling stage (Tuomenpuro, unpubl.). If the first clutch succeeds, the earliest females can lay their second clutch at the beginning of June.

The long laying season indicates that at least a fraction of the Dunnock population regularly lays two clutches in a season. Moreover, at least some of the clutches laid in July are third attempts (Tuomenpuro, unpubl.), but I suspect that third clutches are not laid after two successful breeding attempts.

The difference in the commencement of laying of first broods between southern and central Finland was five days (Table 6); there are hardly any nest cards from northern Finland. Enemar (1987), however, noted that the first Dunnocks

start to lay on about 20 May in the Ammarnäs area of Swedish Lapland, which is almost three weeks later than in southern Finland (Fig. 1). The latest clutch is laid about mid-July. In Swedish Lapland the breeding season is three or four weeks shorter than in southern and central Finland.

In the more southern parts of its range the Dunnock starts breeding as early as April or even March. According to Weitz (1987), in Langenfeld, West Germany, the date of laying of the very first egg of the season varied annually from 13 April to 28 April in 1980–86. In England, where most Dunnocks are sedentary (Davies & Lundberg 1984), the breeding season begins at the end of March and ends in early July (Snow & Snow 1982, see also Davies & Lundberg 1985). The main breeding period spans April and May; according to the B.T.O. nest cards from southern England, 35% of layings are started in April and 33% in May (Snow & Snow 1982). Thus, laying starts approximately a month earlier in England than in southern Finland.

### 4.3. Clutch size

According to several studies (Table 12) the clutch size of the Dunnock varies between 1 and 7 eggs. The average clutch size decreases approximately by 0.7 eggs from northern Europe (i.e. Sweden and Finland) to Central Europe (i.e. West Germany), and by 1.4 eggs to the British Isles. The

Table 12. The clutch size of the Dunnock in four populations grouped according to the commencement of laying; means, standard deviations and sample sizes (in parentheses); and the overall variation in clutch size. \* source for clutch size variation: Davies (1985).

Locality	Source	April	May	June	July	Total	Range
Swedish Lapland	Enemar (1987)	–	5.35±0.49 (20)	5.22±0.61 (73)	5.00±1.41 (2)	5.23±0.64 (155)	3–7
Southern Finland	This study	–	5.11±0.61 (151)	5.44±0.69 (97)	4.24±0.62 (21)	5.16±0.71 (269)	3–7
West Germany	Weitz (1987)	4.40±0.76 (25)	4.63±0.70 (49)	4.29±0.96 (21)	4.00±0.63 (6)	4.46±0.78 (101)	2–6
England	Davies & Lundberg (1985)	3.5±0.5 (23)	3.8±0.8 (23)	4.4±0.6 (16)	3.8±0.8 (6)	3.8±0.7 (68)	*1–5

most common clutch sizes are five and six in northern Europe (Enemar 1987, this study), but five and four in West Germany (Weitz 1987), and four and three in England (Davies 1985).

No continuous decline in clutch size with advancement of season was found in this study (Fig. 1). Instead, the mean clutch size increased by 0.33 eggs from May to June and then declined by 1.2 eggs to July. A similar pattern has also been found by Weitz (1987) in West Germany, and by Davies (1985) and Snow & Snow (1982) in England (Table 12). In Ammarnäs, Swedish Lapland, Enemar (1987) did not find any significant change in clutch size from late May to July. Although laying starts later in Ammarnäs, the mean clutch size (Table 12) is the same as in southern Finland in May ( $t=1.687$ ,  $df=169$ , ns), which is in contrast with findings in many other species (A. Järvinen 1986). In June clutch size is significantly smaller in Ammarnäs than in southern Finland ( $t=2.174$ ,  $df=168$ ,  $P<0.05$ ).

In general, the seasonal clutch size variation of the Dunnock seems to follow the peak-shaped trend observed in many open-nesting species (Klomp 1970, Slagsvold 1982), but interestingly, in northern areas (i.e. Lapland) there is no trend. The initial rise in the curve is missing in Ammarnäs, possibly because the start of the laying season is delayed until the second half of May. However, in NW Finnish Lapland the clutch size in first clutches seems to be smaller (mean 4.87,  $SD=0.99$ ,  $n=15$ , A. Järvinen 1986) than in southern Finland or Swedish Lapland.

Breeding success decreases if May is cool. Evidently it would be advantageous for a female to lay smaller clutches when the expected survival probability is low, but no such adjustment of clutch size was observed. Apparently there is no way for a female to predict the coming weather conditions in May when she starts to lay her first clutch (cf. A. Järvinen 1989). On the other hand, the nest card material may not provide adequate data for discovering possible changes in mean clutch size in relation to weather conditions.

#### 4.4. Breeding success

In almost all calculations (Tables 9, 11) the daily survival rate of eggs was significantly lower than

the survival of nestlings. The difference in daily survival is 0.028 for the first and 0.020 for the replacement clutches. Thus, the laying and incubation stages are more critical than the nestling stage to reproduction in the Dunnock. From May to June/July the daily survival probability of an egg increases by 0.012, which improves the probability of an egg surviving until hatching by 0.093. However, the hatching success is 0.035 better in May than in June/July. The daily survival of nestlings does not change with advancement of the breeding season.

A plausible explanation for the increase in the daily survival of eggs from May to June is the development of vegetation. Deciduous bushes and trees in particular, as well as herbs, offer far less protective cover in May than later. As the eggs of the Dunnock are greenish blue, they are conspicuous to predators when left unattended. On the other hand, the nestlings are more difficult to detect, as they soon acquire protective colouring. Thus, the vegetation cover is probably of greater importance for the protection of eggs than for the nestlings.

Although the mean temperature of one particular month is quite a general variable, the significance of temperature conditions to breeding success could be strikingly demonstrated. In years with a warm May the daily survival of eggs was 0.044 better than in cool years. During cold periods in May the incubating female is probably forced to forage more often and for longer periods than during warm weather. During cold periods the risk of nest predation is thus increased as the conspicuous eggs remain unattended.

Enemar (1987) found that the probability of an egg of producing a fledgling was 0.24, which is markedly less than the value of 0.37 found in the present study. However, he used a slightly different calculation method and a different length for the nesting period than the ones I used, which complicates the comparison. There is no difference in the daily survival rate of eggs between Swedish Lapland (0.956) and southern Finland (0.955), but the hatchability of eggs is better in southern Finland ( $\chi^2=7.80$ ,  $df=1$ ,  $P<0.01$ ). The daily survival rate of nestlings was 0.940 in Swedish Lapland (Enemar 1987), which is less than the rate of 0.980 found in this study ( $t=4.77$ ,  $df=282$ ,  $P<0.001$ ). The heavier losses were caused both by

the failure of whole broods and by the death of single nestlings. The losses are probably due to heavy predation during the early part of the season, when the vegetation offers little protection (A. Enemar, pers. comm.). Later in the season the success would probably be higher, but the data for the second half of June is very scanty (Enemar 1987, and pers. comm.). A further contributory factor may be the weather, which is not so harsh in southern Finland as in Swedish Lapland.

Weitz (1987) estimated that 39.7% of the eggs produced a fledgling in his study area in West Germany. However, this value cannot be directly compared with the values of the present study, as Weitz's (1987) method differed from mine. In accordance with my results, he noted that nest failures were more common during the egg than the nestling period. Almost one fourth (23.1%) of the failures took place during laying and about half (51.1%) during incubation.

#### 4.5. Population increase and breeding biology

The recent population increase of the Dunnock has generally been explained by habitat changes, e.g. by the increasing predominance of spruce-dominated forests in forestry (Järvinen et al. 1977, Järvinen & Väisänen 1977). This explanation was supported by an analysis of habitat preferences of the Dunnock (Tuomenpuro 1989).

My present analysis did not reveal a significant difference between the habitats as regards clutch size or commencement of laying of first clutches (Table 6). However, the habitat classes used were quite general and heterogeneous. Neither was there any difference in the daily survival probability of eggs between the habitats. The effect of May temperature on success did not confound the comparison between habitats as all habitat classes included almost equal numbers of clutches from warm and cool years. In mixed or spruce forests nestling survival seemed to be lower than in other coniferous forests. There is no obvious explanation for this difference.

The population increase of the Dunnock is comparable with that of the Scarlet Rosefinch (*Carpodacus erythrinus*). In the latter species the increase has been nicely attributed to the better breeding success related to habitat changes

(Stjernberg 1979). In the Dunnock, the present study based on nest card data did not provide much supporting or opposing evidence to the habitat change hypothesis. To resolve this problem, an analysis based on more detailed data is required.

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#### Selostus: Rautiaisen pesimäbiologia ja populaatiokoon kasvu Etelä-Suomessa

Rautiaisen pesimäbiologiaa tutkittiin Suomen Tiedeseuran pesäkorttiaineiston (Taul. 1) perusteella. Kuusi- ja sekametsät olivat yleisimpiä elinympäristöjä (Taul. 3); pesä sijaitsi useimmiten pienessä kuusessa (62,5% pesistä) tai katajassa (15,3%, Taul. 4).

Ykköspesyeen muninta alkoi keskimäärin 16.5. (Taul. 5), elinympäristöjen välillä ei ollut eroa (Taul. 6). Uusintajuosten peseyden takia muninta jatkui heinäkuun loppupuolelle saakka (Kuva 1). Keskimääräinen pesyekoko oli toukokuussa 5.11, kesäkuussa 5.44 ja heinäkuussa 4.24 (Taul. 5). Pesyekoko ei vaihdellut elinympäristöjen, leveyspiirien tai viileiden ja lämpimien vuosien välillä.

Mayfieldin menetelmällä laskettuna 37% munista tuotti maastopoikasen. Suurin osa tuhoista tapahtui muninta- tai haudontavaiheessa (Taul. 9). Viileinä keväinä 20% ja lämpiminä keväinä 46% munista tuotti maastopoikasen.

Tuloksia verrataan muihin rautiaistutkimuksiin. Ilmeisesti kuusivaltaisten metsien suosinta metsätaloudessa on vaikuttanut rautiaisen runsastumiseen Suomessa, mutta pesäkorttiaineisto ei mahdollista asian tarkempaa analyysyä.

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