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Farmland birds occupying forest clear-cuts respond to both local and landscape features

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ABSTRACT

Agricultural landscapes have changed fast in Europe, which has led to steep declines in farmland biodiversity. While this has differentially impacted "farmland species", some of these seem to be able to use alternative man-made open habitats in forests, such as forest clear-cuts and powerline rights-of-way. We investigated the use of clear-cuts by two historically declining farmland birds, the Yellowhammer (*Emberiza citrinella*) and the Red-backed Shrike (*Lanius collurio*), to determine both local and landscape habitat characteristics of clear-cuts used for breeding. Among 101 clear-cuts visited in Scania, southern Sweden, 27% were occupied by Yellowhammers and 12% by Red-backed Shrikes. Yellowhammer occurrence in clear-cuts was positively related to local spruce cover (the planted tree species). There was also an interaction between clear-cut size and the proportion of farmland in the landscape, such that the positive effect of the proportion of farmland nearby was stronger for larger clear-cuts. Red-backed Shrike occurrence was positively related to clear-cut size and the local presence of piles of forest residues (tops and branches). The relation between occurrence and the proportion of clear-cuts in the landscape was positive for small clear-cuts and negative for larger ones. Yellowhammers and Red-backed shrikes are affected by both the local habitat structure in the clearcut and on the composition of the surrounding landscape, most likely because they use the clear-cut for nesting and the surroundings as complementary feeding habitat. To what extent clear-cuts as complementary breeding habitat to farmland may contribute to the conservation of Yellowhammers and Red-backed shrikes, as well as other farmland birds, is a promising path for future investigations.

1. Introduction

Agricultural intensification in Europe has led to major and rapid declines in biodiversity and is predicted to lead to further decreases in biodiversity and ecosystem quality, both in cropland and grassland (IPBES, 2018). Birds may be the taxon for which these changes have been best described. The average decline of common farmland bird species across Europe between 1980 and 2017 was estimated to be 57%, compared to a 14% decline for all common European bird species together, and the loss of farmland birds has continued to the present day (PECBMS, 2019). To mitigate this biodiversity loss, conservation efforts are made by implementing programs in which farmers receive financial benefits for adapting their farms to environmental goals called agri-environment schemes (Bright et al., 2015; Żmihorski et al., 2016b), albeit not with sufficient success to reverse trends (Pe'er et al., 2014).

In the past decades, some 'farmland' species have been reported to breed in forest clear-cuts (Paquet et al., 2006; Ram et al., 2020; Söderström and Karlsson, 2011; Stjernman et al., 2013; Żmihorski et al., 2016a). Clear-cutting, i.e. the simultaneous felling of all trees in an area, is the predominant forestry practice in many forest-dominated countries. In Sweden, the average clear-cut size is 4.3 ha (Christiansen and Stridsman, 2014). During a time-window of 5–10 years after the

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removal of the old trees until the re-planted trees form a new young forest, clear-cuts may be attractive to farmland birds by offering a combination of open ground and shrubby vegetation similar to habitat often found in e.g. semi-natural grasslands (Berg, 2002; Fuller et al., 2004; Söderström, 2009). Whether clear-cuts can fully replace farmland as suitable breeding habitat for some of the declining farmland bird species remains to be investigated.

The are several studies describing the composition of bird communities in clear-cuts and young tree plantations (e.g. Gailly et al., 2017; Hansson, 1983; Lindbladh et al., 2017; Ram et al., 2020; Żmihorski et al., 2016a). However, detailed knowledge about the habitat usage of individual species in clear-cuts is still lacking. While birds should be expected to favor specific clear-cut morphologies, landscape context may also play a big role (Caplat and Fonderflick, 2009; Mazerolle and Villard, 1999; Opdam, 1991; Tischendorf et al., 2005). The influence of landscape configuration should be particularly important for organisms such as birds, that can only use them during a short window of opportunity since they need to colonize the clear-cuts from more permanent habitats in e.g. farmland. Hence, we expect clear-cuts near farmland to be more often occupied than those farther away. Detailed knowledge about habitat preferences and the influence of landscape configuration would be critical for informing clear-cut management for conserving farmland birds.

In Sweden, patterns of farmland bird declines have been similar to the rest of Europe (Green et al., 2019; Wretenberg et al., 2007, 2006). In Sweden farmland occupies a low proportion of total land (7–8%) and is mainly concentrated to the south of the country, where it sometimes occurs in a mosaic landscape of forest and farmland. Most of Sweden is covered by forests that are actively managed for wood production (58% of the land area, Nilsson and Cory, 2017), where clear-cutting since the 1940 s has been the most common management practice. Since embedded farmland in much of the forested landscape has been subject to agricultural abandonment, not least semi-natural grasslands (Wretenberg et al., 2006), clear-cuts may contribute to maintaining the mosaic structure of these landscapes.

Yellowhammer (*Emberiza citrinella*) and Red-backed Shrike (*Lanius collurio*) are two “farmland bird species” that have been reported to breed in clear-cuts (Söderström, 2009; Stjernman et al., 2013; Żmihorski et al., 2016a). Both species are traditionally described as associated with semi-natural grasslands and small crop fields (Svensson et al., 1999; Yosef et al., 2014). Hence, the loss of small-scale agriculture and semi-natural grasslands has been suggested as a possible cause for the decline of these species across Europe (IPBES, 2018). It has actually been proposed that significant proportions of the Swedish Red-backed Shrike and Yellowhammer populations nowadays breed outside farmland (63% and 34%, respectively, Stjernman et al., 2013), and the reproductive success of Red-backed Shrike in Sweden has even been found to be higher in clear-cuts than in farmland (Söderström and Karlsson, 2011).

We studied which features underlie the usage of clear-cuts as habitat by Red-backed Shrike and Yellowhammer in a mosaic landscape of farmland and production forests. We hypothesized that habitat usage is determined by a combination of local habitat structure, habitat size, and landscape composition. We predicted (1) that the local presence of shrubby vegetation is positively associated with the presence of both species, by providing nest sites and foraging perch sites. Additionally, (2) we expected that the availability of open ground (areas with no to little vegetation, where cover is characterized by gravel, dirt, or sand) and thorny shrubs in clear-cuts would positively affect Red-backed Shrike occurrence by providing both hunting and nesting opportunities. Finally, (3) we predicted that the abundance of both species would decrease with increasing distance from the nearest farmland. This would be consistent with the hypothesis that the two species only colonize ephemeral habitats like clear-cuts from more permanent farmland.

2. Methods

2.1. Study species

2.1.1. Yellowhammer

The Yellowhammer is a widely distributed bunting (Emberizidae) that occurs in most of Europe and parts of Asia (Copete, 2016). It occurs in most of Sweden and is mainly resident (Ottosson et al., 2012; Svensson et al., 1999), but is regarded as Vulnerable in the red-list because of its strong population decline (Westling, 2015). Yellowhammers are attracted to linear elements such as hedgerows, ditches, and herbaceous vegetation in agricultural landscapes with forest or small forest patches (Svensson et al., 1999; Von Haartman, 1969). Yellowhammers feed mostly on seeds and grains year-round, while insects are important in the breeding season. Breeding in southern Sweden commences from the first week of May (Bradbury et al., 2000). Nests are built by the female in shrubs or on the ground below shrubs (Copete, 2016; Von Haartman, 1969).

2.1.2. Red-backed Shrike

The Red-backed Shrike is a migrating shrike (Laniidae) that breeds throughout most of Europe and parts of Asia and winters in East and South Africa (Yosef et al., 2014). Although it was red-listed in Sweden up to 2005 (Tjernberg and Svensson, 2007), the current conservation status is Least concern, both in Sweden and internationally (BirdLife International, 2017; Westling, 2015). Red-backed Shrikes use semi-open areas with scattered shrubs and low trees (1–3 m), as well as agricultural areas with patches overgrown by shrubs and hedgerows (Svensson et al., 1999; Von Haartman, 1969; Yosef et al., 2014). The diet includes large insects, as well as small mammals, birds, and reptiles (Yosef et al., 2014). Red-backed Shrikes arrive in Sweden between mid-May and early June and initiate breeding one to two weeks after arrival (Söderström and Karlsson, 2011). The nest is built in thorny shrubs such as bramble or hawthorn (Von Haartman, 1969; Yosef et al., 2014).

2.2. Study area

We surveyed clear-cuts in the municipality of Höör, central Scania in southernmost Sweden (56°03′N, 13°51′E, Fig. 1). The extent of the overall study area was 5620 ha, almost exclusively consisting of forest (4130 ha, 79%) and agriculture (1050 ha, 20%), while the remaining 1% mainly consisted of built-up areas and water bodies (Ahlkrona et al., 2018). The agricultural areas consisted of a mixture of semi-natural pastures, improved grasslands, and cropland. The forest in the area was a mosaic of small even-aged stands (0.1–25 ha) of Norway spruce (*Picea abies*) and clear-cuts (278 registered in 2007–2018, Swedish Forest Agency, 2018). The area was selected because of the combination of agriculture with semi-natural pastures and forest with clear-cuts providing both of the most commonly used habitats for these species.

2.3. Site selection

Publicly available shapefile data of all clear-cuts were retrieved from the Swedish Forest Agency’s data portal (Swedish Forest Agency, 2018). This and all other geographical data used in the study was handled in QGIS 3.2 (QGIS Development Team, 2018). All clear-cuts in the study area that were cut between January 1st, 2013, and May 27th, 2017 (the youngest at the time of selection) were selected for surveying ($n = 110$). These dates were chosen based on exploratory visits to the area, where it was observed that many clear-cuts up to approximately five years of age visually resembled the open or shrubland habitats found in agricultural landscapes. Nine clear-cuts could not be reached or could not be found in the field, resulting in a total of 101 visited clear-cuts (mean size ± SD: 1.9 ± 1.7 ha, Fig. 1).

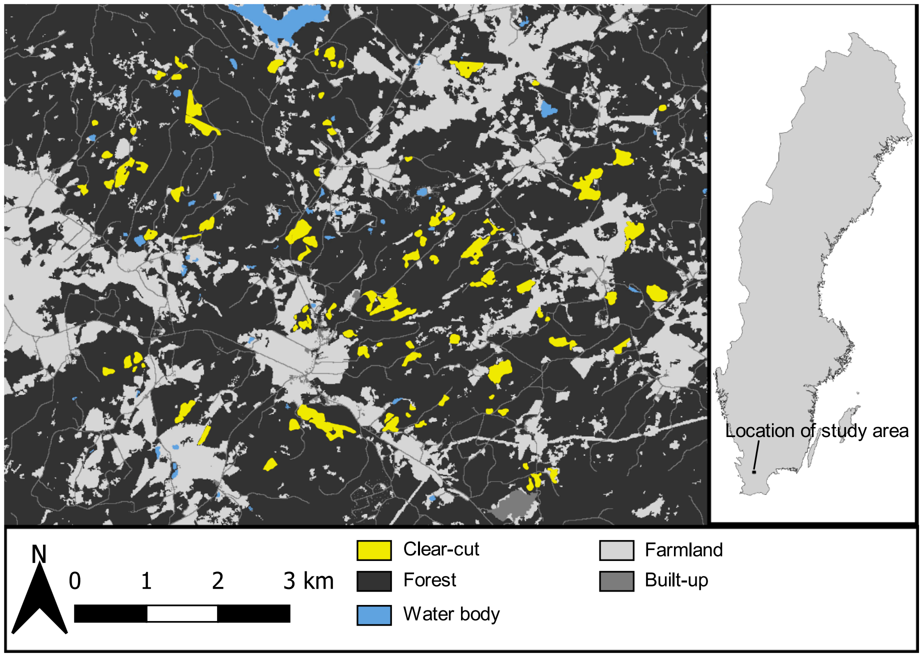

Fig. 1. Distribution of the 101 clear-cuts in the area. The land cover data were extracted from the Swedish national land cover data (Ahlkrona et al., 2018). The farmland category also includes open land with vegetation not used for farming. The built-up category also includes roads.

2.4. Survey

Fieldwork was carried out by a single surveyor (TB) during 18 days between the 15th of May and the 5th of June 2018. Prior to the fieldwork a careful selection of variables was made that describe the structural composition of the habitat relevant to the ecology of both species and field protocols were established. All observations were made between 05:00 am and 10:00 am under dry weather conditions. At each location, the observation started with a five-minute point count from the edge of the location. After the point count, a transect across the location was walked in such a way that the whole location was visually inspected for both species. We made sure that the relative effort per clear-cut was equal and that surveying effort was very high everywhere. Red-backed Shrikes and Yellowhammers were counted based on sight and hearing. Only observations of males were used in the analysis, as (1) it avoids overestimation of the number of breeding pairs, and (2) they are more conspicuous: males of both species sing, and are visually more striking than females, making them easier to observe. Both species are easily detected, Yellowhammers have a distinct and frequently sung song and a distinct plumage, while Red-backed shrikes have an unmistakable shape and plumage compared to other Swedish species. Males of both species perch on top of vegetation and are therefore easily spotted in this environment.

2.5. Environmental variables

2.5.1. Site description

In the first years after felling, clear-cuts vary highly in their morphology. Clear-cuts can be characterized by the presence of heaps of cutting remains (e.g., tops and branches), the growth of different types of vegetation (e.g., grass, birch, or raspberry shrubs, or planted saplings), or the absence of any vegetation or structure (bare ground). Clear-cut morphology depends mainly on management decisions by the forest owner or the contractor responsible for cutting the forest. On each location, we estimated the relative cover of different types of vegetation. The percentage cover of each category was recorded in such a way that the sum of all categories was 100%. Although this method does not take multiple vegetation layers into account, it gives a good estimate of vegetation composition and dominant vegetation types on a clear-cut. The categories were based on the vegetation types encountered during exploratory visits: grass (for all grass and herbaceous vegetation $<$ 1 m tall), spruce (up to 2 m), birch (up to 2 m), raspberry (for all raspberry and blackberry shrubs), shrubs (for all shrubs other than low birch, raspberry, and blackberry), branches (for heaps of branches and tops $\geq$ 0.5 m tall), bare (for bare ground and litter), and stones (for stones $\geq$ 0.3 m $\varnothing$ or heaps of stones). In addition, we recorded whether retention trees or standing deadwood ($>$ 2 m) were present at the location. Finally, mean vegetation height was estimated, rounded up to the nearest 10 cm for heights below 0.5 m, and to the nearest 0.5 m for heights above 0.5 m.

2.5.2. Landscape variables

For each clear-cut, we determined its size, the distance to the nearest clear-cut (the distance between the edges of the location and the nearest clear-cut) and the distance to the nearest farmland patch $>$ 10 ha (the distance between the edges of the location and the nearest patch of farmland). The 10 ha size requirement was chosen as our interest was in the effect of distance of clear-cuts to farmland-dominated areas in the landscape. The landcover data (Ahlkrona et al., 2018) included tiny patches of farmland throughout the forest that would homogenize the distance variable if these were not excluded. The proportion of farmland and clear-cuts in a 250 m buffer around each clear-cut was calculated from the same datasets as the distances. These proportions were calculated to represent the landscape composition around the locations. The buffer distance was similar to known foraging ranges and territory sizes from both species (Söderström, 2001; Stoate et al., 1998; Whittingham et al., 2005). An overview of all collected variables is presented in Table 1.

2.6. Statistical analysis

The analysis was done in R version 3.6.1 (R Core Team, 2018). Since the recorded bird abundances were low (ranging from 0 to 4 per clear-cut, with 15 out of 27 clear-cuts occupied by Yellowhammer and 8 out of 12 clear-cuts occupied by Red-backed Shrike being occupied by only one male individual of the respective species), we converted abundances to presence-absence data. All explanatory variables were standardized according to Gelman (2008). Logistic regression models

Table 1
Description of all the variables used in the analysis.

Variable	Description	Unit
Clear-cut size	Size of the harvested area derived from the felling map	ha
Herbaceous vegetation cover	The relative percentage of clear-cut covered by grasses and other herbaceous vegetation	%
Spruce cover	The relative percentage of clear-cut covered by young spruce (≤2m tall)	%
Birch cover	The relative percentage of clear-cut covered by young birch (≤2m tall)	%
Raspberry cover	The relative percentage of clear-cut covered by raspberry and (occasional) blackberry	%
Shrub cover	The relative percentage of clear-cut covered by shrubby vegetation (≤2m tall) other than the aforementioned categories	%
Cover by branches	The relative percentage of clear-cut covered by heaps of branches or dead wood ≥ 0.5 m tall	%
Bare ground	The relative percentage of clear-cut with little to no vegetation, characterized by open gravel, dirt or sand	%
Cover by stones	The relative percentage of clear-cut covered by stones (≥0.3 m ∅ or heaps of stones).	%
Retention trees	Presence of retention trees (> 2m)	Binary
Standing deadwood	Presence of standing deadwood (> 2m)	Binary
Mean vegetation height	Estimated mean vegetation height, rounded up to the nearest 10 cm for heights below 0.5 m, and to the nearest 0.5 m for heights above 0.5 m	m
Distance to nearest clear-cut	Distance between the edge of the focal clear-cut and the nearest other clear-cut.	m
Distance to nearest farmland	Distance between the edge of the focal clear-cut and the nearest farmland patch > 10 ha.	m
Proportion of clear-cuts in 250 m buffer	The proportion of clear-cut area in a 250 m fixed-width buffer around the edge of the focal clear-cut.	–
Proportion of farmland in 250 m buffer	The proportion of farmland area in a 250 m fixed-width buffer around the edge of the focal clear-cut.	–

predicting occurrence were selected using AIC-based model selection using the dredge function from the MuMIn package (Barton, 2018). The full model (from which all combinations of variables are tested), included all measured variables (see Table 1), except for stones to prevent sum-to-one collinearities amongst the cover variables. In addition to the separate variables, we also included the interactions between (1) clear-cut area and proportions of farmland and clear-cuts in a 250 m buffer, and (2) between clear-cut area and distance to the nearest clear-cut and the nearest farmland, to account for interactions between habitat amount and landscape composition. After the model selection table consisting of the models with all possible combinations of predictor variables was created, the models with ΔAIC ≤ 2 were selected. Overly complex models were removed from sets of nested models because the extra explanatory variables did not add considerable explanatory power compared to the least complex one according to Richards (2008). In this approach, models are considered to be nested in another if they only contain part of the explanatory variables of a more complex model and no other variables. The remaining models were interpreted.

3. Results

In total, 44 male Yellowhammers were observed and 27% (27 out of 101) of the clear-cuts were occupied by one or more Yellowhammers. On 15 of these clear-cuts one Yellowhammer was observed, on 8 clear-cuts two Yellowhammers, on 3 clear-cuts three Yellowhammers, and on 1 clear-cut four Yellowhammers. In addition, 18 male Red-backed Shrikes were found on 12% (12 out of 101) of the clear-cuts. On 8 of these clear-cuts one Red-backed Shrike was observed, on 2 clear-cuts two Red-backed shrikes, and on two clear-cuts three Red-backed Shrikes. Both of the species were observed together on six of the clear-cuts (6%). This was 50% of the clear-cuts that Red-backed Shrikes occurred on (or 22% of the clear-cuts occupied by Yellowhammers). The percentage of occupied clear-cuts per cutting year varied between 8% (2016) and 48% (2013) for Yellowhammer and between 0% (2017) and 15% (2016) for the Red-backed Shrike. The distribution of the predictor variables for the occupied and unoccupied plots are shown in Fig. 2 and Fig. 3.

3.1. Yellowhammer occurrence

Three models had a ΔAIC ≤ 2.0 and were the least complex of sets of nested models (Table 2). Tjur's R^2 of the three models ranged between 0.21 and 0.24 (Table 2). Yellowhammer occurrence was most importantly positively related to the clear-cut size and spruce cover (Table 2) in all models. Also, Yellowhammer occurrence was negatively related to the proportion of bare ground in two of the models. Similarly important was the interaction between the proportion of farmland and clear-cut size in which the positive effect of the proportion of farmland was stronger for large than for small clear-cuts. However, in the model where this interaction was not selected, the interaction between the proportion of clear-cuts in the landscape and clear-cut size was instead selected and had the opposite effect. The separate effects of landscape proportion of farmland, which was positive in two models, and that of clear-cuts, which was negative in one model, was likely related to the negative correlation between the two variables (Spearman's rank correlation = -0.37).

3.2. Red-backed Shrike occurrence

Two models had a ΔAIC ≤ 2.0 and were the least complex of sets of nested models (Table 3). Tjur's R^2 of the two models was 0.48 and 0.43 (Table 3). Six variables appeared in both models (Table 3). Red-backed Shrike occurrence was positively related to the interaction between clear-cut size and proportion of farmland in the surroundings and this was the largest effect in both models. Similar to Yellowhammers, the positive effect of the proportion of farmland was stronger for large than for small clear-cuts. The interaction between clear-cut size and distance to farmland also had a strong effect on Red-backed Shrike occurrence, such that the increase of occurrence with distance to farmland was stronger for large than for small clear-cuts. As a separate effect, the Red-backed Shrike occurrence was positively related to clear-cut size. The cover by branches had a positive effect on Red-backed Shrike occurrence as well, although the effect sizes were smaller (Table 3). The last variables that occurred in both models, the distance to the nearest farmland and the proportion of farmland in the surroundings, were not strongly related to Red-backed Shrike occurrence and had relatively large uncertainty (Table 3). Their inclusion in the models was the consequence of the fact that the interactions between variables could only be incorporated in the models if the separate variables were included as well.

Two variables that were only included in the top model were the proportion of clear-cuts in the landscape and the distance to the nearest clear-cut (Table 3). Both were positively related to Red-Backed Shrike occurrence.

4. Discussion

This study is, to our knowledge, the first to investigate habitat usage of Yellowhammers and Red-backed Shrikes in clear-cuts. We surveyed clear-cuts of different sizes, morphologies, and landscape contexts, and modeled the probability of finding either species to site and landscape variables. The species occurred both separately as well as together on

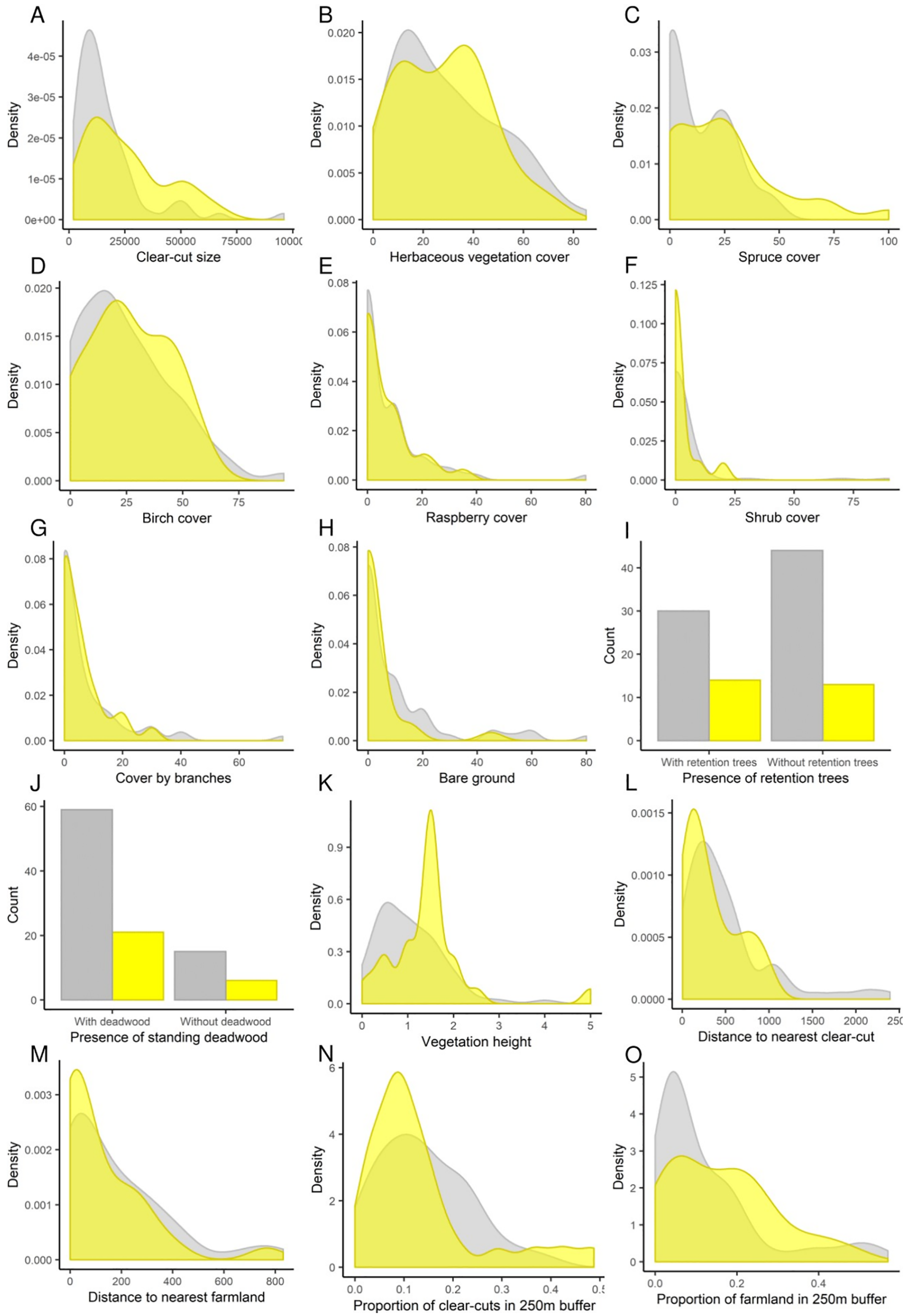

Fig. 2. The distribution of the explanatory variables of the collected data. The distribution is separately represented for clear-cuts with Yellowhammers present (in yellow) and absent (in grey). Continuous variables are displayed as density distributions and discrete variables as bar plots. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

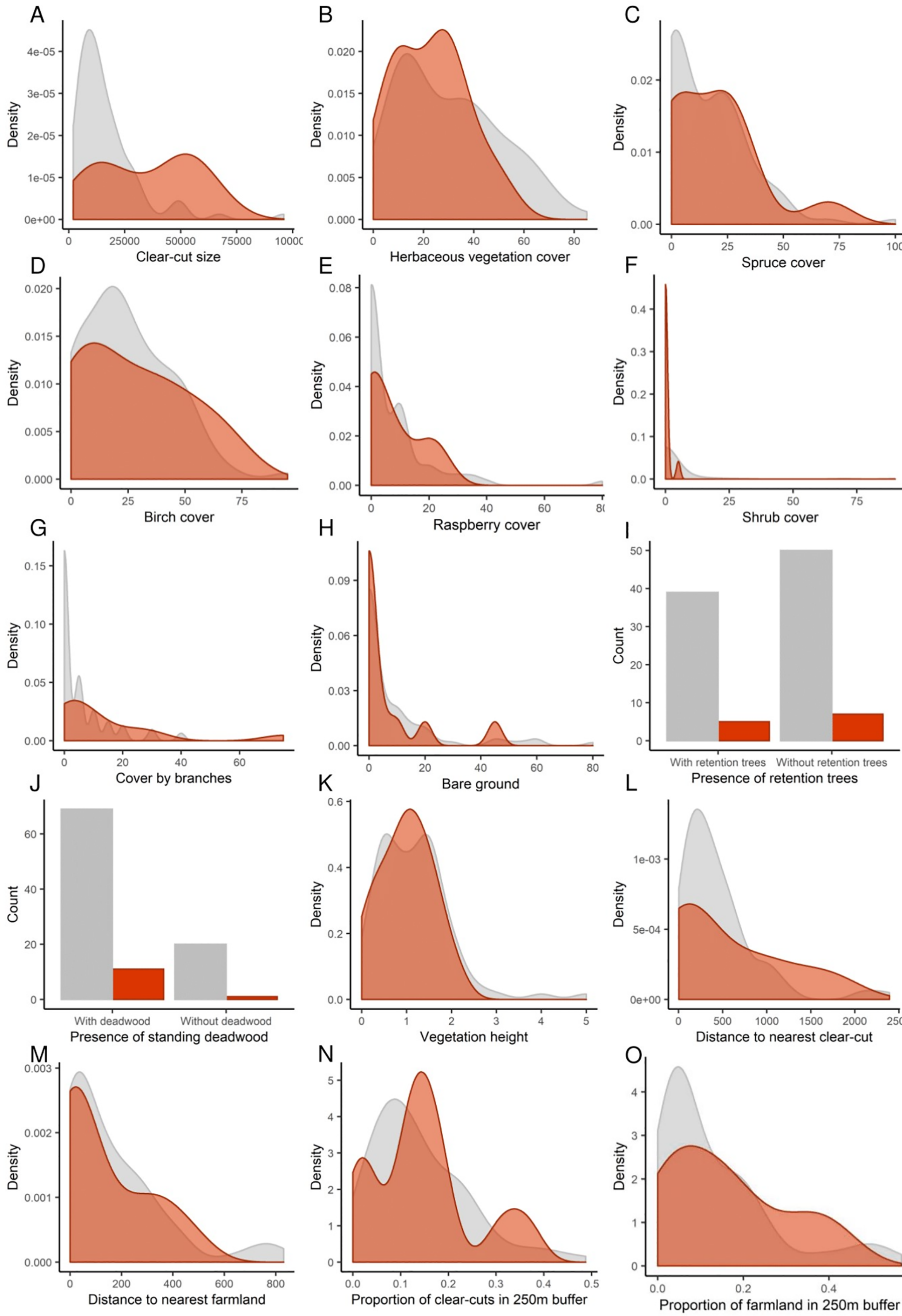

Fig. 3. The distribution of the explanatory variables of the collected data. The distribution is separately represented for clear-cuts with Red-backed Shrike present (in red) and absent (in grey). Continuous variables are displayed as density distributions and discrete variables as bar plots.

Table 2
Model descriptions of the models that were selected (ΔAIC ≤ 2 and only least complex of nested models) for Yellowhammer occurrence. The effect sizes of each variable in the model and the 95% confidence intervals are represented in the respective rows, the other rows show Tjur's R^2, the degrees of freedom, log-likelihood statistic, and AICc.

	Model		
	1	2	3
Intercept	−1.27 (−1.97 to −0.69)	−1.19 (−1.82 to −0.65)	−1.08 (−1.62 to −0.57)
Clear-cut size	1.26 (0.31 to 2.33)	1.42 (0.44 to 2.49)	1.28 (0.33 to 2.38)
Bare ground	−2.00 (−4.77 to −0.06)	−1.50 (−3.77 to 0.09)	NA
Proportion of clear-cuts	NA	−0.81 (−1.96 to 0.24)	NA
Proportion of farmland	1.17 (0.05 to 2.35)	NA	1.14 (0.01 to 2.38)
Cover by spruce	1.20 (0.23 to 2.30)	1.31 (0.30 to 2.40)	1.48 (0.53 to 2.57)
Clear-cut size * proportion of clear-cuts	NA	−3.01 (−6.24 to −0.30)	NA
Clear-cut size * proportion of farmland	3.05 (0.51 to 6.33)	NA	2.36 (−0.03 to 5.84)
Tjur's R^2	0.24	0.23	0.21
df	6	6	5
logLik	−46.51	−47.19	−48.6
AICc	105.91	107.27	107.82

Table 3
Model descriptions of the models that were selected (ΔAIC ≤ 2 and only least complex of nested models) for Red-backed Shrike occurrence. The effect sizes of each variable in the model and their 95% confidence intervals are represented in the respective rows, the other rows show Tjur's R^2, the degrees of freedom, log-likelihood statistic, and AICc.

	Model	
	1	2
Intercept	−2.81 (−4.43 to −1.80)	−2.43 (−3.46 to −1.65)
Clear-cut size	4.69 (2.12 to 8.22)	2.85 (1.11 to 4.98)
Cover by heaps of branches	1.86 (0.42 to 3.71)	1.16 (−0.06 to 2.48)
Distance to nearest clear-cut	2.95 (0.17 to 6.21)	NA
Distance to nearest farmland	−0.48 (−4.54 to 2.37)	0.30 (−2.85 to 2.25)
Proportion of clear-cuts	2.60 (0.20 to 5.45)	NA
Proportion of farmland	1.39 (-1.47 to 4.20)	1.18 (-1.50 to 3.53)
Clear-cut size * distance to farmland	6.55 (2.05 to14.21)	4.54 (1.05 to 10.78)
Clear-cut size * proportion of farmland	13.67 (4.99 to 25.32)	7.69 (1.89 to 16.95)
Tjur's R^2	0.48	0.43
df	9	7
logLik	−19.36	−22.4
AICc	58.7	60.01

the surveyed clear-cuts, which does not indicate that there was avoidance of or preference for co-occurrence by these species. We found that the probability of finding either species increased with clear-cut size, but also that the two species differed in their responses to other morphology and landscape variables.

4.1. Yellowhammers in clear-cuts

The results suggest that the presence of Yellowhammer in a clear-cut is strongly determined by the replantation of spruce, which is in agreement with the hypothesis that Yellowhammer occurrence is related to shrub-like vegetation. It is important to note that our study area only included Norway Spruce as a planted species and that it is probably not the only suitable type of regrowth for Yellowhammers or other "farmland birds" (Christian et al., 1997). However, spontaneous birch regrowth was present in the study area but did not come up in the model selection, indicating that spruce regrowth was more suitable than birch. Previous studies have also shown that clear-cuts, but also Christmas tree plantations in farmland (i.e. not in forests), can be suitable breeding habitats for Yellowhammers and other birds (Fartmann et al., 2017; Gailly et al., 2017; Ottosson et al., 2012; Żmihorski et al., 2016a). The role of spruce plantation in our study is likely to be similar to that of hedges in farmland, i.e. they provide nest-sites (Bradbury et al., 2000). Since nesting is related to vegetation cover, and food provisioning for the chicks is related to bare ground availability (Copete, 2016; Stoate et al., 1998), the negative relation between occurrence and bare ground cover could indicate that clear-cuts are mainly used as a nesting ground and less as foraging grounds, since bare ground cover is negatively related to (mostly) shrub-like vegetation cover.

The occurrence of Yellowhammers was, as hypothesized, also affected by landscape composition, which is demonstrated by the stronger positive effect of the proportion of farmland in the landscape in large clear-cuts than in small clear-cuts. A possible explanation for this landscape effect is that clear-cuts and farmland are seasonally complementary habitats for Yellowhammers. The spruce cover in the used clear-cuts could be used mostly for nesting and this could be complemented by the surrounding farmland for food provisioning or as a immigration source for the clear-cut population. This distinction in habitat requirements might be useful for understanding the positive interaction effect of clear-cut size and the proportion of surrounding farmland in our models. Indeed, in the landscape we surveyed, clear-cuts were always associated with access roads providing heterogeneous habitat. Smaller clear-cuts would provide nesting habitat with few feeding resources but are never far from potential foraging ground (existing farmland as well as the herbaceous vegetation on access roads and edges). Larger clear-cuts, on the other hand, offer more feeding resources, especially during the breeding season, (simply via the sheer effect of size) and benefit in winter from feeding resources from surrounding farmland. The role of young tree plantations as nesting grounds has been previously shown in grasslands in France, where local bird species richness was enhanced by Christmas tree plantations in areas with low hedge density (i.e. areas with little nesting opportunity), but species richness was not enhanced in areas with high hedge density (Gailly et al., 2017).

An alternative explanation for the area effect and the interaction with the landscape composition would be that area and survey effort could be confounded. However, we do not believe this to be the case as, first, the occurrence data and model predictions show a strong clear-cut size threshold for occurrence. Second, we made sure that we surveyed each clear-cut completely and that the time spent per area and therefore the relative effort per clear-cut was equal. Third, based on the ecology of males of both species during the breeding season, we believe that the detection probability was very high. Male Yellowhammers continuously sing their very recognizable song from the top of shrubs and small trees, which makes them easy to both hear and see and detection should not be significantly affected by the time spent surveying. Male Red-backed Shrikes have an unmistakable silhouette and plumage compared to other Swedish species and perch on the top of low growing vegetation (up to a few metres tall). We believe that detection probability for this species was high as well because of this and because of the high visual surveying effort in each clear-cut.

4.2. Red-backed Shrikes in clear-cuts

The interaction between clear-cut size and proportion of farmland was the most important predictor of Red-backed Shrike occurrence and showed a pattern similar to that observed for Yellowhammer. This suggests that for Red-backed shrikes in large clear-cuts the presence of farmland in the surroundings is more important than in small clear-cuts or that breeding in small clear-cuts is more difficult independent of landscape context and that landscape effects only affect occupancy in clear-cuts that are large enough to breed in. The interaction effect between clear-cut size and distance to the nearest farmland was actually opposite to the interaction with the proportion of farmland. The probability of Red-backed Shrike occurrence increased with distance to farmland on big clear-cuts while there was no effect on small clear-cuts. Due to the high collinearity between distance to farmland and the proportion of farmland, we assume that this opposite effect has a dampening function on the effect of the proportion of farmland although it is difficult to disentangle one from the other. The importance of landscape variables suggests that the Red-backed Shrikes that breed in the study area depend on the surrounding farmland, potentially for food. We did not find direct evidence for Red-backed Shrikes foraging in farmland in this study but an inquiry with members of the Swedish birdwatching community quickly returned accounts of people observing this happening. One previous study in Sweden indicated a potential preference of Red-backed Shrikes for clear-cuts over farmland, no difference in food availability between clear-cuts and farmland, as well as a higher number of fledglings in clear-cuts than in farmland, potentially due to decreased nest predation pressure (Söderström and Karlsson, 2011). However, another study showed that food availability was higher in farmland than in clear-cuts in Belgium and that still Red-backed Shrikes preferred to settle in clear-cuts rather than in farmland, resulting potentially in an ecological trap (Hollander et al., 2013). Both studies showed differences in reproductive success between clear-cuts and farmland, however in opposite directions (Söderström and Karlsson, 2011, Hollander et al., 2013). To explain this discrepancy, future studies should investigate reproductive success on clear-cuts in different landscape contexts. The habitat selection of migrant species such as the Red-backed Shrike might be time pressured due to the short window between arrival and the start of nesting. This could lead potentially to poor decisions in specific landscape contexts and explain this apparent poor habitat selection. Yellowhammers on the other hand are resident in the study area and could make more informed decisions in the selection of breeding habitat.

Besides landscape effects, the Red-backed Shrike occurrence was positively related to clear-cut size and the cover by branches, which was in accordance with our hypothesis that vegetation structure and habitat size positively influence occurrence. Red-backed Shrikes are well known to use thorny shrubs for nesting and open ground for feeding (Polak, 2012; Yosef et al., 2014), including open areas in forested landscapes (Lislevand, 2012). The heaps of branches, similar in structure to throny bushes, may well provide nest sites for the Red-backed Shrikes. In fact, during the survey we observed nest-building Red-backed Shrikes in a heap of branches on a clear-cut on one occasion. The clear-cuts where the heaps generally occurred were usually up to two years old with little vegetation and this combination of both shrub-like structures and open habitat on clear-cuts could be sufficient to provide both nesting and feeding opportunities.

4.3. Farmland birds in forest clear-cuts

Considering the potentially large importance of clear-cuts for Yellowhammers, Red-backed Shrikes and other “farmland” species in Sweden (Stjernman et al. 2013, this study) and elsewhere in Europe (Paquet et al., 2006; Żmihorski et al., 2016a), future research should investigate the habitat usage of other species in clear-cuts. For example, other open habitat species such as Linnet (*Linaria cannabina*), Stonechat (*Saxicola torquatus*) and Whinchat (*Saxicola rubetra*) and many more could be similarly related to clear-cuts (Gailly et al., 2017; Ram et al., 2020; Stjernman et al., 2013). It should also be stated that clear-cuts may not be the only alternative habitat for these birds. Before forests were used for timber harvesting and rotation forestry, in the pre-agricultural Holocene, they were likely less dense and more prone to natural disturbances such as windfall and wildfires (Svenning, 2002). The open patches in forests created by these dynamics could have been suitable for these birds as well, as shown as well in treefall gaps in a European old-growth forest (Fuller, 2000).

To mitigate the negative but also complex effects of clear-cutting on forest biodiversity, conservation measures such as green tree retention, and retention and creation of standing deadwood, have been introduced in connection to forest certification (Bremer and Farley, 2010; Ram et al., 2017). Given the potentially large importance of clear-cuts also for “farmland birds”, more research is needed on whether some clear-cuts may be managed to benefit farmland birds. Alternatively, other measures could be used to increase spatial heterogeneity in forests, such as avoiding the forest closure resulting from contemporary intensive forest management (Mitchell et al., 2006). It is also important that conservation measures are not merely informed by habitat selection studies since there are many other factors influencing breeding success and survival, such as, predation and resource availability (Hollander et al., 2011; Söderström, 2001; Söderström and Karlsson, 2011).

Our study confirms that Yellowhammers and Red-backed Shrikes regularly occur in habitats other than farmland in Sweden (Stjernman et al., 2013), which most commonly are clear-cuts such as described in our study. How many clear-cuts in Sweden could actually hold breeding Yellowhammers and Red-backed Shrikes? We estimated this with a calculation based on the total number of clear-cuts harvested within the last five years (Appendix A, Swedish Forest Agency, 2018) in the southern half of Sweden, which is the distribution range of the majority of the population of the two species (83% for Yellowhammer, 86% for Red-backed Shrike, Ottosson et al., 2012). We assumed occupancy rates consistent with our study and estimated that as many as 39,900 and 17,700 clear-cuts could harbor Yellowhammers and Red-backed Shrikes, respectively. With the same number of pairs per occupied clear-cut as in this study, 1.6 and 1.5, respectively this corresponds to 8.5% of the Yellowhammers and 70% of the Red-backed Shrikes that are estimated to breed in this part of Sweden. A more conservative estimate of only one pair per clear-cut gives proportions of 5% and 46%. These estimates are in the same order of magnitude as those by

Stjernman et al. (2013), who suggested that 34% of the Swedish Yellowhammers and 63% of the Red-backed Shrikes breed outside of farmland, most of which are likely to be found in clear-cuts or similar cleared forest habitat, e.g. powerline rights-of-way.

CRediT authorship contribution statement

Tristan Bakx: Conceptualization, Methodology, Investigation, Formal analysis, Visualization, Data curation, Writing - original draft, Writing - review & editing. **Åke Lindström:** Conceptualization, Methodology, Supervision, Investigation, Resources, Writing - review & editing. **Dafne Ram:** Supervision, Writing - review & editing. **Lars B. Pettersson:** Writing - review & editing. **Henrik G. Smith:** Writing - review & editing. **E. Emiel Loon:** Supervision, Formal analysis, Writing - review & editing. **Paul Caplat:** Conceptualization, Methodology, Formal analysis, Funding acquisition, Project administration, Writing - review & editing.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary material

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