
Nest-box in mixed environment

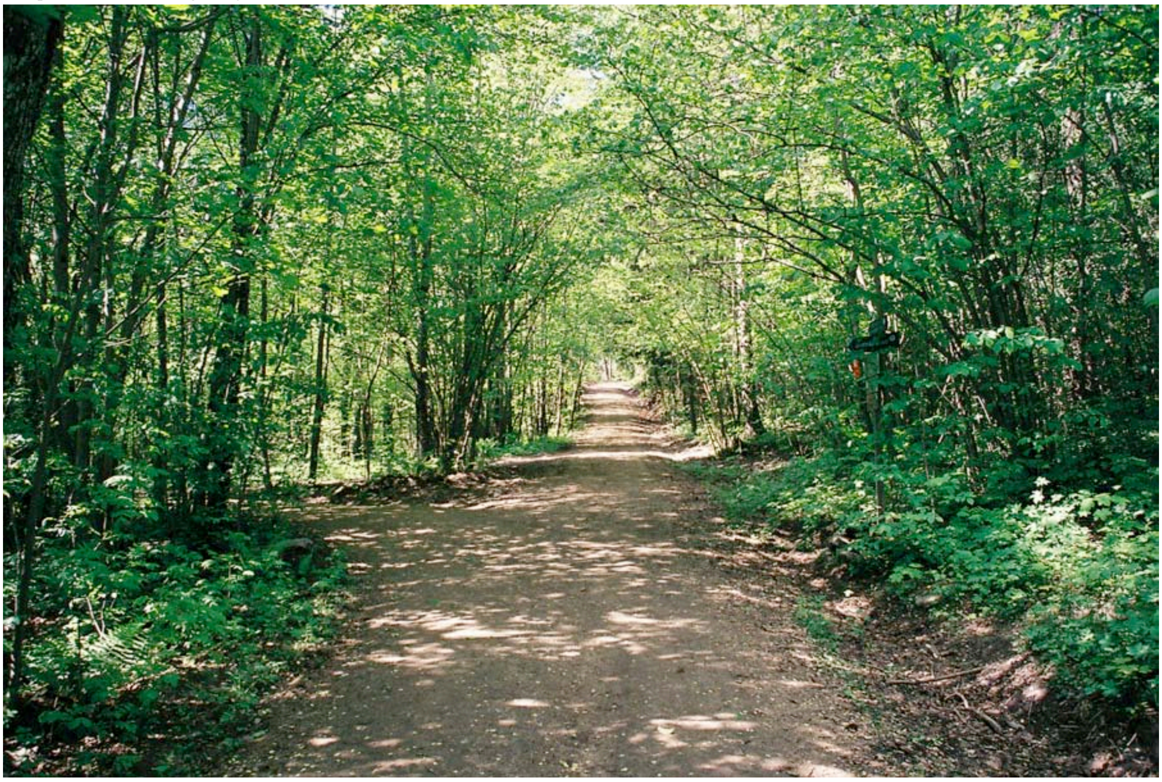
Habitat Choice in Tits: The Effect of Early Learning

Vegetation Analysis at the Lake Dæli Study-Site

Master Thesis 2007

Synne Folsland Olsen

The path between the graveyard and Stein Gård



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Forord

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Abstract

Breeding habitat-choice in two closely related species of passerines, Great Tit (*Parus major*) and Blue Tit (*Cyanistes caereleus*) was studied to reveal if their habitat preferences primarily is a hereditary trait, or if they could be acquired through early learning. We performed a cross-fostering experiment by swapping eggs between nests of the two species, which entailed that a number of broods were reared by hetero-specific foster-parents.

Blue Tits prefer deciduous forests as their breeding habitat, whereas Great Tits often are found breeding in habitats with a higher share of coniferous wood. If preferences for habitat primarily are based upon learning from parents while growing up, we would expect the cross-fostered birds to settle in habitats preferred by their foster-parents. If they did not, habitat preferences would most probably be a hereditary trait.

We detected no significant differences in choice of nesting habitat in coniferous or deciduous forests between cross-fostered birds raised by hetero-specific parents and control-birds raised by con-specific parents. Cross-fostered birds did not choose habitats according to the preferences of their hetero-specific foster-parents though there was a slight tendency in that direction. We found some evidence of early learning, however. The cross-fostered Blue Tits chose large nest-boxes, which are usually preferred by Great Tits.

1. Introduction

Every living organism, directly or indirectly, selects a habitat in which to live and reproduce. Immobile taxonomic groups, especially plants, depend in general on external factors such as wind or water to disperse their pollen and seeds. Once successfully settled, plants cannot easily change their habitat. Choice is made by the habitat rather than the plant, at least at the proximal level (Bazzaz 1991). Zooplankton drift with the ocean currents. Despite their vertical mobile ability to avoid predation or to feed in the water column, their horizontal movements are very restricted (Levinton 2001). In contrast to this, one would expect that more mobile species selects their habitats with great care. The habitat in which a species chooses to settle, has a large impacts on the individual's fitness and other subsequent choices. Of paramount importance in this respect is how many surviving offspring will be able to reproduce, and further; how many of those offspring that will survive to reproduce.

Despite the large number of studies dealing with habitat selection in animals, little is known about the underlying mechanisms and causes of their choices. Birds have due to their mobility a major potential for selecting habitats, and have therefore been subject to many related studies.

Selection of breeding habitat often overrides other components of habitat selection. This is no doubt due to the fact that the nest site is critical for the survival of the species (Orians and Wittenberger 1991). Breeding habitat may, in some species, be different from foraging habitat (Cody 1985). Seasonal change in food availability and weather conditions, can bring about displacements of whole groups or populations to more suitable areas (Ehrenroth 1979). With regard to birds of passage, this results in migrations to other continents.

Many factors have to be considered when selecting nesting-site habitats. Cody (1985) mentions, among other things, provision of shelter from the weather and from predators. Not all of these aspects may be important to all species at all times. Large birds of prey, for example, do not to worry much about being eaten when they are fully-grown.

The breeding habitat should in addition to the above-mentioned factors, possess enough available and usable nesting-holes, and the density of birds should not exceed the carrying-capacity of that particular area. Species richness can differ according to tree type. There are evident differences between the carrying capacity of coniferous and deciduous woodland for birds. Broad leaved woods support more bird species and higher densities than pine forests do (Fuller 1982). The risk of predation should be as low as possible, and the habitat should provide food for the whole breeding period. This fact is extremely important, since choosing to settle in an area which would soon be depleted of food, would lower the parents' fitness. Most probably they would not be able to bring any of their young through the nestling-, hatchling- and subsequent fledgling-period. Birds in the Wytham area (UK) time their onset of egg-laying according to the burst of foliage and the following development of caterpillars. (Perrins 1979). They must infer in advance when this burst of food is coming, since maturing of eggs, laying- and incubating them takes some time. Ideally, the young should hatch just in right time for an abundance of food, which would give them better chances of surviving.

Breeding habitat-choice in two closely related species of passerines, Great Tit (*Parus major*) and Blue Tit (*Cyanistes caereleus*) was studied. The main goal of the investigation was to examine whether the choice of nesting site in these two bird species primarily was a hereditary trait (Harris 1951), or acquired during early development (cp. Davis and Stamps 2004). We performed a cross-fostering experiment by swapping eggs between nests of the two species, which entailed that a number of broods were reared by hetero-specific foster-parents (Slagsvold *et al.* 2002).

In general, Blue Tits prefer deciduous forests as their nesting habitat, whereas Great Tits are found both in coniferous forest, deciduous forest and in a mixed environment (Haftorn 1971; Perrins 1979).

Blue Tits and Great Tits therefore prefer slightly different types of habitats. If their genetic disposition is the most influencing factor, we would therefore expect that the cross-fostered birds would hold an innate preference for a certain type of habitat and would thereby choose the predominant habitat of their species.

If, however, preferences for habitat primarily are based upon learning from parents while growing up, we would expect them to choose habitats usually preferred by their foster-parents. These two alternatives leave us with the following predictions:

1. There are no differences in choice of nesting habitat between cross-fostered birds raised by heterospecific parents and control-birds raised by conspecific parents.

2. Cross-fostered birds choose habitats according to the preferences of their heterospecific foster-parents.

Tits' territories are established during late winter/early spring (Gozler 1993). In winter, they forage in mixed species flocks that roam widely about in the area in search for food. Many of these flocks visits urban regions where they benefit from food put out by humans. In a study of competition at feeding stations in winter, Hansen and Slagsvold (2004) found that the cross-fostered birds were subject to more aggression from con-specifics than control birds were. In addition did they initiate more aggression against hetero-specifics of the foster-species than the controls did.

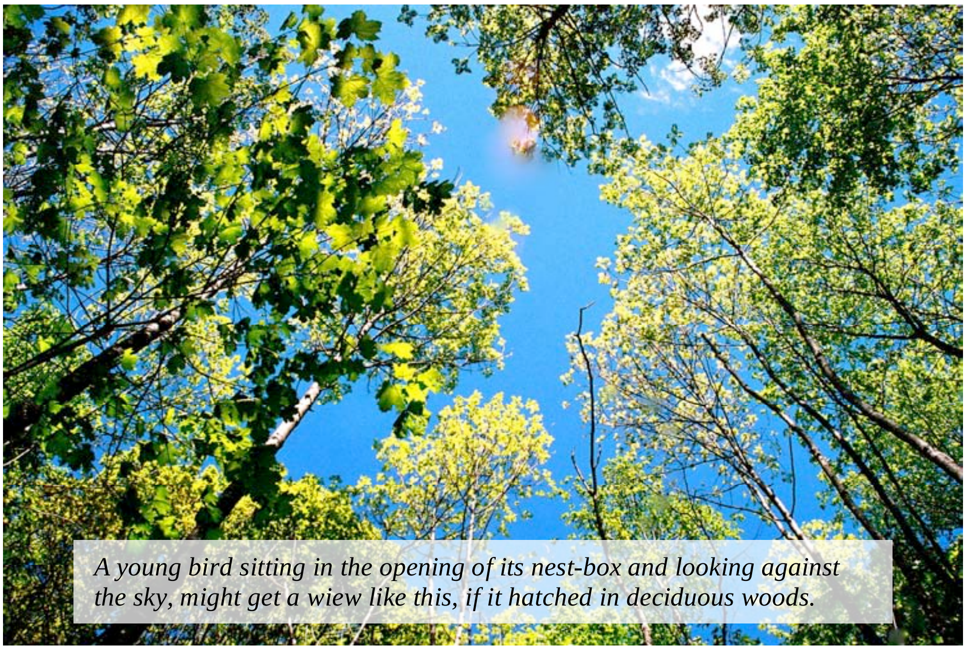
Who will become the victor of the competition for breeding-sites, depends on the individual bird's ranking on the social ladder. Size and sex are usually the determining factors in this respect. Adult Great Tits, weighing approximately 17-20g, are dominant compared to Blue Tits weighing 10-11g. Males in each species are furthermore dominant to females (Hansen and Slagsvold 2004).

The above-mentioned study found that the cross-fostered tits were subdominant compared to controls and immigrants during the winter months. If this trend would continue during mating and breeding habitat choice in spring, they could also end up loosing in the competition to find adequate and preferable nesting sites. This leads to the third prediction:

3. Cross-fostered birds will end up in less preferable habitats if they are subdominant in the competition to chose a breeding territory.

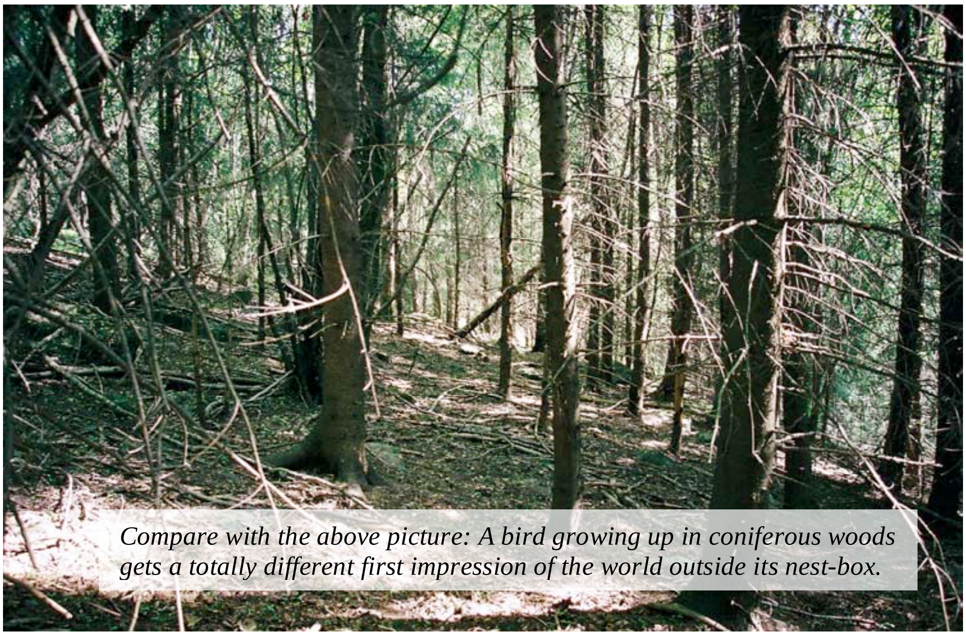
Some earlier studies have focused on the hereditary factors of habitat preferences and choice. (Harris 1951; Partridge 1974; Wecker 1963). These were all laboratory experiments. Though some of them took place in the open air, the subjects were nonetheless captive animals or birds that could not act as they would have done in the wild. All of the above-mentioned studies found that inherited factors are important for preference of habitats. In any case, it was not possible to rule out that learning was a significant factor shaping an animal's choices of where to live.

Imprinting during a relatively short period early in the bird's development has been given much attention since Lorenz first described filial imprinting in ducklings on a mother-object (Barnard 2004). Other themes of great importance in this connection are learning of species-specific song (Johannessen *et al.* 2006), imprinting on a future mating partner (Slagsvold *et al.* 2002), and as in the Cuckoo (*Cuculus canorus*), imprinting on the parasite host (Slagsvold and Hansen 2001). It is therefore reasonable to assume that the same sort of imprinting probably takes place when it comes to habitat preferences. The Blue Tit and Great Tit parents do not leave their offspring on their own straight after fledging, but stay with their young to feed them for about 20 days, depending to some degree on the possible onset of a new brood (Verhulst and Hut 1996). This period of after-fledging brood-care may be important for learning how to use a specific habitat and how to survive in it. Cues encountered by young birds early in their lives may be the same cues they are looking for when they are about to settle in a habitat as mature (natal dispersal). This subject has not been given much attention, but visual cues such as the shape of leaves and the structure of foliage in deciduous woods (Klopfer 1963) have been proposed as relevant in this respect. It is further likely that vision could be an important component in habitat imprinting in birds. It has generally been assumed that their sense of smell probably is lesser developed than their hearing and vision. The latter may be subject to some debate, since it recently has been shown that even passerine songbirds, who have minimal olfactory-bulb sizes, can detect certain odours with the same acuities as rats and rabbits (Gill 2007).



A young bird sitting in the opening of its nest-box and looking against the sky, might get a wiew like this, if it hatched in deciduous woods.

Other cues are openness of landscape and habitat-structure rather than vegetation. Which cues, innate or learned, the animal uses in habitat-selection, are probably species- and habitat-dependent. In his study of habitat selection, Harris (1952) doubted that the Prairie Deer-Mouse (*Peromyscus maniculatus gracilis)* relied on vision and the tactile organs of the *vibrissae* (whiskers). He concluded that sensations received through feet, tail and other parts of the body were more important in this respect.



Compare with the above picture: A bird growing up in coniferous woods gets a totally different first impression of the world outside its nest-box.

Slagsvold and Wiebe (2007) studied foraging niches in Great and Blue Tits, and found that the feeding preferences were strongly based upon early learning. It is therefore reasonable to expect that choices of where to live will be influenced in the same manner, since it would be wise to seek a habitat where one could take advantage of the acquired foraging behaviour. Blue Tits and Great Tits have different foraging niches to which they have adapted. Their morphologies are slightly different, especially regarding size. The lighter Blue Tit forage on the outer buds and leaves, while the larger Great Tit forage a bit further down the trunk, on the thicker branches and more on the ground. Their beak is also slightly thinner and more adapted to forage between needles in coniferous trees than that of the Blue Tits, whose beak is short and broader and adapted to a life in the deciduous woods. The Blue Tits feet are relatively longer than the Great Tits’, which make them more adapted to balancing on thin, deciduous trees than the somewhat clumsier Great Tit.

”King of the food”.

A Great Tit in deep snow; difficult to feed on the ground.

A Great Tit, keeping its balance.

A Blue Tit, wondering if the Great Tit has flown.

Differences in morphology between Blue Tits and Great Tits. The shape and size of the beak:

The Blue Tit: Short, stout beak.

The Great Tit: Long, slender beak.

2. Material and Methods

2.1 Study Site

The fieldwork was carried out from April to September 2005 in a 1.6 km^2 nest-box plot close to Lake Dæli (59°56'N, 10°33E') in Bærum, west of Oslo. Since the start of the project in 1995, the study site has been geographically enlarged, and the number of nest-boxes has been increased from about 200 to about 450. This in fact provides nesting sites for almost all of the Great Tit and Blue Tit pairs holding territories in the area. Consequently, only a few pairs are found nesting in natural cavities. Altogether about 70-80 pairs of Great Tits, 90-100 pairs of Blue Tits and 70-80 pairs of Pied Flycatchers nest in the nest-boxes each year, along with a few pairs of Nuthatches (*Sitta europaea*) and Coal Tits (*Parus ater*). To prevent predation, the wood-made nest-boxes have entrances (32 mm in diameter) surrounded by wire. A wire is also attached over the top of the box to keep it in place. The nest-boxes are fastened to the tree trunks about 1.5 meters above the ground to facilitate easy inspection.

The main nest-predators are Great Spotted Woodpeckers (*Dendrocopos major*), Weasels (*Mustela ermines*) and Cats (*Felis catus*), and for adults it is Pygmy Owls (*Glaucidium passerinum*) and Sparrow Hawks (*Accipiter nisus*). Some parts of the study site are popular for hikers, and from time to time curious or thoughtless people disturb the boxes and damage the nests.

A road divides the box plot area into two parts, along which there are some sparse human settlements. Cultivated areas are found especially around Stein Farm (Fig1: A), to which most of the study fields belong, and in the south, where the study-plot borders on some fields. In the eastern region, the study-site includes a graveyard in addition to an arboretum.

The nest-boxes are situated in different topographical areas, which have bearing on the

Nest-box in open, deciduous woods

results of this thesis. Principally, the study-site is covered by deciduous forest, but there are also patches of coniferous forest in between, and mixed areas consisting of both conifers and deciduous woods. Calcareous bedrock underlies the eastern half of the study site, and this, together with the favourable south-facing slope of the whole Lake Dæli-area, provides for the rich vegetation consisting of lush, broad-leaved forest. Dominating tree species are Hazel (*Corylus avellana*), Ash (*Fraxinus excelsior*) Norway Maple (*Acer platanoides*) Birch (*Betula* sp.), Rowan (*Sorbus aucuparia*), and Elm (*Ulmus* sp). Other species are Grey Alder (*Alnus incana*), European Black Alder (*Alnus glutinosa*), European Aspen (*Populus tremuloides*), and English Oak (*Quercus robur*).

In the mainly coniferous parts of the woods, Pine (*Pinus sylvestris*) is the predominante species in the central area, while Norway Spruce (*Picea abies*) is more dominant on the northern and western edges.

Close to the graveyard (Fig 1: B) in the eastern area, there is an arboretum (Fig1: C) with a number of artificially-introduced tree species. However, the nest-boxes are mainly in areas with natural vegetation. This region is relatively dry, as are most of the habitats lying north of the road, except some moist habitats in the north-western parts. South of the road, both in the south-western and in the central parts, there are moist and swampy areas with brooks.

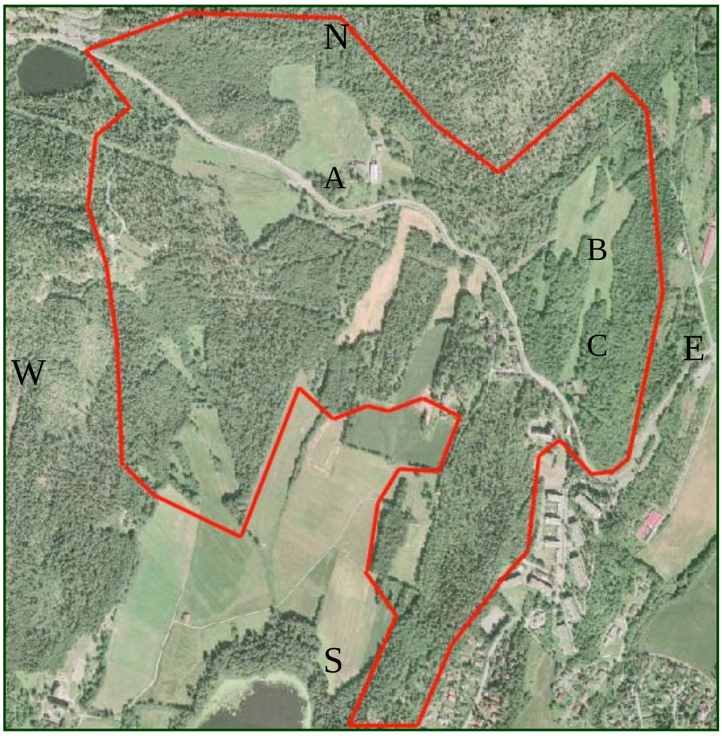


Fig 1. *Air-photo of the lake Dæli study area. Compass-directions and main features are indicated in capital letters.*

Habitat Surrounding Each Nest-box

The area in a 40 m radius around each nest-box was mapped to classify the type of forest. The following methods and variables were used:

1. **Type of nest-box.** All nest-boxes were wooden and could be divided in two main categories: Big boxes (bottom area: 70-180cm^2), and small boxes (bottom area: 70-80 cm^2). Vertical distance for both types is 13-15 cm from base of entrance to bottom.
2. **Direction of nest-box.** A compass was placed along the left side of each nest-box (box-entrance pointing forward), and its direction compared to the magnetic north was read to the nearest 10 degrees. If the nails in the box or the wires attached to it affected the compass, it was held some distance away from the box when used.
3. **Slope-direction.** The direction of the slope of the terrain was deduced from the main inclination of the ground surrounding the box, using a compass.
4. **Diameter of nest-box tree.** Diameter of nest-box tree was measured to the nearest centimetre, about 1.5 m above ground. In cases were the nest-box was attached to one of a number of thin branches originating from one thick trunk, this was noted.
5. **Nest-box tree-species.** Type of species of tree to which the nest-box was attached.
6. **Dominating deciduous tree-species.** This variable was estimated by taking the whole 40 m radius circumference into consideration and then deducing which 2-3 species were most abundant. Biomass of tree was also taken into consideration, since for example one large, old tree may have greater impact on the environment than five small young trees. If there was more than one layer of foliage, the most abundant tree-species in each layer was noted.
7. **Dominating coniferous tree-species.** This variable was divided into three categories: Pine, Spruce and the same amount of each species. It was deduced in the same manner as dominating deciduous tree-species.
8. **Percentage of bush-cover.** The share of the total circumference-area that was covered by bush growth, was estimated to the nearest 10 % by using six categories of different percentage bush-growth.

9. **Percentage of coniferous wood.** The portion of coniferous wood of the total woods (coniferous and deciduous) in the 40-m radius habitat was estimated to the nearest 25 % and put in five categories.
10. **Percentage of open patches.** Small parts of the ground surface different in texture from the surrounding habitat within continuous woods, eg. bare rock or naked ground, was estimated to the nearest 10 %.
11. **Percentage of open edge.** The percentage of habitat not covered by woods, eg. lawn, pasture or parking-ground, was estimated. In areas where different types of edges were found within one habitat, the area of each patch was roughly calculated and summarised.
12. **Edge-type.** Characterisation of the types of edges cutting through the habitat, if there were any, using seven categories. Continuous woods, pasture/field, felling areas, other type of vegetation, lawn, path or meadow/high grass and parking space/road.
13. **Ground-level humidity.** The level of humidity was roughly divided into three categories; dry habitat, moist/swampy habitat and habitat with ponds and/or brooks. In cases where the habitat was mixed, eg. whether it was a dry habitat with just one tiny brook running through it in the periphery, the most prominent type was chosen.

A rather shallow nest-box situated in deciduous habitat (northwest in the area) dominated by Ash and Grey Alder.

The study-area was divided into six parts. The part to explore each day was decided by throwing a die. The number of boxes checked per day (4-60) varied according to the terrain, weather and other aspects beyond control.

2.2 Cross-fostering of Blue Tits and Great Tits

The cross-fostering experiment was performed under license from the Directorate for Nature Management, and the National Animal Research Authority in Norway.

Prior to my habitat-investigation during the summer 2005, an inter-specific cross-fostering of Blue Tits and Great Tits had already taken place. From 1997-2004 eggs were swapped between Blue Tit- and Great Tit nests. Some nests were left undisturbed, as control nests (Slagsvold et. al 2002). The birds were given a combination of colour rings for individual identification. Ownership of the nest-box was recorded in spring 2005.

From early spring 2005 through the nesting period, nests were checked at least every second or third day, to record the onset of nest building and egg-laying. The onset of egg-laying was estimated according to the normal pattern of tits in which the female lays one egg per day (Perrins 1979).

A Blue Tit female and her just hatched young.

2.3 Statistical Procedure

The statistical analyses were performed using the statistical program Statview 5.0.

Due to the fact that the data was not normally distributed, non-parametrical tests were employed. Mann Whitney U-test was used to compare the continuous variables such as diameter of nest-box tree, while the chi-square test was used to compare the categorical discrete variables like eg. dominant deciduous tree species.

The sample size occasionally differed due to missing values. Sample size is therefore specified in each case.

Some of the category variables recorded in the field were grouped together before doing the statistical analyses because the observations were too few to give any meaningful results. Others were judged unsuitable to include in the analysis because of difficulties in judging their differences between habitats. Eg. habitat analyses of ground humidity and degree of bush-growth recorded in May, differed much from those recorded in August, even if they were done in the same habitat. (During summer, the grazing cows cleared the central area of ground vegetation and small bushes.)

The tests were performed in the order described below, and the resulting percentage for each group of birds taken from contingency tables, are shown in tables in chapter 3.

1. Blue Tit-controls versus empty boxes.
2. Great Tit-controls versus empty boxes.
3. Blue Tit-controls versus Great Tit-controls.
4. Cross-fostered Blue Tits versus control Blue Tit.
5. Cross-fostered Great Tits versus control Great Tits.

Control individuals are either immigrants or offspring of con-specific parents born in the study-field. Cross-fostered individuals are tits raised by hetero-specific foster-parents.

3. Results

3.1 Size of Nest-box

The number of nest-boxes checked in the Dæli study area 2005 was 442. Of these were 307 (≈70 %) small boxes, and 135 (≈30%) big boxes.

Table 1. Portion of different types of nest-boxes occupied by Blue Tits (BT), Great Tits (GT) and empty boxes

	Percent distribution			
Species	Small boxes	Big boxes	Total	n
Empty boxes	71	29	100	261
BT controls	97	3	100	69
GT controls	38	62	100	52
BT cross-fostered	63	37	100	19
GT cross-fostered	50	50	100	14

The difference between the Blue Tit-controls and the empty boxes was significant. Almost all the Blue Tit-controls chose small nest-boxes, and there were more empty big boxes than big boxes chosen by Blue Tits (χ^2=19.4 df=1, p=0.00); Table 1.

The difference between the Great Tit-controls and the empty boxes was significant. More of the Great Tit-controls chose big nest-boxes, and there were less empty big boxes than big boxes chosen by Great Tits (χ^2=18.8 df=1, p=0.00); Table 1.

The chi-square test showed that there were significant differences in preference for small and big nest-boxes between the control groups. Almost all of the Blue Tit-controls chose small nest-boxes. Most of the Great Tit-controls chose big nest-boxes, although some of them selected the small ones (χ^2=47.6 df=1, p=0.00); Table 1.

The cross-fostered Blue Tits chose to nest in big boxes in a much higher degree than the control Blue Tits, also significant (χ^2=15.2 df=1, p=0.00); Table 1.

We found no significant differences between the cross-fostered Great Tits and the Great Tit-controls (χ^2=0.2 df=1, p=0.64); Table 1.

3.2 Direction of Nest-box

Table 2. Direction* of nest-box for boxes occupied by Blue Tits (BT), Great Tits (GT) and empty boxes

	Percent distribution					
Species	North	East	South	West	Total	n
Empty boxes	2	27	58	13	100	259
BT controls	1	24	59	16	100	68
GT controls	8	13	52	27	100	52
BT cross-fostered	0	42	47	11	100	19
GT cross-fostered	7	21	50	22	100	14

*North: 315-45°, East: 46-135°, South: 136-225° and West: 226-315°.

Tests between Blue Tit-controls and empty boxes showed no significant difference (χ^2=1.0 df=3, p=0.8); Table 2.

The chi-square test between empty boxes and boxes occupied by Great Tits controls, was significant (χ^2=13.7, df =3 p=0.003). There were more empty boxes facing eastwards and southwards than occupied by Great Tit controls, and more Great Tit-controls inhabiting boxes facing westwards and northwards than empty boxes; Table 2.

Great Tit-controls nested in boxes facing more in the eastern and northern directions than Blue Tits-controls did. The difference was almost significant (χ^2=6.18, df=3, p=0.10). We found no significant difference between control and cross-fostered Blue

Tits (χ^2=2.8, df=3, p=0.4), neither did we find any difference between control and cross-fostered Great Tits (χ^2=0.6, df=3, p=0.9); Table 2.

3.3 Direction of Slope

Table 3. Direction* of the slope for boxes occupied by Blue Tits (BT), Great Tits (GT) and empty boxes

	Percent distribution					
Species	North	East	South	West	Total	n
Empty boxes	3	28	55	14	100	260
BT controls	0	29	46	25	100	69
GT controls	6	19	56	19	100	52
BT cross-fostered	0	37	53	10	100	19
GT cross-fostered	7	28	53	39	99	14

*North: 315-45°, East: 46-135°, South: 136-225° and West: 226-315°.

Test of Blue Tit-controls vs. the empty boxes was not at all significant (χ^2=1.0 df=3, p=0.8). Neither did we find significant differences between the Great Tit-controls and the empty boxes (χ^2=3.40, df=3, p=0.33); Table 3.

There was a tendency towards Great Tit-controls nesting in boxes with a slope facing more in the southern and northern direction than Blue Tits controls did, although the differences were not significant (χ^2=6.02, df=3, p=0.11); Table 3.

No difference was found between Blue Tit-controls and the cross-fostered Blue Tits (χ^2=1.80, df=2, p=0.41), neither was any significance found between the Great Tit-controls and the cross-fostered Great Tits (χ^2=3.44, df=3, p=0.33); Table 3.

Directions of nest-boxes and the slope of the terrain:

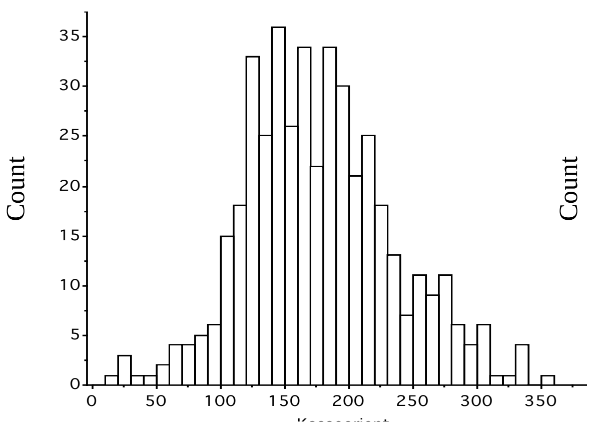


Figure 2. *Direction (in degrees) of nest-box front*

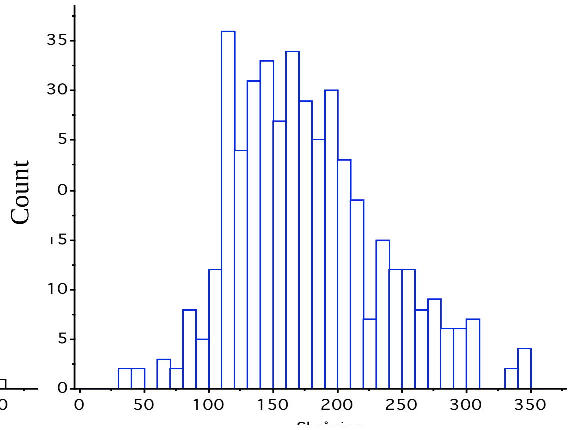


Figure 3. *Direction (in degrees) of the slope of the terrain surrounding nest-box*

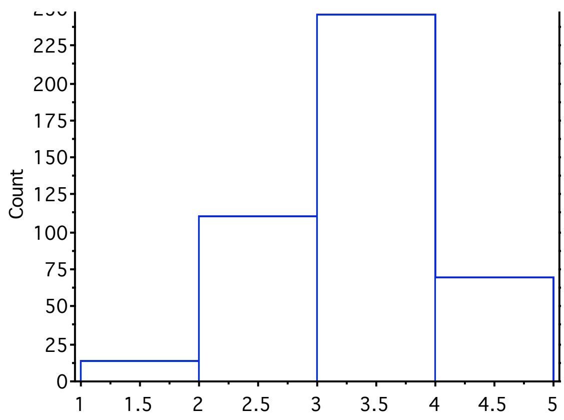


Figure 4*. Number of boxes in each category of direction*

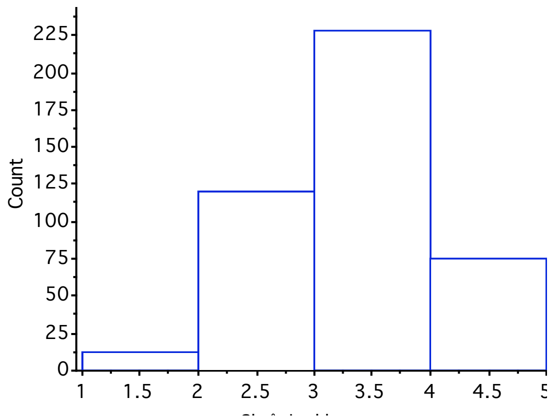


Figure 5*. Number of habitat in each category of slope of terrain-direction*

Fig. 2 shows that most of the nest-boxes at the Dæli study-site were facing directions between ca. 100 and 240 degrees; eg. eastwards.

Fig 3 shows the direction of the slope of the terrain, and this graph relates similar findings as the previous figure, although it is somewhat more skewed towards the left. Consequently, a few more habitats had an eastern-facing slope of terrain than there were boxes facing in this direction.

Fig. 4 and Fig. 5 shows how the boxes are distributed inside the four main categories used in the analysis.

3.4 Dominating Coniferous Tree-Species

One hundred of 112 nests of Blue Tits and Great Tits were situated in a terrain more dominated by Pine than Spruce. For two habitats the amount of the two tree-species was equally divided, and in ten cases spruce dominated. Of these last ten cases, five were Blue Tit- and five Great Tit-nests; consequently there was no difference observed between the two tit-species.

3.5 Percentage of Coniferous Woods

Table 4. Portion of coniferous woods in habitat around boxes occupied by Blue Tits (BT), Great Tits (GT) and empty boxes

	Percent distribution				
Species	0 %	[1-25%⟩	[25-100%]	Total	n
Empty boxes	8	65	27	100	261
BT controls	10	67	23	100	69
GT controls	4	69	27	100	52
BT cross-fostered	0	74	26	100	19
GT cross-fostered	0	57	43	100	14

The last three categories observed in the field were grouped together due to small sample size.

The difference between the control species and the empty boxes was not significant, (Blue Tit vs. empty: χ^2=0.84 df=2, p=0.66, Great Tit vs. empty: χ^2=1.0, df=2, p=0.60). Neither was there any difference between the controls; Blue Tit-controls vs. Great Tit controls: (χ^2=1.8, df=2, p=0.4). None of the cross-fostered birds vs. their respective controls showed any significant deviation: (Blue Tit: χ^2=2.1, df=2, p=0.35 and Great Tit: χ^2=1.7, df = 2, p=0.42); Table 4.

3.6 Dominating Deciduos Tree-species

Table 5. Portion of different categories of dominating deciduous tree-species in habitat surrounding boxes occupied by Blue Tits (BT), Great Tits (GT) and empty boxes

	Percent distribution				
Species	Broad-leaved species*	Mixed; equal amount.	Not broad-leaved**	Total	n
Empty boxes	49	37	14	100	261
BT controls	57	36	7	100	69
GT controls	50	23	27	100	52
BT cross-fostered	47	11	42	100	19
GT cross-fostered	29	21	50	100	14

*Broad-leaved species: Ash, Elm, Maple and Hazel.

**Not broad-leaved species: Aspen, Birch, Sallow, Rowan, Grey and Black Alder.

Blue Tit-controls did not differ from empty boxes: (χ^2=2.9, df =2, p=0.23); Table 5.

Significantly more Great Tit- than Blue Tit-controls chose nest-boxes situated in habitats in which the deciduous share of trees was dominated by others than broad-leaved species (χ^2=6.32, df =2, p=0.04). In addition, more Blue Tit- than Great Tit-controls settled in habitats with an equal amount of the two deciduous categories. Slightly more Blue Tit than Great Tit-controls selected boxes in habitats where the deciduous portion of woods consisted exclusively of species from the broad-leaved group. (χ^2=6.3, df = 2, p=0.04); Table 5.

Great Tit-controls did not differ from empty boxes (χ^2=3.18, df = 2, p=0.20), neither did cross-fostered Blue Tit- differ from Blue Tit-controls (χ^2=2.97, df = 2, p=0.23), or Cross-fostered Great Tits from the control group (χ^2=2.9, df = 2, p=0.23). Neither of these results were significant; Table 5.

Deciduous trees at the graveyard, northeast in the study-area (One coniferous representative can be seen.)

Some of the participants in this study, not caring particularly much about the size of their nest-box tree or the direction of the terrain-slope at this moment.

3.7 Percentage of Open Patches

Table 6. Percentage of open patches for boxes occupied by Blue Tits (BT), Great Tits (GT) and empty boxes

	Percent distribution				
Species	[0 – 10)	[10 – 20)	[20 – 100]	Total	n
Empty boxes	72	21	7	100	261
BT controls	81	13	6	100	69
GT controls	65	33	2	100	52
BT cross-fostered	79	10	10	99	19
GT cross-fostered	71	21	7	99	14

Due to few observations in the last categories of percentage open patches, these categories were grouped together ([20-100]); Table 6.

Blue Tit-controls did not differ from empty boxes: (χ^2=2.62, df=2, p=0.27). More Great Tit-controls chose nest-boxes in habitats which had the properties of habitats lying in the second open-patches category (10-20% open patches) than there were empty boxes in these areas. More empty boxes than boxes inhabited by Great Tit-controls were found in the other two categories (χ^2=4.2, df=2, p=0.12). These results show a slight tendency towards significant findings cp. Table 6.

The chi-square test showed significant differences between Blue Tit and Great Tit controls. More Blue Tit- than Great Tit-controls had selected nest-boxes in habitats with 0-10% open patches. In contrast, the Great Tit-controls selected habitats with 10-20% open patches more than Blue Tit-controls did (χ^2=7.39, df=2, p=0.02);Table 6. Cross-fostered Blue Tits did not differ from controls of the same species: (χ^2=0.57, df=2, p=0.76), neither did cross-fostered Great Tits differ from their controls (χ^2=1.51, df=2, p=0.47); Table 6.

3.8 Percentage of Open Edges

None of the comparisons between the groups were significant, but the Blue Tit control group compared to the Blue Tit cross-fostered group showed a tendency towards significance. (Mann Whitney U-test Z=-0.16, n_1=69, n_2=19, p=0.10)

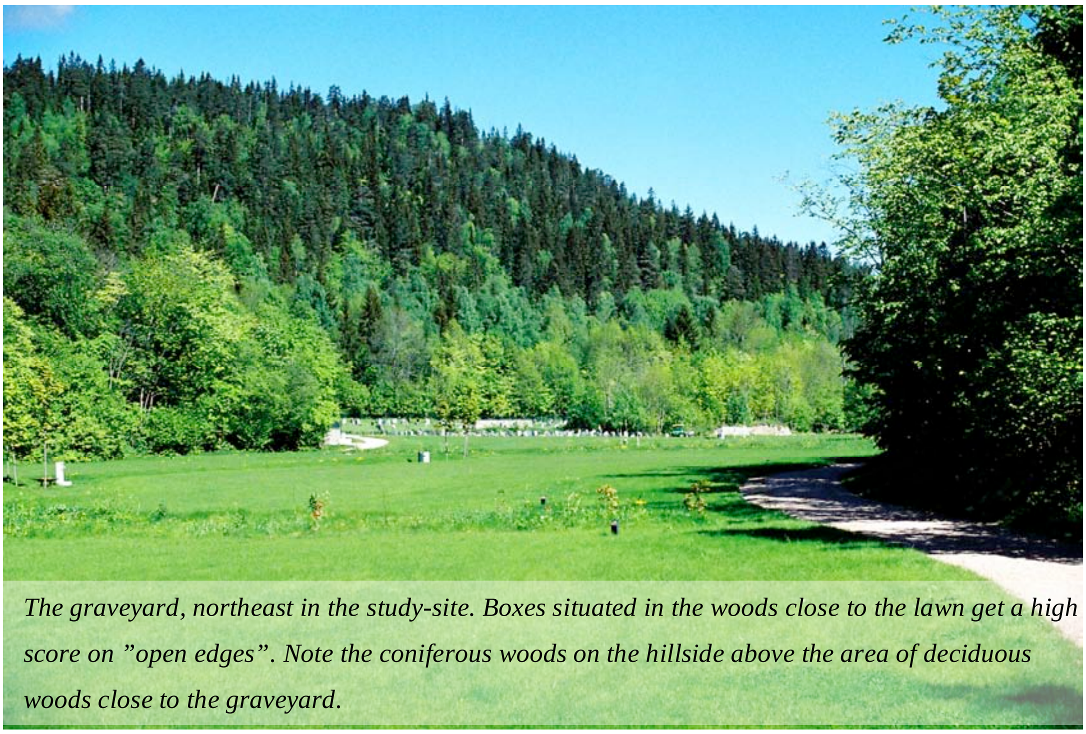
Mean proportion of open edges was 24.1% (SD=21.7) for Blue Tit-controls, and 14.9% (SD=14.5) for cross-fostered Blue Tits.

For the means and standard deviations of all the groups of birds, see Table 7.

Table 7. **Comparison between characteristics of nest sites occupied by Blue Tits and Great Tits**

	Diameter of nestbox-tree (cm)			Number of large trees*			Percent open area		
Group	**Mean**	**SD**	**n**	**Mean**	**SD**	**n**	**Mean**	**SD**	**n**
Empty boxes	15.6	7.0	257	2.3	2.0	261	21.4	21.7	261
Blue tit controls	14.1	5.4	68	2.2	2.4	68	21.4	20.9	69
Great Tit controls	15.7	7.0	51	1.9	1.9	52	24.3	19.6	52
Blue Tit cross-fostered	17.6	6.3	19	2.1	1.6	19	26.5	24.1	19
Great Tit cross-fostered	14.9	7.4	14	2.8	2.2	14	14.9	14.5	14
MWU-test	**Z**	**p**		**Z**	**p**		**Z**	**p**	
Blue Tit controls vs. empty boxes	-1.23	0.22		-1.17	0.24		-0.16	0.87	
Great Tit controls vs. empty boxes	-0.01	0.99		-1.36	0.17		-1.34	0.18	
Blue Tit controls vs. Great Tit controls	-0.94	0.35		-0.24	0.81		-0.98	0.33	
Blue Tit control vs. Blue Tit cross-fostered	-2.07	0.04		-0.52	0.60		-0.81	0.42	
Great Tit control vs. Great Tit cross-fostered	-0.54	0.59		-1.52	0.13		-1.63	0.10	

*Number of trees with diameter > 40 cm within a circumference of 40 m around/about nestbox.



The graveyard, northeast in the study-site. Boxes situated in the woods close to the lawn get a high score on "open edges". Note the coniferous woods on the hillside above the area of deciduous woods close to the graveyard.

3.9 Diameter of Nest-box-Tree

A difference was found between Blue Tit-controls vs. cross-fostered Blue Tits (Mann Whitney U-test $Z=-2.07$, $n_1=69$, $n_2=19$, $p=0.04$). Mean diameter of nest-box trees was 14.1 cm (SD=21.7) for Blue Tit-controls, and 17.9 cm (SD=14.5) for cross-fostered Blue Tits; Table 7.

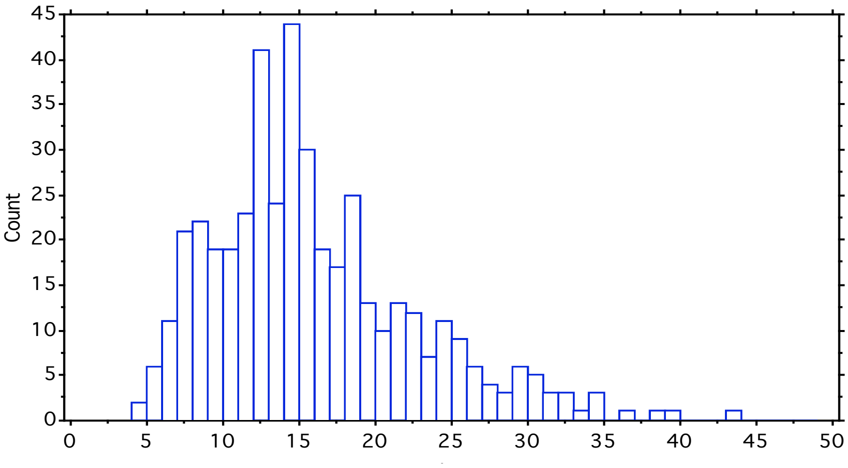


Figure 5. *Diameters (in cm) of the nest-box trees in the study-site.*

3.10 Number of Large Trees with Diameter > 40 cm

None of the comparisons between the groups was significant. In other words; between the different tested groups of birds, there were no differences in choice of habitats containing numerous large trees, and choice of habitats containing fewer, cp. table 7.

A Great Tit checking out the quality of a thick trunk.

Stein Gård.

Nest-box situated in a moist area in the northwest, dominated by Grey Alder and Ash.

4. Discussion

4.1 Main findings

A variety of habitat variables were tested to see whether we could detect differences between control birds and the cross-fostered birds in each of the two species of tits studied. Of most interest were the variables related to the distinction between habitats dominated by coniferous woods and the ones dominated by deciduous woods, since these two habitat types are subjects to different preferences by Great Tits and Blue Tits. Both species can live in the above-mentioned habitats, but Blue Tits generally prefer deciduous woods. Great Tits on the other hand prefer woods with an element of the coniferous species. These are well-known facts, and may be related to the effects of adaptation to different foraging niches as earlier described (Slagsvold and Wiebe 2007). Since early learning has been shown to have such a great importance with regard to foraging behaviour, we would expect that more cross-fostered Blue Tits would select habitats in coniferous areas than cross-fostered Great Tits.

We did not, however, find evidence of this prediction in our investigation of the preferred habitats. Comparisons of the different groups of birds revealed a slight tendency for the cross-fostered groups to select habitats where one or a few of the variables described, were related to the habitat normally preferred by their hetero-specific foster-parents. Examples of these were the diameter of the nest-box tree in cross-fostered Blue Tits and the percentage of open edge in cross-fostered Great Tits. The largest difference in habitat preference found in this experiment, was the difference in preference for size of nest-boxes. These differences were found both between the control groups and between the Blue Tit-controls and the cross-fostered Blue Tits.

4.2 Choice of Habitat in Control Birds

There were significant differences in preference for small and big nest-boxes between the control groups. Almost all of the Blue Tit-controls chose small nest-boxes. Most of the Great Tit-controls chose big nest-boxes, although some of them selected the small ones. This makes sense, since Great Tits are larger birds than Blue Tits and therefore needs more space in the nest-box.

There was a slight tendency for the Great Tit-controls to nest in boxes facing more in eastern and northern directions than Blue Tit-controls. In addition, they had a slight tendency to choose more habitats facing northwards and southwards than was the case for Blue the Tit-controls. The difference between empty boxes and Great Tit-controls was significant, and again more Great Tit-controls chose a nest-box facing a northern direction in addition to western direction. Nest-boxes situated in the coniferous regions of the Dæli study-area are often placed in more varying directions than those in deciduous regions. This can possibly be a part of the explanation why slightly more Great Tits inhabit these areas, and vice versa when it comes to Blue Tits in deciduous habitats. No differences were found between control birds in the comparison between boxes situated in areas with different portion of coniferous woods.

Another way to classify a coniferous habitat, other than to study its portion of conifer trees, is to consider other factors typical for that type of woods. Broad-leaved deciduous species are less likely to be found in coniferous areas to the same extent as not broad-leaved deciduous species, such as for example, birch and rowan. We found significant results related to Great Tit-controls choosing more nest-boxes situated in habitats in which the deciduous portion of woods was dominated by not broad-leaved species. Slightly more of the Blue Tit-controls chose habitats where the deciduous portion of the woods consisted of broad-leaved species. This group also selected more habitats in which there was an equal amount of deciduous tree species.

In coniferous woods, especially in areas where pine is the most dominant species, rock, naked ground and dry patches not covered by vegetation are also found. This means that habitats achieving a high score on the list of percentage of open patches, most probably belong to an area dominated by coniferous woods.

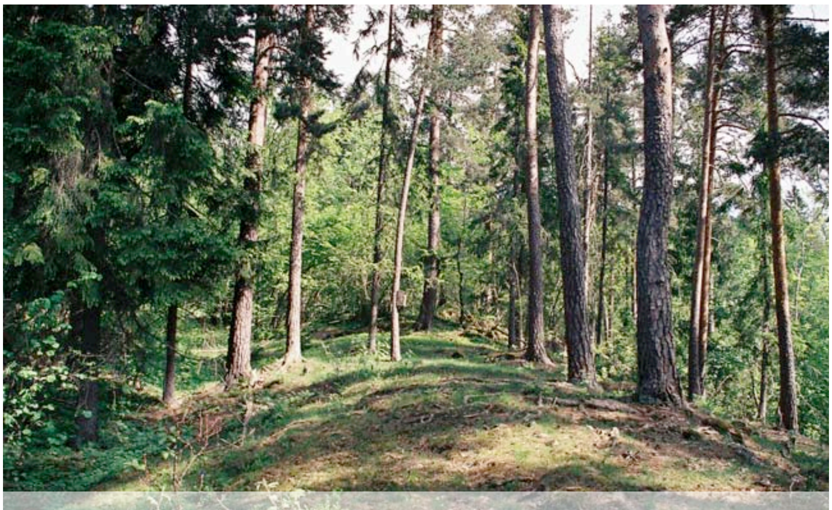
The chi-square test showed significant differences between Blue Tit- and Great Tit-controls in this respect. More Blue Tit- than Great Tit-controls selected habitats with a few open patches or none at all than Great Tits did. Great Tits on the other hand, selected habitats with more than 10 % open patches.

4.3 Choice of Habitat in Cross-fostered Birds

We found significant differences in preference for nest-box size between the Blue Tit-controls and the cross-fostered Blue Tits. The cross-fostered Blue Tits chose to nest in big boxes in a much higher degree than the Blue Tit controls did. This implies that preference for big boxes was imprinted during early age in the Blue Tits growing up in "foster-homes". When they chose their nesting-sites the following spring, these Blue Tits searched for boxes with enough room according to their preferences. The bird should choose a nest-box corresponding to its' size. A too wide box could increase the probability of the young dying of heat-loss. The Blue Tit female (who by the way build the nest on her own) would fill the box with moss until the nest has the preferred level according to the opening (Perrins 1979), so choosing a too big box according to its' size, may not be a serious disadvantage in this species.

We found no significant differences between the cross-fostered Great Tits and the Great Tit-controls. An explanation for this may be that due to their relatively bigger size compared to Blue Tits, the small boxes could be too narrow for incubating and for bringing up the young. A too narrow nest-box could become much too hot if it is situated in the sun, and becomes over-crowded with big, growing Great Tit-hatchlings.

There was a slight tendency for cross-fostered Blue Tits to choose habitats with more open areas ("open edges") than the case was



Nest-box in a coniferous, open habitat where Pine is the dominant tree-specie for the control group. A possible reason for this could be that especially Pine-woods are relatively open compared to thick broad-leaved forests with a dense under-story of hazel. In addition, some of the coniferous areas are felling-areas, which give them a higher amount of "open edges". An image of open land as preferred habitat, could therefore be consolidated in the cross-fostered Blue Tits, and make them more interested in habitats with open edges.

A difference was found between Blue Tit-controls and cross-fostered Blue Tits regarding the diameter of the nesting-tree. Cross-fostered Blue Tits chose larger nesting trees than control birds did. Great Tits forage in general on thicker branches, and further down on thicker tree-trunks than Blue Tits. Therefore, one possibility of why the cross-fostered Blue Tits select nesting-trees with a larger diameter, is that this preference has been learned from the foster-parents.

4.4 Possible Reasons for Findings

- One possible explanation of why we did not detect significant differences regarding the wood-variables, between birds from the control groups and from the cross-fostered ones, is that the Dæli study-area contains somewhat less coniferous woods than deciduous woods. The decision to place the plot in an area with such a distribution of different woods, was originally done deliberately to attract both tit-species to the study-site with the aim of conducting cross-fostering experiments. Because of the lack of coniferous woods in their natal area during adolescence, the young birds might not be sufficiently exposed to this type of habitat. Consequently, they would select habitats with little or no coniferous woods due to the fact that this was the type of woods they were imprinted on.

- Another explanation is related to inter- and intraspecific competition among species. Due to the fact that the cross-fostered individuals become subdominant in feeding places in the winter as shown in the study of Hansen and Slagsvold (2004), they may, because of competition, be forced to select breeding habitats of lesser quality than they would have chosen if they were able to select freely.

- A third explanation is that the choice of habitat is a genetically determined trait, and that cross-fostered birds settle in areas they are adapted to, and have preferences for, regardless of their experiences early in life. This may be the reason why we did not record significant results. However, this is not likely because studies on habitat choice (Partridge 1974; Wecker 1963) show that a learning aspect may be of relevance in addition to genetic aspects.

In addition, it should be taken into consideration that most of the variables recorded in the field were subjective. Some of the variables could be measured relatively easy, like the diameter of the nest-boxes, while others, such as the percentage of coniferous woods, were harder to assess, and could therefore be somewhat misleading when tested in the statistical analysis.

4.5 Conclusion

A large amount of habitat-variables was recorded in order to distinguish differences in choice of habitat between cross-fostered tits and their control groups. There was a slight tendency in the cross-fostered group to select habitats with features indirectly preferred by their foster-parents. When we tested the most obvious variables, for example, percentage of coniferous woods, we found no significant differences between the bird groups. An important exception was the difference in choice of the size of the nest-box between the cross-fostered Blue Tits and the Blue Tit-control group. The cross-fostered Blue Tits chose big nest-boxes, which is usually preferred by Great Tits. This preference has most probably been learned at an early age, since almost all of the control Blue Tits chose small nest-boxes fitting their size.

Some trends in habitat choices related to species were observed. Further studies where more clearly defined coniferous areas are included in the study-field, might help to reveal significant differences between the groups of tested birds. Including nesting-site data from more than one year, could also contribute to this. We cannot, based on the findings of this thesis, rule out the fact that there could be an effect of early learning. The gradient in the habitat studied was, it turned out, too small to be able to document such findings.

A nest-box situated in a habitat dominated by Spruce, in the central area, close to Stein Gård.

Coniferous woods/mixed woods in the north-western part of the study-field, close to the area ”Huset”.

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"Oh, how I love that feeling of those conifer-needles tingling between my toes..."