Habitat and nest site preferences of Red-backed Shrike (*Lanius collurio*) in western Denmark

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Received 22 November 2013, accepted 4 November 2014



In this study we evaluate nest site and habitat preferences of Red-backed Shrike (Lanius collurio) in the national park Mols Bjerge, Denmark. In total, 28 nests were found during 2010 and 2011. To determine nesting site preferences, the species composition of vegetation in scrub used for nesting was compared to that of nearest unused scrub. To evaluate habitat preferences, a Resource Selection Probability Function (RSPF) was modelled based on presence/absence data. The habitat factors were represented by Light Detection And Ranging (LIDAR) derived measures of vegetation height and topographic wetness as well as distance to nearest road/path, as an indicator of human disturbance. Scrub used as nesting sites were characterized by thorny shrub species such as Prunus spinosa and Rubus fruticosus. RSPF showed that shrike presence was positively correlated with vegetation heterogeneity and high topographic wetness, and that it was unaffected by the distance to the nearest road/path. These results provide some guidelines for management, showing that Red-backed Shrike for nesting preferred habitats with high wetness, possibly linked to food availability, and heterogeneous vegetation, consistent with their need for low vegetation for hunting and higher vegetation for hunting perches and nest sites, with thorny shrubs especially important for the latter.

1. Introduction

Over the last century the landscape in Europe has undergone major changes. The historical mosaic rural landscape with often extensive non-cultivated, often grazed areas, a diversity of small arable areas, and numerous hedgerows has disappeared and is now replaced with large areas of arable monocultures (Lefranc 1997, Potter 1997). This reduction in mosaic habitats has led to a massive decline in wildlife, especially notable in farmland birds (e.g. Tucker & Heath 1994, Pain & Dixon 1997, Donald *et al.* 2006). One of these birds is the Red-backed Shrike (*Lanius collurio*), which has declined since the 1970's (Tucker & Heath 1994, Pihl *et al.* 2006) and is now listed on Annex I of the EU Birds Directive (Bird Directive 2009/147/EC). For birds on this list specific actions must be done by the members of the EU to protect these birds and especially their habitats. Agricultural intensification has been proposed as one of the main reasons for the overall decline of

Red-backed Shrike as it has led to both loss of suitable habitat and decreased prey availability (Lefranc 1997, Kuper *et al.* 2000).

In Denmark the number of Red-backed Shrikes is estimated to be relatively stable with 1,500-3,000 breeding pairs (Pihl et al. 2006), although there has been a geographic shift over the last 30 years, with fewer now breeding in the eastern part of Denmark and more in the western part (Grell 1998). Some of the Red-backed Shrikes in Denmark breed in Mols Bjerge, which was defined as a national park in 2009 in order to conserve the unique nature, flora and fauna in the area. Presence of Red-backed Shrike has been proposed as a good indicator for biodiversity in semi-open habitats by Brambilla et al. (2009), as they found a higher floral diversity in areas occupied by this species. Safriel (1995) also proposed that shrikes (Laniidae) would be good bioindicators due to their sensitivity to changes in habitats. Therefore, it will be an advantage to maintain the area suitable for this bird species, as it will benefit the biodiversity in Mols Bjerge in general.

Habitat preferences for the Red-backed Shrike have been studied previously, and it has been found associated with open land with scattered scrub such as low-intensive farming areas, meadows and waste land (Olsson 1995a, Lefranc 1997, Lefranc & Worfolk 1997, Grell 1998, Kuzniak & Tryjanowski 2000, Vanhinsbergh & Evans 2002, Brambilla et al. 2007, Golawski & Golawska 2008, Brambilla et al. 2009). However, several outstanding questions exist, notably as concerns the role of vegetation height, as well as the role of topography. Red-backed Shrike uses different vegetation heights; higher vegetation like scrub are used as nesting sites and hunting perches, and lower vegetation provides prey items. Topography may influence habitat selection via effects on prev availability (Titeux et al. 2007). Here, we use Light Detection And Ranging (LIDAR), a remotesensing technology (Vierling et al. 2008), to investigate Red-backed Shrike's habitat selection in Mols Bjerge. LIDAR has the important advantage that it allows broad-scale, but detailed mapping of vegetation height and topography (see review in Vierling et al. (2008)). To maintain Mols Bjerge as a suitable breeding area it is also important to investigate specific choice of nest sites for Redbacked Shrike. Some authors (Holan 1995,

Söderström 2001) found that Red-backed Shrike uses scrub of the most frequently plant species in the breeding area, others found that Red-backed Shrike, more specifically, chose spiny scrub as nest sites (Olsson 1995b, Farkas *et al.* 1997, Campos & Lizarraga 2000).

Habitat preferences of Red-backed Shrike have not yet been studied in Denmark. Therefore, we specifically aimed to investigate if Red-backed Shrike had specific preferences in (1) their choice of vegetation for nest sites and in (2) overall local nesting habitat, as a basis for management to favour the persistence or increased presence of the species both generally as well as specifically in Mols Bjerge.

We focused on three descriptors of local habitat conditions: (i) height of vegetation, as Redbacked Shrike uses shrubs for nesting sites and for hunting perches in areas of low vegetation; (ii) topographic wetness, as Titeux *et al.* (2007) have put avoidance of drained fields as a recommendation for Red-backed Shrike habitat management in order to optimize prey availability; (iii) distance to nearest road or path, to investigate whether Redbacked Shrike is affected by human disturbance, to address if low-intensity nature tourism within nature reserves such as Mols Bjerge poses a threat to the species.

2. Material and methods

2.1. The study area

The study was conducted in the National Park Mols Bjerge, Denmark (56.225 N, 10.58 E), in two areas (near Mols Laboratoriet and at Trehøje) – a well-known breeding area for Red-backed Shrike (Fig. 1). Mols Bjerge has a unique landscape with many different habitat types. We only surveyed opened areas and used natural limits like dense forest. The areas are often grazed by livestock, but parts of the area at Trehøje are also mown.

2.2. The study period

Data were collected in May–August 2010 and 2011, as part of the Red-backed Shrike project, run by Natural History Museum, Aarhus (Sell *et al.*



Fig. 1. Map showing the study area in Mols Bjerge, Denmark. The white squares represent the Red-backed Shrike's nests (n = 20), the black circles represent the pseudo-absence points (n = 280), which were randomly distributed within the surveyed areas.

2013). In the beginning of May the area was visited weekly until the first Red-backed Shrikes arrived. Hereafter, the area was visited almost daily to locate the nests by observing the parent birds. Data on vegetation composition and GPS positions of the nests and vegetation were collected, when the juveniles had left the nest.

2.3. Data collection and analyses

In total, 28 nests were located during the two years. Observations of Red-backed Shrikes displaying territorial behaviour where the nests could not be found (n=6) were not included in the dataset. Dur-

ing both years, Red-backed Shrikes were captured and colour-ringed to be able to identify the shrikes individually. Seven (two females, five males) of the 30 (17 adult, 13 juveniles) ringed shrikes in 2010 returned to the study area in 2011. All the returning shrikes had a new mate in 2011, but three of the males returned to the same territory. Having repeating individuals can result in pseudoreplication. The dataset is not large enough to use the individuals as a random factor in the analysis, so instead we developed a reduced dataset to account for any pseudoreplication introduced by individuals observed in both years. The reduced dataset was made by excluding one of the two observations of individuals that were represented twice (i.e., in two years) in the dataset. The exclusion was done randomly, except for the constraint that the two years should be equally presented. Hence, in the final dataset each individual only occurs once and only with one nest (n = 20 nests). Data from both years are used as part of the same sample, as weather data (mean monthly temperature, monthly sum of precipitation and monthly hours with sunlight) from both years did not differ when compared on a monthly base (Wilcoxon signed rank sum test – temperature: W = 5; P = 1; precipitation: W=6; P=0.88; sunlight: W=3; P=0.63). The weather data used was a mean of the data from Aarhus and Grenaa, as the study site is located in between these cities, collected by the Danish Meteorological Institute for the months May, June, July and August 2010 and the same month in 2011 (http://www.dmi.dk/vejr/arkiver/ maanedsaesonaar/).

2.3.1. Nest habitat

The species composition of the scrub vegetation was quantified in the scrub types: nest scrub, nearest scrub, nearest thornless scrub and nearest thorny scrub (abbreviated as: nest, bush, thornless and thorn, respectively). In a virtual column with the nest as centre, a radius at 1 m and the height from ground to the top of the vegetation, we estimated the volume that each plant species occupied (in percentage of the total vegetation in the column; hereafter referred to as percentage scrub occupancy volume). The same method was used to quantify the species composition in the scrub nearest to the nest scrub with a virtually point placed 1 m into the scrub from its surface facing the nest scrub selected as centre. If the nearest scrub contained thorny scrub species, the method was used on the nearest thornless scrub, too, and if it did not contain any thorny scrub species, the method was used on the nearest thorny scrub as well. A scrub was defined as thorny if it contained > 1% scrub occupancy volume of at least one of the following species: rose (Rosa spp. L.), Raspberry (Rubus idaeus L.), Blackberry (Rubus fruticosus L.), hawthorn (Crataegus spp. L.) or Sloe (Prunus spinosa L.). All herbaceous plants such as Stinging Nettle (Urtica dioica L.), Common Yarrow (Achillea millefolium L.), Mint (Mentha spp. L.), and

grasses (Poaceae spp. L) were grouped as a single herbaceous ground-layer category, as they did not constitute part of the nest-holding vegetation (see appendix for a list of all plant species found).

2.3.2. Territory habitat

The GPS positions of the nests (n = 20) were imported to ArcMap 9.3.1 (ESRI **®** 2009) (Fig. 1). Random distributed points (n = 280) were generated as pseudo-absence points to represent points with an absence of Red-backed Shrikes (Fig. 1). These points were only distributed in the area that was surveyed for Red-backed Shrike and, furthermore, did not overlap any of the real nests or any of the six areas where a potential nest could not be located.

Buffer zones with the centre at the nest or at the random points were generated in ArcMap 9.3.1 (ESRI 8 2009). The buffer zones were laid as a circle with 10 m radius (the 10 m buffer zone) and two annular defined by concentric circles with 20 m radius (the 20 m buffer zone) and 40 m radius (the 40 m buffer zone), respectively. Brambilla & Ficetola (2012) showed in their study that the territory size of Red-backed Shrike is correlated with the suitability of the environment and that the size can vary from 2,500 m² to 20,000 m². We estimated home ranges at our study site to vary from 3,743 m² to 43,226 m², with 15,923 m² as mean value. So, the buffer zones include most of the home ranges.

For each of the buffer zones, the mean, maximum (max) and standard deviation (sd) of the vegetation height (vegh) and the topographic wetness (twi) were computed. The mean was chosen as it describes how the habitat was in general, the maximum captures any tall vegetation or wet areas that were present, whereas the standard deviation describes spatial heterogeneity in vegetation height or wetness. Vegetation height was estimated as the difference between a Digital Surface Model (DSM), describing the elevation of the surface and objects like buildings and vegetation and a Digital Terrain Model (DTM), describing the elevation of the bare ground. Both dataset are produced in 1.6 m horizontal resolution and have an estimated vertical accuracy of 0.10 m. They are based on airborne Light Detection And Ranging (LIDAR) and

Table 1. Variables used for the logistic Resource Selection Probability Function (RSPF) (Manly *et al.* 2002), which describes the Red-backed Shrike's habitat preferences in Mols Bjerge.

Variables	Variable description
SHRIKE	Presence/absence of Red-backed Shrike
TWI	Topographic Wetness Index
TWI_10M_MEAN	Mean TWI for the buffer zone 0–10 m from nest
TWI_10M_MAX	Maximum TWI for the buffer zone 0–10 m from nest
TWI_10M_SD	SD TWI for the buffer zone 0–10 m from nest
TWI_20M_MEAN	Mean TWI for the buffer zone 10–20 m from nest
TWI_20M_MAX	Maximum TWI for the buffer zone 10–20 m from nest
TWI_20M_SD	SD TWI for the buffer zone 10–20 m from nest
TWI_40M_MEAN	Mean TWI for the buffer zone 20–40 m from nest
TWI_40M_MAX	Maximum TWI for the buffer zone 20–40 m from nest
TWI_40M_SD	SD TWI for the buffer zone 20–40 m from nest
VEGH	Vegetation height
VEGH_10M_MEAN	Mean VEGH for the buffer zone 0–10 m from nest
VEGH_10M_MAX	Maximum VEGH for the buffer zone 0–10 m from nest
VEGH_10M_SD	SD VEGH for the buffer zone 0–10 m from nest
VEGH_20M_MEAN	Mean VEGH for the buffer zone 10–20 m from nest
VEGH_20M_MAX	Maximum VEGH for the buffer zone 10–20 m from nest
VEGH_20M_SD	SD VEGH for the buffer zone 10–20 m from nest
VEGH_40M_MEAN	Mean VEGH for the buffer zone 20–40 m from nest
VEGH_40M_MAX	Maximum VEGH for the buffer zone 20–40 m from nest
VEGH_40M_SD	SD VEGH for the buffer zone 20–40 m from nest
DIST	Distance from the nest/random control point to the nearest road/path

available as GIS layers from National Survey and Cadastre Denmark (2008). Topographic wetness was estimated from the DTM by the Topographic Wetness Index (TWI), which describes the topographic wetness in a point according to the upland area and the slope of the terrain in the point (Wilson & Gallant 2000). The distance (dist) from a nest site or potential nest site to the nearest road/path, calculated from "Kort 10", (Kort 10 is the official collection of basic topographic data from the Danish Geodata Agency 2006, the resolution is 40×40 cm per pixel), was used as an indicator of human disturbance, i.e., by the low-intensity nature tourism in Mols Bjerge. While the Kort10 layer contained most of the roads and paths in the study area, some extra paths were added manually, as they have been observed used in the study period (J.K. Svendsen, pers. obs.).

2.4. Statistical analyses

2.4.1. Nest habitat

Multi-Response Permutation Procedure (MRPP)

was used to test the null hypothesis that the composition in vegetation did not differ between the four scrub types (nest, nearest, nearest thornless and nearest thorny scrub). The number of permutations was set to 999,999 to obtain stable significance estimates. The distance used was the Sørensen's index as recommended by McCune & Grace (2002). The significance level was set to 0.05 / 4 = 0.0125 after Bonferroni correction for multiple testing, i.e., the four MRPP tests)

To identify which plant species were driving the obtained differences between the different scrub types (as found by the MRPP analysis), we used the Wilcoxon signed rank test to compare the percentage scrub occupancy volume for each plant species in nest scrub vs. nearest scrub and in nest scrub vs. nearest thorny scrub. As the sample size for the nearest thornless scrub type (n = 7) varied from that of the other scrub types (n = 20), we used the Wilcoxon rank sum test rather than a pairwise test, to test for differences in percentage scrub occupancy volume for each plant species between this scrub type and nest scrub, in order to use the full dataset.



Fig. 2. Nest site preferences for Red-backed Shrike in Mols Bjerge, Denmark: Mean scrub occupancy volume values for the five most frequently plant species (mean > 10%) in the four different scrub types.

2.4.2. Territory habitat

Binary logistic regression (a generalized linear model with logit link function and binomial error distribution) was used for analysing habitat selection in Red-backed Shrike, modelling a Resource Selection Probability Function (RSPF) (Manly *et al.* 2002). A logistic regression RSPF is given by Eq. 1:

$$\pi = \frac{e^{\beta_0 + \beta_1 X_1 + \beta_2 X_2 + \dots + \beta_p X_p}}{1 + e^{\beta_0 + \beta_1 X_1 + \beta_2 X_2 + \dots + \beta_p X_p}}$$
(1)

where π here is the probability that a given site is used by Red-backed Shrike, X_i are the different variables which describes data (listed in Table 1), β_i are regression coefficients. The models were built with maximum three variables at the time because of the small sample size (n = 20), as recommended by Harrell *et al.* (1996).

The set of models investigated were first all variables alone together with a null model containing only the slope, then all possible combinations of two variables representing different potential drivers, so either dist and a vegh variable, dist and a twi variable, or a vegh variable and a twi variable. Then all possible combinations of three different variables were tested, again with no models containing two vegh or twi variables. In total, 200 models were investigated. An information-theoretic approach was used for the final evaluation of the model selection, with the models being evaluated based on Akaike's Information Criterion, corrected for small-sample bias (AIC) and by Akaike weights (w_i) to assess the statistical support for a given model as well as a given predictor variable (Burnham & Anderson 2002). Akaike weights can be interpreted as the probability that a given model is the best model or factor belongs in the best model for the data, given the set of candidate models (Johnson & Omland 2004).

All statistical analyses were run in R (R Development Core Team 2011).

3. Results

3.1. Nest habitat

A total of 28 nests (12 nests in 2010 and 16 nests in 2011) were detected and located in the study period, the results are based on 20 nests of these nests (9 nest in 2010 and 11 nest in 2011). The shortest distance between two nests was 36.03 m. The mean distance from a nest to the nearest adjacent scrub was 10.0 m (sd 12.1 m), the mean distance from a nest to the nearest adjacent thorny scrub was 15.3 m (sd 17.9 m) and the mean distance from a nest to the nearest adjacent thornless scrub was 26.9 m (sd 25.2 m). All nest scrub contained some

Table 2. Ten best ranked models from the logistic Resource Selection Probability Function (RSPF), which describes the Red-backed Shrike's habitat preferences in Mols Bjerge. Rankings are based on Akaike's Information Criterion, corrected for small-sample bias (AIC_c). *K* is the number of parameters in the model, AIC_c is the difference in AIC_c compared to the best model and w_i (%) are the Akaike weights given as percentages.

Model no.	Model variables	К	AIC _c	AIC _c	<i>w</i> , (%)
1	SHRIKES = 0.183 × TWI_20M_MAX	4	128.98	0.0	29
2	+ $0.446 \times VEGH 10M_SD - 5.57$ SHRIKES = $8.76 \times 10^{-3} \times DIST$ + $0.183 \times TWI_20M_MAX$ + $0.446 \times VEGH 10M_SD - 5.63$	5	130.99	2.0	11
3	SHRIKES = 0.169 × TWI_20M_MAX + 0.314 × VEGH_20M_SD = 5.39	4	131.34	2.4	9
4	SHRIKES = 0.189 × TWI_40M_MAX + 0.422 × VEGH_10M_SD = 6.32	4	131.84	2.9	7
5	SHRIKES = 0.913 × TWI_40M_SD + 0.358 × VEGH_10M_SD_4 84	4	132.61	3.6	5
6	SHRIKES = 0.184 × TWI_40M_MAX + 0.326 × VEGH_20M_SD_6 30	4	132.84	3.9	4
7	SHRIKES = 1.25 × 10 ⁻³ × DIST + 0.169 × TWI_20M_MAX + 0.316 × VEGH_20M_SD = 5.49	5	133.31	4.3	3
8	SHRIKES = 1.42× 10 ⁻³ × DIST + 0.189 × TWI_40M_MAX + 0.422 × VEGH_10M_SD_6 43	5	133.78	4.8	3
9	SHRIKES = 0.880 × TWI_40M_SD + 0.263 × VEGH_20M_SD - 4.81	4	133.96	5.0	2
10	SHRIKES = 5.18 × 10 ⁻⁴ × DIST + 0.911 × TWI_40M_SD + 0.358 × VEGH_10M_SD - 4.88	5	134.65	5.7	2

thorny vegetation; the mean being 64% scrub occupancy volume (sd 36%) with 7% as the minimum.

Species composition of the different plant species in percentage scrub occupancy volume differed significantly between nest scrub and nearest thornless scrub ($n_{\text{nest}} = 20$; $n_{\text{thomless}} = 7$; P = 0.0037). A tendency towards a difference between nest scrub and nearest scrub was found ($n_{\text{nest}} = 20$; $n_{\text{bush}} = 20$; P = 0.065), while there was no significant difference between nest scrub and nearest thorny scrub ($n_{\text{nest}} = 20$; $n_{\text{thom}} = 20$; P = 0.15). When comparing the different scrub types

When comparing the different scrub types (Fig. 2) no significant differences were found for *Prunus spinosa* in nest scrub compared to nearest scrub (Wilcoxon signed rank test: $n_{nest} = 20$; $n_{bush} = 20$; V = 60, P = 0.11) nor in nest scrub compared to nearest thorny scrub (Wilcoxon signed rank test: $n_{nest} = 20$; $n_{thom} = 20$; V = 69, P = 0.11). Nest scrub contained less herbaceous ground-layer vegetation volume than nearest scrub (Wilcoxon signed

rank test: $n_{\text{nest}} = 20$; $n_{\text{bush}} = 20$; V = 41, P = 0.02) as well as less than the nearest thorny scrub (Wilcoxon signed rank test: $n_{\text{nest}} = 20$; $n_{\text{thorm}} = 20$; V = 46.5, P = 0.05). Significantly more *Prunus spinosa* (Wilcoxon rank sum test: $n_{\text{thormless}} = 7$; $n_{\text{nest}} = 20$; W = 105, P = 0.01) and more *Rubus fruticosus* (Wilcoxon rank sum test: $n_{\text{thormless}} = 7$; $n_{\text{nest}} = 20$; W = 101, P = 0.03) were found in nest scrub than in the nearest thornless scrub.

3.2. Territory habitat

According to the model selection analysis presence of Red-backed Shrike was dependent on heterogeneity of vegetation height 0–10 m from a potential nest site and topographic wetness 10–20 m from a potential nest site. The best model for explaining the presence of Red-backed Shrikes is given by the equation in Table 2. This model had an AIC_c on 128.98 which gave $w_i = 29\%$. The ten best ranked models and their AIC_c values are shown in Table 2.

4. Discussion

Within territories, the preferred nest site vegetation for Red-backed Shrike was *Prunus spinosa*rich scrub. The territories themselves were preferentially located in areas with highly heterogeneous vegetation and close to, but not in wet areas. No effect of distance to nearest road or path could be detected.

4.1. Nest habitat

Overall, nest scrub and nearest non-nest scrub differed in plant species composition, indicating that the Red-backed Shrike in Mols Bjerge has preferences for specific plant species in terms of its nest location. This is contrary to other studies which found that Red-backed Shrike does not selectively choose specific plant species; but simply use the dominant plant species in the breeding area (Holan 1995, Söderström 2001).

Selection of scrub with thorny shrub species as nest sites were behind these compositional differences. Notably, there was more *Prunus spinosa* and *Rubus fruticosus* in nest scrub than in the nearest thornless scrub within nesting territories. *Prunus spinosa* has been described as an important nesting plant for Red-backed Shrike before (Olsson 1995b, Farkas *et al.* 1997, Söderström 2001) together with Dog Rose (*Rosa canina* L.), Common Hawthorn (*Crataegus monogyna* L.), *Rubus fruticosus*, Juniper (*Juniperus communis* L.) and Norway Spruce (*Picea abies* L. Karst.) (Gorban & Bokotej 1995, Campos & Lizarraga 2000, Nikolov 2000, Väli 2005, Lislevand 2012), all more or less spiny or prickly species.

Several behavioural factors may explain this pattern. One such would be caching behaviour. It is well-known that Red-backed Shrike sometimes collects and storages food on thorns and spines in the vegetation for use on days with poor conditions for hunting (Cramp & Perrins 1993). This behaviour requires thorny vegetation in the area where the Red-backed Shrike breeds. Hernández (1995) found that Red-backed Shrike preferred to store prey in thorny bushes like *Crataegus* spp. and *Pru-nus spinosa*.

A more likely explanation, however, could be protection against nest predation. Several studies have found that nest predation is the main reason for nest failure in the Red-backed Shrike (Roos & Pärt 2004, Farkas et al. 1997, Söderström 2001) and in birds in general (Lima 2009). Comparisons between nest sites and the surrounding habitats have shown that nest site is chosen to minimize predation risk (Caro 2005). In this study a higher cover by ground-layer herbaceous vegetation was found in the nearest scrub than in nest scrub. This could indicate that scrub chosen for nesting is denser - and thus provide more heavy shadow than the surrounding scrub and thereby provides more cover for the nest. Several studies support this interpretation. Müller et al. (2005) found that nesting success in the Red-backed Shrike was higher when the nest was more concealed. Gorban & Bokotej (1995) found that the Red-backed Shrike nesting in Rubus fruticosus rather than in trees had a higher breeding success, while Tryjanowski et al. (2000) showed that the number of young fledged was significantly higher in thorny compared to thornless scrub. Contrary to these, Farkas et al. (1997) found no difference in breeding success between thorny closed and open thornless bushes.

4.2. Territory habitat

The best habitat model indicated that Red-backed Shrike nest occurrence was positively related to the standard deviation in vegetation height within 10 m from the potential nest site (vegh_10m_sd) and maximum topographic wetness within 10–20 m from the potential nest site (twi_20m_max). This indicates that Red-backed Shrike prefers areas with heterogeneous vegetation, especially just around the nest (0–10 m), and high wetness near the nest (10–20 m), but not right by it. The model did not contain the distance to nearest road or path (dist), indicating occurrence was unaffected by human disturbance associated with roads and paths.

The positive association of Red-backed Shrike nest occurrences to locally high vegetation heterogeneity is in agreement with previous studies. Landscape heterogeneity in vegetation height is well-known as an important factor for Red-backed Shrike and many other farmland birds (Berg 2002). Several studies on habitat preferences mention open areas with scattered scrub and trees as the main habitat for Red-backed Shrikes (Cramp & Perrins 1993, Olsson 1995a, Lefranc & Worfolk 1997, Vanhinsbergh & Evans 2002, Brambilla et al. 2007, Brambilla et al. 2009). According to several studies (e.g. Olsson 1995a, Brambilla et al. 2007, Brambilla et al. 2009), the Red-backed Shrike prefers habitats with hedgerows or forests edges. Such areas will give heterogeneity near the nest scrub, supporting the results in this study. Many of the nests in our study were located near edges of forest or bigger scrub areas. Landscape heterogeneity provides vegetation suitable for nesting sites and perches for hunting as well as low-vegetation areas with good hunting opportunities. Food availability may influence the choice of habitat, as Golawski & Golawska (2008) showed that habitat preference of Red-backed Shrike corresponds with the differences in prey biomass in these habitats. Prey, especially insects, are easier to spot in the open areas with grass and other low vegetation, but Red-backed Shrike need scattered scrub in the habitat to be used as perches from which it often hunts by dropping to the ground (Olsson 1995a, Karlsson 2004). The length of these hunting drops are often much less than 10 m (Cramp & Perrins 1993). Vanhinsbergh & Evans (2002) also showed that shrike abundance increased with scrub cover up to 15% of cover and then declined again with higher levels of cover. This is consistent with the findings in Brambilla et al. (2007) where the areas with the highest density of Red-backed Shrikes had a scrub cover between 10 and 30%. Vanhinsbergh & Evans (2002) found that the Red-backed Shrike is positively associated with grassland grazed by livestock and scattered trees and scrub. Livestock grazing is used as the primary method to maintain many of the open areas in Mols Bjerge, and this is also the case for the habitat of all the Red-backed Shrike territories in this study. Open pastures grazed by livestock at low intensity provide good hunting places for the species, if scattered small trees and scrub are able to grow up in the pastures to serve as hunting perches. Free-living wild herbivores may provide similar vegetation height

(Svenning 2002, Vera 2009). Many insects will also benefit from the presence of livestock, and especially their dung, providing more prey items for the Red-backed Shrike.

The positive effect by maximum topographic wetness variable (twi_20m_max), indicates that the Red-backed Shrike has a preference for having relatively wet areas in the vicinity of the nest site. As *Prunus spinosa* and other preferred nest shrub species prefer less wet habitats, which could explain why Red-backed Shrike prefers wetness in the buffer zone 10–20 m and not near the nest site.

In their study Titeux et al. (2007) also found Red-backed Shrike breeding in areas with higher soil wetness than in unoccupied areas. Lefranc & Worfolk (1997) write that the habitat choice for Red-backed Shrike is very variable, from heathland over grasslands to bogs. This is consistent with several other studies that categorized preferred breeding habitats as pastures (Cramp & Perrins 1993, Vanhinsbergh & Evans 2002, Brambilla et al. 2007, Golawski & Golawska 2008), meadows (Lefranc 1997, Kuzniak & Tryjanowski 2000, Golawski & Golawska 2008), marshes (Cramp & Perrins 1993, Lefranc & Worfolk 1997) and bogs (Grell 1998). Although the preferences for habitat types vary, the authors in general agree that the preferred habitats are correlated with food availability (Olsson 1995a, Karlsson 2004, Golawski & Golawska 2008). Large insects, such as beetles (Coleoptera spp. L.), wasp, bumble bees and bees (Hymenoptera spp. L.) and grasshoppers (Orthoptera spp. Latrielle) constitute the preferred prey for Red-backed Shrikes (Tryjanowski et al. 2003), and wetter areas likely provide greater densities of these large insects species (ex Carabidae spp. Latreille in Holland 2002). This lends support to the strong effect of wet areas observed in our study.

The distance to roads/paths did not seem to have an effect on the presence of Red-backed Shrike, indicating that low-intensity nature tourism such as practised in the Mols Bjerge area does not affect nest site selection. Morelli (2011) showed that Red-backed Shrikes preferred nesting in scrub near roads although suitable scrub were presented in the whole study area, probably because the roads provided good hunting opportunities, as they were used as corridors for the ground insects. Smith-Castro & Rodewald (2010) found that human use of recreational trails only had a short-term effect on the behaviour of nesting birds and that the use of the trails did not affected the nesting success. Still, our results do not address

more severe human disturbance than that occurring along small roads and foot paths. In summary, the Red-backed Shrike preferred territory habitats with high wetness, possibly linked to food availability, and heterogeneous vegetation, consistent with their need for low vegetation for hunting and higher vegetation such as bushes or small trees to be used as hunting perches and nest sites. Red-backed Shrike did not seem to be affected by human disturbance associated with roads or paths within their territories. These results provide some guidelines for management to favour Red-backed Shrike breeding populations. Vegetation should be a mix of open areas and patches of woody vegetation, with many thorny shrub species like Prunus spinosa and Rubus fruticosus, as they constitute preferred nest sites and are also used by Red-backed Shrikes for caching food items. This type of landscape would not only benefit the Red-backed Shrikes, but also many other birds, arthropods and plants (Holland & Luff 2000, Berg 2002, Brambilla et al. 2009).

whether the Red-backed Shrike is affected by

Acknowledgements. We would like to thank Mols Laboratoriet, Naturhistorisk Museum, Aarhus, for letting us use their facilities during the field period. Special thanks to Christina Vedel-Smith, for helping with fieldwork and commenting an earlier version of the manuscript. We also thank Kent Olsen, for starting the project on Red-backed Shrikes in Mols Bjerge, from which this project has evolved, and providing the data from 2010. JCS was supported by the European Research Council (ERC-2012-StG-310886-HISTFUNC) and Aarhus University and Aarhus University Research Foundation under the AU IDEAS program (via Center for Informatics Research on Complexity in Ecology, CIRCE). In addition, we are grateful to SCALGO (www.scalgo.com) for allowing us to use their algorithms for computing the topographic wetness index.

Törnskatans val av habitat och boplats i västra Danmark

I denna studie undersökte vi törnskatans (*Lanius collurio*) val av habitat och boplats i nationalparken Mols Bjerge, i Danmark. Vi hittade totalt 28

bon under 2010-2011. För att fastställa preferens för boplats jämfördes vegetationens artsammansättning i buskage som användes för häckning, med närmaste buskage utan häckning. För att undersöka val av habitat estimerade vi sannolikheten för häckning med hjälp av närvaro/frånvaro-data (med s.k. RSPF; Resource Selection Probability Function). Habitatet beskrevs med mätningar av vegetationens höjd och topografisk våthet (baserat på LIDAR-metoden; Light Detection And Ranging), samt avståndet till närmaste stig/väg, som en indikator på antropogen störning. Buskage som användes som boplats präglades av taggiga buskarter så som slån (Prunus spinosa) och björnbär (Rubus fruticosus). RSPF visade att törnskatans närvaro korrelerade positivt med vegetationens heterogenitet och topografisk våthet, men saknade statistiskt samband med avstånd till närmaste stig/väg. Dessa resultat kan användas som riktlinjer vid förvaltning. Törnskatans preferens att bygga bo i habitat med högre fuktighet, har troligen att göra med bättre tillgång till föda. Mer heterogen vegetation motsvarar bättre artens behov: att jaga i låg vegetation, samt hålla utkik och häcka i högre vegetation. Framför allt högre vegetation med taggiga buskar är viktig som häckningsplats.

References

- Berg, Å. 2002: Composition and diversity of bird communities in Swedish farmland-forest mosaic landscapes. — Bird Study 49: 153–165.
- Bird Directive 2009/147/EC of the European Parliament and of the Council of 30 November 2009 on the conservation of wild birds.
- Brambilla, M., Rubolini, D. & Guidali, F. 2007: Between land abandonment and agricultural intensification: habitat preferences of Red-backed Shrikes *Lanius collurio* in low-intensity farming conditions. — Bird Study 54: 160–167.
- Brambilla, M., Casale, F., Bergero, V., Matteo Crovetto, G., Falco, R., Negri, I., Siccardi, P. & Bogliani, G. 2009: GIS-models work well, but are not enough: Habitat preferences of *Lanius collurio* at multiple levels and conservation implications. — Biological Conservation 142: 2033–2042.
- Brambilla, M. & Ficetola, G.F. 2012: Species distribution models as a tool to estimate reproductive parameters: a case study with passerine bird species. — Journal of Animal Ecology 81: 781–787.
- Burnham, K.P. & Anderson, D.R. 2002: Model Selection

and Multi-Model Inference : A Practical Information-Theoretic Approach. 2nd ed. — Springer, USA.

- Campos, F. & Lizarraga, A. 2000: The Red-backed Shrike (*Lanius collurio*) — an indicator of climate and vegetation type? — The Ring 22: 59–64.
- Caro, T. 2005: Antipredator defenses in birds and mammals. 1st ed. — The University of Chicago Press, Chicago.
- Cramp, S. & Perrins, C. 1993: Handbook of the Birds of Europe, the Middle East and North America. The Birds of the Western Paleartic, Vol. 7. — Oxford University Press, New York.
- Danish Geodata Agency (previously National Survey and Cadastre Denmark) 2006: Kort10 – en del af den geografiske infrastruktur. — Copenhagen. URL: http:// www.gst.dk/produkter-og-ydelser/produktkatalog/topografiske-data/vektordata/kort10/ (In Danish)
- Donald, P.F., Sanderson, F.J., Burfield, I.J. & van Bommel, F.P.J. 2006: Further evidence of continent-wide impacts of agricultural intensification on European farmland birds, 1990–2000. — Agriculture, Ecosystems and Environment 116: 189–196.
- ESRI ® 2009: ArcMapTM. Vers 9.3.1. Environment Research System Inc., Relands, USA.
- Farkas, R., Horváth, R. & Pásztor, L. 1997: Nesting success of the Red-backed Shrike (*Lanius collurio*) in a cultivated area. Ornis Hungarica 7: 27–37.
- Golawski, A. & Golawska, S. 2008: Habitat preference in territories of the Red-backed Shrike *Lanius collurio* and their food richness in an ectensive agriculture landscape. — Acta Zoologica Academiae Scientiarum Hungaricae 54: 89–97.
- Gorban, I. & Bokotej, A. 1995: Distribution of Laniidae in western Ukraine, and the breeding biologi of *Lanius collurio*. — Proceedings Western Foundation Vertebrate Zoology 6: 70–71.
- Grell, M.B. 1998: Fuglenes Danmark. Gads Forlag. (In Danish)
- Harrell, F.E., Lee, K.L. & Mark, D.B. 1996: Multivariable prognostic models: Issues in developing models, evaluating assumptions and adequacy, and measuring and reducing errors. — Statistics in Medicine 15: 361– 387.
- Hernández, Á. 1995: Temporal-spatial patterns of food caching in two sympatric shrikes species. — The Condor 97: 1002–1010.
- Holan, V. 1995: Population density and breeding biology of Red-backed Shrikes in Czechoslovakia. — Proceedings Western Foundation Vertebrate Zoology 6: 76– 77.
- Holland, J.M. & Luff, M.L. 2000: The effects of agricultural pratices on Carabidae in temperate agroecosystems. — Integrated Pest Management Reviews 5: 109–209.
- Holland, J.M. 2002: Carabid Beetles: Their Ecology, Survival and Use in Agroecosystems. In The Agroecology of Carabid Beetles (ed. Holland, J.M.): 1–40. Intercept, Andover.

- Johnson, J.B. & Omland, K.S. 2004: Model selection in ecology and evolution. — Trends in Ecology & Evolution 19: 101–108.
- Karlsson, S. 2004: Season-dependent diet composition and habitat use of Red-backed Shrikes *Lanius collurio* in SW Finland. — Ornis Fennica 81: 97–108.
- Kuper, J., van Duinen, G.-J., Niejssen, M., Geertsma, M. & Esselink, H. 2000: Is the decline of the Red-backed Shrike (*Lanius collurio*) in the Dutch coastal dune area caused by a decrease in insect diversity? — The Ring 22: 11–25.
- Kuzniak, S. & Tryjanowski, P. 2000: Distribution and breeding habitat of the Red-backed Shrike (*Lanius collurio*) in an intensively used farmland. — The Ring 22: 89–93.
- Lefranc, N. & Worfolk, T. 1997: Shrikes. A guide to the shrikes of the world. Pica Press, Succex.
- Lefranc, N. 1997: Shrikes and the farmed landscape in France. — In Farming and Birds in Europe: The Common Agricultural Policy and its Implications for Bird Conservation, Vol. 1 (ed. Pain, D.J. & Pienkowski, M.W.): 236–268. Academic Press, London.
- Lima, S.L. 2009: Predators and the breeding bird: behavioral and reproductive flexibility under the risk of predation. — Biological reviews of the Cambridge Philosophical Society Cambridge Philosophical Society 84: 485–513.
- Lislevand, T. 2012: Habitat and nest placement of Redbacked Shrikes *Lanius collurio* breeding in clear-cuts in southern Norway. — Ornis Norvegica 35: 28–36.
- Manly, B.F.J., McDonald, L.L. & Thomas, D.L. 2002: Resource Selection by Animals: Statistical Design and Analysis for Field Studies. 2nd ed. — Kluwer Academic Publishers, The Netherlands.
- McCune, B. & Grace, J.B. 2002: Analysis of ecological communities. — MjM Software Design, Gleneden Beach, Oregon, USA.
- Morelli, F. 2011: Importance of road proximity for the nest site selection of Red-backed shrike (*Lanius collurio*) in an agricultural environment in central Italy. — Journal of Mediterranean Ecology 11: 21–29.
- Müller, M., Pasinelli, G., Schiegg, K., Spaar, R. & Jenni, L. 2005: Ecological and social effects on reproduction and local recruitment in the red-backed shrike. — Oecologia 143: 37–50.
- National Survey and Cadastre Denmark 2008: Proceedings of the 2nd NKG workshop on national DEMs. — Copenhagen, 11–13 November 2008, Technical report no. 04.
- Nikolov, B.P. 2000: An investigation of nest building and nests of the Red-backed Shrike (*Lanius collurio*) in Bulgaria. — The Ring 22: 133–146.
- Olsson, V. 1995a: The Red-backed Shrike *Lanius collurio* in southeastern Sweden: Habitat and territory. — Ornis Svecica 5: 31–41.
- Olsson, V. 1995b: The Red-backed Shrike Lanius collurio in southeastern Sweden: Breeding biology. — Ornis Svecica 5: 101–110.

- Pain, D.J. & Dixon, J. 1997: Why farming and birds in Europe? In Farming and Birds in Europe: The Common Agricultural Policy and its Implications for Bird Conservation, Vol. 1 (ed. Pain, D.J. & Pienkowski, M.W.): 1–24. Academic Press, London.
- Pihl, S., Clausen, P., Lauridsen, T.L., Madsen, J. & Bregnballe, T. 2006: Conservation status of bird spiecies in Denmark covered by the EU Wild Birds Directive. National Environmental Research Institute, NERI Technical Report no 570. URL: http://faglige-rapporter.dmu.dk
- Potter, C. 1997: Europe's changing farmed landscapes. In Farming and Birds in Europe: The Common Agricultural Policy and its Implications for Bird Conservation, Vol. 1 (ed. Pain, D.J. & Pienkowski, M.W.): 25– 42. Academic Press, London.
- R Development Core Team 2011: R: A language and environment for statistical computing. — R Foundation for Statistical Computing Vienna, Austria. URL: http://www.R-project.org
- Roos, S. & Pärt, T. 2004: Nest predators affect spatial dynamics of breeding red-backed shrikes (*Lanius collurio*). — Journal of Animal Ecology 73: 117–127.
- Safriel, U.N. 1995: What's special about shrikes? Conclusions and recommendations. — Proceedings Western Foundation Vertebrate Zoology 6: 299–308.
- Sell, H., Olsen, K., Vedel-Smith C. & Svendsen, J. 2013: Effects of anthropogenic disturbance on Red-backed Shrike (*Lanius collurio*) breeding in different habitat types. — Flora & Fauna 119: 55–64. (In Danish with English summary)
- Smith-Castro, J.R. & Rodewald A.D 2010: Behavioral responses of nesting birds to human disturbance along recreational trails. — Journal of Field Ornithology 81: 130–138.
- Söderström, B. 2001: Seasonal change in Red-backed

Shrike *Lanius collurio* territory quality – the role of nest predation. — Ibis 143: 561–571.

- Svenning, J.-C. 2002: A review of natural vegetation openness in north-western Europe. — Biological Conservation 104: 133–148.
- Titeux, N., Dufrene, M., Radoux, J., Hirzeld, A.H. & Defoumy, P. 2007: Fitness-related parameters improve presence-only distribution modelling for conservation practice: The case of the red-backed shrike. — Biological Conservation 138: 207–223.
- Tryjanowski, P., Kuzniak, S. & Diehl, B. 2000: Does breeding performance of Red-backed Shrikes *Lainus collurio* depend on nest site selection? — Ornis Fennica 77: 137–141.
- Tryjanowski, P., Karg, M.K. & Karg, J. 2003: Diet composition and prey choice by red-backed shrike *Lanius collurio* in western Poland. — Belgian Journal of Zoology 133: 157–162.
- Tucker, G.M. & Heath, M.F. 1994: Birds in Europe: their conservation status. — BirdLife International, Cambridge.
- Väli, Û. 2005: Habitat use of the Red-backed Shrike in Estonia. — Hirundo 18: 10–17.
- Vanhinsbergh, D. & Evans, A. 2002: Habitat associations of the Red-backed Shrike (*Lanius collurio*) in Carinthia, Austria. — Journal of Ornithology 143: 405–415.
- Vera, F.W.M. 2009: Large-scale nature development the Oostvaardersplassen. — British Wildlife 20: 28– 36.
- Vierling, K.T., Vierling, L.A., Gould, W.A., Martinuzzi, S. & Clawges, R.M. 2008: Lidar: shedding new light on habitat characterization and modeling. — Frontiers in Ecology and the Environment 6: 90–98.
- Wilson, J.P. & Gallant, J.C. 2000: Terrain analysis: principles and applications. — Wiley, New York.

Appendix 1. A full list of the plant species found in the nest scrub, nearest scrub and nearest thorny scrub and how they were grouped (ground-layer species, thornless species, thorny species). The last column (Occupancy%) presents the average percentage scrub occupancy volume in nest scrub (n = 20).

English name	Latin name	Author	Category	Occu- pancy%
Bird's-foot Trefoil	Lotus corniculatus	L.	Ground-layer	0.15
Buttercup	Ranunculus spp.	L.	Ground-layer	0.05
Cleavers	Galium aparine	L.	Ground-layer	0.60
Cock's-foot	Dactylis glomerata ssp. glomerata	L.	Ground-layer	0.30
Common Silverweed	Argentina anserina	(L.) Rydb.	Ground-layer	0.10
Common Stitchwort	Stellaria graminea	Ĺ.	Ground-layer	0.05
Common Toadflax	Linaria vulgaris	Miller	Ground-layer	0.05
Common Wormwood	Artemisia vulgaris	L.	Ground-layer	0
Common Yarrow	Achillea millefolium	L.	Ground-layer	0.05
Dandelion	<i>Taraxacum</i> spp.	Wigg.	Ground-layer	0.10
Dock	Rumex spp.	L.	Ground-layer	0.05
Fern	Polypodiopsida spp.	Ritgen	Ground-layer	0.10
Grasses	Poaceae spp.	L.	Ground-layer	1.35
Gypsy's Rose	Knautia arvensis	(L.) Coult.	Ground-layer	0
Harebell	Campanula rotundifolia	È.	Ground-layer	0.05
Hedge Parsley	Torilis japonica	(Houtt.) DC.	Ground-layer	0.25
Horsetail	Equisetum spp.	È.	Ground-layer	0.05
Lady's Bedstraw	Galium verum ssp. verum	L.	Ground-laver	0
Mint	Mentha spp.	L.	Ground-laver	0.25
Mosses	Bryopsida spp.		Ground-laver	0
Ragwort	Senecio spp.	L.	Ground-layer	0
Red Clover	Trifolium pratense	L.	Ground-laver	0
Ribwort Plantain	Plantago lanceolata	L.	Ground-laver	0
Rosebay Willowherb	Epilobium angustifolium	(L.) Scop.	Ground-laver	0.50
Soft Rush	Juncus effusus	Ĺ.	Ground-laver	0.45
Stinging Nettle	Urtica dioica	L.	Ground-laver	2.45
St. John's wort	Hypericum spp.	L.	Ground-laver	0
Thistle	Carduus spp.	L.	Ground-laver	0.05
Tufted Vetch	Vicia cracca	L.	Ground-laver	0.10
Violet	Viola spp.		Ground-laver	0.10
Birch	Betula spp.	L.	Thornless	0
Elder	Sambucus nigra	L.	Thornless	7.25
Bittersweet	Solanum dulcamara var. dulcamara	L.	Thornless	0.35
Crab Apple	Malus sylvestris	(L.) Mill.	Thornless	2.80
Honevsuckle	Lonicera periclymenum	Ĺ.	Thornless	4.25
Juniper	Juniperus communis	L.	Thornless	10.60
Mirabelle Plum	Prunus domestica ssp. svriaca	Janch.	Thornless	0.25
Oak	Quercus spp.	L.	Thornless	3.80
Sour Cherry	Prunus cerasus	L.	Thornless	0
Spindle	Euonymus europaeus	L.	Thornless	0
Unspecified tree	, , , , , , , , , , , , , , , , , , , ,		Thornless	0
Willows	Salix spp.	L.	Thornless	0
Blackberry	Rubus fructicosus	 .	Thorny	14.30
Hawthorn	Crataeous spp.		Thorny	0.15
Raspberry	Rubus idaeus	 L.	Thorny	0.20
Rose	Rosa spp.	 .	Thorny	15 75
Sloe	Prunus spinosa	L.	Thorny	33.60
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