Effect of nest site on nest survival in the Dunnock *Prunella modularis*

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Nest survival and breeding success were studied in relation to nest site at 134 Dunnock nests in southern Finland. The nests were grouped according to three site categories: 1) small spruce, 2) shrub, and 3) heap of spruce twigs and branches (brush pile). Of the 110 nests under observation during the egg stage, 56 failed; 54 failures were attributable to predation. During the egg stage the daily survival rate of a nest was 91.3% in spruces, 91.2% in shrubs, and significantly higher, 96.7%, in brush piles. The probability of a nest surviving throughout the egg stage was 24%, 23% and 59%, in spruces, shrubs and brush piles, respectively. The hatchability of eggs varied from 89.3% in spruces to 95.4% in brush piles, but the differences were non-significant.

During nestling stage, 10 out of 77 nests were destroyed by predators, but no other failures were observed. The daily survival rate of nests varied from 96.8% in spruces to 99.1% in shrubs, and the daily survival rate of nestlings exceeded 99%, irrespective of the nest site. The differences were non-significant. The size of first clutches did not vary between the nest sites.

On average, successful nests were better concealed both from above and from the sides than failed nests, but no other differences in nest site characteristics were found. The brush pile nests were better concealed from the sides than other nests. Dunnocks used nest sites that offered better cover and were surrounded by denser vegetation than potential but unoccupied sites.

1. Introduction

Reproductive failures of small passerines are largely attributable to predation during the egg or nestling stages (Nice 1957, Ricklefs 1969). Strategies to reduce losses due to nest predation are colonial nesting (e.g. Wiklund & Andersson 1980, Hoogland & Sherman 1976, Wilkinson & English-Loeb 1982) and nesting in tree-holes (e.g.

Nice 1957, von Haartman 1957, Nilsson 1984). In open-nesting passerines selecting a safe and well-protected nest site can be of crucial importance to reproductive success. Nest predation should thus be a major selective force in the evolution of nest site selection.

In this paper I examine the nesting and breeding success of the Dunnock (*Prunella modularis*) in relation to nest site in southern Finland; I also

relate the success of a nest to quantitative nest site characteristics. Commencement of laying and clutch size are compared across nest sites. Finally, I compare nest sites with potential unoccupied sites, in order to find out how the nest sites differ from sites that have not been chosen.

The nesting and reproductive success of Finnish Dunnocks is of special interest, as the population size has increased rapidly from the 1950s onwards (Merikallio 1958, Järvinen & Väisänen 1977, 1978). The increase has generally been explained by habitat changes (for references, see Tuomenpuro 1989). The expansion to new favourable habitats may have been due to improved reproductive success of the Dunnock in Finland, or to increased immigration caused by improved reproduction in other regions, or both.

2. Material and methods

The main study area, located in Heinola, southern Finland (61°12′N, 26°05′E), measures 4.08 km^2 and is largely covered by spruce-dominated or spruce/pine-dominated forest (see Tuomenpuro 1989). Some additional data were gathered in an area of about 1.6 km^2 at Pertunmaa, some 50 km north of the main study area. The second area contains forests dominated by spruce, pine or birch.

The field data relate to 111 nests found in the main study area in 1984–88; most analyses include another set of 23 nests found in the main study area in 1983 or at Pertunmaa in 1984–88. For each nest records were made of the commencement of laying, clutch size, number of hatchlings and nestlings, nest fate (failure/success) and the number of days the nest was under observation at the different stages. When the breeding sucess was calculated by Mayfield's method (Mayfield 1961, 1975, see also Hensler & Nichols 1981, Johnson 1979), the following lengths were asumed for the different nesting stages: laying 4 days, incubation 11.8 and nestling stage 10.9 (based on my unpublished data). In all calculations the laying and incubation stages were combined (term "egg stage" applied), due to the scantiness of the data for the laying stage.

In July and August, after the breeding season, nest site characteristics were determined for 69

nests in the main study area. To obtain a sample of potential nest sites, each of the 69 nests was paired with a randomly chosen potential nest site ("unused site") inside the territory (i.e. male's song polygon) by locating a point at a random distance (≤ 75 m) and direction from the nest and choosing the nearest potential nest site (one of a site type actually used by Dunnocks) as an unused site. Eleven quantitative structural characteristics were determined at the sites (see Appendix).

For statistical comparisons non-parametric tests were usually chosen. When ANCOVA was applied, the square root transformation of $(x_i + 3/8)$ was performed, except for ACOV, SCOV, GC and CC (see Appendix), which were transformed to arcsine $(x_i/100)$.

3. Results

3.1. Nest placement

The nest site most often used was a small (≤ 3.0 m high) spruce (*Picea abies*); this was the site of 51 (40%) of the 134 nests. Twenty-six nests (19%) were in heaps of spruce twigs and branches formed by forest clearance (brush piles). Thirty-one nests were placed between two close-growing spruce bushes, 14 in juniper (*Juniperus communis*) bushes, and 12 in other sites. In all subsequent analyses the last three site classes are combined and the term "shrub" applied to this category. Thus, three nest site classes are recognised: spruce, shrub, and brush pile.

3.2. Reproductive success in relation to nest site

Of the 110 nests under observation during the egg stage, a total of 56 failed to produce fledglings. Only two nests were deserted, one due to heavy rainfall and the other due to disturbance by me. All the other 54 nests were robbed by predators. These were seldom identified, but Hooded Crows (*Corvus corone*), Jays (*Garrulus glandarius*) and red squirrels (*Sciurus vulgaris*) were known to have destroyed some of the nests, and presumably they, and possibly stoats (*Mustela erminea*), caused most of the other losses. During

the nestling stage 77, nests were under observation; ten were lost to predators, but no other failures took place.

The daily survival rate of nests during the different nesting stages is given in Table 1. During the egg stage, the daily survival probability was highest (96.7%) in brush piles. The difference between brush piles and spruces or shrubs was significant (t-test, P < 0.05). In brush piles 59% of the nests survived for the entire egg stage. During the nestling stage there were no differences in the daily survival probability between the sites. The survival probability of a nest was significantly (t-test, P < 0.05) lower during the egg than the nestling stage in spruces and shrubs, but not in brush piles.

No single eggs were lost from nests during the egg stage, but 30 eggs failed to hatch. In spruces, hatchability was 89.3% (117 eggs hatched), in shrubs 92.9% (143) and in brush piles 95.4% (104). The proportion of nests containing unhatched eggs did not vary between the sites ($\chi^2 = 3.06$, n = 77, df = 2, P = n.s.).

Only 14 nestlings were lost from successful nests (Table 2), and the survival probability of

nestlings varied from 99.3% (in spruces) to 99.6% (in shrubs); the differences between the nest sites were not significant.

3.3. Nest fate in relation to nest site characteristics

Comparison of successful nests with failed nests revealed statistically significant differences in three out of eleven nest site variables. Nest cover, viewed both from above (ACOV) and from the sides (SCOV), was better in successful nests than in failed nests (Table 3). As ACOV and SCOV were highly correlated ($r_s = 0.77$, P < 0.001), usually both the variables had high or low values. ACOV was less than 60% in only two (3%) successful nests, but in 19 (50%) failed nests (Fig. 1). SCOV was higher than 60% in 26 (84%) successful, but in only 6 (16%) failed nests (Fig. 1). DIST was greater in successful nests (median 56 cm) than in failed nests (median 47 cm). The correlation between DIST and ACOV was $r_s = 0.30$ (P < 0.01), and between DIST and

Table 1. Survival rates (±SD) of Dunnock nests in relation to nest site during egg and nestling stages.

Nest site	n	Nest days	Losses	Survival rate	
				daily	throughout stage
Egg					
Spruce	45	298	26	0.913 (±0.016)	0.24
Shrub	45	294	26	0.912 (±0.166)	0.23
Brush pile	20	122	4	0.967 (±0.016)	0.59
Nestling					
Spruce	25	185	6	0.968 (±0.013)	0.70
Shrub	31	213	2	0.991 (±0.007)	0.90
Brush pile	21	153	2	0.987 (±0.009)	0.87

Table 2. Survival rates (±SD) of Dunnock nestlings in relation to nest site.

	n	Nestling days	Losses	Survival rate	
				daily	throughout stage
Spruce	87	811	6	0.993 (±0.003)	0.92
Shrub	134	947	4	0.996 (±0.002)	0.96
Brush pile	94	720	4	0.994 (±0.003)	0.94
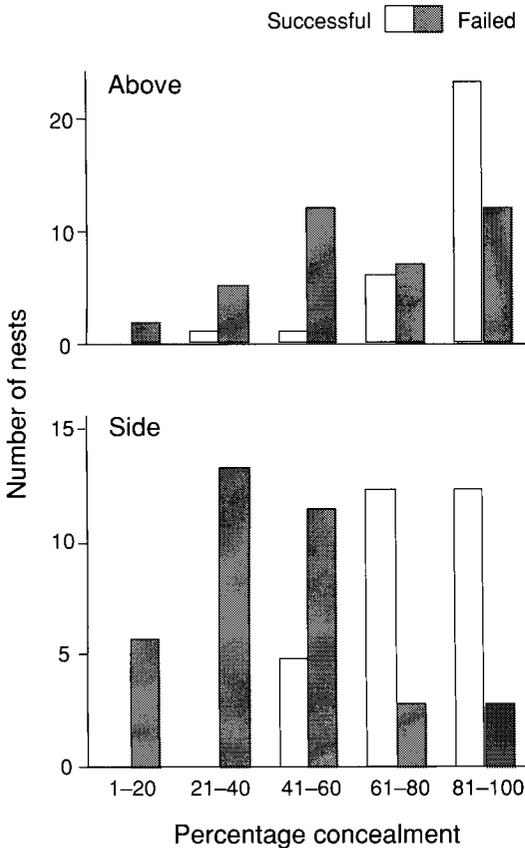
Successful ☐ ▨ Failed

Fig. 1. Concealment (%) of successful and failed Dunnock nests viewed from above and from the side.

3.4. Differences between nest sites and unused sites

Comparison between the nest sites and "unused sites" revealed significant differences in 10 out of 11 nest site variables (Table 4). Both cover for the nest and canopy cover were higher, but ground cover was lower among the nest sites. The nearest coniferous bush and nearest tree were closer for the nests, and the total number of coniferous bushes, and also of trees, was greater around the nests.

3.5. Laying date and clutch size in relation to nest site

As the median laying date and the median clutch size in the first broods could be determined only in the main study area, the following analyses comprise 65 clutches. The commencement of laying is expressed as the deviation from the yearly median date of all the first clutches.

The commencement of laying differed significantly between the sites (F = 4.01, df = 2, 62, P < 0.05). Laying started later in spruces (mean +1.8, SD = 4.8 days) than in brush piles (0.0, SD = 2.2) or shrubs (mean –1.4, SD = 4.1).

In all years the median clutch size in the first broods was five eggs. The mean clutch size was 5.13 in spruces, and 5.07 in shrubs and brush piles; the differences are not significant (F = 0.11, df = 2, 62, P = n.s., Table 5).

SCOV r_s = 0.37 (P < 0.001). All the other variables showed negligible differences.

Among the different nest sites, SCOV was, on average, higher in brush piles (median 70%, QD = 20%) than in spruces (median 55%, QD = 15%) or shrubs (median 60%, QD = 24%; Kruskal-Wallis test H = 6.86, df = 2, P < 0.05). The other nest site variables showed no significant differences between the nest sites. Two-way ANCOVA did not reveal significant interactions between nest fate (success/failure) and nest site (spruce/shrub/brush pile) for any of the variables. When the effects for a particular variable were tested, all the other variables were used as covariates.

4. Discussion

The analyses presented here may be subject to at least two sources of error. Firstly, if only well concealed brush pile nests and poorly concealed spruce and shrub nests were found, the nesting success calculations would be biased. However, there is no reason to assume such a biased data-gathering pattern. Although there was a significant difference in the mean lateral concealment of nests between the nest sites, no interaction between nest fate and nest site was found in any of the nest site variables (see above). Secondly, my visit to the nest might increase the vulnerability of nests to predation in spruce or shrub

Table 3. Nest site differences between successful (n = 31) and failed (n = 38) Dunnock nests. Kruskal-Wallis test (H).

Nest site variable	Successfull nests Median	QD	Failed nests Median	QD	H	P
ACOV	90.0	10.0	65.0	20.0	14.91	0.0001
SCOV	80.0	10.0	40.0	15.0	31.58	< 0.0001
DIST	56.0	17.5	46.5	20.3	5.92	< 0.05
CC	54.0	12.0	54.0	12.3	0.54	ns
GC	12.0	15.0	15.0	12.1	2.80	ns
CONF	0.7	0.7	0.8	0.7	0.11	ns
DEC	1.2	0.6	1.0	0.5	0.42	ns
TREE	1.0	0.4	1.0	0.5	0.09	ns
NC	4.0	3.0	3.0	4.5	0.56	ns
ND	5.0	2.5	5.0	2.5	0.18	ns
NT	6.0	2.0	5.0	2.5	0.04	ns

Table 4. Differences between sites of Dunnock nests (n = 69) and unused sites (n = 69). Wilcoxon matched-pairs test (T).

Nest site variable	Nests Median	QD	Unused sites Median	QD	T	P
ACOV	90.0	17.5	30.0	22.5	98.5	< 0.0001
SCOV	60.0	20.0	30.0	17.5	278.0	< 0.0001
DIST	52.0	19.8	36.0	15.8	617.5	< 0.01
CC	54.0	12.0	46.0	16.0	783.0	< 0.05
GC	15.0	13.3	30.0	14.3	633.5	< 0.01
CONF	0.7	0.7	1.1	0.8	696.5	< 0.05
DEC	1.1	0.5	0.9	0.4	760.5	< 0.05
TREE	1.0	0.4	1.3	0.6	680.5	< 0.05
NC	3.0	4.3	2.0	3.0	635.0	0.05
ND	5.0	2.5	6.0	6.0	725.0	ns
NT	5.0	2.0	3.0	2.0	545.5	< 0.001

Table 5. Clutch size of first broods in different nest sites.

Site	Clutch size distribution 3	4	5	6	Mean	SD	n
Spruce	1	2	13	7	5.13	0.16	23
Shrub	–	6	13	8	5.07	0.73	27
Brush pile	–	2	10	3	5.07	0.59	15

nests but not in brush pile nests (cf. Willis 1973). In fact, more time may have been spent in checking the brush pile nests; this should increase, not decrease, the vulnerability of brush pile nests to predation.

In a previous paper (Tuomenpuro 1990) I found that on average 37% of Dunnock eggs produced a fledgling in southern Finland, which suggests considerably better breeding success than was found in the present study. The difference is probably due to the exceptionally high predation pressure in my main study area. Indeed, about one half of the nests under observation during the egg stage were robbed by predators. The fate of a nest was strongly related to the nest site chosen. The probability of failure was considerably lower if the nest was built in a heap of

spruce twigs and branches rather than in any other site available (Table 1). It was found that only the variables contributing to nest concealment (ACOV, SCOV, DIST) influenced nesting success (Table 3). Other variables describing essentially the patch around the nest site showed no difference between failed and successful nests. The better lateral concealment of brush pile nests (see above) is presumably one reason for the better success of these nests, though it may not fully explain the difference. In addition, predators may not have learnt to search effectively for brush pile nests, as the availability of brush piles varies annually and also spatially. Brush pile nests may also be more difficult to approach than other nests.

In contrast to the egg stage, no significant difference in nest survival between the nest sites was found during the nestling stage. Nor were there any differences in the hatchability of the eggs or in the nestling survival between the nest sites.

As the breeding success increased considerably when the nest was placed in a brush pile rather than a spruce or shrub (see above), it would evidently be advantageous for a female to choose a brush pile when possible. The present data do not allow us to test this hypothesis. However, the availability of brush piles in the study area varies between years as a consequence of forest management and experimental manipulation of the availability would make it possible to examine this matter. A preference for the most productive type of nest site has been found, for example, in Field Sparrows (*Spizella pusilla*) in Michigan (Evans 1978), which preferred to nest in juniper bushes when the availability of junipers increased. Furthermore, nests built in junipers suffered considerably less predation during both the incubation and nestling stages than nests built in other sites.

The importance of nest concealment or cover in determining the nest fate has been demonstrated earlier in a variety of passerines, including, for example, the Eastern Kingbird (*Tyrannus tyrannus*, Murphy 1983), Hermit Thrush (*Catharus guttatus*, Martin & Roper 1988), Blackbird (*Turdus merula*, Osborne & Osborne 1980) and Superb Fairy Wren (*Malurus cyaneus*, Nias 1986). In contrast, Best (1978) found that the vulnerability of Field Sparrow nests to predation was independent of the relative nest concealment, probably because the most important predators in his study area were snakes. In an experimental study Gottfried & Thompson (1978) failed to find differences in predation rate between well- and poorly-concealed experimental nests.

Other structural attributes of the nest site have also been shown to affect the nesting success of several bird species. These include, for example, the height of the nesting substrate (Yahner 1983, Best & Stauffer 1980, see also Nilsson 1984), distance of the nest from the tree trunk (Yahner 1983), tree species (Knupp et al. 1977) and patchiness of the vegetation (Joern & Jackson 1983).

Comparison of the sites of Dunnock nests with unused sites revealed that the female Dunnocks probably also pay attention to other nest site characteristics than those directly influencing nest fate. The sites actually used are surrounded by denser bush and tree layers than unused sites (Table 4). This preference undoubtedly serves to reduce the probability of nest predation, though the comparison between failed and successful nests suggested that in determining the nest fate the immediate concealment of the nest is far more crucial than the density of surrounding vegetation.

In conclusion, the nesting success of the Dunnocks clearly best in brush piles. In Finland the area of clear-cuttings and young forests (≤ 20 yr) has increased from 850 000 ha in 1952 to 3 630 000 ha in 1973, due to forest management (for example, Järvinen et al. 1977). This trend has continued since the early 1970s. The new techniques applied in forestry (i.e. heavy machinery) may have increased the amount of twigs and branches left in forests compared with that in earlier decades. Besides the increase of favourable habitats (Järvinen et al. 1977, Järvinen & Väisänen 1977, Tuomenpuro 1989) there may thus also have been a general increase in the availability of favourable nest sites, which in turn may have contributed to the increase of the Dunnock population in Finland.

Selostus: **Pesäpaikan vaikutus rautiaisen pesän menestyvyyteen**

Rautiaisen pesän tuhoutuvuutta ja rautiaisen pesimismenestystä tutkittiin pääasiassa Heinolassa vuosina 1984–88 kerätyn aineiston (134 pesää) avulla.

Muninta- ja haudontakaudella 56 pesää 110:stä tuhoutui (Taul. 1); 54 tapauksessa tuho oli pedon aiheuttama. Pesän päivittäinen selviytymistodennäköisyys oli 96,7% jos pesä sijaitsi risukasassa ja merkitsevästi pienempi, noin 91% jos pesä sijaitsi muilla paikoilla. Munista kuoriutui pesäpaikasta riippuen 89,3–95,4%; pesäpaikkojen välillä ei ollut merkitsevää eroa.

Pesäpoikaskaudella 10 pesyettä 77:stä joutui petojen saaliiksi (Taul. 1); pesäpaikkojen välillä ei ollut merkitsevää eroa. Maastopoikasia tuottaneissa pesyeissä tuhoutui 10 poikasta; poikasten selviytymistodennäköisyys ylitti 99% kaikilla pesäpaikoilla.

Maastopoikasia tuottaneet pesät olivat keskimääräistä paremmin näkösuojassa sekä ylhäältä päin että sivuilta kuin tuhoutuneet pesät (Taul. 3). Risukasoissa sijainneet pesät olivat keskimääräsitä suojatumpia sivuilta. Rautiaisten valitsemat pesäpaikat tarjosivat paremman näkösuojan ja olivat tiheämmän kasvillisuuden ympäröimiä kuin satunnaisesti valitut potentiaaliset, mutta käyttämättömät pesäpaikat (Taul. 4).

Pesäpaikkojen välillä ei ollut eroa ykköspesyeiden keskimääräisessä koossa (Taul. 5), mutta muninta alkoi keskimääräistä varhemmin pienissä kuusissa sijaitsevissa pesissä.

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Appendix. Abbreviations and descriptions of nest site variables.

Abbreviation	Description
ACOV	Percentage nest cover of nest viewed from above.
SCOV	Percentage nest cover of nest viewed from the side.
DIST	Maximum direct distance between nest and outside edge of shrub (cm).
CC	Percentage canopy cover of trees > 3 m. Mean of five sightings.
GC	Percentage ground cover.
CONF	Distance from nest to nearest coniferous bush (m).
DEC	Distance from nest to nearest deciduous bush (m).
TREE	Distance from nest to nearest tree (m).
NC	Number of coniferous bushes within 2 m of the nest.
ND	Number of deciduous bushes within 2 m of the nest.
NT	Number of trees within 3 m of the nest.

Bushes were defined as woody plants 0.3 – 3.0 m high.

Trees were defined as woody plants > 3.0 m high.

The *canopy cover* of trees was estimated at the nest, and 2 m from the nest in each cardinal direction. A scale from 0 (no cover), 10, 20, ... to 100 (complete cover) was used.

Ground cover was estimated from a 2 m^2 plot around the nest; the overall coverage of ferns, grasses and herbs was estimated. The scale was the same as for CC.