The influence on natal habitat, and previous breeding habitat, in the habitat selection of the Ortolan Bunting



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By Peder Christiansen

Cand. scient. thesis Department of Biology and Nature Conservation Agricultural University of Norway

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Innflytelsen av fødehabitat, og tidligere hekkehabitat, for habitatvalg hos hortulan.

By Peder Christiansen

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Peder Christiansen

Abstract

Habitat selection is the choice of a type of place in which to live. Perhaps no other taxonomic group has, and presumably exercises, the potential for habitat selection that birds do.

Ortolan Bunting (*Emberiza hortulana*) in Norway use several habitats. Peat bog, forest clear-cut, areas cleared for cultivation, and one forest fire site are the most common habitat types. It is generally assumed that for many species, the habitat in which the juvenile period is passed becomes the bird's later choice of habitat. My results from the Ortolan Bunting differ from these general assumptions. For natal habitat choices there was no evidence for a return to same habitat types more often than random. The same was the case for adult males. After breeding dispersal there was no evidence for a return to same habitat type more often than random. In tests for preference for some habitat types rather than other there were generally no significance. In spite of no significance in the tests, there was a tendency for Ortolan Bunting to prefer habitats with areas being cleared for cultivation. In these cultivation habitats there are embankments, which are popular nest- and song- sites. Grain fields often surround these embankments, and these fields are god foraging sites.

One of the reasons why Ortolan Bunting were not imprinted on natal habitat, or earlier breeding habitat, may be that the structure of the habitat was more important than the vegetation type. That is, an open habitat with little vegetation was a more important factor in habitat choice than whether it was for instance peat bog or forest clear-cut. The Ortolan Bunting seemed to have separated feeding and nesting areas. It fed in grain fields, while the nests territories were in open and dry areas. This was probably to reduce nest predation.

I discuss the importance of knowledge about habitat selection for the management of the small and endangered Norwegian Ortolan Bunting population.

Sammendrag

Habitat valg er valget om hvilket sted en skal leve. Kanskje er det ingen taksonomisk gruppe som har hatt, eller har, så stort potensial for habitat valg som fugler.

Hortulanen (*Emberiza hortulana*) i Norge bruker flere forskjellige habitater. Torvmyr, hogstfelt, nydyrkingsområder, og ett brannfelt er de mest brukte habitat typene. Generelt er det antatt at for mange arter, vil habitatet som ungetiden er tilbrakt i, bli fuglenes valg av habitat senere i livet. Mine resultater fra hortulan skiller seg fra disse generelle antagelsene. For ungefuglers habitat valg var det ikke vist en forflytning til samme habitat oftere enn forventet ut fra tilfeldig forflytning. Det samme gjelder for voksne hanner. Etter hekkeforflytning er det ikke vist en forflytning til samme habitat oftere enn forventet ut fra tilfeldig forflytning. I tester av om noen habitater er foretrukket foran andre var det generelt ingen signifikans. Til tross for at det ikke var signifikans i testene, er det en tendens til at hortulaner prefererer habitater med nydyrking. I disse habitatene med nydyrking er det voller, som er populære reir- og sang- steder. Disse vollene er ofte omkranset av kornåkrer, som er gode områder for å finne mat.

En av grunnene til at hortulan ikke ble preget til føde habitatet, eller til habitat hvor den har hekket tidligere, kan være at strukturen på habitatet er viktigere enn vegetasjonstypen. Med det menes at det var viktigere at habitatet var åpent med lite vegetasjon enn om det for eksempel var torvmyr eller hogstflate. Hortulanen så ut til å ha separate spise- og reirområder. Den søkte etter mat i kornåkrer, mens reir-territoriet var i åpne og tørre områder. Dette var trolig for å unngå reirpredasjon.

Jeg diskuterer viktigheten av kunnskap om habitat valg for forvaltning av den lille og truede populasjonen av hortulan i Norge.

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1. Introduction

1.1 Habitat selection

Habitat selection is the choice of a type of place in which to live. Perhaps no other taxonomic group has, and presumably exercises, the potential for habitat selection that birds do. Birds are extremely mobile and wide ranging, and of the range of habitats they pass through or over, only specific ones are used for breeding or foraging or wintering (Cody 1985). For the average small temperate passerine, the choice of suitable habitat must be made repeatedly, often in both wintering quarters and in breeding territory, and perhaps continuously during migration (Cody 1985).

The selection, or choice, of the proper habitat, that is the area which provides optimum conditions for survival and reproduction, presumably provides a far more secure prospect for a long life than would a random choice. Ultimately, individuals exercising wise choices must do much better than those that do not (Klopfer and Ganzhorn 1985).

Birds are guided to the breeding areas by a primarily innate reaction released by certain environmental stimuli, on the principle of summation of heterogeneous stimuli (Hildèn 1965). Hildèn considered the ultimate factors of habitat selection of birds to be: a) food, b) the requirements imposed by structural and functional characteristics of the species, and c) shelter from enemies and adverse weather. Furthermore, he considered the proximate factors to be stimuli of: a) landscape, b) terrain, c) nest-, song-, look-out, feeding and drinking sites, and d) other animals. In certain species, e) food also directly influences the choice of territory. In addition to these, f) internal motivation contributes to the release of the selection response, in some way determining the sensitivity of the bird to external stimuli.

There are also stimuli which have an opposite, repelling effect, and which thus decrease the combined effect of the stimuli mentioned above. According to the

principle of stimulus summation, not every habitat approved as suitable need possess the entire suite of features characteristic of the bird's optimal environment, or in the same proportions as in the optimal environment; it is enough that the combined effect of the individual stimuli exceeds the threshold of the settling reaction. As the threshold in addition depends on the motivation of the bird, a species has at its option a potential more or less wide habitat range (Hildèn 1965). Although Hildèn referred to the "release" of the habitat selection reaction and its "threshold", settling in the territory still cannot, he thinks, be considered completely comparable with a simple, schematic instinctive activity. If so, he says, a bird would remain in the first place that it encounters in its breeding area that releases its territorial occupation reaction. In fact this does not happen: the bird usually tries out many places, where it sings and displays other territorial behaviour, before it finally settles down in its breeding station (Haartman 1949). The bird consequently without doubt makes a selection, and if there are many suitable places it chooses the best one (Hildèn 1965).

Hildèn explained habitat selection as involving two stages. The first stage, to settle down and explore the place, is released by features of the landscape and general characteristics of the terrain. The second stage, whether the place is approved as a breeding territory or discarded, depends on how closely certain of its details conform to the other sign stimuli constituting the proximate factors in the bird's habitat selection mechanism.

Klopfer and Ganzhorn (1985) agree with Hildèn (1965) that habitat choice may consist of a sequence of choices, the various criteria being hierarchically ordered. So if there is a principle of stimulus summation (threshold): What about imprinting on to certain habitat, and experience from earlier breeding? Cody 1985 states that both experience and the natal circumstances may play a role in habitat selection.

Studies of the development of habitat preferences have taken the form of demonstrations either that differences in preferences are partly genetic in origin or that preferences are modifiable by early experience of particular environments (Partridge 1979). If two animals are reared in identical environments and differ in their habitat preferences, then the difference must be hereditary. When individual Blue Tits (*Parus caeruleus*) and Coal Tits (*Parus ater*) were reared in aviaries with no experience of vegetation and then presented with a choice between various species of oak and pine branches, Coal Tits perched more on the pine branches than Blue Tits did, who perched more than the Coal Tits on oak branches. This difference corresponds to the habitat difference between these two species in nature, and the difference between wild birds in aviaries (Partridge 1979).

Klopfer (1963) described an experiment of the role of early experience. In this study young Chipping Sparrows (*Spizella passerina*) were hand reared, in an environment with oak foliage. These birds naturally spend most their time in pine. Birds that were reared in the presence of oak foliage showed a decreased preference for pine. Thus the obviously innate preference for pine could be somewhat modified by altering the rearing environment.

A similar study of mammals, Deer Mouse (*Peromyscus maniculatus bairdi*), has investigated the significance of early experience to the habitat selection. The study indicated that both heredity and experience play a role in determining the preference of this animal for the field habitat (Wecker 1963).

When does imprinting on the environment occur? Klopfer and Hailman refers to Löhrl (1959), who reports that the Collared Flycatcher, (*Ficedula albicollis*), returns in the spring to the habitat to which it was exposed for about two weeks after fledging during the preceding year.

Juveniles are often less specific in their preferences than older birds, with feedback from their experiences in different locations apparently influencing later choices (Klopfer and Ganzhorn 1985). Herlugson (1981) show that birds consider breeding success when evaluating and selecting habitat. The majority of adult females successful in fledging young during the previous year either returned to the same territory and nest box or selected the same type of nest box if they changed territories. If they were unsuccessful, adult females tended to change territories and nest box types.

One behavioural aspect of habitat selection concerns the degree to which free choices of habitat are made as opposed to individuals imprinting on and returning to natal habitats. Certainly the extensive data on site fidelity, where adult individuals returning to exactly or approximately the same territories year after year, indicate that there may be a very limited choice in some species (Cody 1985). There is extensive data on site fidelity (Cody 1985). Imprinting on to a certain environment is also discussed, although convincing evidence is meagre (Hildèn 1965). This imprinting may occur after leaving the natal area (Löhrl 1959). Experience, both good and bad, can influence the bird's habitat selection (Herlugson 1981). There is little knowledge about whether individuals choose the same habitat, especially after breeding dispersal.

1.2 Study species: Ortolan Bunting

In Norway, as in several other European countries (Kutzenberger 1994), the population of Ortolan Bunting (*Emberiza hortulana*) has declined dramatically. The species is listed as vulnerable in Europe (Tucker and Heath 1994). Before 1970 the bird has decreased both in distribution and number in Norway (Haftorn 1971). The Ortolan Bunting was first listed as "vulnerable" on the Norwegian red-list, but has later been categorised as "directly threatened" (Størkersen 1999). In 1996, a field study of the Norwegian Ortolan Bunting was started. Since then the total male population has been estimated. During the study period estimates of the population size indicate a decline of about 8 % per year (Dale 2001).

Several hypotheses try to explain the decline of the Ortolan Bunting. Both trapping during autumn migration (Stolt 1996), and conditions in wintering areas (Kutzenberger 1994) has been suggested. Dale (2001) showed high survival rates of Ortolan Bunting, and suggested therefore that mortality during migration and over wintering cannot be a major cause of the population decline in Norway. Dale (2001) instead suggested that the initial decline of the Ortolan Bunting during the 1950`s and 1960's was because of changes in agricultural practices and landscape structure, and possibly the use of mercury-treated seed grains in Norway. Dale (2001) also considered it unlikely that habitat loss or change can explain the current decline of the Ortolan Bunting in Norway. He said that there have not been any significant losses of habitats in recent years. Dale and Hagen (1997) reported a high proportion of unpaired males in the Norwegian population. Dale (2001) stated that in 1999 not more than 75% of the males attracted females. He suggested that dispersal of females lead to the fact that many males do not find a mate. This is because in the small isolated population, birds that have a large dispersal distance will disperse to areas without Ortolan Bunting. He concluded that the decline of the Ortolan Bunting in Norway seems to have been a two-staged process. First an initial decline due to human habitat change and destruction, and a subsequent decline due to the species' inability to cope with a low population density and a fragmented distribution.

Mixed farmland used to be the most common habitat for Ortolan Bunting in Norway (Haftorn 1971). Later on the distribution range of Ortolan Bunting has contracted and the species has become nearly extinct in mixed farmland areas (Dale and Hagen 1997). Today the habitats with most birds are raised peat bogs. In 2002 there were 68 Ortolan Bunting territories on peat bogs. Forest clear-cuts are the second most used habitat with 34 territories in 2002. One forest-fire site, 9 km² burned in 1976, is used by 15 males. The number of Ortolan Bunting on the forest-fire site has declined dramatically the recent years. In 1996 there were 52 males (Dale and Hagen 1997). Ortolan Bunting also use sand pit, gravel pit, embankment, agriculture cultivation, fallow land, industrial areas, and edges of forest, agriculture and bog.

To better understand the ecology of Ortolan Bunting it is important to examine the process of habitat selection. This will be of great help for conservation of habitats and for conservation of the Ortolan Bunting. If there were a preference for any habitat it would be constructive to improve the conservation of this habitat. These might be useful tools for conservation of the threatened Norwegian Ortolan Bunting population.

1.3 Hypothesis and Predictions

This paper looks at all recorded Ortolan Bunting changes of location by male bird, and therefore habitat selection, known in Norway from breeding season 1999 until breeding season 2002. These dispersals have been analysed separately as natal dispersals and breeding dispersals. The analysis tries to find a pattern of dispersal, especially whether or not the birds disperse to the same habitat as where it previously has been. In addition to this the question about whether or not some of the habitats are more preferred than others are considered. The breeding dispersals, which have the largest data sample, were in addition analysed separately for dispersals from peat bog and forest clear-cut. This was done statistically by three different methods, and by two different tests.

Klopfer and Ganzhorn (1985) state that for many species, the habitat in which the juvenile period is passed becomes the bird's later preference choice. Hildèn (1965) states that even though convincing evidence is meagre so far, he considers the phenomenon proved. Site tenacity will strengthen over the years. The young birds will not be so well acquainted with their home area as a bird that has already once nested does with regard to its territory (Hildèn 1965).

These studies leads to the hypothesis that preferred habitat is imprinted at an early stage in life, and that the bird will prefer this habitat through life. The present paper analysed dispersal from the bird's natal place were they hatched, to the breeding place the following year. Especially whether the young would return to the same habitat category was analysed. The prediction was that natal dispersals more often than random would be to the same habitat type as it was reared. (In this paper it is by random dispersal meant random within habitat categories described in methods, and not random in its most wide sense). The present paper also looked at dispersals from breeding territories (breeding dispersal). Especially whether the adult would return to the same habitat category was analysed. The prediction was that breeding dispersal more often than random would be to the same habitat category as analysed. The prediction was that breeding dispersal more often than random would be to the same habitat type as it dispersed from. Another hypothesis is that the birds do not get imprinted on a certain habitat, but at all

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times choose the habitat with the best stimuli of suitable features characteristic of the optimal environment. This is described by Hildèn (1965). This hypothesis is that the birds have a genetic origin for a specific habitat preference, whether or not it was born in that kind of habitat, or had bred there earlier. This predicts that natal dispersal will more often than random be to the habitat type where the bird was reared. For breeding dispersal it predicts that dispersals more often than random would be to the same habitat type as where it bred the previous year. A third hypothesis is that for dispersals the birds did not have neither a innate or imprinted habitat preference, but choose habitat types at random. This predicts a random dispersal.

Thus, I test whether or not some of the habitat categories were preferred more than the others.

2. Methods

2.1 Study area

The study area was situated in Hedmark County, South-eastern Norway. The data were collected in May and June from 1996 until 2002. This was done by slowly walking through each habitat patch with Ortolan Bunting with binocular and telescope, looking and listening for birds. From 1999 all known populations in central Hedmark were visited throughout the breeding season, and visits were made with 1-3 days interval. During the first years from 1996-98, the study was concentrated to a forest fire area, Starmoen, near Elverum in Hedmark County. The Starmoen population was followed on a nearly daily basis through the breeding seasons in these years. Most other populations in Hedmark County were also visited during the nestling period during 1997-98 (see also Dale and Hagen 1997). Since the study was concentrated on Starmoen, there was a lack of knowledge about the other potential breeding habitats. Therefore the analyses of dispersal could not be made, and dispersals before 1999 are excluded from this analysis. Populations known in the southern part of Hedmark and Akershus counties (about 10 % of the total Norwegian population) were visited only 1-3 times during each breeding season during the whole

study period. Personally, I participated in the fieldwork during the breeding season (May and June) of 2002.

2.2 Breeding habitats of Ortolan Bunting

In Norway the typical breeding habitat of Ortolan Bunting was formerly mixed farmland (Haftorn 1971), but now the species is nearly extinct in such areas (Dale & Hagen 1997). Today the main breeding habitat of Ortolan Buntings is raised peat bogs (Dale & Hagen 1997), and forest clear-cuts (Dale 2000). There are also several birds on Starmoen, an area where there was a forest fire in 1976. Common for all the locations is that they are close to farmland, which is important for Ortolan Buntings as foraging areas (Dale 1997).

The habitat categories presented in this paper are described as:

- Peat Bog: This was both natural peat bog, and peat bog used or previously used for peat extraction. There were typically open habitats with some trees of pine (*Pinus sylvestris*) and birch (*Betula pubescens*), and vegetation dominated by heather (*Calluna vulgaris*), mosses (*Sphagnum* spp.) and (*Eriophorum vaginatum*).
- 2. Forest clear-cut: This habitat had some few trees (*Pinus sylvestris*), and was typically an open habitat. The ground was dry, and often with branches lying on it. The ground was dominated by heather (*Calluna vulgaris*) and lichens.
- Forest fire site: This one site with 9 km² forest burned in 1976. This area was dominated by pine (*Pinus sylvestris*) and birch (*Betula pubescens*). The ground was dry, and dominated by e heather (*Calluna vulgaris*), lichen (e.g. *Cladonia stellaris*), often with exposed sand. Some birds were also in rather closed forest, dominated by pine.
- 4. Land being cleared for cultivation (From now on called Cultivation): This habitat was typically previously clear-cut, where trees, branches, and other organic material had been gather in embankment. Grain fields often surrounded these embankments. These were open habitats.

- 5. Edge: This was a narrow zone between grain fields, forest, forest fire site, and peat bog. The vegetation was varied, often dominated by birch.
- 6. Other habitats: This includes sand pit, gravel pit, fallow land, and industrial area. All these was open habitats. A further description was difficult to make.

2.3 Colour ringing

The identity of all birds was recorded every year, and unique colour ring combinations on their feet identified each bird. Birds were captured in their territory in mist nets, by playback of Ortolan Bunting song, and given three colour rings and one numbered metal ring. Some were also ringed as young in nests. Almost all birds captured in nets were males. In nests both males and females were ringed. Thus, most birds with colour rings are males. Therefore the data on dispersal is almost entirely made up of males, and it is male habitat selection that is analysed in this paper.

2.4 Analyses of dispersal

Dispersal is here defined as a change of habitat patch. Thus, dispersals within or between years within a habitat patch are not recorded as dispersal. To record what choice the bird had in regard to habitat selection, analyses of all the potential locations between start and end of the recorded dispersal were made. All habitat patches were places where there had been recorded Ortolan Bunting. For each recorded Ortolan Bunting that changed habitat patch, dispersal was analysed to determine what locations that were potential for the bird during the dispersal. That is, when dispersing from A to B, what locations in between is it likely that the bird had passed, and therefore potentially could select for breeding habitat? When potential locations between A and B had been defined, the proportions of different habitats within the locations were calculated. Number of occupied territories in each habitat was used as a measure of habitat availability. Since the number of different territories within a location differs between years, each year was dealt with separately. Number of territories occupied by Ortolan Buntings in the year each individual dispersed was used as a measure of what type of habitats that was available to the birds. The values for expected habitat selection in the statistical tests are calculated from these numbers of territories within the dispersal path (see below) of each Ortolan Bunting.

2.5 Defining dispersal paths

The analyses of dispersal paths were made by three different methods:

 Method 1 used a 2 km wide area, 1 km to both sides in the straight line between the location the bird left to the habitat patch where the bird was registered next time (See figure 1). All locations that were within this band were analysed as potential locations for the bird. If the bird dispersed less than 1 km, patches that were further away than where the bird stopped, even if it was within the 2 km sector, was rejected as a potential habitat. This was done because only locations between the start and the end of dispersal were regarded as potential alternatives to the birds.



Figure 1. Schematic figure of dispersal path, for dispersal analyses by method 1.

2. Method 2 used a 4 km wide area, 2 km to both sides, from the location the bird left to the location where the bird was recorded next time. All locations that were within the 4 km wide area were analysed as potential patches for the bird. If the bird dispersed less than 2 km, locations that were further away than where the bird stopped, even if they were within the 4 km sector, was rejected

as potential sites. This was done because locations only between start and end of dispersal were regarded as potential to the birds.

3. Method 3 used a sector of 90°, 45° to each side, between location where the bird left and where the bird settled down. The location closest to start location, and within the sector, was registered as the next potential site. From this patch a new sector was made from here to the location where the bird settled down. The closest location within the sector was again regarded as the next potential site. This was done for all patches within sector from start to end for all bird dispersals. This test assumes that the birds will avoid dispersing over large forest areas. Therefore a 5 km limit was set for dispersal over forest. In some few cases there were no locations within the 90° sector that were not over 5 km forest. Then the sector was made wider until there was a location that came within the sector.

Norwegian topographical maps (series M711, scale 1:50 000) were used to measure the 2 and 4 km wide range for bird dispersal. This was also used to measure the range of 90° sector in Method 3. If a part of a location was within the sector, all of the location was regarded as within this sector. This assumes that a bird, which has found a location, then has found all of the location, and all of its habitats were potential for the bird.

The three different methods where analysed by two different tests, Test 1 and Test 2:

- Test 1 assumed that all territories in all the different locations have equal preference by the Ortolan Bunting. In this test all territories in all locations that came within the sector of dispersal, were used equally to calculate expected value of habitat choice made by the bird.
- 2. Test 2 assumed that all locations have equal preference by the birds. That is, if the bird has two locations that are potential for the bird, there is an equal chance for the bird to settle down in either location. A location with one territory and a location with ten territories had the same weighting by the bird. That is, in both cases, the bird saw a potential site, and either accepted it or moved further. This from the threshold theory that combines positive and negative characteristics of the habitat: if the sum exceeds the threshold, the

bird occupies the territory; if not, the bird leaves to seek another site. Within each location, the expected values for habitat choice were calculated by numbers of territories, as in Test 1.

Expected values for habitat choice were used to compare with recorded habitat choice. This was done for natal dispersal and breeding dispersals. In this analyses the expected value for dispersal to the same habitat were compared to the expected value for dispersal to a new habitat. For natal and breeding dispersals this was done by chi-square tests by method 1 test1 and 2. For breeding dispersals, separate chi-square tests for dispersals between habitat categories from peat bog and forest clear-cut were used. These dispersals were analysed by method 1-3, test 1 and 2. In these tests it was analysed whether or not there was a random dispersal between habitat categories. Dispersals from forest fire site were in all chi-square tests excluded. This is because there only is one patch with forest fire site, so therefore dispersal from and to a forest fire site is impossible. Then an expected value for dispersal from forest fire site was not calculated.

The chi-square test can only be used if the tested observations are independent from each other. Therefore a bird cannot be used twice in the same test, even though the Ortolan Bunting had dispersed from the specific habitat twice. Thus, for two individuals, mean values of recorded habitat choices were used. In table 5 these dispersals were set as separated. Therefore ten birds have been counted for twice, and one bird counted for three times. Because of small sample sizes in some comparisons, there were expected values that were less than five in some cases. This is not preferable in chi-square tests. Then habitat types were joined into one combined category. For tests for dispersal from peat bog, this yields the habitats: edges, forest fire site, sand pit, gravel pit, embankment, cultivation, fallow, industrial area. For tests for dispersal from forest clear-cut this yields the habitats peat bog, in addition to the former habitats.

Even with these combined categories, there were five tests with an expected value of slightly less than five. Since any more combining was impossible, and because the

values were very close to five, the chi-square test was used anyway. Some locations were only used one season by one bird. These were regarded as unrepresentative observations and were rejected as a location offer for Ortolan Bunting. This excludes five locations.

Many birds were recorded at one location one year, and then seen on a different location the following year. Since we cannot know what year the bird dispersed, a mean of offered habitats between the two years was used as the expected value in analyses of habitat selection.

2.6 Statistical analyses

Data were analysed statistically by a chi-square test, which compare observed data distributions against expected data distributions. The chi-square value and P-value in the statistical test were calculated from the Internet site "Vassarstat: Web Site For Statistical Computation". (http://faculty.vassar.edu/lowry/VassarStats.html)

3. Results

3.1 Number of territories and habitat patches

Peat bog was the habitat with most Ortolan Bunting territories (Table 1). Forest clearcut was the habitat with most patches and second most territories. Forest fire site, with only one patch, was the habitat with most birds per habitat patch (Table 1). Cultivation, edge, and other habitats are relatively similar, with 4-7 habitat patches and 11-13 territories (Table 1).

Table 1. The mean number of territories per year. The percentage of territories for each habitat patch.Mean number of habitat patches per year. The percentage of all habitat patches for each habitat patch.Mean number of territories per habitat patch per year.

Mean number of:	Peat	Forest	Forest fire	Cultivation	Edge	Other	Mean
	bog	clear-	site			habitats	
		cut					
Territories	74.8	34.3	22.3	11.3	12.8	12.3	28.0
% of all territories	45.0	20.0	13.0	7.0	8.0	7.0	16.7
Habitat patches	12.0	16.8	1.0	4.5	6.8	5.0	7.7
% of all habitat patches	26.0	36.4	2.2	9.8	14.8	10.9	16.7
Territories pr.	6.2	2.0	22.3	2.5	1.9	2.5	6.2
habitat patch							

3.2 Dispersal and habitat selection

3.2.1 Natal dispersal and habitat selection

A total of 16 natal dispersals were recorded (Table 2). 15 (94 %) natal dispersals were to peat bog or forest clear-cut. The only exception was a dispersal that was made from the same habitat type that the bird dispersed from (Other habitat). 7 of 16 (44 %) natal dispersals were made to the same habitat type that the bird left.

For 15 dispersals the expected values for random dispersals to same habitat were calculated. Dispersal from forest fire site was excluded. This was done by method 1 test 1, and these values were compared with the recorded values of dispersal to the same habitat. The expected and recorded values were not significantly different ($\chi^2 = 0.02$, df = 1, P = 0.89). See figure 2. Nor dispersal by method 1 test 2 was significantly different from a random dispersal ($\chi^2 = 0$, df = 1, P = 1). See figure 3.



Figure 2. Expected and recorded dispersals to same or new habitat type. Analysed by method 1 test1.



Figure 3. Expected and recorded dispersals to same or new habitat type. Analysed by method 1 test 2

	To habitat										
From habitat	Peat bog	Forest clear-cut	Forest fire site	Cultivation	Edge	Other habitats					
Peat bog	4	2									
Forest clear-cut	2	2									
Forest fire site	1										
Cultivation											

Table 2. The number of natal dispersals between the habitat categories.

Edge			
Other habitats	2	2	1

Other habitats include the habitats: sand pit, gravel pit, fallow land, and industrial area.

3.2.2 First breeding dispersal and habitat selection

There were 60 first breeding dispersals. 15 (25 %) of these were to the same habitat type. 11 of these 15 were from peat bog, and three from forest clear-cut. No dispersals made from forest fire site, cultivation or edge was made to the same habitat type, and 1 of 3 dispersals from other habitats was to the same habitat (Table 3). For 54 dispersals, 6 dispersals from forest fire were excluded, the expected values for random dispersals to same habitat were calculated. These were not significantly different from the recorded values (method 1 test 1: $\chi^2 = 1.24$, df = 1, P = 0.27, method 1 test 2: $\chi^2 = 1.15$, df = 1, P = 0.28).

		То	o habitat			
From habitat	Peat bog	Forest clear-cut	Forest fire site	Cultivation	Edge	Other habitats
Peat bog	11	7	3	7		2
Forest clear-cut	6	3		1	1	2
Forest fire site	2	2		1	1	
Cultivation	1					
Edge	2	1		1		
Other habitats	1					1

Lubic of The humber of first breeding dispersions bein cent the hubble cure solves	Table 3.	The	number	of first	breeding	dispersals	between	the	habitat	categories.
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Other habitats include the habitats: sand pit, gravel pit, fallow land, and industrial area.

3.2.3 Second breeding dispersal and habitat selection

5 of 12 (41.7 %) second breeding dispersals were to the same habitat category as the bird dispersed from. In addition there were one third breeding dispersal from clear-cut to clear-cut (Table 4). This was the only third breeding dispersal in this study.

The expected number of dispersals to same habitat by random dispersal was calculated. It was not significantly different from the recorded dispersal (method 1 test 1: $\chi^2 = 0$, df = 1, P = 1, method 1 test 2: $\chi^2 = 0$, df = 1, P = 1).

-		То	habitat			
From habitat	Post bog	Forest	Forest fire	Cultivation	Edgo	Other
	Peat bog	clear-cut	site	Cultivation	Luge	habitats
Peat bog	3		1	1		1
Forest clear-cut	2	2*				
Forest fire site						
Cultivation	1					
Edge						
Other habitats		1				

Table 4. The number of second breeding dispersals between the habitat categories.

*: There were in addition to these dispersals one third breeding dispersal. This was the only recorded third time breeding dispersal in the study.

Other habitats include the habitats: sand pit, gravel pit, fallow land, and industrial area.

3.2.4 All breeding dispersal and habitat selection

For both first and second dispersal there was no significance for a non-random dispersal. These dispersals were joined together to increase the data material in each test. 20 of 72 breeding dispersals were to the same habitat as were the dispersals started (Table 5). The expected values for random dispersals to same habitat were calculated. It was not significantly different from the recorded dispersal (method 1 test 1: $\chi^2 = 0.59$, df = 1, P = 0.44 method 1 test 2: $\chi^2 = 0.52$, df = 1, P = 0.47).

Table 5. The number of all breeding dispersals between the habitat categories.

To habitat

From habitat	Peat bog	Forest	Forest fire	Cultivation	Edgo	Other
		clear-cut	site		Luge	habitats
Peat bog	14	7	4	8		3
Forest clear-cut	8	5		1	1	2
Forest fire site	2	2*		1	1	
Cultivation	2					
Edge	2	1		1		
Other habitats	1	1				1

*: There were in addition to these dispersals one third breeding dispersal. This was the only recorded third time breeding dispersal in the study.

Other habitats include the habitats: sand pit, gravel pit, fallow land, and industrial area.

In the tests with all breeding dispersals there were some birds that were recorded several times. This means that some birds will influence the results more than others. To avoid this there were made new tests. In these tests, a mean for each bird of expected value for dispersals to the same habitat category, were used. It was not significantly different from the recorded dispersal (method 1 test 1: $\chi^2 = 0.64$, df = 1, P = 0.42 method 1 test 2: $\chi^2 = 0.59$, df = 1, P = 0.44).

3.2.5 Breeding dispersal and habitat selection for dispersals from peat bog

37.9 %, 12 of 37, of all breeding dispersals form peat bog were to another peat bog (Table 5). Dispersals from peat bog were analysed by three different methods, and to different tests. It was in all 6 different tests. Dispersal from peat bog was in only one test significantly different from random. In the five other tests it was not significant from random. When a path with width of two km were used, and were all locations were measured with equal preference, there was a significant difference between recorded dispersal and a random dispersal (method 1 test 2: $\chi^2 = 5.96$, df = 2, P = 0.05). For the five other different tests of dispersal from peat bog it was not significantly different form random. Method 1 test 1: $\chi^2 = 2.24$, df = 2, P = 0.33. Method 2 test 1: $\chi^2 = 1.71$, df = 2, P = 0.43. Method 3 test 1: $\chi^2 = 1.76$, df = 2, P = 0.41. Method 2 test 2: $\chi^2 = 4.99$, df = 2, P = 0.08. Method 3 test 2: $\chi^2 = 4.27$, df = 2, P

= 0.12). All analyses in test 2 had a higher χ^2 -value than the analyses in test 1.

3.2.6 Breeding dispersal and habitat selection for dispersals from clear-cut

26.3 %, 5 of 19, breeding dispersals from forest clear-cut were to another clear-cut. Dispersals from clear-cut were analysed by three different methods, and to different tests. It was in all 6 different tests. Inn all tests the recorded and expected values of dispersal were not significantly different. (Method 1 test 1: $\chi^2 = 0.03$, df = 1, P = 0.86. Method 2 test 1: $\chi^2 = 0.02$, df = 1, P = 0.89. Method 3 test 1: $\chi^2 = 0.04$, df = 1, P = 0.89. Method 3 test 1: $\chi^2 = 0.52$, df = 1, P = 1. Method 1 test 2: $\chi^2 = 0.42$, df = 1, P = 0.52. Method 2 test 2: $\chi^2 = 0.52$, df = 1, P = 0.47. Method 3 test 2: $\chi^2 = 0.13$, df = 1, P = 0.72. Like for dispersal from peat bog, dispersal from forest clear-cut had in all tests a higher χ^2 -value in test 2 than the analyses in test 1.

4. Discussion

The results of the analyses showed that the Ortolan Bunting did not have a special preference for any habitat. After natal dispersal there were no more return to the habitat type in which the bird fledged than expected by random. After breeding dispersal there were no more dispersals to same habitat type than expected by random. There was no significance in the analyses of whether some habitat types that were more preferred than others. The term random dispersal is in this paper not a random dispersal per se, including forest, mountain, and riversides, but a comparison of dispersal between the habitat types described in this paper.

The amount of data material in the different tests varies a lot. There are some tests with less than preferable number of observations. This applies to natal and second breeding dispersal tests. In these tests there are only 16 and 12 observations, respectively. This limits the number of tests that can be made for these two categories. A higher number of data sample may have shown a pattern in these dispersals, although the analyses in the present paper does not indicate this. Also for analyses of dispersal from peat bog and forest clear-cut there were in each category of habitat type too little data sample. Therefore several categories had to be combined in to one category, and this made these tests less precise. For test for any habitat preference for birds dispersed form peat bog, there were three categories. The categories were peat bog, forest clear-cut, and combined category. In the tests there were no significance for preference of any of these three categories. In the combined category there were several habitat types. The Ortolan Bunting may have preferred some of these, and some not. This may have equalised preferred and not preferred habitats, and these habitats in the combined category may have outweighed each other. Because of little data sample, a further analysis of the habitat types in the combined category was impossible. The same applies for the tests for any preference for habitat types for birds that dispersed form forest clear-cut.

In the present paper some of the dispersals were analysed with several different

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methods and tests. The three different methods represents different ways in with the birds dispersed, these are described in methods. There was little difference between these methods. Therefore it would seem unlikely that further methods, for example a wider or narrower path, would give very different results. Test 2 had higher chi-square values than test 1 in all tests for dispersal from clear-cut or peat bog. Test 2 was a test where expected dispersal to clear-cut was higher than in test 1. Clear-cut was a habitat with many patches, but few territories in each patch. For example if a bird dispersal had an offer of 2 clear-cut and 2 peat bog patches. In all 4 patches this was the only habitat in the patch. If a mean of territories in each patch were used (Table 1), test 1 and 2 would give very different expected values. Test 1 would give an expected value of 2 x 6.2 = 12.4 territories to peat bog. To clear-cut it would give 2 x 2 = 4. In test 1 expected value of clear-cut would then be $4 / 16.4 \approx 1 / 4$. In test 2 it would be 1 / 2. This is why the expected number of dispersals to clear-cut was much higher in test 1 than test 2. This applies to both dispersals from peat bog and from forest clear-cut. To decide which method that are closest to the real situation are difficult. Although the methods in some cases give different values, the results of the tests are the same. There were by neither of the methods found any patterns of dispersal. The variation in habitat types made it more difficult to capture males in some habitats than others. This may influence the analyses in the present paper. This is however unlikely considering that no tests indicate that the birds' choice of dispersal was influenced by what habitat the birds stayed in.

4.1 Natal dispersal

The high amount of natal dispersals to forest clear-cut and peat bog (15 of 16 natal dispersals) may indicate a preference for these habitats in natal dispersal. This may also be a consequence of that older birds, which are superior in territorial fights, will occupy other more preferable habitats.

The chi-square test of return to natal habitat does not support a strong imprinting onto a certain habitat type. Klopfer and Ganzhorn (1985) state that for many species the

habitat in which the juvenile period is passed becomes the bird's later preference choice. This is also described by Hildèn (1965), and he considered the phenomenon proved, even though convincing evidence was meagre so far. There is in this paper no support for this theory. The analysis of Ortolan Bunting natal dispersal does not support dispersal to same habitat as hatched more often than random. Klopfer and Hailman referees to Löhrl (1959), who reports that the Collared Flycatcher, (*Ficedula albicollis*), returns in the spring to the habitat to which it was exposed for about 2 weeks after fledging during the preceding year. During these 2 weeks the birds may have moved so far that they have changed habitat. For instance, a young hatched in a habitat described as edge may have moved from the edge and on to a peat bog. Some of the locations in this study have several habitats, and the boundaries between them are vague. This means that the birds may have been imprinted on a habitat other than were they were hatched. There is little knowledge about where the newly fledged young Ortolan Bunting stays. An analyses based on this theory (Löhrl 1959) is therefore impossible at present time.

The lack of imprinting to the bird's natal habitat may be a consequence of the Ortolan Buntings use of habitats. The Ortolan Buntings apparently do not have the classical all-purpose territory typical of most passerine birds, but have more or less separated nesting and feeding areas. Feeding areas appears to be in farmlands, often grain fields, where seeds and insects may be abundant. The nest is on the ground and usually in open, rather dry areas with sparse vegetation. The Ortolan Bunting may use these habitats to reduce nest predation (Dale 2000). Thus, the structure and vegetation of the habitat, preferred open with little vegetation, may play a bigger role than vegetation type in the selection of nest territory. This basis for habitat preference may result in the lack of imprinting on the natal habitat defined by vegetation communities.

4.2 Breeding dispersal

Klopfer and Ganzhorn (1985) refers to Bairlein (1985) and says that juveniles are often less specific in their preferences than older birds. Older birds have experiences

in different locations apparently influencing later choices (Partridge, 1979).

The tests of first breeding dispersal, which was not significantly different from random, does not support the imprinting theory described by Hildèn (1965), Klopfer (1963), and Partridge (1978). This may be because of the separated feeding and nesting areas, as described above. It may support the learning theory, where experience from earlier breeding attempts influences the habitat choice. Herlugson (1981) showed that birds with successful breeding would use the same territory and nest box the following year, while unsuccessful breeders will change territory and nest box. The number of unsuccessful breeding by the dispersers is not considered in this paper. From Herlugson's theory it can be assumed that birds with successful breeding the previous year will stay in the same territory, while unsuccessful breeders will disperse and change territory and habitat. The large amount (73.2 %) of dispersals to another habitat may be because of unsuccessful breeding the previous year. In addition to unsuccessful breeders, males who did not attract females and therefore did not breed at all, made many of the breeding dispersals. A large amount of males did not attract females. In 1999 not more than 75% of the males attracted females (Dale 2001). This lack of females may cause breeding dispersal and therefore a possible change of habitat.

The results of second breeding dispersal gave the same results and conclusions as for first breeding dispersal. Also the tests where first and second breeding dispersal where joined together in one test, with a mean value of each bird so that each bird had the same influence on the test, showed the same results.

4.3 Habitat preferences

Overall there were no clear patterns of dispersal from and to the habitat category peat bog. There was no conclusion for preferences or patterns of dispersal from or to forest clear-cut. The 6 dispersals from fire site dispersed to 4 different habitats. This does not indicate a strong preference for any of the habitats for dispersals form forest fire site. Cultivation may be a habitat that was preferred by Ortolan Bunting. 11 birds dispersed to this habitat, but only 2 dispersed from this habitat. One of these to dispersals was from an embankment close to peat bog. Ortolan Bunting only used this embankment one year, and it was nearly not classified as cultivation habitat (Location Jevne in year 2000). Cultivation was a habitat where it was difficult to capture birds. Therefore few birds are caught in nets in this habitat type, and therefore there are few birds that are recorded dispersing from cultivation. This may give the numbers of 11 dispersals to and 2 dispersals from cultivation areas an incorrect picture of the situation. In all 12 tests for dispersals from peat bog and forest clear-cut the number of expected dispersals to cultivation are less than observed. For dispersals from other habitats (n = 10), analysed by method 1 test 1 and 2, the expected and observed numbers of dispersals to cultivation are about equal. In these tests there were observed one (1) dispersal to cultivation, and expected value were 1.17 and 1.23. To cultivation there were totally 11 dispersals (15.3 %). This is higher than territory percentage (7) and habitat patch percentage (9.8). This may indicate that cultivation is a habitat that is preferred by Ortolan Bunting in Norway. More data material over the following years will help to confirm this trend.

There were 4 dispersals from edge, and 2 dispersals two edge. In all analyses for dispersals from peat bog and forest fire-site the expected number of dispersals were a little higher than observed. Edge is a habitat that is diffuse to categorise. These edges vary between grain fields, forest, peat bog and forest fire site. Therefore these territories may not be similar, and to conclude some trends of dispersal is difficult. To define edge was also difficult, because it was always near and close to another habitat, and therefore the boundary between edge and another habitat were vague. Other habitats are a category with several habitats. Therefore it was difficult to analyse the dispersals from this category.

4.4 Conclusions

Overall there was no support for non-random habitat selection. Only one of 20 tests were significant different from random. All 8 tests for a habitat selection more often

than random to same habitat as previous were not significant. One of 12 tests was significantly different from a random habitat selection between the different habitats. This does not support the expected theory that Ortolan Bunting gets imprinted on a certain environment. Hildèn (1965), Klopfer (1963), and Partridge (1978) described this as a general assumption, not specific for the Ortolan Bunting. The reason that Ortolan Bunting did not get imprinted on certain habitat types may be because of the separate feeding and nest areas. While feeding in other places, the nests seem to be placed in open and dry areas with little production and therefore presumably little nest predation. This might leads to a low preference for any of the nest territory habitats described in this paper. Although it was not possible to make a test of dispersal and habitat choice for the habitat cultivation, there was some support for this to be a preferred Ortolan Bunting habitat. More data for dispersal form and to cultivation the next years would possibly clarify this pattern.

For conservation of the threatened Norwegian population of Ortolan Bunting a conservation of some particular habitats would not expect to give a big increase in number of birds. This was tested for the habitats peat bog and forest clear-cut. There might be a little response of population increase in conservation of areas being cleared for cultivation. There was some support for that Ortolan Bunting preferred these habitats with embankments.

All habitats used by the threatened Ortolan Bunting are valuable. The birds may use all habitats during dispersal.

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