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Habitat selection of ortolan buntings (*Emberiza hortulana*) on forest clear-cuts in northern Sweden

Hortulanens (*Emberiza hortulana*) habitatvalg på hogstflater i Nord-Sverige

Julianna Anne Percival

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ABSTRACT

The ortolan bunting (*Emberiza hortulana*) is one of the most severely declining farmland birds in Europe. Since the 1970s, the population in Sweden has declined more than 80%, and in Norway the population is close to extinction. While ortolan buntings are traditionally linked to farmland, a large proportion of the remaining population in Sweden is found on forest clear-cuts in northern Sweden. Few studies have investigated habitat selection of ortolan buntings outside of farmland in Sweden, and even fewer studies have identified the types of clear-cuts that ortolan buntings prefer.

The main objective of this study was to identify specific habitat characteristics influencing presence and abundance of ortolan buntings on forest clear-cuts in Västerbotten County, northern Sweden. 123 clear-cuts were visited during the breeding season (present N = 48, absent N = 75) and the results of the regression models showed that clear-cut size, the number of remaining trees, bare soil percentage (≥10%) and narrow-leaved grass vegetation had a positive influence on ortolan bunting occupancy and abundance on clear-cuts. Further, vegetation litter and few large rocks had a negative effect on the number of territories on clear-cuts. Although larger clear-cuts had a higher probability of occupancy and a higher number of territories, an additional linear regression showed that territory density (the average number of territories per hectare) did not increase with clear-cut size.

In addition, proximity to farmland was not important, and combined with behavioural observations in the field, this suggest that forest clear-cuts also provide suitable foraging habitat. This contrasts with Norwegian clear-cuts occupied by ortolan buntings, where breeding habitats are always found close to cultivated areas, which are used for foraging. In Sweden, post-harvest conditions create a mosaic of microhabitats and successional stages that provide suitable nesting sites and apparently sufficient food supplies. However, it is important to keep in mind that clear-cuts are transitional, short-lived habitats that develop into young forest within 5-10 years. This thesis therefore offers some important insights on ortolan buntings outside of farmland in Sweden, and based on this knowledge, appropriate management policies can be implemented for the conservation of this species.

SAMMENDRAG (IN NORWEGIAN)

Hortulanen (*Emberiza hortulana*) er en av de mest utrydningstruede fugler i jordbruksområder i Europa. Siden 1970-tallet har bestanden i Sverige sunket med mer enn 80%, mens bestanden i Norge nå står i fare for å bli utryddet. Hortulanen blir vanligvis forbundet med jordbruksland, men en stor del av den gjenværende bestanden i Sverige befinner seg imidlertid på hogstflater i nordlige deler av Sverige. Få studier har sett på hortulanens habitatvalg utenfor jordbruksland i Sverige, og enda færre studier har forsøkt å identifisere hvilke typer hogstflater hortulanen foretrekker.

Hovedmålet med denne oppgaven var å identifisere trekk ved habitatet som spiller inn på hortulanens tilstedeværelse og antall territorier på hogstflater i Västerbotten fylke i Nord-Sverige. 123 hogstflater ble undersøkt i hekkesesongen (tilstedeværende N = 48, fraværende N = 75) og resultatene fra regresjonsmodellene viste at hogstflatenes størrelse, antall gjenværende trær, prosentandelen av bar jord (≥10%), samt vegetasjon dominert av smyle hadde en positiv innvirkning på hortulanens tilstedeværelse og antall territorier på hogstflatene. Hogstavfall og lavt antall større steiner hadde en negativ innvirkning på antall territorier. Selv om større hogstflater hadde en høyere sannsynlighet for tilstedeværelse og et større antall territorier, viste en ytterligere lineær regresjon at territorietettheten (gjennomsnittlig antall territorier per hektar) ikke økte proporsjonalt med hogstflatens størrelse.

I tillegg viste det seg at nærhet til jordbruksland ikke var en avgjørende faktor, og sett i sammenheng med atferdsobservasjoner i felt, tyder dette på at hogstflater også fungerer som passende habitat for næringssøk. Dette står i kontrast til observasjoner av hortulaner på hogstflater i Norge, hvor hekkehabitatet alltid befinner seg i nærheten av dyrket mark, som også benyttes til å skaffe mat. I Sverige bidrar forholdene etter hogst til å skape en mosaikk av mikrohabitater og suksesjonsstadier, som tilbyr passende hekkeområder og tilsynelatende tilstrekkelig mattilbud. Det er imidlertid viktig å huske på at hogstflater er kortvarige habitater som utvikler seg til ung skog innen 5-10 år. Denne oppgaven presenterer viktige sider ved hortulanens habitatvalg utenfor jordbruksområder i Sverige, og basert på denne kunnskapen vil det være mulig å implementere passende strategier for å bevare arten for fremtiden.

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1. INTRODUCTION

The ortolan bunting (*Emberiza hortulana*) is a long-distance migratory bird currently experiencing large population declines and range contractions across most of Europe (Dale & Steifetten 2011; Menz & Arlettaz 2011). These declines have occurred since the 1950s, and in the last 15 years declines have been reported in 21 out of 36 European countries (BirdLife International 2004).

Ortolan bunting breeding habitats are traditionally linked to farmland (Ottvall et al. 2008) and the species decline has paralleled the loss of other farmland bird species (Tucker & Heath 1994). Changes in farming practices are identified as the most important drivers in the decline of ortolan buntings, and increased agricultural intensification and homogenisation of landscapes has resulted in widespread habitat loss and degradation of suitable breeding habitat (Kutzenberger 1994; Donald et al. 2001; Newton 2004; Vepsäläinen et al. 2005; Wretenberg et al. 2006; Menz & Arlettaz 2011). Other major drivers include increased pesticide use and mercury-treated seed grain (Svensson et al. 1999). Studies by Dale (2001) and Steifetten & Dale (2006) also found that female-biased natal dispersal limits population growth in the already small Norwegian population and explains the high proportion of unpaired males. In addition, illegal trapping of birds in southwestern France kills approximately 50,000 birds annually during autumn migration (Stolt 1993). Other possible causes of declines include environmental changes in wintering areas and possible loss of wintering habitats in Africa (Menz & Arlettaz 2011).

Ortolan bunting populations in northern Europe have experienced one of the most dramatic declines (Dale 2001; Vepsäläinen et al. 2005; Ottvall et al. 2008). Consequently, the ortolan bunting is classified as vulnerable in Sweden (Gärdenfors 2010) and critically endangered in Norway (Kålås et al. 2010). In Sweden, less than 7,000 breeding pairs remain – equivalent to less than 20% of the population found in the 1970s (Ottvall et al. 2008). While in Norway, the species is effectively extinct – the entire population is restricted to a small area in Hedmark County and consists of about 25 males, only half of which have females (S. Dale, personal communication 2014).

Ortolan bunting breeding habitats vary greatly throughout Norway, Sweden, and the rest of Europe, but a common feature is that they prefer sunny, semi-open or sparsely vegetated areas and are attracted to exposed patches of soil (Berg 2008). Today the Norwegian population of ortolan buntings are found on raised peat bogs, forest clear-cuts on poor sandy soils, newly cultivated land, and on one old forest burn from 1976 (Dale & Hagen 1997; Dale 2000; Dale & Olsen 2002). These breeding habitats are always found close to cultivated areas, which ortolan buntings use for foraging (Dale 2000; Dale & Olsen 2002).

Ortolan buntings have almost disappeared in south and central Sweden. However a significant population (an estimated 2,000-7,000 birds) is found in north-eastern Sweden, where they are found mostly on 3-10 year old forest clear-cuts (Stolt 1993; Ottvall et al. 2008). Unlike the Norwegian ortolan bunting population, studies have shown that nearby farmland is not essential for breeding habitats, as forest clear-cuts may provide both suitable nesting and foraging habitat (Ottvall et al. 2008).

Besides studies by Ottvall et al. (2008), few studies have investigated habitat selection of ortolan buntings outside of farmland areas in Sweden. Even fewer studies have identified the types of forest clear-cuts that ortolan buntings prefer, and which habitat features influence habitat selection at the site and micro-habitat scales. Lucas (2013) studied ortolan buntings on burnt and non-burnt clear-cuts in northern Sweden, but did not find birds on burnt areas. However, her study found that presence of ortolan buntings was positively correlated with clear-cut size. My study therefore provides a more detailed understanding of the characteristics of suitable breeding and foraging habitat of ortolan buntings on forest clear-cuts in northern Sweden. This study also identifies whether ortolan buntings breeding on forest clear-cuts need nearby farmland for foraging, as this appears to be necessary in Norway.

Further, this knowledge can help develop recovery strategies or conservation practices that can help expand existing ortolan bunting populations or establish new populations outside of farmland in northern Europe.

1.1. Research objectives

The main objectives of this study are to (i) identify the main habitat variables influencing habitat selection of ortolan buntings on forest clear-cuts at the landscape level; (ii) investigate foraging behaviour and habitat use at the individual clear-cut level; and (iii) compare used clear-cuts in northern Sweden with used clear-cuts in Norway, and draw comparisons between the two populations.

The following specific research questions were addressed at the three spatial scales:

(i) At the landscape level in Västerbotten, Sweden:
   a. Is there a relationship between the presence and abundance of ortolan bunting territories, and specific forest clear-cut characteristics (e.g. vegetation type, age, size) in the whole study area?
   b. Is there a relationship between the presence and abundance of ortolan buntings and distance to nearby farmland?
   c. How do used clear-cuts differ from adjoining clear-cuts that were not used?

(ii) At the individual clear-cut (habitat) level in Västerbotten, Sweden:
   a. Do used sites within a clear-cut differ from the overall clear-cut characteristics?
   b. Are there any common characteristics of observed foraging sites?

(iii) Comparison between Norwegian sites and northern Swedish Sites
   a. How do used clear-cuts in Norway differ from used sites in northern Sweden?

2. MATERIALS AND METHODS

2.1. Study species

Ortolan buntings are small (20-25 g), long-distance migratory passerine birds that over-winter in western Africa (Cramp & Perrins 1994). Males start returning to their breeding grounds in Sweden around early to mid-May, with females arriving about one week later (Durango 1948). The species is a ground-nesting bird that produces one brood per year with a clutch size of 4-5 eggs (Cramp & Perrins 1994). Females carry out incubation, which lasts between 11-12 days and nestlings leave the nest after 12-13 days. During the breeding season, the nestlings are fed mainly a diet of insects, while outside of the breeding season their diet consists of mainly seed grain (Cramp & Perrins 1994).

2.2. Study area in Västerbotten County, Sweden

The main fieldwork was conducted in Västerbotten County, north-eastern Sweden (63.8–64.4°N, 19.6–21.9°E; Fig. 1) during the breeding season for six weeks from mid-May to late-June 2013.

The study area is located in the northern boreal forest where forests are dominated by Norway spruce (*Picea abies*) and Scots pine (*Pinus sylvestris*), and interspersed with deciduous species such as birch (*Betula spp.*) and aspen (*Populus tremula*) (Arnborg 1990). The Swedish boreal forest covers 22.9 million ha of Sweden's land area (about 55%) (Swedish Forest Agency, 2013), of which more than 97% is managed for timber and pulp production (Kruys et al. 2013).

Since the 1950s, modern clear-felling practices have replaced selective cutting practices in Sweden and nearly all managed forest consist of dense, homogenous conifer stands with an even age distribution (Axelsson & Angelstam 2011; Swedish Forest Agency 2013). After clear-cutting, clear-cuts are primarily reforested through planting (or otherwise through natural seed-tree regeneration), which is followed later by commercial pre-thinning and thinning (Kruys et al 2013). Rotation times vary from 60 to 100 years (Kruys et al 2013). A more detailed account of site preparation methods and vegetation changes after clear-cutting is described in the discussion.

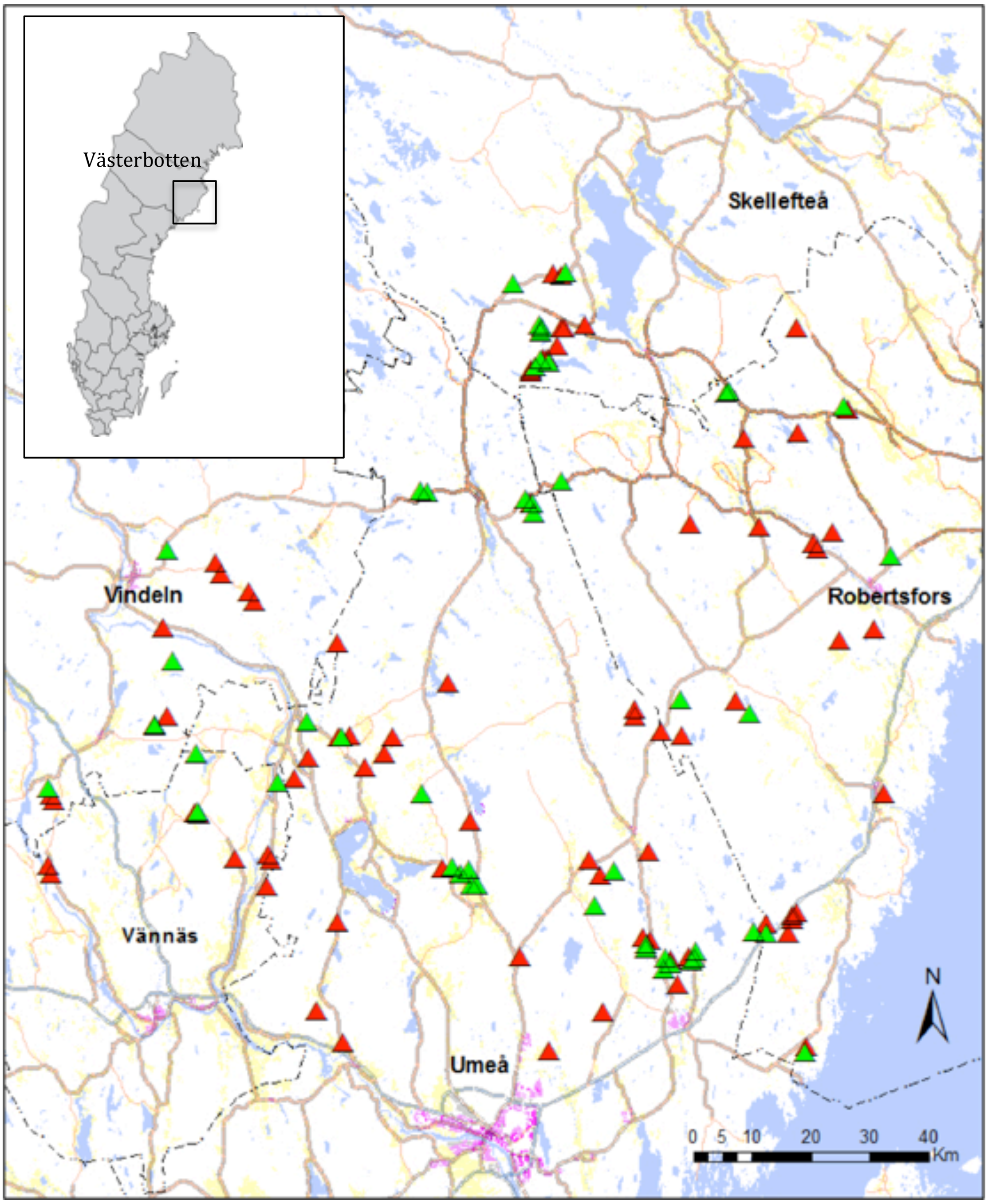

Figure 1: Map of study area showing clear-cuts visited in Västerbotten County, northern Sweden (municipalities included: Robertsfors, Umeå, Vindeln, Vännäs and Skellefteå). Solid green triangles show clear-cuts where ortolan buntings were present, and solid red triangles show clear-cuts where ortolan buntings were absent. See Appendix 1 for GPS coordinates of sampled clear-cuts.

2.2.1. Data collection

Site selection

Forest clear-cuts were identified from a map obtained from the Swedish Forest Agency (scale 1:250 000). Clear-cuts in different parts of the study area were selected prior to sampling and included areas of regional variability, including those close to farmland. Noticeable and easily accessible clear-cuts along the way were also visited. In total, 123 clear-cuts were visited.

A different part of the study area was visited each day to avoid a time-bias, meaning that clear-cuts in the northern, southern, eastern and western part of the study area were systematically alternated over time. If an ortolan bunting was found on a clear-cut, adjoining clear-cuts were also sampled (if possible), which provided paired comparisons of occupied and unoccupied clear-cuts (see below). Sites were not randomly selected due to differences in accessibility (e.g. closed roads, road condition, long driving distances on unmaintained roads), and this study design prioritized sample size over random selection. The differences between accessible and inaccessible sites are most likely differences in topography; whereby main roads generally go into valleys, and clear-cuts at higher elevations (e.g. hilltops) may therefore be under-represented. However, since hilltops were not in areas of high altitude and all vegetation types were present in the sample, such areas probably do not include important habitat variation that was not already found in my sample.

The clear-cut distribution was not homogenous across the study area and some areas, particularly between Botsmark and Bullmark in the centre-east of the study area (see Fig.1), had few sampled clear-cuts. To the best of my knowledge, this area did not differ from sampled parts of the study area - there were no noticeable differences in regional variability, e.g. elevation, slope, and other characteristics that would affect the range of variation in the sample.

At the time of fieldwork, recent clear-cuts that were felled in 2013 were not registered on the Swedish Forestry Database; therefore clear-cuts less than one year old (post-harvest) were only sampled when they were seen by chance in the field. The database also did not include clear-cuts older than 13 years (post-harvest) and these sites were therefore not included in the sample. Overgrown clear-cuts with more than 50% regrowth were excluded from the sample, as ortolan buntings are known to prefer sparsely vegetated areas.

Despite some potential biases in site selection, the sample included in this study covered a wide range of site types and environmental conditions available to the species; therefore I believe this is a representative sample that adequately reflects the overall variability in the area.

Field procedures

Each clear-cut was visited between 04:00 – 14:30 hours, and sampling at each clear-cut took between 45 minutes – 3.5 hours, depending on size. I walked around in a loop on each clear-cut, ensuring an approximate equal distance from the centre to the edge of the clear-cut, and on larger clear-cuts I also made cross transects to minimize the risk of false absences of ortolan buntings and to assess habitat characteristics.

Playback was not used to provoke a response, as male ortolan buntings have a loud and conspicuous song, and use song-posts (e.g. trees or artificial perches) to call their mates or to establish a territory. Although singing activity of mated birds is usually low during the incubation period, ortolan buntings have a distinct and loud alarm call which may be heard from quite a distance. In addition, the time spent walking around at each clear-cut and taking frequent pauses to listen, further increased the chances of detection.

Clear-cuts were classified as used (present), if birds were seen or heard. If birds were present, I tried to determine the number of territories in the clear-cut. Individual territories were distinguished based on singing activity and distance between territories. In some cases, it was difficult to determine the exact number of territories, particularly on large clear-cuts. In these cases, I indicated an approximate number of territories, e.g. 2-3 (indicated as 2.5 in the statistical analysis). The approximate position of each ortolan bunting and their respective territories were also noted on a sketch of the clear-cut. Clear-cuts were not visited during heavy rain or wind.

Coordinates at each site were stored on a Garmin GPS (Montana 600); these coordinates (waypoints) were later transferred to ArcGIS 10.1 using the application DNRGPS 6.0.0.15.

Habitat variables collected

Habitat variables were collected both from the field and by using ArcGIS 10.1. An overview of all habitat variables is summarised in Table 1.

Table 1: Overview of habitat variables collected

Variables	Type	Categories	Units
Field-collected			
Vegetation type	Categorical	Broad-leaved grass, narrow-leaved grass, sedge-horsetail, bilberry, lingonberry, crowberry-heather, poor dwarf-shrub, lichen	
Regeneration age	Continuous		years
Remaining trees	Continuous		trees / ha
Regrowth density	Categorical	0, 1-5, ≥10	%
Bare soil	Categorical	0, 1-5, ≥10	%
Vegetation litter	Categorical	0, 1-5, ≥10	%
Rockiness	Categorical	Medium rocks (none, few, medium, many), large rocks (none, few, medium, many)	rocks / ha
Soil type	Categorical	Sand, moraine, peat, rocky	
Topography	Categorical	Bottomland, slope, hill	
Aspect	Categorical	North, North-East, East, South-East, South, South-West, West, North-West	
ArcGIS-collected			
Size	Continuous		ha
Post-harvest age	Continuous		years
Distance to farmland	Continuous		m

Field-collected habitat variables

Vegetation type was classified according to the Swedish Classification System developed by Hägglund and Lundmark (1984) and was based on the abundance of indicator species found in the field-layer. Percentages of individual plant species that indicated a specific vegetation type were recorded and were visually estimated. Eight different vegetation types were recorded in the field: broad-leaved grass, narrow-leaved grass, sedge-horsetail, bilberry, lingonberry, crowberry-heather, poor dwarf-shrub, and lichen vegetation types. When a clear-cut consisted of more than one vegetation type, the percentage of each vegetation type was indicated: for example one clear-cut could be classified as 70% bilberry type and 30% narrow-leaved grass type. Vegetation types were only separated when a single vegetation type was large enough for an ortolan bunting territory, or composed more than 10% of the entire clear-cut area. Otherwise, small, localized vegetation patches were pooled within the dominant vegetation type(s).

Regeneration age, the age of planted seedlings, was estimated by counting the yearly shoots of planted trees. If no planted trees were observed, then the regeneration age was indicated as zero.

Remaining trees was based on a visual estimation of the average number of individual isolated trees, above the height of two metres, which were remaining per hectare. Retention patches (groups of trees) were not included because these patches varied considerably in size from small clusters of individual trees to remnants of intact forest covering several hectares.

Regrowth density was based on an overall visual estimation of the percentage ground coverage of regenerating vegetation in the bush-layer, i.e. below the height of two metres (e.g. birch and rowan regrowth, planted trees). Regrowth density at each site was classified as no regrowth (0%), little regrowth (1-5%) and significant/substantial regrowth (≥10%). Intermediate values were either rounded down to the middle category (1-5%) or rounded up to last category (≥10%). The same reasoning applied to the variables *bare soil* and *vegetation litter* (see below).

Bare soil was based on a visual estimation of the percentage ground coverage of exposed soil from soil disturbance, wheel tracks and root upheaval. Bare soil at each site was classified as undisturbed (0%), partly disturbed (1-5%), and heavily disturbed (≥10%).

Vegetation litter was based on a visual estimation of the percentage ground coverage of freshly fallen or slightly decomposed organic debris, e.g. leaf litter, needles, twigs, branches. Vegetation litter at each site was classified as no vegetation litter (0%), little vegetation litter (1-5%) and significant vegetation litter (≥10%).

Rockiness was measured in the field by counting the number of medium-sized rocks (rocks visible up to 1 m tall) and large-sized rocks (rocks more than 1 m tall) per ha. Medium-sized rocks were categorized into the following groups: none, few (<10 per ha), some (10-50 per ha), many (>50 per ha). Large-sized rocks were categorized into the following groups: none, few (1-2 per ha), some (3-5 per ha), many (>5 per ha). A rockiness index was created to account for both medium and large rocks. Medium-sized rock categories had the following values assigned: none (0), few (1), some (2), many (3). Large-sized rock categories had the following values assigned: none (0), few (1), some (2), many (3) and were multiplied by 2. The rockiness index combined the values from the medium-sized rocks and the large-sized rocks to create a scale from 0-9.

Soil type and *topography* were based on visual estimation in the field, and wet areas indicated bottomland topography.

Aspect was measured with a compass to indicate the slope direction. If the clear-cut had a rolling topography and it was difficult to determine the exact slope direction, the most dominant direction was used to indicate the aspect. Three clear-cuts (#003, #006, #020) were not measured in the field, but ArcGIS 10.1 was used to estimate the general direction, using the Swedish topographic map of the study area (scale 1:50 000).

ArcGIS-collected habitat variables

All visited clear cuts were identified on ArcGIS 10.1 using the GPS coordinates obtained from the field.

Clear-cut size was retrieved on ArcGIS 10.1 from the shapefile "notification of felling" (in Swedish: Avverkningsanmälningar), which was downloaded from the Swedish National Forest Agency Website (http://www.skogsstyrelsen.se/Aga-och-bruka/Skogsbruk/Karttjanster/Skogens-Kalla/) on September 1., 2013. The clear-cut sizes were extracted from the attribute table (under the Swedish attribute category: areal (ha) avverkning). As some clear-cuts were fragmented and therefore not identical to the surveyed clear-cuts, all clear-cut polygons were checked against the clear-cut sketches from the field. In these cases, new clear-cut polygons were drawn in ArcGIS 10.1, and the new size was calculated using the "calculate geometry" tool. Some clear-cuts were classified as one site during fieldwork, even though they were two individual clear-cuts in the ArcGIS database (i.e. neighbouring clear-cuts with similar age), in these cases, a new clear-cut polygon was created to obtain the size.

Post-harvest age, the number of years since initial felling occurred, was extracted from the same shapefile as above (under the Swedish attribute category: Avverkningsäsong). During fieldwork, clear-cuts were classified as separate sites if they had a distinct age difference, i.e. based on the year of planting and the degree of soil disturbance. However, differences of 1-2 years were not always obvious in neighbouring clear-cuts, and clear-cuts were sometimes classified as one site even though they were classified as two in the database, because they were felled in different years. These differences were always within 1-2 years of each other, and in these cases the clear-cuts were still treated as one site, and the average year was taken to indicate the post-harvest age.

The database had no information on the number of years between initial felling and planting/regeneration. Because of this, both age variables (regeneration age and post-harvest age) were collected. While the post-harvest age provides a more objective variable, it does not account for differences in vegetation density and height, as planting of new seedlings occurred at different time intervals after initial harvesting. While the regeneration age is a more subjective variable, it can be difficult to estimate the exact age of planted trees (since counting the number of shoots is not always clear). However, it does provide a more biologically important measurement for ortolan bunting habitat than post-harvest age, and better reflects reality and the attractiveness of the clear-cut to ortolan buntings.

To calculate *distance to farmland*, all visited clear-cuts were first exported as a separate map layer. Then, using a Swedish topographic map obtained from Lantmäteriet (scale 1:50 000, Swedish reference system: SWEREF99, vector format), farmland data was extracted from the attribute table and separated into three groups: All farmland ≥ 1ha, all farmland ≥ 10 ha, and all farmland ≥ 100 ha, and then exported as separate shapefiles. The distance to the nearby farmland categories was then calculated using the "near analysis geoprocessing tool", which measures the distance from one feature (clear-cut polygon) to the nearest line in another feature class (farmland).

Behavioural observations

Nineteen focal observations were conducted on an opportunistic basis when foraging individuals were active. These focal observation periods lasted for 30 continuous minutes. Focal observations recorded time periods and positions during singing and foraging, and noted movements within or away from the clear-cut, e.g. toward nearby farmland. When possible, detailed information was recorded on foraging activity, such as habitat of foraging sites. If an individual was lost for more than five minutes (unless it was seen leaving the clear-cut to nearby farmland), the sampling period was not considered as a focal observation, but instead used as a casual behavioural observation (see below).

Eleven casual behavioural observations were recorded in the field when birds were seen directly foraging, and these observations also included aborted focal observations. Detailed information about foraging sites was included, such as vegetation type and availability of bare soil.

2.3. Study area in Hedmark County, Norway

Additional fieldwork was carried out in three municipalities (Elverum, Våler, Åsnes) in Hedmark County, south-eastern Norway, on September 12, 2013 (60.3–60.5°N, 11.4–12.2°E). Hedmark County is located in the Norwegian boreal zone where forests are typically dominated by Norway spruce (*Picea abies*) and Scots pine (*Pinus sylvestris*), and interspersed with deciduous species such as birch (*Betula spp.*) and aspen (*Populus tremula*).

The primary purpose of data collection was to investigate the vegetation types in former and current ortolan bunting clear-cut sites in Norway and to see how they differed from vegetation types used in northern Sweden. Sites were determined on the basis of sites reported in Dale and Christiansen (2010), using clear-cuts regularly occupied by ortolan bunting(s). Vegetation types were classified according to Hägglund and Lundmark (1984), the same classification system used in the study site in northern Sweden.

Although a proportion of the visited sites were considerably overgrown, some parts had remnant vegetation growth that represented the vegetation type found when previously occupied by ortolan buntings. One site, Kjellåsen, was too overgrown to provide a representative sample and therefore an old photograph from the time ortolan buntings were present was used to determine the vegetation type. In total, 15 sites were visited.

2.4. Statistical analyses

2.4.1. Selection of habitat variables

All continuous variables were first tested for multicollinearity and variables that were strongly correlated were excluded from the models. Pairwise correlations were performed with Spearman's rank correlation coefficient using a threshold of $\rho > 0.6$, consistent with similar studies on ortolan buntings in the same area (Lucas 2013).

Subsequently, post-harvest age was removed from the regression models due to collinearity with regeneration age ($\rho = 0.88$, $P \leq 0.0001$). Distance to farmland ≥ 1 ha was correlated with distance to farmland ≥ 10 ha ($\rho = 0.76$, $P \leq 0.0001$), therefore two separate models were performed to test the effect of different farmland sizes: one with distance to nearest farmland ≥ 1 ha, and one with distance to nearest farmland ≥ 10 ha. Distance to large farmland was removed from both models as it had too few observations. Although regeneration age was correlated with regrowth density (ρ = 0.67, P ≤ 0.0001), and vegetation litter was correlated with bare soil (ρ = 0.80, P ≤ 0.0001), none of these variables were excluded from the models because they represent different and important aspects of clear-cut characteristics. Additional tests were run selecting only one variable from the correlated pairs above, to check that the model results were qualitatively the same. The results did not change and are therefore not shown in the Results section.

Prior to fitting the models, all non-normally distributed continuous variables were transformed either with log10 or log10(x+1). Two variables, clear-cut aspect and rockiness, were recoded to reduce the number of degrees of freedom used and to increase the stability of the model. Clear-cut aspect was recoded from eight categories (N, NW, E, SE, S, SW, W, NW) to two categories (North and South). Northeast, East, and Northwest facing clear-cuts were recoded as North-facing, and Southeast, West, and Southwest facing clear-cuts were recoded as South-facing. Rockiness was recoded from ten categories (0, 1, 2, 3, 4, 5, 6, 7, 8, 9), to the following three categories: 0-1, 2-5, 6-9.

Of all visited clear-cuts, 23 clear-cuts were composed of more than one vegetation type. In clear-cuts that had more than one vegetation type, the dominant vegetation type was used for the analysis, except in two cases where the ortolan bunting(s) were found in the non-dominant vegetation type. In one case, the density of birds was higher in the non-dominant vegetation type, and therefore the non-dominant vegetation type was used to indicate the vegetation type of the clear-cut. Clear-cuts with two different vegetation types that were equally dominant (i.e. 50% coverage each) were excluded from the model (N = 3).

The model was further simplified by removing clear-cuts with vegetation types that only had a few observations. Subsequently, clear-cuts with the following vegetation types were excluded from all models: broad-leaved grass (N = 3), sedge-horsetail (N = 4), and lichen (N = 4). The total sample size for the logistic and linear regression models was therefore reduced from 123 to 109.

In addition, for the presence-only linear regression model of the number of territories, clear-cuts with crowberry-heather vegetation were removed (N = 1). The following habitat variables were also excluded from all analyses, as they had almost no variation: soil type, moisture type, and topography.

2.4.2. Logistic regression models of presence-absence

Once all variables were selected for the model, a backward, stepwise logistic regression was performed to identify key habitat variables influencing the presence of ortolan buntings on forest clear-cuts. The first logistic regression model included all selected habitat variables. Then, the least significant variable was removed, and a second model was fitted with the remaining variables. This process was repeated until all remaining habitat variables in the model were significant ($P \leq 0.05$). The final reduced model from stepwise backward-selection corresponded well with the full logistic regression model; therefore the full model output is given in the results. All statistical analyses were performed with the software JMP® Pro 10.0.0.

2.4.3. Linear regression models of number of territories

A least-squares linear regression was used to identify significant habitat variables influencing the number of territories (abundance) of ortolan buntings on forest clear-cuts. Two models were performed: one model using presence-absence data (N = 109) where unoccupied clear-cuts had zero territories, and one model using presence-only data (N = 46). An additional regression analysis was performed to assess the relationship between the average number of territories per ha and clear-cut size.

2.4.4. Paired comparisons of neighbouring clear-cuts

Two types of paired comparisons were made between neighbouring clear-cuts: (1) comparisons between neighbouring clear-cuts where ortolan buntings were present on one clearcut, and absent on a neighbouring clear-cut, and (2) comparisons between neighbouring clear-cuts where ortolan bunting densities were higher on one clear-cut, and lower on a neighbouring clear-cut.

Each of the habitat variables was first summarized into two categorical groups to ensure sufficient observations (> 6) within each category. Vegetation types were simplified into “narrow-leaved grass”, and all other vegetation types were pooled into the “other” (vegetation type) category. Clear-cut sizes were simplified to “smaller” or larger". Bare soil, vegetation litter, tree density, and regrowth variables were each simplified to "less" or "more". Regeneration age was simplified to "younger" or "older".

Pearson chi-square tests were then used to identify any differences in selection (presence/absence) between neighbouring clear-cuts (N = 19) to see whether the observed frequency of ortolan buntings in one category (for each habitat variable) differed from the expected frequency. Of the nineteen possible comparisons between neighbouring clear-cuts, seven clear-cuts (present N = 3, absent N = 4) were counted more than once as they neighboured more than one clear-cut.

A two-tailed Wilcoxon sign-rank test was used to compare differences in territory densities (number of birds per ha) of neighbouring clear-cuts (both occupied), to determine how habitat variables in clear-cuts with higher densities of ortolan buntings differed from adjoining clear-cuts with lower densities. Vegetation types were not analysed because of the small sample size (N = 2). Fourteen comparisons between territory densities in adjoining clear-cuts were possible. Three clear-cuts were counted more than once as they were neighbouring more than one other occupied clear-cut.

Some clear-cuts were counted twice as they were adjoining more than one sampled clear-cut. Although some cases of pseudo-replication may represent a potential problem, including these clear-cuts was necessary to increase the sample size and perform statistical testing. However, the patterns were qualitatively the same when these cases were excluded from the analyses.

2.4.5. Paired comparisons within clear-cuts

Paired comparisons were done between vegetation types within a clear-cut, i.e. clear-cuts with > 1 vegetation type, where ortolan buntings were present on one vegetation type and absent on another. Vegetation types were first summarized into the same two categorical groups as above: "narrow-leaved grass" and all other vegetation types pooled into the "other" (vegetation type) category.

Pearson chi-square tests were then used to test whether ortolan buntings use vegetation types (narrow-leaved grass or other) based on their availability/proportion within the clear-cut (N = 11). The observed occurrence of ortolan buntings in each vegetation type was compared to the expected values (calculated as the proportion of the vegetation types available within the clear-cut).

2.4.6. Differences between Norwegian and Swedish clear-cuts

Vegetation types were first ranked according to 'richness', from rich to poor types. Each of the vegetation types was assigned the following values: narrow-leaved grass (7), bilberry (6), lingonberry (5), crowberry- heather (4), poor-dwarf shrub (3), lichen-rich (2), and lichen (1). The non-parametric Mann-Whitney U-test was then used to test for differences in vegetation types between occupied Norwegian and Swedish clear-cuts (N = 15 Norwegian sites, N = 47 Swedish sites).

3. RESULTS

3.1. Selection of forest clear-cuts: presence and absence

Ortolan buntings were found on 48 of the 123 clear-cuts. Occupied clear-cuts were on average significantly larger than unoccupied clear-cuts (Table 2; Fig. 2a), and occupied clear-cuts had on average more remaining trees per ha (Table 2; Fig. 2b).

Ortolan buntings were found on clear-cuts with exposed bare soil present and with no bare soil present (Fig. 2c, Fig. 3). Ortolan buntings were found on five out of the eight vegetation types, and were mostly found on clear-cuts with narrow-leaved grass vegetation type, followed by bilberry, lingonberry and crowberry-heather (Fig. 2d, Fig. 3). Occupied and unoccupied clear-cuts were similar in terms of regeneration age and post-harvest age (Table 2). Occupied clear-cuts were on average slightly further away from both farmland ≥ 1 ha and farmland ≥10 ha than unoccupied clear-cuts (Table 2; Fig. 2e,f). 42% of occupied clear-cuts were more than one kilometre from nearby farmland.

Table 2: Mean ± standard error (SE) for continuous variables from occupied clear-cuts (n = 48) and unoccupied clear-cuts (n = 75) by ortolan buntings

Variable	**Occupied clear-cuts (mean ± SE)**	**Unoccupied clear-cuts (mean ± SE)**
Size (ha)	17.21 ± 1.32	13.39 ± 1.24
Remaining trees (trees per ha)	3.69 ± 0.36	3.29 ± 0.43
Regeneration age (years)	3.32 ± 0.37	3.31 ± 0.29
Post-harvest age (years)	6.38 ± 0.42	6.32 ± 0.38
Distance to farmland ≥ 1 ha (m)	854.25 ± 121.75	643.00 ± 85.23
Distance to farmland ≥ 10 ha (m)	1617.55 ± 218.20	1489.31 ± 175.78

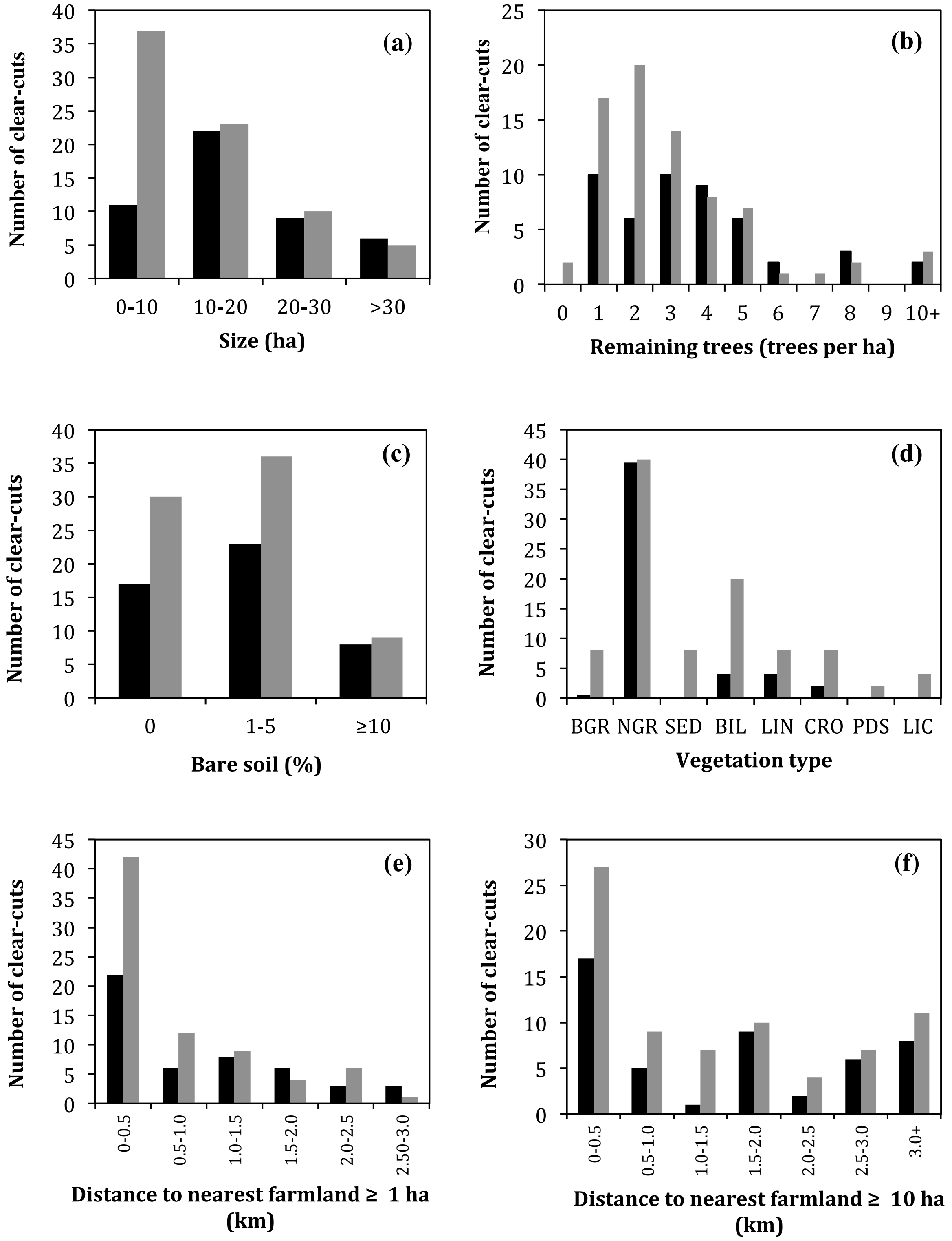

Figure 2: Frequency distributions of main habitat variables at occupied (N = 48) and unoccupied clear-cuts (N = 75). *Black columns* = occupied; *grey columns* = unoccupied **(a)** size frequency distribution **(b)** relative frequency of remaining trees **(c)** bare soil percentage frequency distribution **(d)** Vegetation type frequency distribution (BGR = Broad-leaved grass, NGR = Narrow-leaved grass, SED = Sedge-horsetail, BIL = Bilberry, LIN = Lingonberry, CRO = Crowberry-heather, PDS= Poor dwarf-shrub, LIC = Lichen) *Note:* Larger sample size (present N = 50, absent N = 98) because some sites had > one vegetation type **(e)** frequency distribution showing distance to nearest farmland ≥ 1 ha **(f)** frequency distribution showing distance to nearest farmland ≥ 10 ha

(a)

(b)

Figure 3: Photographs showing examples of occupied forest clear-cuts in Västerbotten County, Sweden **(a)** Clear-cut with 3-4 male territories, showing narrow-leaved grass vegetation type, 0% bare soil, and individual trees used as song posts **(b)** More recent clear-cut with 1 male territory, showing narrow-leaved grass vegetation, >10% bare soil.

3.2. Presence and absence logistic regression model

The logistic regression model of habitat variables influencing the presence of ortolan buntings on forest clear-cuts showed that four variables – clear-cut size, number of remaining trees, percentage of bare soil, and vegetation type – had a positive influence on ortolan bunting occupancy (Tables 3 and 4). The outputs were similar under both models: distance to nearest farmland ≥ 1 ha and distance to nearest farmland ≥ 10 ha.

The individual tests for each categorical variable showed that ortolan buntings prefer clear-cuts with more than 10% bare soil (distance to farmland ≥ 1 ha: $\chi^2 = 6.99$, $P = 0.0082$; distance to farmland ≥ 10 ha: $\chi^2 = 6.74$, $P = 0.0094$) and strongly favoured clear-cuts with narrow-leaved grass vegetation types (distance to farmland ≥ 1 ha: $\chi^2 = 7.35$, $P = 0.0067$; distance to farmland ≥ 10 ha: $\chi^2 = 7.73$, $P = 0.0054$).

Vegetation litter, regeneration age, regrowth density, rockiness, and both distance to farmland over ≥ 1 ha and distance to nearest farmland ≥ 10 ha, had no effect on occupancy (Tables 3 and 4). Ortolan buntings were found on all clear-cut aspects, with no difference found between north and south-facing slopes (Tables 3 and 4).

Table 3: Logistic regression (likelihood-ratio tests) of the habitat variables on presence of ortolan buntings on clear-cuts with distance to nearest farmland ≥ 1 ha (N = 109, $R^2 = 0.29$). Significant variables ($P < 0.05$) are indicated in bold.

Variables	**df**	χ^2	***P***
Vegetation type	3	9.92	**0.019**
Regeneration age	1	0.17	0.68
Size	1	22.80	**<0.0001**
Remaining trees	1	18.06	**<0.0001**
Regrowth	2	0.43	0.81
Bare soil	2	8.52	**0.014**
Vegetation litter	2	2.03	0.36
Distance to farmland ≥ 1ha	1	1.45	0.23
Rockiness	2	2.91	0.23
Aspect	1	0.38	0.54

Table 4: Logistic regression (likelihood-ratio tests) of the habitat variables on presence of ortolan buntings on clear-cuts with distance to nearest farmland ≥ 10 ha (N = 109, $R^2 = 0.29$). Significant variables ($P < 0.05$) are indicated in bold.

Variables	**df**	χ^2	***P***
Vegetation type	3	10.75	**0.014**
Regeneration age	1	0.20	0.66
Size	1	22.69	**<0.0001**
Remaining trees	1	17.76	**<0.0001**
Regrowth	2	0.42	0.81
Bare soil	2	8.52	**0.014**
Vegetation litter	2	1.89	0.39
Distance to farmland ≥ 10 ha	1	1.40	0.24
Rockiness	2	2.84	0.24
Aspect	1	0.70	0.40

3.3. Selection of forest clear-cuts: number of territories

A total of 96.5 territories were found on the 123 sampled clearcuts (range 1-4, median 2). Of these, 29 clear-cuts had more than one ortolan bunting territory. Most territories were found on clear-cuts between 10-20 ha, however the number of territories increased linearly with clear-cut size, and the largest clear-cuts (>30 ha) had the highest average number of territories (Fig. 4a,b). The average number of territories was spread through both low and high number of remaining trees (Fig. 4c,d).

Clear-cuts with 1-5% bare soil also had both the highest number of territories and the highest average number of territories (Fig. 4e,f). Clear-cuts with narrow-leaved vegetation type had the highest total number of territories while bilberry, lingonberry, and crowberry vegetation types had few territories, reflecting the sample size (Fig. 5a). Although clear-cuts with bilberry, lingonberry, and crowberry vegetation types were not often used, the average number of territories in clear-cuts with these vegetation types was similar to those found on clear-cuts with narrow-leaved vegetation type (Fig. 5b). Lower numbers of territories were also associated with more vegetation litter (Fig. 5c,d) and intermediate rockiness (Fig. 5e,f).

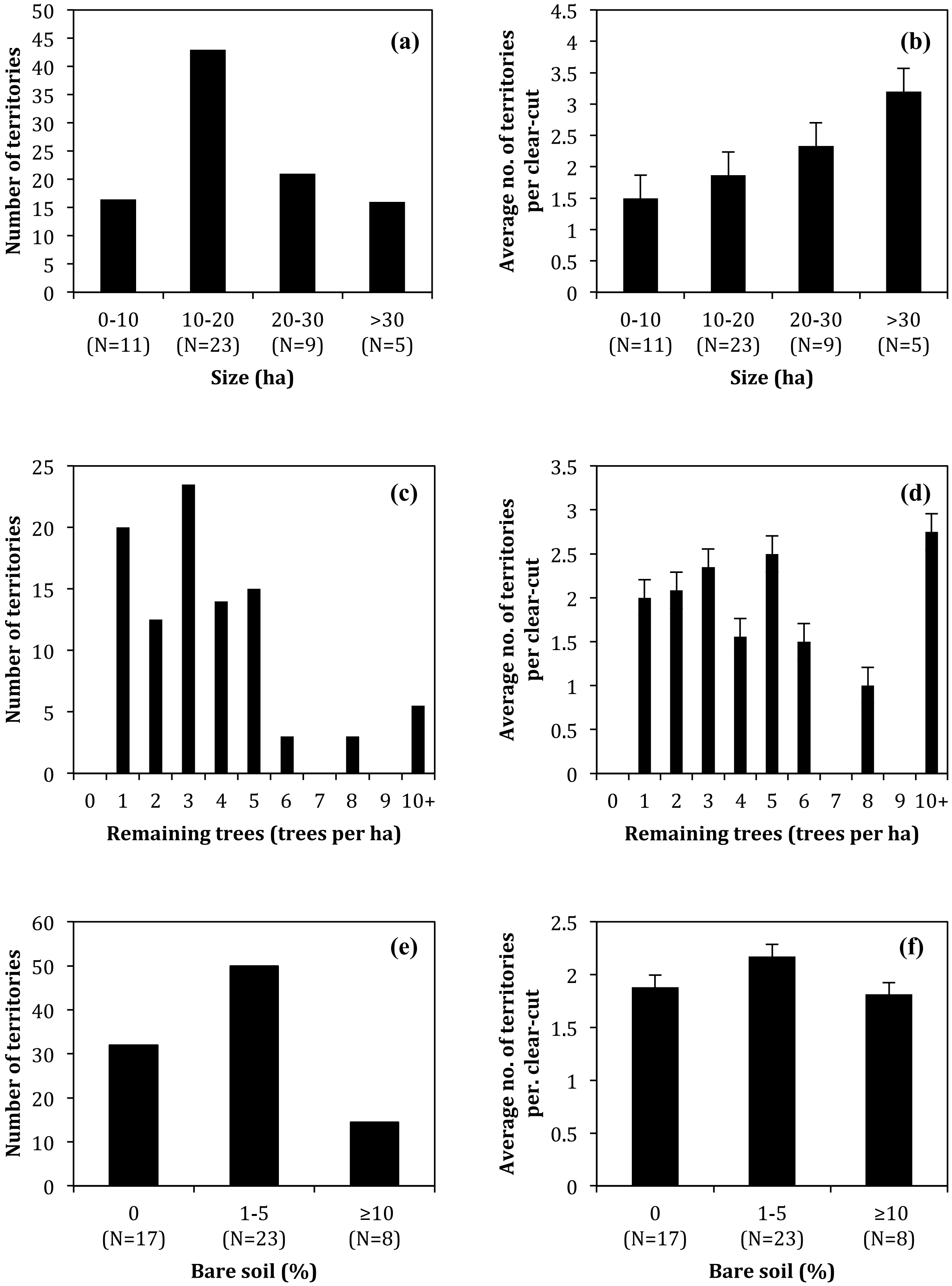

Figure 4: Frequency distribution of significant habitat variables at occupied clear-cuts **(a)** total number of territories per clear-cut size **(b)** size frequency distribution (mean + SE) **(c)** total number of territories per number of remaining trees **(d)** remaining trees frequency distribution (mean + SE) **(e)** total number of territories per percentage of bare soil remaining **(f)** bare soil frequency distribution (mean + SE)

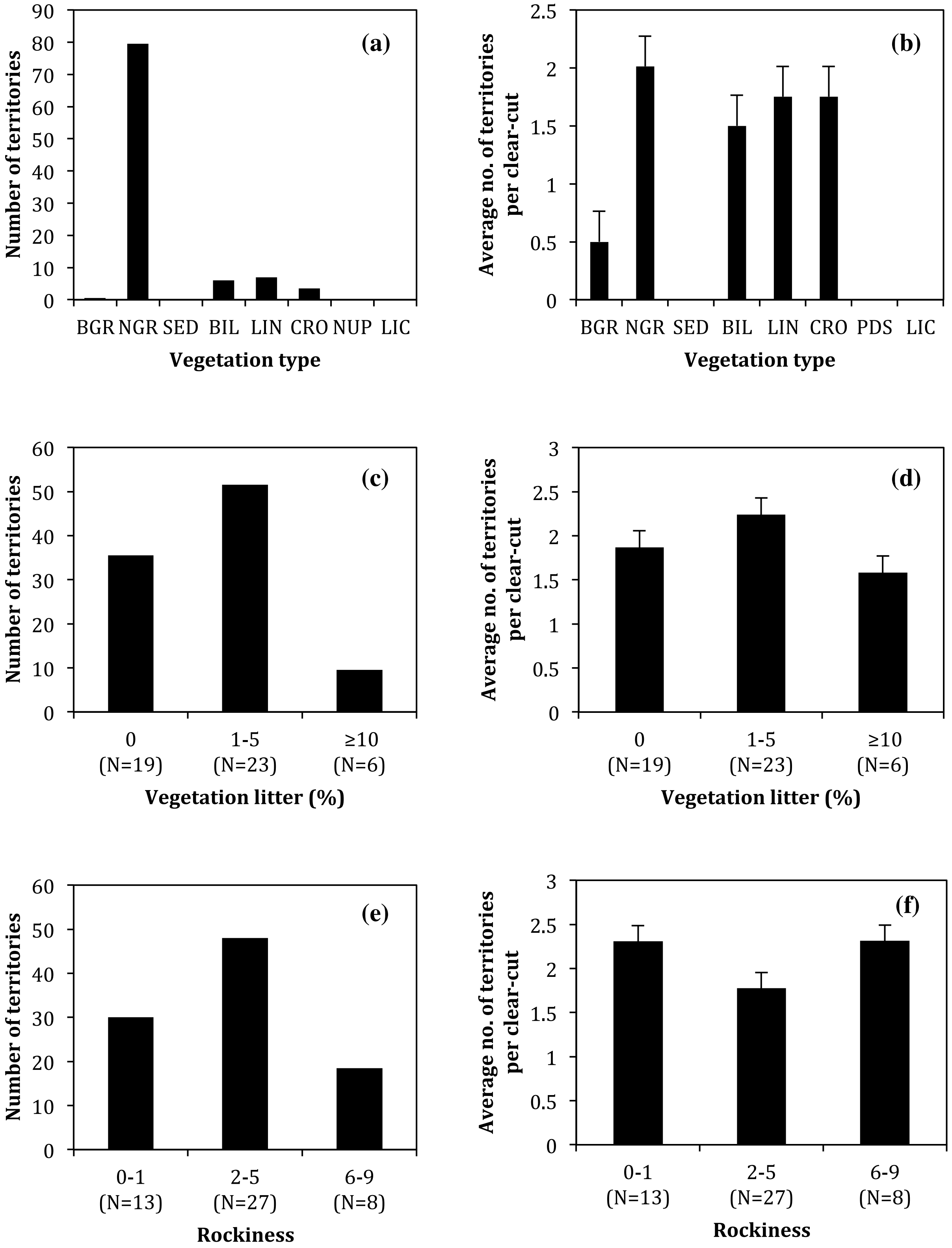

Figure 5: Frequency distribution of significant habitat variables at occupied clear-cuts **(a)** total number of territories per vegetation type (N = 50) (BGR = Broad-leaved grass, NGR = Narrow-leaved grass, SED = Sedge-horsetail, BIL = Bilberry, LIN = Lingonberry, CRO = Crowberry-heather, PDS = Poor dwarf-shrub LIC = Lichen **(b)** vegetation type frequency distribution (mean + SE) **(c)** total number of territories per percentage of remaining vegetation litter **(d)** vegetation litter frequency distribution (mean + SE) **(e)** total number of territories per rockiness class **(f)** rockiness frequency distribution (mean + SE)

3.4. Number of territories linear regression model

The results of the least-squares linear regression with the number of territories as the dependent variable showed that two variables – clear-cut size and the number of remaining trees – had a positive influence on ortolan bunting abundance, both when all clear-cuts (presence-absence, N = 109) and presence-only (N = 46) sites were included in the model (Tables 5 and 6). The outputs were similar under both farmland sizes: distance to nearest farmland ≥ 1 ha or distance to nearest farmland ≥ 10 ha. Therefore, only the results for distance to nearest farmland ≥ 1ha are mentioned here (See Appendix 2, Table A1 and Table A2 for distance to nearest farmland ≥ 10 ha).

When all clear-cuts were included in the model (with distance to farmland ≥ 1 ha), the individual tests for each categorical variable showed a positive effect of narrow-leaved grass vegetation type (t = 2.69, p = 0.0084) and bare soil above 10% (t = 2.14, p = 0.035) on the number of territories. In addition, the model showed that vegetation litter over 10% had a negative effect on the number of territories (t = -2.03, p = 0.046).

When presence-only sites were included in the model (with distance to farmland ≥ 1 ha), the individual tests for each categorical variable showed that few medium-sized rocks (corresponding to less than 2-5 on the rockiness index) had a negative effect on the number of territories (t = -2.07, p = 0.047).

Although larger clear-cuts had a higher total number of territories in both models (presence-absence, and presence-only), an additional linear regression revealed that territory density (i.e. the average number of territories per hectare) did not increase with clear-cut size, but actually declined ($r = -0.51$, $n = 46$, $p = 0.0003$; Fig. 6).

Table 5: Standard least-squares linear regression (effect tests) of habitat variables influencing the number of territories on clear-cuts with distance to nearest farmland ≥ 1 ha (presence-absence model, N = 109, $R^2 = 0.36$). Significant variables ($P < 0.05$) are indicated in bold.

Variables	**df**	**F-ratio**	***P***
Vegetation type	3	2.44	0.07
Regeneration age	1	0.01	0.91
Size	1	34.96	**<0.0001**
Remaining trees	1	17.93	**<0.0001**
Regrowth	2	0.03	0.97
Bare soil	2	2.53	0.09
Vegetation litter	2	2.14	0.12
Distance to farmland ≥ 1 ha	1	0.21	0.65
Rockiness	2	1.85	0.16
Aspect	1	0.78	0.38

Table 6: Standard least-squares linear regression (effect tests) of habitat variables influencing the number of territories on clear-cuts with distance to nearest farmland ≥ 1 ha (presence-only model, N = 46, $R^2 = 0.47$). Significant variables ($P < 0.05$) are indicated in bold.

Variables	**df**	**F-ratio**	***P***
Vegetation type	2	2.01	0.15
Regeneration age	1	0.17	0.68
Size	1	13.57	**<0.0009**
Remaining trees	1	5.14	**<0.031**
Regrowth	2	0.27	0.76
Bare soil	2	1.33	0.28
Vegetation litter	2	0.27	0.77
Distance to farmland ≥ 1 ha	1	0.04	0.84
Rockiness	2	2.79	0.08
Aspect	1	0.32	0.58

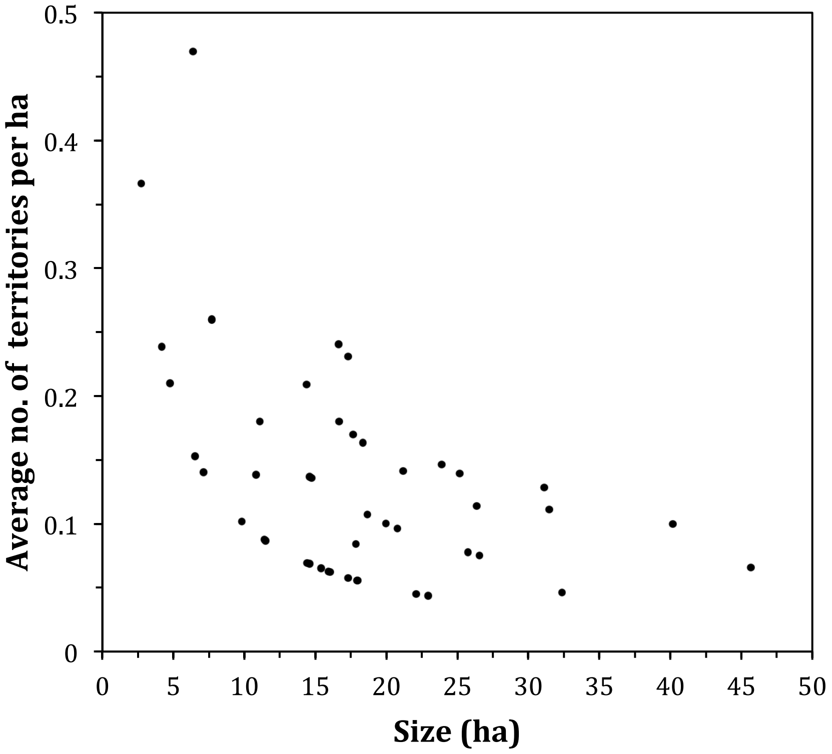

Figure 6: Relationship between clear-cut size and number of territories per ha ($r = -0.51, n = 46, p = 0.0003$)

3.5. Paired comparisons of neighbouring clear-cuts

The Pearson chi-square analysis of individual habitat variables between neighbouring clear-cuts with and without birds indicated that ortolan buntings showed no strong preference or avoidance of any of the habitat variables (Table 7). Clear-cut size was the only habitat variable that suggested a difference, which is also consistent with results from the logistic and linear regression analyses, although the difference is still not significant. The small sample size in these tests could however limit the ability to detect a statistically significant difference.

The Wilcoxon signed-rank tests yielded no differences (P < 0.05) in territory densities between neighbouring occupied clear-cuts for any of the six habitat variables (Table 8). Again, a larger sample size may increase the ability to detect statistically significant differences.

Table 7: Chi-squared analysis of habitat characteristics of neighbouring clear-cuts with and without ortolan buntings

Habitat variable	Observed no. of sites	χ^2	P-Value
Vegetation type ***(N = 12)***			
Narrow-leaved grass	8		
Other	4	0.67	0.25
Size ***(N = 20)***			
Smaller	6		
Larger	14	3.20	0.07
Bare soil ***(N = 17)***			
Less	7		
More	10	0.53	0.47
Vegetation litter ***(N = 10)***			
Less	5		
More	5	0.00	1.00
Tree density ***(N = 17)***			
Less	6		
More	11	1.47	0.23
Regeneration age ***(N = 19)***			
Younger	7		
Older	12	1.32	0.25
Regrowth ***(N = 15)***			
Less	7		
More	8	0.07	0.80

Table 8: Wilcoxon signed rank tests of differences in territory density of individual habitat variables at neighbouring occupied clear-cuts. Mean for Group 1 (lower values) = smaller sites (size), less bare soil, less vegetation litter, fewer remaining trees, younger regeneration age, and less regrowth. Mean for Group 2 (higher values) = larger sites (size), more bare soil, more vegetation litter, more remaining trees, older regeneration age, and more bare soil.

Habitat variable	Mean density for Group 1 (lower values)	Mean density for Group 2 (higher values)	Test statistic (S)	P-value
Size *(N = 14)*	0.16	0.13	-8.5	0.58
Bare soil *(N = 7)*	0.25	0.11	-8.5	0.09
Vegetation litter *(N = 8)*	0.22	0.11	-10.0	0.12
Remaining trees *(N = 13)*	0.12	0.18	13.0	0.34
Regeneration age *(N = 13)*	0.10	0.19	24.0	0.06
Regrowth *(N = 10)*	0.08	0.16	17.5	0.08

3.6. Paired comparisons of vegetation types within clear-cuts

The Pearson chi-square analysis of differences between vegetation types within one clear-cut (occupied clear-cuts with > 1 vegetation type) showed that ortolan buntings occurred on narrow-leaved vegetation types with a greater frequency than was expected based on the availability of other vegetation types (observed frequency = 10/11, expected frequency = 6.1/11) ($\chi^2 = 5.60$, d.f. = 1, $p = 0.018$).

3.7. Behavioural observations

Ten of the nineteen focal observations occurred at clear-cuts within 500 m from nearby farmland, and in only three of these observations did I observe individuals flying toward farmland. In two cases, nearby farmland was directly adjoining the clear-cut (distance to nearest farmland: 0 m and 2.6 m) and birds were away for 16-20 minutes. In the third case, the clear-cut was 252 m from nearby farmland, and the individual was away for 26 minutes. In all other focal observations where birds were seen foraging within the clear-cut, individuals were seen making 1-3 foraging attempts on the ground during the 30-minute focal period. Each foraging attempt lasted between 30 seconds – 9 minutes (total foraging attempts observed = 27, mean foraging time = 3.8 minutes).

Seven of the eleven casual behavioural observations occurred at clear-cuts within 500 m from nearby farmland (five of these were less than 100 m from farmland), and only one individual was seen flying toward nearby farmland. In all other casual observations, individuals were seen engaging in foraging activities on the clear-cut, even when farmland was nearby. Foraging lasted between 1-10 minutes on the ground (total foraging attempts observed = 12, mean foraging time = 2.9 minutes).

Common vegetation of foraging areas included a high proportion of wavy hairgrass, fireweed, and some moss (Fig. 7a,b). Individuals were also observed on the ground pecking at small grass seeds (*Deschampsia flexuosa* and *Melica nutans*) and spore capsules from haircap moss (*Polytrichum spp*.). Foraging areas included those with exposed bare soil, quite often in old wheel tracks, but also in areas nearly or completely void of exposed bare soil (Fig. 7c,d). Individuals were also observed with insects in their bill (beetles, caterpillars) in foraging areas without exposed bare soil. Five focal observations (26% of focal observations) and two casual observations (18% of casual observations) occurred on sites without bare soil.

(a)

(b)

Figure 7: Photographs showing examples of observed foraging sites **(a)** one male was observed foraging in a patch dominated by wavy hairgrass and small seeds from *Melica nutans* (narrow-leaved grass vegetation type, 0% bare soil) **(b)** one male was observed foraging in a patch of bare soil (lingonberry vegetation type, 1-5% bare soil)

(c)

(d)

Figure 7: Photographs showing examples of observed foraging sites in old wheel tracks **(c)** one male was observed in a site dominated by wavy hairgrass and patches of fireweed (narrow-leaved grass vegetation type, ≥10% bare soil) **(d)** one male was observed with an insect in his bill in an area dominated by fireweed (narrow-leaved grass vegetation type, 0% bare soil)

3.8. Selection of forest clear-cuts in Hedmark County, Norway

A total of 15 forest clear-cut sites were visited. These sites had six different vegetation types: bilberry, lingonberry, crowberry-heather, poor-dwarf shrub, lichen-rich, and lichen. Occupied sites consisted mostly of lingonberry vegetation type, followed equally by bilberry, crowberry-heather, lichen-rich (> 25% lichen), and lichen types (> 50% lichen) (Fig. 8). No occupied site consisted of narrow-leaved vegetation type. Two sites with peaty soil had a ground layer dominated by heather (*Calluna vulgaris*), lingonberry (*Vacciium vitis-idaea*), bilberry (*Vaccinium myrtillus L.),* sphagnum mosses (*Sphagnum spp*.), and to a lesser extent northern bilberry (*Vaccinium uliginosum*) and bog rosemary (*Andromeda polifolia*). All of the other forest clear-cuts were found on nutrient-poor sandy soils, mostly characterised by lingonberry, heather and *Cladonia* lichens.

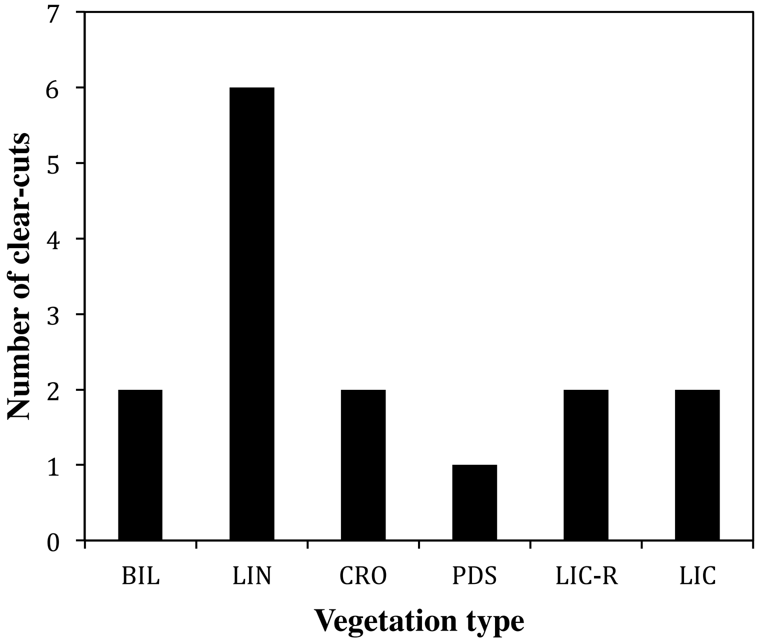

Figure 8: Frequency distribution of vegetation types of used forest clear-cuts in Hedmark County, Norway (N = 15). BIL = Bilberry, LIN = Lingonberry, CRO = Crowberry-heather, PDS = Poor dwarf-shrub, LIC-R = Lichen-rich, LIC = Lichen

Ortolan buntings were found on clear-cuts with significantly 'poorer' vegetation types in Norway compared to clear-cuts in Sweden (Mann-Whitney U-test: $z = -5.83$, $N = 15$ Norwegian sites, $N = 47$ Swedish sites, $P < 0.0001$).

4. DISCUSSION

4.1. Habitat characteristics of used forest clear-cuts

In this study, the four most important variables positively influencing the occurrence and abundance of ortolan buntings on forest clear-cuts in Västerbotten, Sweden were clear-cut size, the number of remaining trees per ha, percentage of bare soil (≥10%) and narrow-leaved grass vegetation. Further, vegetation litter (≥10%) and few large rocks showed a negative effect on territory abundance. In addition, proximity to farmland did not influence presence or abundance of ortolan buntings on forest clear-cuts, which suggests that forest clear-cuts may provide both suitable nesting and foraging habitat.

To my knowledge, this is the most comprehensive study identifying multiple characteristics affecting habitat selection of ortolan buntings on forest clear-cuts in northern Sweden, at both the landscape and individual clear-cut level. This study therefore offers some important insights into the ecology of ortolan buntings breeding outside of farmland in Europe.

Size

Ortolan bunting occupancy and abundance on clear-cuts was most strongly influenced by clear-cut size, although the size of occupied clear-cuts varied considerably, and clear-cuts as small as 2.7 ha were also occupied. Compared to small habitat patches, larger patches will generally have higher habitat heterogeneity and more resources, which in turn can support larger local populations with lower extinction probabilities, and will therefore have a higher probability of occupation (Levins 1970). Moreover, ortolan buntings are known to be attracted to semi-open and open areas, which may serve as an environmental cue to encourage settlement (Cramp & Perrin 1994).

These findings are consistent with studies by Lucas (2013) and Gustafsson (2014) who found that the probability of ortolan bunting occupancy on clear-cuts in northern Sweden increased with clear-cut size. Further, after a long period of decline in in Sweden in the early 1960s (Stolt 1974), a slight increase in ortolan buntings was observed during the 1970s, and according to Stolt (1994) this coincided with the creation of large-scale forest clear-cuts in the central and northern parts of the country.

The higher number of territories found on larger clear-cuts could also indicate the possible role of social cues such as conspecific attraction, as ortolan buntings have a tendency to form breeding groups or “semi-colonies” (Durango 1948; Vepsäläinen et al. 2007). Individuals are attracted to conspecifics because they may signify high quality breeding habitat as well as provide territory defence, predator protection, and increase their chances of attracting females (Stamps 1988; Smith & Peacock 1990; Reed & Dobson 1993; Muller et al. 1997). However, Vepsäläinen et al. (2005) have suggested that clustering of ortolan bunting territories is often due to a combination of conspecific attraction and quality-related characteristics of the habitat.

In my study, although larger clear-cuts had a higher number of territories, the density of ortolan buntings (i.e. number of territories *per* ha) declined with clear-cut size. Long-term monitoring (between 1941 and 1991) of ortolan buntings in different habitats in Finland, including forest clear-cuts in eastern and northern Finland, found that the density of ortolan buntings was also higher in small and medium-sized clear-cuts than in larger clear-cuts (Väisänen 1992). Väisänen (1992) classified large clear-cuts as those exceeding 200 ha. However, clear-cuts of that size are no longer common in Sweden or Finland and most clear-cuts in Sweden are less than 100 ha (EEA 2006), with the average clear-cut size at 4.4 ha (Swedish Forest Agency 2013). Due to regional variation in clear-cut sizes, the average clear-cut size in my study was 14.9 ha. Still, large clear-cuts sampled in my study area were significantly smaller than in Finland, with a maximum clear-cut size of 62.8 ha. However, both my findings and Väisänen (1992) are still in agreement, and both show a negative relationship between clear-cut size and territory density. Still, the total number of territories increased with clear-cut size and 83% of birds were found on clear-cuts larger than 10 ha.

The negative relationship between clear-cut size and territory density suggests that ortolan buntings may not prefer large clear-cuts. The higher occupancy rates and territory abundance of ortolan buntings on larger clear-cuts could exist for two reasons: first, larger clear-cuts may simply have a higher chance probability of occupation, and second, conspecific attraction may partially account for the number of territories on larger clear-cuts. If ortolan buntings showed a real selection for larger clear-cuts, one might also expect territory density to increase with clear-cut size, particularly as larger areas have a higher capacity to support higher densities of birds.

To analyse the significance of clear-cut size on habitat selection in more detail, site selection patterns of individual birds should be studied to see if birds visit/sample multiple clear-cuts of varying sizes, and choose according to size. The size of clear-cuts should also be considered in view of the shape, composition and configuration of clear-cuts within the broader landscape, which may affect colonisation probability of nearby clear-cuts.

Habitat structures: remaining trees and rocks

Ortolan buntings are known to use single large trees, large shrubs, large rocks, electricity wires and other similar features as song posts and perching sites (Kutzenberger 1994; Tryjanowski 2001). My findings highlight the importance of retaining structural elements after harvesting, such as single isolated trees and rocks. I found that the number of individual trees (above two metres tall) per ha positively affected occupancy and abundance of ortolan buntings. I also found that no or few large rocks over 1 m (corresponding to 2-5 on the rockiness index) negatively affected the number of territories. This reinforces studies by Vepsäläinen et al. (2005; 2007) which highlight the importance of large structures in ortolan bunting territories, as they provide song posts to help attract females and conspecifics, as well as create structural diversity and habitat heterogeneity in otherwise open environments.

Vepsäläinen et al. (2005; 2007) found that bush- or tree covered ditches and large rocks were important habitat elements positively affecting the occurrence of ortolan buntings in agricultural environments in southern Finland. More specifically, Vepsäläinen et al (2007) found that removing two kilometres of bush- and tree covered ditches from ortolan bunting farmland habitats contributed to the significant population decline of ortolan buntings in his study area – ortolan buntings declined from 11pairs/km^2 to 1pair/km^2 between 1989 and 1992. Berg (2008) also found that ortolan buntings on farmland in south-central Sweden preferred heterogeneous habitats mixed with patches of taller vegetation and patches of bare soil (see below).

Bare soil and vegetation litter

My observations are consistent with previous findings which show that ortolan buntings, and other ground-foraging insectivorous birds, prefer foraging in habitats with a high proportion of bare soil due to increased prey availability (Vepsäläinen et al. 2005; Berg 2008; Menz et al. 2009b; Schaub et al. 2010; Morelli 2012). For example, studies on ortolan buntings in farmland habitats in Italy (Morelli 2012) and Switzerland (Menz et al. 2009a), and on post-fire habitats in Catalonia (Menz et al. 2009b), found that bare soil was an important variable influencing habitat selection.

Immediately following clear-felling, clear-cuts generally have a high proportion of vegetation litter, including freshly fallen or slightly decomposed organic debris. I found that the percentage of vegetation litter (≥ 10%), negatively affected territory abundance (but not occupancy), which may indicate that freshly felled clear-cuts (prior to soil preparation/scarification) may not be optimal habitats for ortolan buntings, either because (1) vegetation litter could impede movement and reduce available areas for foraging, (2) soil preparation/scarification has not yet occurred, (3) pioneer species such as wavy hairgrass have not yet established, or (4) sites have simply not had enough time to attract individuals via conspecific attraction.

In Sweden, mechanical soil scarification is the most common method of site preparation after clear-cutting, and is practiced in 92% of Sweden's forested areas (Swedish Forest Agency 2013). Soil scarification is intended to increase the survival and growth of seedlings by exposing the mineral soil underneath and increasing soil temperatures (Örlander et al. 1990). However, it is important to emphasize that there are different methods of soil scarification with varying degrees of intensity, e.g. disc trenching and mounding. My study did not distinguish between the methods of soil scarification, but only between the degree of disturbance, i.e. undisturbed (no bare soil), some disturbance (1-5% bare soil), and heavily disturbed (≥ 10% bare soil).

Further, the heavily disturbed category (≥ 10% bare soil) had a maximum bare soil percentage of 20% for occupied sites, and 45% for unoccupied sites. Therefore the ≥ 10% bare soil category should be interpreted with caution to not overemphasize the significance of heavily disturbed clear-cuts. Some site preparation may be favourable to the ortolan buntings, but too much may be unfavourable. Ortolan buntings were present on only 1 of 5 sites with ≥ 20% bare soil, which may indicate that sites that are very heavily disturbed (i.e. ≥ 20% bare soil) may not be optimal, however the sample size was too small to show a statistically significant difference. Further studies would be needed to increase the number of clear-cuts sampled with ≥ 10% bare soil, in order to distinguish any differences between ≥ 10%, and ≥ 20% bare soil.

In contrast to my findings, Lucas (2013) found that ortolan buntings on forest clear-cuts in northern Sweden were more likely to occur on clear-cuts with no or little bare soil. She found ortolan buntings on 35.7% of clear-cuts with 0-5% bare soil, while only 6.9% and 4.2% of clear-cuts with 5-20% and >20% bare soil (respectively) had ortolan buntings present. Fonderflick et al. (2005) also found that bare soil was not a requirement for ortolan bunting presence on a limestone plateau habitat (Causse Mejean) in southern France. These studies suggest that while bare soil may be an important driver of habitat selection, it may not be a requirement. One would expect clear-cuts with a high proportion of bare soil to be first settled, and then abandoned as they become less optimal (i.e. as pioneer species begin to grow and reduce the amount of exposed soil). However, an additional factor, site fidelity, may affect settlement patterns because birds may return to breed in the same site as the previous year(s). This may explain why birds occupied older clear-cuts completely void of soil, even when higher quality habitats might have been available.

Dale et al. (2005) studied the entire ortolan bunting population in Norway and found that younger males had unusually high dispersal rates, but showed higher breeding site fidelity when older. However, site fidelity can differ between populations of the same species (Fuller 2012). The Norwegian population is small and isolated which may explain the high dispersal rates in younger birds (Dale et al. 2005). However, the ortolan bunting population in Sweden is much larger, with greater availability of breeding habitat, and individuals may therefore show less dispersal and higher site fidelity – which could explain why ortolan buntings were still found on clear-cuts with no or little bare soil. This study is however limited to one breeding season, and it is difficult to conclude whether, and to what degree, breeding dispersal and/or site fidelity is an underlying mechanism affecting habitat selection of ortolan buntings in northern Sweden.

Vegetation type

One of the most important findings of this study is the strong influence of vegetation type on both occupancy and the number of territories. In almost all analyses, narrow-leaved grass was the most preferred vegetation type, even when other vegetation types were available. To my knowledge, these findings have established, for the first time, a direct relationship between vegetation type on forest clear-cuts and the suitability of forest clear-cuts as habitat for ortolan buntings.

A temporal settlement pattern could exist whereby ortolan buntings are first attracted to clear-cuts with a high proportion of bare soil (clear-cuts in the early stage of succession), then, as the clear-cuts develops with fast-growing pioneer species, vegetation type rather than bare soil (or a combination of the two) becomes a driving mechanism for habitat selection. Individuals may also choose to remain faithful to regenerating clear-cuts because of site fidelity (see above).

Before clear-felling, the field-layer vegetation typically consists of late-successional dwarf-shrubs such as bilberry (*Vaccinium myrtillus*) in spruce-dominated forests, and crowberry (*Empetrum nigrum*) and lingonberry (*Vaccinium vitis-idaea*) in pine-dominated forests (Arnborg 1990). After clear-cutting, mechanical soil scarification increases mineral nutrient availability and decreases the abundance of late successional dwarf shrubs and increases the abundance of fast-growing, early-successional species like grasses and forbs (Bergstedt & Milberg 2001; Strengbom et al. 2004). Wavy hairgrass (*Deschampsia flexuosa*) is the most dominant and widespread grass species in the northern boreal forest, and increases in abundance with increased intensity of soil preparation and increased light (Bergstedt & Milberg 2001; Strengbom et al. 2004).

Narrow-leaved grass vegetation types included sites with more than 25% of the narrow-leaved grass species, but could also have a high percentage (i.e. up to 75%) of species from other vegetation types such as bilberry and lingonberry. Individual species composition differed among narrow-leaved grass sites, but in all sites the most common species was the perennial wavy hairgrass, and to a lesser extent, fireweed

(*Epilobium angustifolium L.*, also known as *Chamerion angustifolium L.)* and raspberry (*Rubus idaeus L.*). In addition, other common plants include mosses, sedges (*Carex pilulifera*), *Melica nutans*, and patches of herbs such as lily of the valley (*Convallaria majalis*) and arctic starflower (*Trientalis europaea*).

Narrow-leaved grass vegetation types typically occur on dry and mesic areas and indicate fertile soils (Hägglund & Lundmark 1984). Narrow-leaved grass vegetation types are probably richer in invertebrates than those vegetation types found on nutrient-poor soils, i.e. vegetation types characterised by dwarf shrubs such as heather (*Calluna vulgaris*) and crowberry (*Emptrum nigram L.*). Clear-cuts with narrow-leaved grass vegetation type may in turn have a higher abundance and accessibility of prey, which may explain why ortolan buntings did not need nearby farmland for foraging – this is supported by behavioural observations in the field, where birds were seen foraging in the clear-cuts, even when nearby farmland was available.

Distance to nearby farmland

Similar to studies by Ottvall et al (2008), my study shows that proximity to farmland did not influence ortolan bunting presence or abundance on forest clear-cuts in northern Sweden. In all analyses neither distance to farmland nor size of farmland (≥ 1 ha, ≥ 10 ha) had an effect on occupancy or abundance of ortolan buntings on clear-cuts. 42% of occupied clear-cuts were found more than one kilometre from the closest farmland. Ottvall et al (2008) found that over half of the occupied clear-cuts in northern Sweden (55%) had no adjacent farmland, and the density of ortolan buntings was higher in clear-cuts without nearby farmland.

My findings are also consistent with both Lucas (2013) and Gustafsson (2014) who found no effect of nearby farmland on occupancy of clear-cuts in northern Sweden. While my study does not distinguish between active and abandoned farmland, Gustafsson (2014) only included active farmland into his analysis, and still found that nearby farmland did not affect ortolan bunting occupancy. However, his results should be interpreted with caution, as his sample size was very small (N = 6).

These findings suggest that outside of farmland habitat, forest clear-cuts may provide both suitable nesting and foraging habitat for ortolan buntings. This in turn could correspond with the richer vegetation type found in Swedish ortolan bunting habitats, meaning that nearby farmland is not needed for foraging. Although nearby farmland may not be a requirement, it may still be used for opportunistic feeding as some birds were seen leaving the clear-cut in the direction of nearby farmland (pers. obs) (see below for comparison with Norwegian sites where nearby farmland seems to be necessary).

Regeneration age and regrowth

This study found no evidence that regeneration age or regrowth density affected occupancy or abundance of ortolan buntings on clear-cuts. Site fidelity may partially account for this, as individuals may be reluctant to move even though regrowth may change the habitat of the territory over time. The range of clear-cut ages sampled was also relatively narrow (maximum regeneration age of 10 years), and Stolt (1992) states that most ortolan buntings in Västerbotten County are found on clear-cuts between 3-10 years old, which means my entire sample is within the suitable age range for ortolan buntings.

If my study expanded to include clear-cuts older than 10 years (i.e. young forests), one would probably expect to find a negative effect of age, as ortolan buntings are known to prefer sparsely vegetated areas (Cramp & Perrins 1994). Sirami et al. (2007) studied songbird occurrences and changes in vegetation cover/density in the Mediterranean over a 25-year period and found that as grasslands changed to woodland habitat, five open-habitat bird species (including the ortolan bunting) decreased significantly.

This study also excluded clear-cuts with more than 50% regrowth (i.e. regrowth in the bush layer), and sites with the most regrowth (≥ 10% regrowth) still had many open patches with low vegetation. If sites with more than 50% regrowth were included into the study, then one might expect to find a negative effect of regrowth, similar to age. For example, Deutsch and Südbeck (2009) compared vegetation height and density of winter rye in farmland habitat in Lower Saxony, Germany, and found that permanent ortolan bunting territories (where a male was detected at least three times near or on the same singing post) had significantly shorter and less dense crops (i.e. 50% ground cover) compared to temporary territories (where a male was detected only once), which had 60% ground cover.

4.2. Differences between Norwegian and Swedish clear-cuts

The most important differences between the Norwegian and Swedish ortolan bunting clear-cut habitats are between vegetation types, soil types, and proximity to farmland. While ortolan buntings in northern Sweden are found on biologically productive sites, predominately characterised by narrow-leaved grass vegetation with moraine soils, Norwegian ortolan bunting habitats are found on low productivity sites, characterised by lingonberry, heather and *Cladonia* lichens with either sandy or peat soils.

The Norwegian habitats are suitable for breeding, but they are generally poor foraging habitats with low insect and seed abundance. Previous studies have shown that ortolan buntings in Norway have spatially segregated nesting and foraging habitats (Dale 2000). Ortolan buntings on forest clear-cuts (S. Dale, personal communication 2014), raised peat bogs (Dale 2000), and the Starmoen forest burn in Elverum (Dale & Olsen 2002) use nearby farmland such as oat fields for seed foraging early in the season, and insect foraging later in the season.

The current habitats in Norway and northern Sweden each represent a different kind of habitat to the former traditional farmland habitat that was once common for ortolan buntings (Dale & Christiansen 2010). This variability appears to reflect the species flexibility in habitat selection as a response to current and historical landscape changes, such as changes in agricultural practices in Norway and abandoned farmland in northern Sweden reverting to forest. Studies by Dale and Christiansen (2010) on ortolan buntings in Norway found that 86% of males changed their habitat at least once during their lifetime, which provides some indications of the species flexibility regarding habitat choice and specific vegetation types. Given that Norwegian ortolan buntings show flexibility to some degree, they seem to be fixed in the need for nearby farmland, as ortolan buntings in Norway have not been found using richer clear-cuts, which would probably remove the need for nearby farmland (S. Dale, personal communication 2014). However, richer clear-cuts in Norway appear to regrow at a much faster rate than the rich clear-cuts in Sweden (S. Dale, personal communication 2014), which is probably related to regional variation in climate, soil and vegetation.

4.3. Management recommendations

Identifying the specific habitat variables influencing habitat selection of ortolan buntings on forest clear-cuts gives forestry managers the opportunity to play a distinct role in promoting the conservation of ortolan buntings in northern Sweden. Post-harvest conditions create a mosaic of microhabitats and successional stages that may resemble traditional farmland habitat, and studies have shown that clear-cuts may also benefit other early-successional or farmland bird species (Brawn et al. 2001; Swanson et al. 2011). However, it is important to keep in mind that clear-cuts are transitional, short-lived habitats that develop into young forests within 5-10 years and are therefore only suitable for a limited time (Stolt 1993; Ottvall et al. 2008).

The results of this study show the positive relationship between clear-cut size and ortolan bunting presence and abundance. However large clear-cuts represent a major disturbance to the local landscape – causing habitat fragmentation and loss of connectivity to forest-interior species. Clear-cuts of varying sizes affect the avian community in different ways, and conservation strategies should also focus on maintaining large tracts of contiguous mature forest (Nilsson et al. 2001). How open-habitat and forest-interior birds respond to clear-cuts of varying sizes and configurations is complex. However, since territory density decreased with size, large clearcuts may not be essential, although most ortolan buntings were found on clear-cuts larger than 10 ha, and a minimum clear-cut size should be considered to maintain viable populations.

This study also shows the importance of single isolated trees on clear-cuts, particularly because ortolan buntings tend to breed in groups. The practice of leaving retention trees after clear-felling to benefit biodiversity and sustain ecological functions was introduced in Sweden in the 1970s and is required under current legislation, i.e. the Swedish Forestry Act (Gustafsson et al. 2012; Kruys et al. 2013). The average number of live retention trees on clear-cuts in Sweden is 7 per ha, although a minimum of 10 per ha is required to meet forest certification standards within the FSC (Swedish Forest Stewardship Council) and PEFC (Programme for Endorsement of Forest Certification), of which 70% of Sweden's forested land is certified under (Swedish Forest Agency 2013). Forestry practices should therefore continue to promote tree retention policies as they provide song posts and sources of food for ortolan buntings.

Ortolan buntings also preferred clear-cuts with a high proportion of exposed bare soil. Disturbances from mechanical soil scarification may also create suitable habitats for species that previously benefited from fire-disturbed habitats (Granström 2001). However, while soil scarification increases nutrient turnover rates and enhances growth and survival of seedlings, it also effects the future productivity of the forest (Örlander et al. 1996; Bergstedt & Milberg 2001). For example, soil scarification compacts the mineral soil and reduces nutrient levels and soil carbon in the long term (Örlander et al. 1996). These results raise some important questions about the association between the intensity and frequency of soil scarification and ortolan bunting populations.

After logging, different post-harvest regeneration strategies may affect later successional processes and affect the long-tem suitability of the clear-cut for ortolan buntings. Natural regeneration of clear-cuts may keep sites open for longer, but does not require soil scarification, which means that sites may be less attractive as exposed bare soil disappears. Planting of seedlings does require prior site preparation, however rapid growth of seedlings may reduce the suitability of the clear-cut. Post-harvest regeneration practices could extend the suitability of clear-cuts by letting clear-cuts regenerate for a few years (scars after felling may initially provide enough exposed soil), and then rejuvenate the soil with late soil preparation and planting.

Previous studies have shown that burnt areas and post-fire habitats are attractive to ortolan buntings (Dale & Hagen 1997; Dale & Olsen 2002; Menz et al. 2009b). In Sweden, prescribed burning is not required under the Swedish Forestry Act regulations, but FSC-certification requires prescribed burning on at least 5% of the annual clear-cut area on dry-mesic land (although this area can be adjusted based on the type of burning) (FSC Sweden 2013). Although, Lucas (2013) did not find ortolan buntings on burnt clear-cuts in northern Sweden, prescribed-burning does increase variation in the landscape, and many fire-adapted species including birds and rare and threatened insect species benefit from prescribed burning and burnt trees (Granström 2001; Nilsson et al. 2001).

Ultimately, a variety of forest policies and practices that support broader ecosystem-based philosophies may be needed to support viable populations of ortolan buntings and maintain species diversity across Sweden's forested landscape. Current practices should continue to recognise the importance of early-successional forest ecosystems, and any practices that maintain structural diversity and heterogeneity should therefore be encouraged. Although clear-cuts are temporary habitats, new clear-cuts are created at the same time as older clear-cuts become overgrown.

5. FUTURE RESEARCH AND CONCLUSIONS

The major limitations of this study are that sampling occurred over one breeding season and each clear-cut was only visited once (except for a few cases when I did follow-up visits for behavioural observations). However territory settlement decisions are not static and strategies for habitat selection depend on both suitability and availability of habitat (Rodenhouse et al. 1997). High-quality habitats tend to be occupied before low-quality habitats and individuals may change territory sites over time – individuals may first settle in sub-optimal habitat, and then disperse to higher-quality habitat as they become available or based on environmental or conspecific cues (Rodenhouse et al. 1997; Betts et al. 2008).

Studies conducted over multiple years, with colour-ringed individuals, could identify dispersal patterns both within and between breeding seasons and detect movements toward higher-quality habitats. In addition, long-term studies could identify whether site fidelity was higher in individuals initially breeding in high-quality habitats compared to low-quality habitats, and determine whether site fidelity was higher in older male ortolan buntings, as found in Norway. Information on dispersal and site fidelity patterns may also play a vital role in understanding the overall metapopulation dynamics of the species and identify potential source populations.

Ortolan buntings on forest clear-cuts in northern Sweden may constitute a stronghold for the species and provide net contributors to the greater metapopulation, as the general pattern of decline across Europe points to a gradual contraction toward core areas, with more severe declines occurring in peripheral and edge populations. An understanding of metapopulation dynamics may contribute to the long-term persistence of the species through recolonisation or reestablishment of locally extinct or declining subpopulations. Furthermore, while presence-absence and abundance data are important indicators of habitat use, future research could also record breeding success to determine how habitat affects productivity.

In the case of ortolan buntings in Norway, the population has likely decreased below a critical population size, and despite high survival rates of adult males, the population continues to decline (Dale 2001). The skewed sex ratio and female-biased natal dispersal limits population growth, and extinction is almost inevitable (Steifetten & Dale 2006). Hence, conservation efforts are best allocated to larger remaining populations such as those in northern Sweden. This further highlights the importance of continued research efforts into the ecology of ortolan buntings in Europe.

The present study has showed that clear-cut size, the number of remaining trees per ha, bare soil percentage (≥10%), and narrow-leaved grass vegetation have a significant positive influence on ortolan bunting occupancy and the number of territories on forest clear-cuts in northern Sweden. Vegetation litter and few large rocks also have a negative influence on the number of territories. Further, unlike ortolan buntings breeding on forest clear-cuts in Norway, proximity to farmland did not affect occupancy or abundance of ortolan buntings on clear-cuts in northern Sweden. These results, combined with behavioural observations in the field, show that clear-cuts in northern Sweden provide both suitable nesting and foraging habitats.

To conclude, this study has provided detailed knowledge about habitat selection of ortolan buntings in northern Sweden, and thus provides a baseline for developing optimal forestry practices directed at improving productivity and population size in this key area for the survival of ortolan buntings in Scandinavia.

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APPENDICES

Appendix 1 – Coordinates of clear-cuts sampled in Västerbotten County, Sweden.

Site	Latitude	Longitude	No. of territories
1	63.889427	20.040409	0
2	63.970758	20.031412	0
3	63.889016	20.746744	0
4	63.880564	20.746733	2
5	63.963577	20.687370	1
6	63.968186	20.685272	0
7	64.013042	19.928708	0
8	64.015567	19.929533	0
9	64.064474	19.936075	4
10	64.104092	19.984604	1
11	64.005459	20.229824	2
12	64.009227	20.206204	3
13	64.054404	20.163500	3
14	63.996066	20.239473	1
15	63.996235	20.243559	3-4
16	64.118933	20.556620	4
17	64.098409	20.525270	0
18	64.109164	20.483770	0
19	64.112416	20.483262	0
20	64.097321	20.554605	0
21	64.264948	20.376381	1
22	64.252778	20.317229	1
23	64.244133	20.326135	1
24	64.250990	20.329053	2
25	64.251003	20.328566	0
26	63.883302	20.355207	0
27	63.946876	20.307444	0
28	64.013652	20.415941	0
29	64.337508	20.328535	0
30	64.339869	20.326385	0
31	64.339138	20.331739	1
32	64.343992	20.343825	2
33	64.343825	20.352728	3
34	64.346227	20.352421	0
35	64.346141	20.346143	0
36	64.070134	19.969209	0
37	64.081035	19.987662	0

Site	**Latitude**	**Longitude**	**No. of territories**
38	64.095961	20.050249	0
39	64.156617	20.029761	0
40	64.167258	20.847285	0
41	64.110757	20.660096	2
42	64.118406	20.639361	0
43	64.013312	19.872185	0
44	64.043757	19.818702	1
45	64.043039	19.819440	0
46	64.043742	19.815708	0
47	63.939642	20.526845	1
48	64.018118	20.505240	0
49	64.073253	20.075475	0
50	64.082873	20.101341	0
51	64.094350	20.114545	0
52	64.131218	20.202566	0
53	64.254754	20.167542	4
54	64.257667	20.159252	1
55	64.218545	19.774138	2
56	64.168378	19.762286	0
57	64.004753	20.195625	0
58	64.036648	20.234504	0
59	64.221023	20.766811	0
60	64.222009	20.761416	0
61	64.291444	20.650250	0
62	64.323690	20.630599	1
63	64.323146	20.622714	3
64	64.005914	20.448648	1
65	63.999994	20.434043	0
66	63.979842	20.421615	3
67	64.366935	20.370795	0
68	64.365979	20.376892	0
69	64.352991	20.369018	0
70	64.368306	20.343117	1-2
71	64.367225	20.341027	1
72	64.367083	20.340300	1
73	64.102120	19.746416	1-2
74	64.101990	19.752019	1
75	64.145797	19.783959	3-4
76	63.957379	20.505701	0
77	63.961351	20.496845	0
78	63.956002	20.501311	1

Site	Latitude	Longitude	No. of territories
79	63.955281	20.501708	2-3
80	63.976787	20.729178	0
81	63.975700	20.727200	0
82	63.972623	20.730142	0
83	63.964034	20.718381	0
84	64.055535	20.869839	0
85	64.367781	20.409469	0
86	64.402169	20.379499	2
87	64.401604	20.375172	0
88	64.403024	20.357959	0
89	64.394746	20.299868	1
90	64.002460	19.593645	0
91	64.005981	19.590155	0
92	64.059320	19.591641	2
93	64.058055	19.592183	0
94	64.053734	19.599437	0
95	64.093647	20.038902	1
96	64.094185	20.034820	0
97	64.183324	19.904471	0
98	64.191446	19.898096	0
99	64.204052	19.846900	0
100	64.210757	19.843309	0
101	63.911219	19.997985	0
102	63.929091	20.550893	0
103	63.942487	20.538314	3
104	63.944447	20.541263	0
105	63.946503	20.533249	2
106	63.949525	20.579201	1
107	63.947767	20.575201	2
108	63.947087	20.577463	1-2
109	63.945929	20.570666	0
110	63.963739	20.667908	3
111	63.908964	20.440360	0
112	64.160392	20.794984	0
113	64.231094	20.788165	0
114	64.213655	20.878282	4
115	64.236127	20.565832	0
116	64.233711	20.679261	0
117	64.296215	20.735796	0
118	64.313030	20.806602	3
119	64.311787	20.808829	0

Site	Latitude	Longitude	No. of territories
120	64.368188	20.732550	0
121	63.994500	19.924318	0
122	64.083682	19.812988	3-4
123	64.110035	19.768171	0

Appendix 2 – Table A1 and A2

Table A1: Standard least-squares linear regression (effect tests) of habitat variables influencing the number of territories on clear-cuts model with distance to nearest farmland ≥ 10 ha) (presence-absence model, N = 109, $R^2 = 0.36$). Significant variables ($P < 0.05$) are indicated in bold.

Variables	**df**	**F-ratio**	***P***
Vegetation type	3	2.48	0.07
Regeneration age	1	0.02	0.88
Size	1	35.17	**<0.0001**
Remaining trees	1	18.09	**<0.0001**
Regrowth	2	0.02	0.98
Bare soil	2	2.58	0.08
Vegetation litter	2	2.21	0.12
Distance to farmland ≥ 10 ha	1	0.33	0.57
Rockiness	2	1.91	0.15
Aspect	1	0.79	0.38

Table A2: Standard least-squares linear regression (effect tests) of habitat variables influencing the number of territories on clear-cuts model with distance to nearest farmland ≥ 10 ha) (presence-only model, N = 46, $R^2 = 0.47$). Significant variables ($P < 0.05$) are indicated in bold.

Variables	**df**	**F-ratio**	***P***
Vegetation type	2	2.02	0.15
Regeneration age	1	0.17	0.69
Size	1	13.20	**<0.001**
Remaining trees	1	5.11	**<0.031**
Regrowth	2	0.27	0.77
Bare soil	2	1.33	0.28
Vegetation litter	2	0.24	0.79
Distance to farmland ≥ 1 ha	1	0.02	0.90
Rockiness	2	2.86	0.07
Aspect	1	0.33	0.57

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