Habitat preferences and territory size of the Dunnock *Prunella modularis* in southern Finland

Jari Tuomenpuro

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An area of 4.08 km^2 was studied in Heinola, southern Finland, mainly in 1984–85. The mean song polygon size was 1.53 ha (SD 0.42 ha, n=51) and, on average, unpaired males defended 0.27 ha smaller territories than paired males. The territories defended by two males were largest, averaging 2.17 ha (SD 0.54 ha, n=3).

Spruce-dominated forests were used disproportionatelly often by the Dunnock. Statistically significant differences between the territories and control quadrats were found in 9 out of 18 habitat-structure variables. The most striking difference was the great number of small spruces and spruce bushes in the territories. In addition medium-sized spruces were more numerous, the dominant trees were taller, and the canopy cover denser in the territories. In 49 out of 59 territories an edge of some kind was present inside the territory or formed a boundary for the territory. In the upper tree layer of the territories, spruce was very prominent, but in the lower tree layer deciduous trees (mainly birch) were almost as numerous. In the bush layer deciduous bushes were most abundant. It is concluded that small spruces and spruce or juniper bushes are essential features of the habitat for the Dunnock; spruce bushes are important nest sites, and Dunnocks also search for food in thick cover under the deciduous and coniferous bushes.

The males arriving early preferred young open bushy forests. In biandrous territories, the edge was nearer the centre and bushes were more numerous than in territories defended by one male.

Jari Tuomenpuro, Dept. of Zoology, Univ. of Helsinki, P. Rautatiekatu 13, SF-00100 Helsinki, Finland.

Introduction

The Dunnock *Prunella modularis*, the commoner of the two accentor species (family Prunellidae) in Europe (Glutz & Bauer 1985), has a remarkably variable mating system (Davies & Lundberg 1984; also Birkhead 1981, Snow & Snow 1982, Weitz 1987). In Finland the number of Dunnocks has increased dramatically at least since the beginning of the 1950s (v. Haartman et al. 1963–72, Järvinen & Väisänen 1977, 1978). In the 1940s Merikallio (1958) estimated that the breeding population comprised ca. 8000 pairs, though his result may have been a slight underestimate (Järvinen & Väisänen 1977). In the mid-1970s, the population had reached the level of 240000 pairs (Järvinen & Väisänen 1977). This increasing trend is continuing (Väisänen 1984, Hildén & Väisänen 1986, Väisänen et al. 1989).

No detailed study has been made of the factors that may have contributed to the increase, but it has generally been explained by habitat changes. The area of favourable forest has increased during recent decades, mainly due to forest management. According to v. Haartman et al. (1963–72), the habitat changes include the increase in the coverage of spruce-dominated forests and the increase in the patchiness of the forests. A further contributory factor suggested by Järvinen et al. (1977) is the increase in the cover of both deciduous and coniferous bushes in forests older than 20 years. Indeed, v. Haartman (1973) observed that in his study area (Lemsjöholm, SW Finland) the increase started only after the cessation of forest grazing. This cessation altered the structure of the forests, allowing the bush layer to develop.

No detailed quantitative information is available on the habitat requirements of the Dunnock in Finland. Accordingly, the first purpose of this paper is to describe quantitatively the structure of the vegetation in Dunnock territories in southern Finland, and to examine the characteristics differentiating the territories from forest not used by the species.

My second aim is to examine whether the vegetation structure of a male's territory is related to the time of arrival of the male. Possible structural differences between the territories of early and late males might suggest intraspecific competition, as the first males are free to settle in the territory of their choice.

Davies & Lundberg (1984) have shown that the social structure of the Dunnock population is very complicated during the breeding season. In their study area in Cambridge, England, they found that the mating combinations comprised both monogamy and several forms of polygamy, depending on the male's ability to monopolize females. Male's success was determined, among other factors, by the vegetation density in his territory (for further details, see Davies & Lundberg 1984, Davies 1985).

In my study area the Dunnock population also comprised both monogamous and polygamous units, and unpaired males (Tuomenpuro unpubl.). The third purpose of this paper is to compare the vegetation of the territories defended by one male with those defended by two, in order to see whether the vegetation characteristics of the territory are related to the mating unit composition, as in Cambridge. The sizes of the males' song territories are also presented, and compared across the different mating units.

Throughout this paper, *habitat* signifies the structure of vegetation in which a species occurs (Grinnell 1917).

Material and methods

Study area

The study area (about 2.0×2.5 km) is located in Heinola, southern Finland (61°12′N, 26°05′E). The area includes seven small lakes, and the land area of 4.08 km^2 is covered mainly by forests.

Deciduous wood lots, mainly birch *Betula* spp., cover an area of 15 ha; 219 ha bear predominantly Norwegian spruce *Picea abies* and 133 ha Norwegian spruce and/or Scots pine *Pinus sylvestris*. The forest is generally 45 to 120 years old, the median age being 65 years, but the area includes four stands of spruce and pine saplings younger than 20 years. There are also small spruce and pine bogs, covering altogether 21 ha, and rather sparsely vegetated patches of bedrock covering 20 ha.

Field data

The field data were gathered mainly in 1984–85; some additional data were obtained in 1983 and 1986–88. Song territories of males were located and mapped by marking the singing perches of the males on field maps (scale 1:2000). The mapping began as soon as the males arrived in the study area, in late April or early May, and lasted until the end of May.

The size of a male's song territory was defined by connecting the outermost singing sites to form a song polygon. However, singing sites which situated far (75 m or more) from others were excluded. Some males (19 out of 59) occasionally sang outside their normal territory, even inside some other male's territory. Typically a male flew 100–250 m to sing on the top of a large spruce, after which he returned to his territory. Usually a male had one to four such occasional singing perches and did not defend the area between them and the normal singing sites, which is the reason for the exclusion of these sites. The field data include observations of clashes and chases between neighbouring males, or alfa- and beta-males. Territory size was determined to the nearest 50 m^2.

In July and August the vegetation characteristics were recorded in all the territories. A total of 59 territories were sampled, 30 in 1984 and 29 in 1985. An additional sample of 12 biandrous territories was obtained in 1983 and 1986–88. To obtain a control sample of all the other habitats available for the Dunnock, the study area was divided into 125-m quadrats (n=277). Of these 71 were chosen at random for comparison. In gathering the control sample, the bedrock areas (see earlier, Table 2) were excluded. As none of the 71 quadrats covered a true territory, though 18 included fragments of territories, these two data sets can be regarded as independent.

In each territory the approximate centre was located with the help of a territory map, and a 50-m transect (width 4 m) was drawn from this point in a randomly chosen direction. Four additional transects were drawn from the central point at 72-degree intervals from the basic transect. Thus, a total area of 1000 m^2 was sampled in each territory.

Fifteen structural characteristics (variables) of the habitat were recorded and three other variables were created by summing some of the original variables. A detailed description of the variables and the abbreviations used for them are presented in the Appendix.

Table 1. Territory size (ha) of the Dunnock males in Heinola. The difference between unpaired and paired males is significant.

Mating status	Mean	SD	Min	Max	N
Unpaired	1.32	0.42	0.79	1.86	10
Paired	1.59	0.41	0.77	2.79	41
Monogamous	1.54	0.36	0.77	2.30	38
Biandrous	2.17	0.54	1.83	2.79	3
All	1.53	0.42	0.77	2.79	51

Data analysis

Each variable, except HDB, HDS and EDGE (see Appendix), was recorded separately on each of the five transects in the territory, but the results were combined for each territory. Heterogeneity within the territory is therefore not considered.

The sample distribution of most variables deviated significantly from the normal distribution; the distribution was tested with the Shapiro-Wilk test (Shapiro & Wilk 1965, see also Zar 1984). Due to the non-normal sample distributions, the differences between the sample means of the variables were tested with the Kruskal-Wallis test.

Discriminant function analysis (DFA) was used to identify the variables giving maximal discrimination between the territories and control quadrats. Before DFA was performed, the original values for all the variables, except HDB, HDS, EDGE and CC, were transformed to the square root of $(x_i+3/8)$, as recommended by Zar (1984). CC was transformed to arcsine (CC). Several variable combinations were tested to find the combination giving maximal discrimination between the groups. Two-group DFA was carried out using program BMDP7M (for details, see Dixon et al. 1985). All the other statistical analyses were also performed with BMDP statistical software.

Results

Size of a male's singing territory

The size of the song territory was determined for 10 unpaired and 38 monogamous males, and for three biandrous male groups. The mean size of the song polygon was 1.53 ha (SD 0.42, n=51; Table 1). The territories defended by two males (alpha-male and beta-male, see Davies & Lundberg 1984) were, on average, the largest, their size being 1.83, 1.88 and 2.79 ha (mean 2.17, SD 0.54). However, the largest territories of the monogamous and unpaired males were of the same size (Table 1). The territories defended by unpaired males were on average 0.27 ha smaller than those defended by monogamous males and biandrous male groups (Kruskal-Wallis test, H=4.02, df=1, P<0.05).

Table 2. Proportion of different forest types in the Heinola study area, and forest types of the Dunnock territories. The difference between the observed and expected distribution of the territories among different categories is significant (for details, see text).

	OMaT, OMT	MT	VT	CT, ClT	Bog	Bed-rock
Study area (ha)	26.8	207.3	98.6	34.0	21.5	19.7
(%)	6.6	50.8	24.2	8.3	5.3	4.8
Territories						
Observed (n)	4.0	38.0	13.0	1.0	3.0	0.0
(%)	6.8	64.4	22.0	1.7	5.1	0.0
Expected (n)	3.9	30.0	14.3	4.9	3.1	2.8

OMaT and OMT represents luxuriant birch/spruce forest; MT spruce-dominated forests, and VT, CT and ClT spruce/pine-dominated forests (for details, see Cajander 1926). Bedrock signifies areas covered with very sparse pine vegetation.

Vegetation structure of the territories and control quadrats

To obtain a preliminary approximation of the habitat preferences of the Dunnock on the scale of the study area, the use of different forest types (see Cajander 1926) was compared with their availability. The expected forest type distribution for the territories was derived by assuming that their use will correspond to the proportions available. The observed distribution (OMaT, OMT, MT vs. other types, Table 2) differed significantly from the expected one (χ^2=4.58, df=1, P<0.05). Deciduous forests, luxuriant spruce forests and spruce-dominated mixed forests (classes OMaT-MT) were used more frequently, and pine-dominated forests less frequently than expected (cf. v. Haartman et al. 1963–72).

To analyse the habitat preferences of the Dunnock in detail, the 18 habitat variables were compared between the territories and control quadrats. As a significant correlation existed between many of the variables, the significance level of the Kruskal-Wallis

Table 3. Habitat-structure variables compared between the territories and control quadrats. Means, standard deviations (SD), coefficient of variation (CV) and tests statistic of Kruskal-Wallis test (H) and its significance (P) are given. For variable abbreviations, see Appendix.

	Territories (n = 71)			Control quadrats (n = 71)				
	Mean	SD	CV	Mean	SD	CV	H	P
HDB	20.2	4.7	23.4%	16.5	4.6	28.1%	20.54	<0.001
HDS	23.0	5.2	22.4%	17.7	5.4	30.7%	31.67	<0.001
CC	50.9	12.6	24.8%	43.6	14.1	32.3%	6.69	<0.01
GC	89.7	23.5	26.2%	99.6	28.0	28.1%	1.51	ns
EDGE	77.2	48.2	62.4%	80.1	57.2	71.1%	0.08	ns
NDA	81.9	58.7	71.7%	60.5	44.8	74.0%	4.28	<0.05
NDB	10.0	11.3	113.3%	9.4	14.7	157.3%	1.67	ns
NSA	96.5	51.1	53.0%	41.8	32.8	78.5%	39.58	<0.001
NSB	38.3	21.5	56.0%	28.4	28.2	99.3%	7.62	<0.01
NSC	4.8	5.2	108.1%	3.6	4.8	132.0%	4.07	<0.05
NPA	6.2	10.1	163.0%	11.4	19.4	170.1%	3.44	ns
NPB	12.4	12.3	98.8%	24.3	23.8	98.2%	7.55	<0.01
ND	91.9	61.2	66.6%	69.8	51.2	73.3%	4.21	<0.05
NS	139.7	57.1	40.9%	73.9	54.4	73.6%	33.58	<0.001
NP	18.6	18.7	100.1%	35.6	34.6	96.9%	8.83	<0.01
DBU	206.2	75.2	36.1%	200.2	73.8	36.9%	0.14	ns
SBU	109.3	71.8	65.7%	62.6	52.7	84.2%	13.26	<0.001
CBU	47.2	48.4	102.4%	59.3	69.9	117.8%	0.43	ns

tests was set at 0.01 in all the following analyses. Using this conservative criterion, there is a significant difference in 9 of the 18 variables (Table 3). The most striking feature is the great number of small spruces (variable NSA) and spruce bushes (SBU) in the territories compared with the control quadrats. Only one quarter (25%) of the control quadrats, but over one half (52%) of the territories contained more than 100 spruce bushes per 0.1 ha. In contrast, the number of deciduous bushes (DBU) was exactly the same in the two groups. Medium-sized (NSB) and possibly also large (NSC) spruces were more numerous in the territories.

The number of large pines (NPB) in the territories was, on average, only half of that in the control quadrats (12.4 vs. 24.3). There seemed to be slightly fewer small deciduous trees (NDA) in the control quadrats ($P<0.05$). In the territories the height of the dominant trees (variables HDB, HDS) was greater and the canopy somewhat denser (CC).

Edges seemed to be at the same distance from the centre of the control quadrats and territories. However, in some cases it is difficult to assess the exact distance from the centre to the nearest edge, due to the ambiguity of the edge concept (see Appendix for a definition). Thus, caution is required in interpreting results for this variable. In 1984–85 the edge was inside the territory, or formed a territory boundary in 49 of the 59 territories (83%). In one extreme case the edge was as far as 150 m from the territory boundary.

The coefficient of variation was considerable in many of the variables in both groups, the variation being especially great in the numbers of pines (NPA, NPB, NP), coniferous bushes (CBU), large spruces (NSC) and large deciduous trees (NDB). In seven variables CV was significantly ($P<0.01$) greater among the control quadrats, which suggests that the Dunnock avoids some parts of the available habitat spectrum.

To study the vertical variation in tree species composition among the territories, the tree layer was divided into two height classes (trees with dbh ≤10 cm and with dbh >10 cm); bushes were treated as a third layer. There was a marked difference in the proportion of different tree species in these classes. In the lower layer, on average, spruce made up 54% (range 3–93%), pine 4% (0–32%) and deciduous trees 42% (6–90%) of the total number of tree trunks. In the upper layer spruce made up 69% (18–100%), pine 18% (0–68%) and deciduous trees 15% (0–82%) of the trunks. In the upper layer spruce was very prominent; in 54 cases its proportion exceeded 50%. In the lower layer, on the other hand, deciduous trees were almost as numerous as spruces. Birches and alder

Alnus glutinosa were the most abundant deciduous species.

In the bush layer the proportion of deciduous species was greatest. On average, deciduous bushes made up 58% (29–94%) of all the bushes in the territory. In 54 territories the number of deciduous bushes was over 160 per 0.1 ha, the maximum being 395. The most common species was rowan *Sorbus aucuparia*, but birches and alder were also numerous. Only 15 territories had fewer than 40 spruce bushes per 0.1 ha, the minimum being 4. On average spruce bushes made up 29% (1–64%), and other coniferous bushes (i.e. junipers and pines) 13% (0–53%) of all bushes, though there were over 80 pine/juniper bushes per 0.1 ha in only 11 territories.

DFA between territories and control quadrats

To study whether the variables chosen were sufficient to dicriminate between territories and non-territories, DFA was performed. Both the territory and control quadrat samples were divided into two subsamples (n_a=30, n_b=29) and only one of the subsamples of each group was used in calculating the discriminant function. The other subsamples were used as independent test material, to test the ability of the discriminant function to classify cases correctly.

After testing several variable combinations, it was found that a model incorporating variables NSA and HDB gave the best result. Of all the territories in the original subsample (that was used to calculate the discriminant function) 90% were again assigned to this group. Of the control quadrats, 79% were reclassified correctly. In the two test groups, 67% of the territories and 93% of the control quadrats were classified correctly. The combined result is presented in Fig. 1.

Habitat characteristics vs. territory size

In general, the correlation between habitat variables and territory size was low (r_s<0.25, n=51, ns). Only NDB correlated significantly with territory size (r_s=–0.28, n=51, P<0.05); the larger the territory was the fewer large deciduous trees it tended to include.

Relation of arrival time to habitat choice

The first males arrived in the study area on 17 April 1984 and 28 April 1985, and the last males settled on 10 May 1984 and 13 May 1985. The first half of the males arrived within a week after the earliest male.

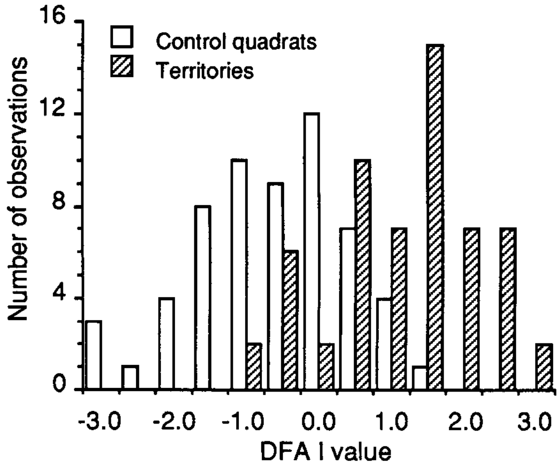

Fig. 1. Frequency distribution of territories and control quadrats along the discriminant function axis. On the DFA-axis the upper limits of each of the classes are presented.

If males arriving early and late choose different habitats, this might suggest that some territories are of better quality than others. Therefore, the males and their territories were grouped into early-comers (n=29) and late-comers (n=29; the arrival time of one male was unknown, and this bird was thus excluded). There were slight differences in the means of several habitat variables between early and late males, which suggested that males arriving early tended to choose younger forests with an open canopy. However, only one of these differences was significant. There were more bushes (variables DBU, SBU and CBU summed) in the territories occupied early (mean 375.0 vs. 288.0, H=6.94, df=1, P<0.01). This was mainly due to the great number of coniferous bushes (CBU) in the teritories of early males (68.9 vs. 27.1, H=9.10, P<0.01).

Since the probability of a male returning to the study area after overwintering was extremely low (only 1 of 29 colour-ringed males returned), it is possible to study the relation between the arrival time of a male and the vegetation structure by examining the order of selection of 12 territories which were occupied in both 1984 and 1985. If marked differences in the quality of the territories exist, these twelve should be among the best sites, and in consequence, should be occupied first. In this context quality need not be related to vegetation structure. On the other hand, if there are no essential differences in the quality of the sites, the order of settlement should be random. This proved to be the case. In 1984 six of these 12 territories were occupied by the early-comers, and the other six by the late-comers. In 1985 seven of the sites were settled early and five were settled late, but this distribution does not deviate significantly from the random (χ^2=0.33, df=1, ns).

Vegetation structure of one-male and two-male territories

Comparison of the vegetation structure of territories defended by one male (n=56) with those defended by two (n=15) revealed only two differences. First, the edge seemed to be (P=0.05) further from the centre in territories defended by one male. Second, the number of bushes (variables DBU, SBU and CBU summed) was greater in biandrous territories (means for biandrous territories 423.0, for others 354.7, Kruskal-Wallis test, H=6.25, df=1, P=0.01). This was due to the abundance of spruce and pine/juniper bushes in the biandrous territories. Nearly one half (45%) of the one-male territories, but only one quarter (27%) of the biandrous territories had fewer than 80 spruce bushes per 0.1 ha. Two-thirds (70%) of the one-male territories, and 37% of the biandrous territories had fewer than 40 pine/juniper bushes.

In general, there was no differences in the CV between the groups; only the coefficient of variation of CBU seemed to be greater in the group of monogamous and unpaired males.

Discussion

Territory size

In this study the mean size of a male's song polygon was found to be 1.31 ha for unpaired and 1.54 ha for monogamous males, and 2.17 ha for biandrous male groups (Table 1). In Cambridge Davies & Lundberg (1984, their Table 3) found that territories defended by two males covered an area of 0.66 ha (SD 0.07, n=17), and territories defended by one male 0.26 ha (SD 0.04, n=13). Two unpaired males had a song polygon smaller than 0.05 ha (Davies & Lundberg 1984, their Fig. 2). Snow & Snow (1982) estimated that in Buckinghamshire the territory size was 0.1–0.6 ha. In Langenfeld, West Germany, Weitz (1987) noted that the territory size was, on average, 0.24 ha (SD 0.10, n=26), the minimum size being 0.05 and the maximum 0.44 ha. Tomek (1988) reported that the territory size varied from 1 to 3 ha in her study area in South Poland.

In Finland, at least in my study area, the average territory is about five times as large as in England or West Germany. At least two factors may contribute to this difference. First, the general habitat is different. In my study area Dunnocks are almost restricked to spruce-dominated forests, whereas in England and West Germany they have a variety of habitats (Glutz & Bauer 1985, Weitz 1987). In Cambridge, for example, they inhabit different types of small wood lots, hedgerows, areas of long grass or open lawn, and flower-beds (Davies 1985, own obs.). In Buckinghamshire the habitats comprise a mixture of woodlands and patches of bramble, bracken and gorse (Snow & Snow 1982). Second, and related to the habitat differences, the density of the Dunnock population is strikingly greater in West Germany and England than in Finland. In Cambridge the density is approximately 3 males/ha (Davies & Lundberg 1984), in Langenfeld 0.6 males/ha (Weitz 1987), but in Heinola only 8 males/100 ha (Tuomenpuro unpubl.)!

Habitat preferences of the Dunnock

Several factors affect the selection of a breeding territory (for a review, see Hildén 1965, Cody 1985, see also Cody 1981, Morse 1985, Partridge 1978). One of the most important of these is often considered to be the habitat or vegetation structure (for example, Hildén 1965, James 1971, Cody 1981).

In the present study, a comparative approach was adopted in an attempt to identify the structural features that characterize the breeding sites of the Dunnock in southern Finland. Some differences were found between these sites (i.e. song territories) and sites that were not chosen.

In my study area Dunnocks inhabit almost pure spruce forest or mixed spruce-dominated forest, and the few deciduous stands are also in regular use. These forests have normally three well-developed canopy layers: 1) bush layer, 2) lower tree layer and 3) upper tree layer, and in some territories there is a distinct third tree layer. Without exception (Table 3), the bush layer comprises considerable numbers of both deciduous bushes (variable DBU) and spruce bushes (SBU); in some territories, however, there are junipers (CBU) instead of spruce bushes. In some territories the lower tree layer (NDA, NSA, NPA) is not separable from the bush layer; instead, these two form one continuous layer of trees and bushes less than 5–10 m tall. The upper tree layer (NDB, NSB, NSC, NPB) is nearly always distinct, but some territories are situated in stands of young spruce (and pine) saplings, which include only a few larger trees.

It seems plausible that, when evaluating the suitability of the habitat, a male Dunnock pays attention to the bush and lower tree layer, without making a distinction between the two. The most important feature of these layers for a Dunnock male selecting his territory is apparently the presence of spruces (or junipers). Other favourable feautures seem to be that the dominant trees are taller, and the canopy cover greater than in the surrounding areas. The species composition of the upper tree layer seems to be of minor importance, though spruce is usually the dominant species. In my study area, Dunnocks avoid forest areas where the only tree species is pine and where a bush layer of spruces or junipers is lacking. Such sites are rare in this area comprising only a few bedrock patches with thin soil.

This study failed to show whether a male prefers edges or not, but the significance of edges is difficult to evaluate because of methodological problems. However, the territories were so located that an edge was normally present inside the territory or at the territory boundary.

These results can, at least partly, be interpreted on the basis of the nesting biology of the Dunnock. In the study area the nests are usually located either in a spruce bush or between two spruce bushes. Of all the nests, 58% (n=75) fell into these categories, and 9% of the nests were situated in junipers (Tuomenpuro unpubl.). Thus, as a nesting site, spruce bushes are important for the Dunnock.

The Dunnock is a ground feeder; 85% of its foraging takes place on the ground (Bishton 1986). In the study area Dunnocks usually search for food in thick cover under deciduous or coniferous bushes or herbs. The bush layer, including deciduous bushes, probably offers protection during feeding. A forest with a dense bush layer can also be expected to provide a better food supply than a forest with a sparse bush layer.

Large trees, especially the tops of tall spruces, are usual song posts for males, though the males also sing in smaller trees and inside the canopy. It is not clear, however, whether the upper tree layer is an essential feature of the habitat for the Dunnock.

Only a few Finnish studies provide quantitative information on habitat use by the Dunnock. Some difficulties are encountered in comparing my data with these, because other researchers have examined distribution patterns on a broader scale, using a community approach, in which the resolution is less fine. Recently, Haila & Hanski (1987) studied the habitat relationships of the most abundant passerines on the Åland Islands, SW Finland, using principal components analysis. In their study area, the density of Dunnocks did not correlate with the number of saplings, horizontal denseness of the habitat, proportion of junipers among the bushes, canopy height or number of large trees. This is in contrast with what I found. Haila & Hanski (1987) concluded that the relatively small degree of habitat segregation between species in their study area was due to the peculiar mosaic structure of the habitats.

In another recent study, Haila et al. (1987) examined the effect of forest fragmentation on bird distribution in southern Finland. The bird distribution observed in four forest fragment classes in old coniferous forest was compared with the expected distribution derived from random placement model (Coleman 1981). The Dunnock was found to show particularly good agreement with the expected distribution. This finding is in contrast with suggestions based on a broader geographical scale (Järvinen & Väisänen 1978, Järvinen et al. 1977), but in this case the sample is fairly small (n=21 Dunnocks).

Outside Finland, only qualitative data are available on the habitat requirements of the Dunnock. Weitz (1987) found that in his study area the cover for foraging sites (i.e. cover provided by the bush vegetation) was important, but that the species composition of the bush layer was of little significance. He concluded that patchiness (mosaicism) of the habitat is an essential feature for the Dunnock. When summarizing the habitat requirements of the Dunnock introduced in New Zealand, Mauersberger (1977) suggested that dense shrubbery with open places inside or on the edges is important.

Other factors affecting habitat selection

There were no major differences in the vegetation structure of the territories between early and late males. However, early-comers seem to prefer younger forests with an open canopy. These areas are characterized by a considerable number of bushes, both spruces and junipers, as well as small trees, but fewer tall trees. Males arriving late tend to settle in more mature forests. The probable preference of younger and open forests by the early males may simply be due to the early snow melt in these forests compared with older forests with a dense canopy. When the first males occupy their territories in late April, snow still covers the forest floor. Snow-free patches, which are foraging areas for the males, are more probably encountered in bushy wood lots with an open canopy, and near open edges between different habitats.

The present data do not allow an analysis of factors other than habitat structure, though some observations may be made. No major differences were found between the territories of early and late males, which indicates that suitable, but unused habitat are still available in the study area. In fact, the number of males in the area has increased continuously since 1985 and was over 50% greater in 1988 than in 1985 (Tuomenpuro unpubl.). These findings point to the conclusion that the study area is not yet saturated, and that there is probably no keen competition for territories between the males.

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Selostus: **Rautiaisen elinympäristön rakenne ja reviirin koko**

Rautiaisen elinympäristön rakennetta ja reviirin kokoa tutkittiin Heinolassa erityisesti vuosina 1984–85. Koiraan laulureviirin koko oli keskimäärin 1.53 ha (hajonta 0.42; n=51; Taulukko 1); parittomien koiraiden reviiri oli keskimäärin 0.27 ha pienempi kuin pariutuneiden koiraiden. Kahden koiraan yhteisesti puolustamat reviirit olivat kookkaimpia (2.17 ha, hajonta 0.54).

Rautiaiset karttoivat vain mäntymetsiä ja hyvin harvapuustoisia kallioalueita (Taulukko 2). Mitatuista 18 habitaattimuuttujasta 9 keskiarvossa oli merkitsevä ero (P<0.01) reviirien ja vertailuruutujen välillä (Taulukko 3). Erityisesti pieniä kuusia sekä kuusipensaita, mutta myös keskikokoisia kuusia oli reviireillä enemmän. Ylispuuston keskikorkeus ja puuston lehvästön peittävyys oli suurempi reviireillä; tavallisesti (83% reviireistä) jonkinlainen reuna sijaitsi joko reviirillä tai muodosti reviirin rajan. Erotteluanalyysin perusteella (Kuva 1) pienten kuusipuiden määrä ja ylispuukerroksen koivujen keskikorkeus erottelivat hyvin reviirit ja vertailuruudut toisistaan.

Todennäköisesti pienten kuusten sekä kuusi- tai katajapensaiden määrä on merkittävä elinympäristön valintaperuste rautiaiselle; sen sijaan puuston lajisuhteet ovat vähämerkityksisiä. Kuusipensaat ovat tärkeitä pesäpaikkoja; lisäksi pensaikkoinen ympäristö tarjonnee enemmän ravintoa ja suojaa kuin avoimemmat alueet.

Varhain pesimäalueelle saapuvat koiraat näyttivät suosivan nuorta, suhteellisen avointa pensaikkoista metsää. Myös kahden koiraan yhteisillä reviireillä pensaskerros oli tiheämpi kuin muilla reviireillä.

References

Birkhead, M. E. 1981: The social behaviour of the dunnock Prunella modularis. — Ibis 123:75–84.

Bishton, G. 1986: The diet and foraging behaviour of the dunnock Prunella modularis in a hedgerow habitat. — Ibis 128:526–539.

Cajander, A. K. 1926: The theory of forest types. — Acta For. Fennica 29(3):1–100.

Cody, M. L. 1981: Habitat selection in birds: the roles of vegetation structure, competition, and productivity. — BioScience 31:107–113.

Cody, M. L. 1985: An introduction to habitat selection in birds. — In: Cody, M. L. (ed.), Habitat selection in birds, pp. 3–56. Academic Press, London.

Coleman, B. D. 1981: On random placement and species-area relations. — Math. Biosci. 54:191–215.

Davies, N. B. 1985: Cooperation and conflict among dunnocks, Prunella modularis, in a variable mating system. — Anim. Behav. 33: 628–648.

Davies, N. B. & Lundberg A. 1984: Food distribution and a variable mating system in the dunnock Prunella modularis. — J. Anim. Ecol. 53:895–912.

Dixon, W. J., Brown, M. B., Engelman, L., Frane, J. W., Hill, M. A., Jennrich, R. I. & Toporek, J. D. (eds.) 1985: BMDP Statistical Software. — University of California Press, Berkeley.

Glutz von Blotzheim, U. W. & Bauer, K. M. 1985: Handbuch der Vogel Mitteleuropas. Band 10/II. — Aula-Verlag, Wiesbaden.

Grinnell, J. 1917: Field tests and theories concerning distributional control. — Amer. Nat. 51:115–128.

v. Haartman, L. 1973: Changes in the breeding bird fauna of North Europe. — In: Farner, D. S. (ed.), Breeding Biology of Birds, pp. 448–481. National Academy of Sciences, Washington D. C.

v. Haartman, L., Hildén, O., Linkola, P., Suomalainen, P. & Tenovuo, R. 1963–72: Pohjolan linnut värikuvin. — Otava, Helsinki.

Haila, Y. & Hanski, I. K. 1987: Habitat and territory overlap of breeding passerines in the mosaic environment of small islands in the Baltic. — Ornis Fennica 64:37–49.

Haila, Y., Hanski, I. K. & Raivio, S. 1987: Breeding bird distribution in fragmented coniferous taiga in southern Finland. — Ornis Fennica 64:90–106.

Hildén, O. 1965: Habitat selection in birds. A review. — Ann. Zool. Fennici 31:107–113.

Hildén, O. & Väisänen, R. A. 1986: Suomen pesivä maalinnusto 1984–1985 piste- ja linjalaskentojen valossa. (Summary: Population monitoring of Finnish land birds in 1984–1985 by using point counts and line transects.) — Lintumies 21:114–125.

James, F. C. 1971: Ordination of habitat relationships among breeding birds. — Wilson Bull. 83:215–236.

Järvinen, O. & Väisänen, R. A. 1977: Recent quantitative changes in the populations of Finnish land birds. — Pol. Ecol. Stud. 3:177–188.

Järvinen, O. & Väisänen, R. A. 1978: Long-term population changes of the most abundant south Finnish forest birds during the past 50 years. — J. Orn. 119:441–449.

Järvinen, O., Kuusela, K. & Väisänen, R. A. 1977: Metsien rakenteen muutoksen vaikutus pesimälinnustoomme viimeisten 30 vuoden aikana. (Summary: Effects of modern forestry on the numbers of breeding birds in Finland in 1945–1975.) — Silva Fennica 11:284–294.

Mauersberger, G. 1977: Über die Heckenbraunelle (Prunella modularis) in Neuseeland. — Zool. Abh. Mus. Tierk. Dresden 34:101–126.

Merikallio, E. 1958: Finnish birds. Their distribution and numbers. — Fauna Fennica 5:1–181.

Morse, D. H. 1985: Habitat selection in North American parulid warblers. — In: Cody, M. L. (ed.), Habitat selection in birds, pp. 131–157. Academic Press, London.

Partridge, L. 1978: Habitat selection. — In: Krebs, J. R. & Davies, N. B. (eds.), Behavioural ecology, an evolutionary approach, pp. 351–376. Blackwell, Oxford.

Shapiro, S. S. & Wilk, M. B. 1965: An analysis of variance test for normality (complete ranks). — Biometrika 52:591–611.

Snow, B. K. & Snow, D. W. 1982: Territory and social organisation in a population of dunnocks Prunella modularis. — J. Yamashina Inst. Ornithol. 14:281–292.

Tomek, T. 1988: The breeding biology of the dunnock Prunella modularis modularis (Linnaeus, 1758) in the Ojców National Park (South Poland). — Acta Zool. Cracov. 31(3): 115–166.

Väisänen, R. A. 1984: Suomen pesivän maalinnuston yleiskehitys 1978 — 84 ja tila 1984. (Summary: Population changes of land birds in Finland in 1978–84.) — Lintumies 19:134–153.

Väisänen, R. A., Hildén, O. & Pulliainen, E. 1989: Suomen pesivä maalinnusto 1979–88 piste- ja lintulaskentojen valossa. — Lintumies 24:60–67.

Weitz, H. 1987: Habitat, ausserbrutzeitliche Aktivitaten, Brutbiologie und Sozialstruktur einer Population der Heckenbraunelle (Prunella modularis modularis). — Ph.D. Thesis, University of Koln, Koln. 182 pp.

Zar, J. 1984: Biostatistical analysis, 2nd ed. — Prentice-Hall, Englewood Cliffs. 718 pp.

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Appendix. Abbreviations and description of the variables considered in the analysis of territories and control quadrats.

Abbreviation	Description
HDB	Height of dominant birches *Betula* spp. (m).
HDS	Height of dominant spruces *Picea abies* (m).
CC	Percentage canopy cover of trees taller than 3 m. The mean of 10 sightings.
GC	Percentage ground cover. The mean of five sightings.
EDGE	Distance from central point of territory to nearest edge (m).
NDA	Number of deciduous trees per 0.1 ha with dbh less than 10 cm.
NDB	Number of deciduous trees per 0.1 ha with dbh greater than 10 cm.
NSA	Number of spruces per 0.1 ha with dbh less than 10 cm.
NSB	Number of spruces per 0.1 ha with dbh 10–34.9 cm.
NSC	Number of spruces per 0.1 ha with dbh greater than 35 cm.
NPA	Number of pines per 0.1 ha with dbh less than 10 cm.
NPB	Number of pines per 0.1 ha with dbh greater than 10 cm.
ND	NDA + NDB.
NS	NSA + NSB + NSC.
NP	NPA + NPB.
DBU	Number of deciduous bushes per 0.1 ha.
SBU	Number of spruce bushes per 0.1 ha.
CBU	Number of other coniferous bushes (junipers and pines) per 0.1 ha.

Bushes were defined as woody plants with a height of 0.3–3.0 m.
Trees were defined as woody plants with a height of > 3.0 m.
Edge was defined as a boundary between the forest and a road or electric powerline or clear-cut area. A boundary between old mature forest and a young sapling stand or open bedrock area was also accepted as an edge.
The *Canopy cover* of trees was estimated in the middle and at the end of each of the five transects through the territory (see methods). A scale from 0 (no cover), 10, 20,...to 100 (complete cover) was used.
Ground cover was estimated at the end of each of the five transects through the territory (see methods). The overall coverage of mosses, ferns, grasses and herbs was estimated from 2×2-m plot, the scale being the same as for CC.