Ornis Fennica 100: 00–00. 2023

Breeding biology of Red-backed Shrikes (*Lanius collurio*): distribution, performance and post-fledging survival in Denmark

Daniel A. F. Bloche*, Kasper Thorup, Kent Olsen, Per Ekberg, Peter Ellegaard Larsen, Knud-Erik Strange & Anders P. Tøttrup

D.A.F. Bloche, K. Thorup, A.P. Tøttrup, Natural History Museum of Denmark, University of Copenhagen, DK-1350 Copenhagen, Denmark
D.A.F. Bloche, Department of Evolutionary and Environmental Biology, University of Haifa, IL-3498838 Haifa, Israel
K. Olsen, Research and Collections, Natural History Museum Aarhus, DK-8000 Aarhus, Denmark
P. Ekberg, Caretaker Gribskov, Dansk Ornitologisk Forening, DK-3400 Hillerød, Denmark
P.E. Larsen, K.-E. Strange, Rørvig Fuglestation, DK-4581 Rørvig, Denmark
**Corresponding author's e-mail: danielbloche@hotmail.de*

Received 18 November 2022, accepted 10 May 2023

Agricultural intensification and habitat degradation across Europe have caused declines since the 20th century in populations of birds adapted to open landscapes, such as the Red-backed Shrike (*Lanius collurio*). Effective conservation strategies require knowledge on species' breeding biology. To understand the status of the Danish breeding population better, we investigate which factors affect their breeding parameter (*i.e.* distribution, performance, post-fledging survival and behaviour). Our focus on the post-fledging period addresses present knowledge gaps due to the importance of this, yet under-studied, phase of passerines' breeding cycle. We studied breeding pairs on different habitat types with Denmark-wide Citizen Science data, complemented by data of local projects in Northern Zealand and Northern Jutland (Denmark). Significantly fewer pairs were found in agricultural habitats and more in forests, semi-natural open habitats and synanthropic habitats. Pairs in forests had a significantly higher breeding productivity compared to agricultural or semi-natural open habitats for data from the years 2000 to 2021. Some project sites showed significantly higher number of fledglings compared to others, indicating that these sites are potential core areas for breeding productivity. Over the last two decades, the mean breeding productivity across Denmark was stable with 2.3 fledglings per successful pair. The survival rate of ringed fledglings increased during the post-fledging period, likely due to their increase in more active and independent behaviour. The relatively low breeding productivity found in this study calls for further studies including detailed data from potentially secondary habitats like agricultural areas to understand the effects of habitat on population fluctuations.

1. Introduction

Birds adapted to open landscapes inhabit nowadays mostly anthropogenic managed areas, in which intensified agricultural practices have caused degradation of suitable habitats and subsequent severe declines of these bird populations since the 20th century (Krebs *et al.* 1999, Tryjanowski *et al.* 2011, Bowler *et al*. 2021). Implementations of effective conservation strategies are crucial to prevent further population losses (Donald *et al.* 2001), which requires thorough knowledge on species biology, including detailed information on species specific environmental preferences (Titeux *et al*. 2007, Tryjanowski *et al.* 2011). Knowledge on breeding performance as well as post-fledging survival is important to fully understand mortality, dispersal and trends in avian populations (Anders & Marshall 2005, Hušek *et al*. 2012, Cox *et al.* 2014). Despite its importance for the first-year survival and consequently for the breeding performance (Marcum & Yosef 1998), the post-fledging period is under-studied across most passerines (Anders & Marshall 2005, Cox *et al.* 2014). Especially birds with short nestling periods depend on prolonged parental care during the post-fledging period (Grüebler & Naef-Daenzer 2010). The Red-backed Shrike (*Lanius collurio*, family Laniidae) stays only for a relatively short period of approximately two weeks in the nest. Hereafter follows the post-fledging period with prolonged parental care of the fledglings for approximately three to four weeks (Cramp & Perrins 1993). This study will pay particular attention to the post-fledging period to address knowledge gaps on this key period (Marcum & Yosef 1998).

The Red-backed Shrike is adapted to breed in open and semi-open habitats, with shrubs as perches for its hunting strategy as well as nest-site (Cramp & Perrins 1993). It mainly feeds on large invertebrates, which it catches and tears apart with a hooked bill and tomial tooth that all member of the Laniidae family developed (Yosef *et al.* 2020). In the anthropogenically altered landscape, it depends on the high abundance of invertebrates promoted by extensive land use and landscape heterogeneity (Brambilla *et al*. 2007, Titeux *et al.* 2007, Bakx *et al*. 2020). Therefore, Red-backed Shrikes can be considered as a good indicator species to evaluate landscape changes and nature management (Latus *et al*. 2004, Tryjanowski *et al.* 2011, Bech *et al.* 2020). Although the species is a long-distance migratory bird which only spends a relatively short period of its annual life cycle in the European breeding ground (Tøttrup *et al*. 2012), conditions in their breeding grounds seem to affect population developments strongly (Marcum & Yosef 1998). The populations of Red-backed Shrikes in Europe – as with most other members of the Laniidae family worldwide – have declined drastically due to landscape changes and increased mortality in their breeding range, along migration routes and in their wintering grounds (Marcum & Yosef 1998). The breeding distribution ranges across most parts of Europe and Western Siberia (Keller *et al*. 2020, Yosef *et al*. 2020), with the Danish population located on the north-western edge (Yosef *et al*. 2020). The species has become more widespread across Denmark since the 1970s (Vikstrøm & Moshøj 2020). However, it cannot be explained by an increasing Danish breeding population because during the same time the breeding population has not shown a positive trend (Grell 1998) and the numbers in point-count data have even declined (Heldbjerg & Fox 2008). Thus, changes in the habitat selection might explain better why Red-backed Shrikes became more widespread, which stresses the need to study differences in their breeding performance across habitat types.

The Red-backed Shrike is listed in the EU Birds Directive (EU 2009), emphasising conservation responsibilities in the European Union (EU). To implement effective conservation measures, a better understanding of its breeding biology, life history parameters and population trends is crucial (Greenwood 2007, Cox *et al.* 2014, Pedersen *et al*. 2018b). This study aims to address present knowledge gaps regarding major parts of the breeding biology of Red-backed Shrikes, focussing on the post-fledging period. In order to study this poorly understood phase of their breeding cycle, we combine Denmark-wide Citizen Science data from the ornithological web-portal DOFbasen (DOF 2020) with detailed studies from different sites in the region of Northern Zealand and Northern Jutland (Denmark) on breeding parameters, such as the distribution, performance (*i.e.* success and productivity), post-fledging survival and behaviour. We expect to deepen the knowledge on Red-backed Shrikes breeding biology in Denmark with these three objectives: 1) On a national scale we analyse the distribution of breeding pairs in different habitat types. Furthermore, we test on a local scale whether habitat type, breeding phenology or predation pressure effect their breeding performance. 2) In addition to analysing the mean breeding productivity between different sites and across Denmark, we give novel insights on the post-fledging survival of young Red-backed Shrikes. 3) During the post-fledging period, we describe the survival rate of fledglings and their behavioural activity. Knowledge gained from this study helps to improve our understanding of the status and trends of the Danish population of Red-backed Shrikes and can contribute to further develop effective conservation strategies to achieve objectives of passerine bird conservation within anthropogenically altered landscapes (Latus *et al*. 2004, Cox *et al*. 2014).

2. Materials and methods

2.1. Study area

This study combines data from two ecological scales in order to answer questions on Red-backed Shrikes breeding biology. On a national scale, we used Citizen Science data on breeding distribution and productivity across Denmark. On local scale, we used data on the breeding performance from various study site with different habitat types. Hulsig Hede (57°41′00″N, 10°28′00″E) in the northernmost part of Jutland and Melby Overdrev (56°01′00″N, 11°99′00″E) at the northern coast of Northern Zealand are both heathland-dune habitats surrounded by coniferous plantations. They differ in size and are respectively 35 km^2 and 2 km^2 large. Rørvig (55°97′00″N, 11°77′00″E) is a 6 km^2 large area in the north-western coast of Northern Zealand with heathland-dune habitats in the North and extensively managed pastures in the South. Gribskov (55°99′00″N, 12°29′00″E) is a 56 km^2 mixed forest area in Northern Zealand, consisting of several forest clearings. In the north-east part of Northern Zealand (55°87′00″N, 12°30′00″E), we studied breeding pairs using sites within the agriculture, which is with approximately 812 km^2 the dominant land cover type in this area.

2.2. Breeding distribution on different habitat types

To describe which habitat types are used by Red-backed Shrikes, breeding distribution across Denmark from data of the Third Danish Breeding Bird Atlas Survey for the years 2014 to 2017 (n = 1534 pairs, Vikstrøm & Moshøj 2020) was analysed. Classes of the Corine Land Cover (CLC) from 2012 in 100-metre resolution (CLC 2012) were grouped into the three main habitat types used in this study – forests (CLC classes: forests, woodland-shrubs), agricultural habitats (CLC classes: agriculture and natural vegetation, arable land, complex cultivation pattern, pastures, fruit trees) and semi-natural open habitats (CLC classes: beach and dunes, moors and heathlands, natural grasslands, wetlands) – as well as into synanthropic habitats (CLC class: artificial surfaces). A random distribution pattern was created by simulating 1534 random points 1000-times across Denmark. The percentage of the random and observed breeding pair points in each habitat type were calculated by spatial analyses and compared by conducting a Chi-square test.

2.3. Potential factors affecting breeding success and productivity

During the breeding season from May to August 2021, detailed data on the breeding biology of Red-backed Shrikes was collected. To find territories of breeding pairs, forest clearings in Gribskov and the heathland-dune area at Melby Overdrev were visited and locations of observed breeding pairs were collected to later search for their nest. In the agricultural landscape matrix of Northern Zealand, we used old breeding sites from Citizen Science data and revisited these sites to search for breeding pairs and later for their nest. To reveal differences in breeding success, we compared the percentage of pairs observed with fledglings from the total number of breeding pairs found with established territories at each study site (n = 72 pairs). Unsuccessful pairs which either lost or abandoned their brood, did not show any behaviour indicating the presence of fledglings for at least two subsequent visits.

In order to test which factors can explain the variation in number of fledglings, we used a Generalized Linear Model (GLM) of the Poisson family to test three factors: (1) The main breeding habitat type. (2) The breeding start, indicated by the hatching date which was estimated based on the age of the ringed nestlings (n = 34 individuals, Olsson 1995, Van den Burg 2011). For individuals that were found after fledging (n = 16 individuals), their age was estimated in an approximate interval (three to seven days), following a guide based on morphological changes in fledglings with known age (Bloche 2023, in prep.). (3) The predation risks at each site, calculated as observation per hour of the main avian predators for their young – Eurasian Magpie (*Pica pica*), Eurasian Jay (*Garrulus glandarius*), Hooded Crow (*Corvus cornix*) and Eurasian Sparrowhawk (*Accipiter nisus*, Matyjasiak 1995, Söderström & Karlsson 2011, Van den Burg 2011).

Additionally, we combined this detailed field study with data on the breeding productivity from other project sites, Rørvig (n = 55 pairs for the years 2016 to 2021) and Mols Bjerge (n = 20 pairs for the years 2010 to 2011), as well as previous study years at Gribskov (n = 553 pairs for the years 2006 to 2011 and 2018 to 2021). We included also long-term Citizen Science data in form of breeding bird observations ("Ynglepar Observationer") with comments on the number of fledglings collected from DOFbasen for the years 2000 to 2021 (n = 351 pairs, DOF 2020). We identified the main habitat types for the breeding bird observations from DOFbasen using their reported location and recent aerial images in 0.6-metre resolution (Esri Inc. 2021). With this larger data set we tested three factors: (1) The main breeding habitat type. (2) The variation in mean breeding productivity between years. (3) The mean breeding productivity for each area (Gribskov, Rørvig, Mols Bjerge and Denmark-wide) and its variation between the years from 2018 to 2021.

2.4. Post-fledging survival

To study post-fledging survival, nestlings were ringed with metal- and colour-ring combinations below their tarsi at the age of approximately eight days to allow individual recognition of birds in the field after fledging (Van den Burg 2011). At the age of two weeks, the young fledge but stay together in family groups for around four more weeks until they disperse or initiate autumn migration (Cramp & Perrins 1993). During that post-fledging period, fledglings were resighted every second to fourth day, using binoculars, telescope and camera. Detection probability and apparent survival rate were calculated by running "Young Survival for marked adults" models, an extension to the Cormack-Jolly-Seber model, with encounter histories for each pair (Cooch 2008). The detection probability describes the likelihood of observing an individual at each visit. We used a constant detection probability to study the variation in apparent survival rate, the probability that an individual is still alive at each age stage. From the apparent survival rate for each age, we calculated the survival over the study period (8 to 44 days after hatching) which indicates the post-fledging survival.

2.5. Post-fledging behavioural activity

Fledgling activity during the post-fledging period was studied by collecting different behavioural traits during the post-fledging period: non-familiar mixing between fledglings, maximum flying distances and different types of hunting attempts. Flying and hunting behaviour were used to create an activity score from 0 (no activity) to 5 (Table 1). The relationship between fledglings' activity score and their age in days was tested with a GLM. ANOVA and further Tukey's post-hoc tests analysed the significance of the regression. The frequency of the observed values for each behavioural trait was analysed along different age. For flying behaviour, natural groups of 15- to 30- and 31- to 44-day-old birds were observed within the data, and therefore tested for significant differences by using a Chi-square test. For the non-familiar mixing of fledglings, the percentage of pairs with mixing fledglings was calculated for each age in days after hatching of the young. We did a GLM and ANOVA test for significance of the regression. To additionally describe behavioural changes in a spatial context, the maximal distance to the nest-site of each fledgling was calculated and compared between the nest visits.

All statistical analyses were performed in R (R Core Team 2021) and $p < 0.05$ was set as the significance level. Survival analyses from the resighting data of ringed fledglings were performed in the program MARK 9.0 (White 2021) and spatial analyses in ArcGIS 10.6.1 (Esri Inc. 2021).

Table 1. Values in the activity score from flying and hunting behaviour for the ringed fledglings at the project sites Gribskov, Melby Overdrev and agricultural habitats in Northern Zealand for the year 2021 (n = 74 observation visits).

Activity score	Flying behaviour	Hunting behaviour
0	No	No
1	< 2 metres	No
2	> 2 metres	No
3	> 2 metres	Unsuccesful try
4	> 2 metres	Succesful try
5	> 2 metres	Contant over longer periods

3. Results

3.1. Breeding distribution on different habitat types

Compared to expected by a random distribution, significantly fewer breeding pairs of Red-backed Shrike used agricultural habitats whereas more pairs used forests, semi-natural open habitats ($p < 0.001$ for the three habitat types) and synanthropic habitats ($p < 0.01$, Fig. 1, Table S2). However, most breeding sites were located in agricultural dominated areas, 44%, as this is the dominating available habitat type. Whereas, 30% of the breeding sites were in forests and less than 20% in semi-natural open habitats.

3.2. Potential factors affecting breeding success and productivity

We found a significantly ($p < 0.001$) higher breeding site fidelity in the forest areas compared to agricultural habitats between the year 2021 and previous years. Whereas 82% of the forest clearings with breeding pairs in the last years also had pairs during the territory search in this study, previous breeding sites within agricultural habitats only contained in 17% of the sites still breeding pairs this year. Furthermore, breeding pairs in forest areas had a significantly ($p < 0.05$) higher breeding success compared to agricultural and semi-natural open habitats, where more than half of the breeding pairs abandoned or lost their brood (Table 2).

Table 2. Success of finding possible breeding birds during the territory search in different habitat types: Agricultural habitat includes sites visited in agricultural habitats of Northern Zealand (n = 29), forest clearing includes the sites in Gribskov (n = 33) and heathland and dune only the one site Melby Overdrev (n = 10). All sites visited from May to August 2021. Chi-square test to calculate p-value with significance values (0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ').

Habitat type	Sites with possible breeding birds	Successful breeding pairs
Agricultural habitat	17%	40%
Forest clearing	82%	63%
Heathland and dune	–	44%
p-value (Chi-square test)	<0.0001 ***	0.046 *

The breeding productivity (*i.e.* number of fledglings) of successful pairs differed significantly between habitat types and years (respectively $p < 0.001$, Table S3). Pairs in forest clearings produced significantly more fledglings compared to pairs in agricultural habitats and semi-natural open habitats ($p < 0.001$), but no difference was found between the latter two habitat types (Fig. 2, Table S4). However, when analysing only data from the 1-year study in the year 2021, none of the three factors explained variations in the number of fledglings significantly (habitat type: $p = 0.83$, hatching date: $p = 0.99$, potential avian predators per hour: $p = 0.78$, Table S5). The mean hatching date was 5.5 days earlier in Gribskov than in the agricultural and semi-natural open habitats, however, the difference was not significant ($p = 0.39$, Table S6).

Denmark-wide Citizen Science data and local project data for the years 2018 to 2021 showed significant differences in the mean number of fledglings of successful pairs between areas ($p < 0.001$). Pairs in Gribskov had with 3.6 fledglings (se = 0.36) a significantly ($p < 0.001$) higher

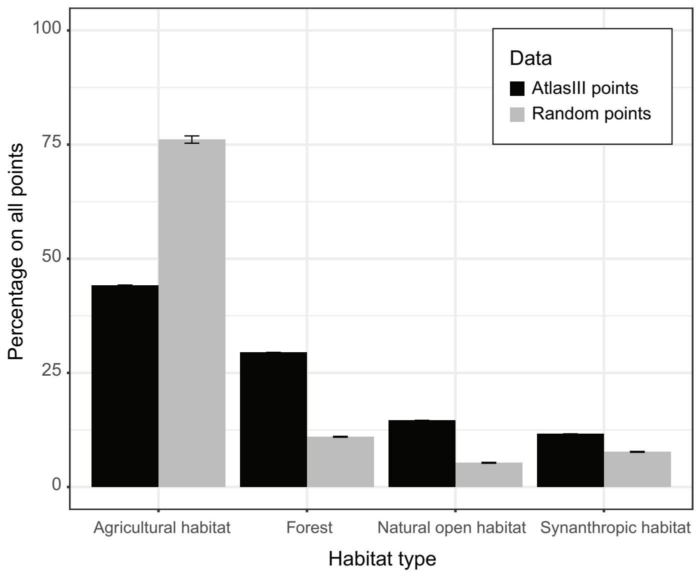

Fig. 1. Bar plot, comparing the percentage of points from breeding pairs of Red-backed Shrikes in the Third Danish Breeding Atlas Survey for the years 2014 to 2017 (AltasIII, black bars, n = 1534 pairs, Vikstrøm & Moshøj 2020) and mean of the 1000 times simulated random points (grey bars with standard error, n per simulation = 1534) in different habitat types of the Corine Land Cover data from the year 2012 (Table S1, CLC 2012).

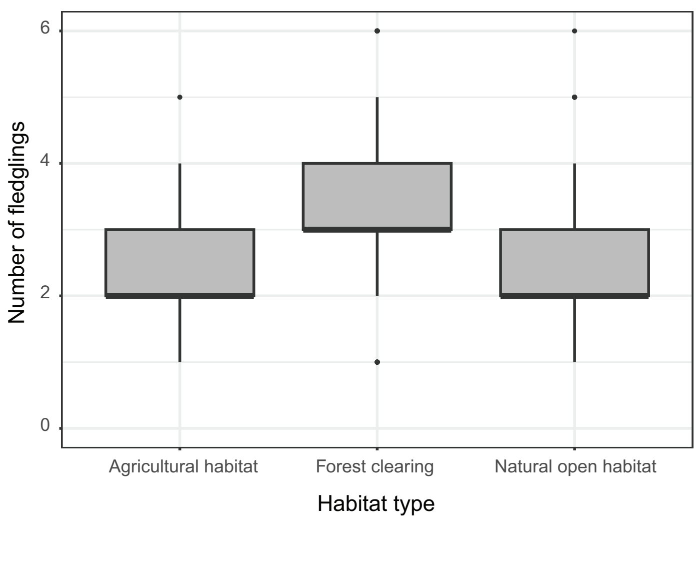

Fig. 2. Number of Red-backed Shrike fledglings in different habitat types for the years 2000 to 2021. Boxplot showing median (bold black line), 25th to 75th percentile interquartile range (grey box), largest values within 1,5 times interquartile range (vertical black line) and residuals outside this range (black dot) for the number of fledglings in agriculture, forest clearings and semi-natural open habitats from DOFbasen data from the years 2000 to 2021 (n = 351 pairs, DOF 2020), as well as project data from Rørvig for the years 2016 to 2021 (n = 55 pairs), Gribskov for the years 2006 to 2011 and 2018 to 2021 (n = 553 pairs), Melby Overdrev for the year 2021 (n = 4 pairs) and the agricultural landscape in Northern Zealand for the year 2021 (n = 2 pairs).

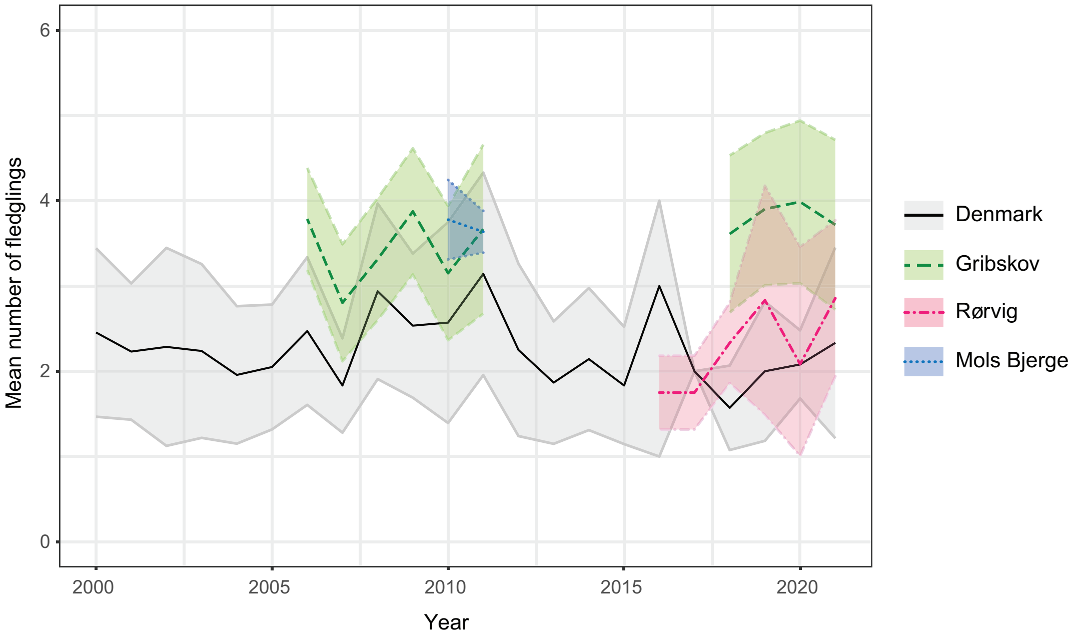

Fig. 3. Changes in mean number of fledglings of Red-backed Shrikes from the years 2000 to 2021 (means shown as lines and standard errors shown as shaded areas). Data of Denmark-wide breeding bird observations from DOFbasen (black solid line and grey area, n = 351 pairs, DOF 2020) are shown for the entire period, data from Rørvig (red dash-dotted line and area, n = 55 pairs) from the years 2016 to 2021, data from Mols Bjerge (blue dotted line and area, n = 20 pairs) from the years 2010 to 2011 and data from Gribskov (green dashed line and area, n = 553 pairs) from the years 2006 to 2011 and 2018 to 2021.

mean breeding productivity compared to pairs from DOFbasen data across Denmark and project data from Rørvig, with respectively 2.3 fledglings (se = 0.39, 0.45, Fig. 3, Tables S7 and S8). Denmark-wide, the mean breeding productivity shows a stable trend over the last two decades, though with some yearly fluctuation.

3.3. Post-fledging survival

All eight pairs with ringed nestlings were successful in producing at least one fledgling. The young survival model calculated a constant detection probability of 0.77 (se = 0.03). The model using this constant detection probability had an AIC value of 237.6, which is 1.8 AIC points better than the AIC value of the model with an age-dependent detection probability (Table S9). Therefore, we calculated the likelihood of surviving each day, the apparent survival rate, with the constant detection probability. The apparent survival rate increased logistically with the age of the young (Fig. 4). Over the study period, the young had a survival rate of 0.73 (se = 0.07).

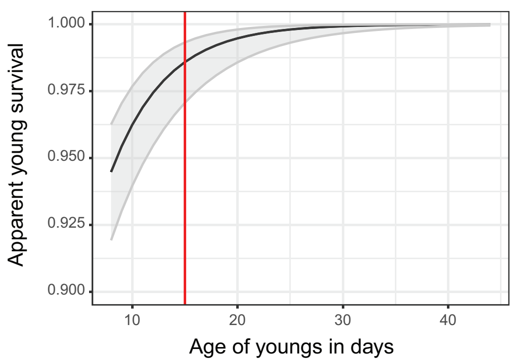

Fig. 4. Apparent survival rate (black line) with limits of lower and upper 95% Confident Interval (grey area) of 8- to 44-day-old Red-backed Shrikes for data from Gribskov, Melby Overdrev and agricultural habitats in Northern Zealand for 2021 (n = 74 pairs). The red vertical line indicates the age they usually fledge (15 days after hatching, Cramp & Perrins 1993).

3.4. Behavioural activity during the post-fledging period

The fledglings' activity increased significantly ($p < 0.001$) during the post-fledging period, with significant ($p < 0.05$) differences between pairs (Fig. 5, Table S10). A significant ($p < 0.001$) increase in long flying distances was found two weeks after fledging (Fig. S1, Table S11). Moreover, fledglings start to forage more independently with days passing since they left the nest: first successful hunting attempts were observed after 22 days and at least 35-day-old birds hunted constantly over longer periods (Fig. S2). Two weeks after leaving the nest, fledglings were observed further than 200 metres away from the nest site, while they stayed within that radius before. At the same time fledglings were observed more often to mix between non-familiar members. The percentage of pairs with fledglings that non-familiar mix increased significantly ($p < 0.001$) over the post-fledging period (Fig. 6, Table S12).

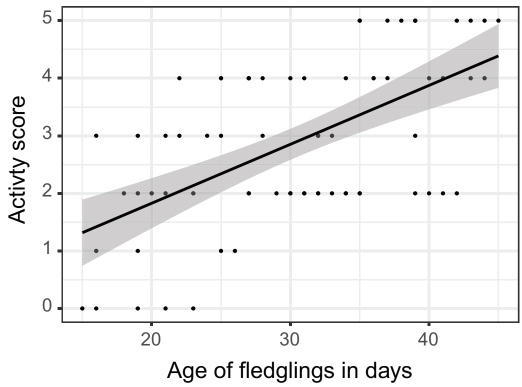

Fig. 5. Activity score (from 0 to 5, Table 1), calculated using flying and hunting behaviour of Red-backed Shrike fledglings with different age in days, for data from Gribskov, Melby Overdrev and agricultural habitats in Northern Zealand for the year 2021 (n = 74 pairs). Regression line was calculated using a Poisson Generalized Linear Model (black line) with standard error (grey area).

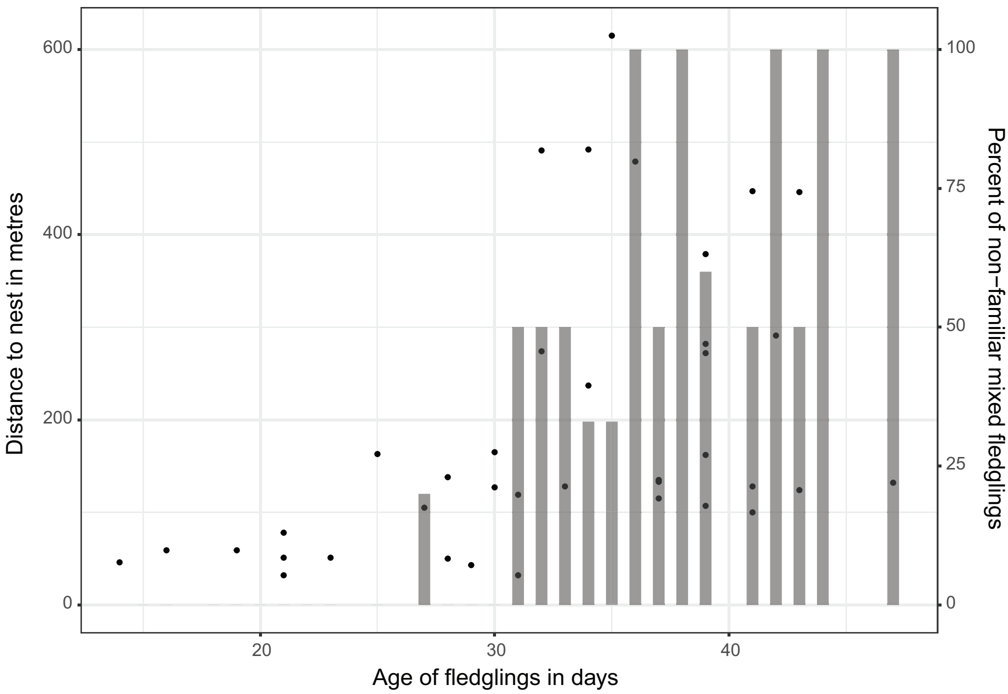

Fig. 6. Observed maximal distance to the nest in metres of Red-backed Shrikes fledglings (black points) and the percentage of pairs observed with non-familiar mixed fledglings (grey bars) across different age in days for data from Gribskov, Melby Overdrev and agricultural habitats in Northern Zealand for the year 2021 (n = 74 pairs).

4. Discussion

4.1. Effects of habitat types on breeding distribution and breeding performance

In this study, Red-backed Shrikes were found significantly more often in forests, semi-natural open habitats and synanthropic habitats but less often in agricultural habitats than expected from a random distribution. Significantly higher probability of occupying previous territories again and the earlier mean hatching date in forests further indicates a preference for nest-sites in this habitat, since territories of higher habitat quality are usually occupied first and over several years (Marcum & Yosef 1998, Söderström & Karlsson 2011). Söderström & Karlsson (2011) found this shift to higher occurrence in forests also for Red-backed Shrikes in Sweden and it can also be found in other birds which were previously mainly found in farmlands, like the yellowhammer (*Emberiza citrinella*) and the Eurasian wryneck (*Jynx torquilla*, Söderström & Karlsson 2011, Bakx *et al*. 2020). Although this study is limited by the low resolution of CLC data (Matyjasiak 1995), several studies also revealed that Red-backed Shrikes avoid arable land as well as prefer heterogenous and extensively managed habitats, like forests (Marcum & Yosef 1998, Vanhinsbergh & Evans 2002, Latus *et al*. 2004, Golawski & Golawska 2008, Morelli *et al*. 2012, Bakx *et al*. 2020). Furthermore, the importance of suitable habitat types is underlined by the link of local population declines to landscape changes (Kuper *et al.* 2000, Tryjanowski *et al*. 2006, Morelli *et al*. 2016, Tellería 2018).

Results in this study indicate that habitat types also influence the breeding performance of Red-backed Shrikes, besides their distribution. A significantly higher number of successful breeding pairs were found in forests compared to agricultural or semi-natural open habitats. Moreover, the breeding pairs in forests produced more fledglings. Most studies on post-fledging survival of passerines found effects of the habitat type (Cox *et al.* 2014) and other studies on Red-backed Shrikes also support that habitats with high heterogeneity have positive effects on both, the breeding success and productivity, while intensive agriculture has negative effects (Matyjasiak 1995, Golawski & Meissner 2008, Söderström & Karlsson 2011). However, the effect of breeding productivity was only significant for the larger dataset and not from the 1-year study solely, likely due to fluctuations of productivity between years and bias caused by a small sample size (Schmidt *et al.* 2008). It is noteworthy, that also our data on breeding success was limited by a small sample size (n = 72 pairs) due to the lack of certain failure records in larger data sets.

Distribution and breeding performance of Red-backed Shrikes might differ between habitat types because of differences in food abundance and availability, as well as the predation risk (Roos 2002, Pedersen *et al*. 2012). Heterogeneous and extensively managed semi-natural open habitats are correlated with high invertebrate richness and abundance (Latus *et al*. 2004, Bech *et al*. 2020). Windthrows or artificial clearings within forests create sun-exposed patches which can act as invertebrate biodiversity hot spots (Bouget & Duelli 2004), while farmlands show a vast decline in invertebrate biodiversity (Stoate *et al*. 2001). Moreover, Red-backed Shrikes are adapted to these heterogeneous forest-steppe habitats with perches and open patches, which are crucial for their hunting strategy (Baláž 2007, Svendsen *et al*. 2015, Morelli *et al*. 2016). Although our data on avian predators was too limited, other studies found that the higher abundance of Eurasian Magpie, Hooded Crow and Eurasian Jay in farmland territories increase the predation risk (Söderström 2001). Nest-sites in spatially aggregated shrub patches within open habitats are likely also more conspicuous for nest predators (Matyjasiak 1995, Roos 2002, Söderström & Karlsson 2011).

4.2. Mean breeding productivity and post-fledging survival at different sites and across Denmark

This study revealed a stable but striking low mean breeding productivity of 2.3 fledglings per successful breeding pair across Denmark. To compensate for mortality and maintain a stable population each pair should produce between 2.3 and 3.0 fledglings per year (Jakober & Stauber 1987, Ryttman 1996, Hemerik *et al*. 2015). It is noteworthy that these studies also include unsuccessful pairs with no fledglings, which usually leads to a severely lower number than by including solely successful pairs, as done in our study (Olsson 1995). Other stable populations across Europe show a remarkable higher breeding productivity of 3.6 to 4.4 fledglings per successful pair (Jakober & Stauber 1987, Kuźniak 1991, Olsson 1995, Horvath *et al.* 2000, Jørgensen *et al.* 2013, Hemerik *et al.* 2015, Table S13). Nevertheless, our results on Denmark-wide productivity should be treated as a minimum number, since Citizen Science data does not consist of a targeted effort, likely necessary for an accurate monitoring (Ekberg *et al.* 2011). Moreover, the high standard error in the data indicates variation between sites and fluctuation over the years, due to varying environmental factors (Schmidt *et al.* 2008).

Spatial variation in the breeding productivity of Red-backed Shrikes can be also explained by potential core areas, besides solely the habitat types. High breeding productivity of pairs in forest clearing of Gribskov, but also in the extensively managed dune-heathland and grassland areas Hulsig Hede (Jørgensen *et al.* 2013) and Mols Bjerge, indicates that potential core areas can be also found in semi-natural open habitats. In these sites, we found a higher mean breeding productivity compared to Denmark-wide data and Rørvig, despites the also high breeding pair abundance at Rørvig. The data from Hulsig Hede and Mols Bjerge was not suitable for statistical comparisons because it was recorded over different and shorter time periods. For Gribskov the difference was significant, which supports statistical evidence that this site is likely a core area regarding breeding productivity. Furthermore, the low return rates of individuals with geolocators and colour-rings in previous studies (Tøttrup *et al.* 2017, Pedersen *et al.* 2018a) could reveal a connectivity of Gribskov to a larger metapopulation. A low breeding site fidelity, caused by this connectivity, was also seen in other local populations with high reproductive success (Geertsma *et al.* 2000, Tryjanowski *et al.* 2007). The high importance of Gribskov as a breeding location could be explained because it is a relatively large forest on Danish scale and contains many grazed clearings with deadwood, which show an especially high habitat quality over many years (Ekberg *et al.* 2011, Overballe-Petersen *et al.* 2014, Bakx *et al.* 2020). Also, the predation risk is lower in patches within large forests than along the forest edge, because many nest predators are adapted to forage and breed in habitat edges (Matyjasiak 1995, Roos 2002). Potential core areas might improve the breeding productivity also due the high density and clustering of breeding pairs (Fornasari *et al.* 1994). For true colonially nesting passerines like Fieldfares (*Turdus pilaris*), it has been shown that larger colonies are more effective in defending their nests (Wiklund & Andersson 1994). Cooperative nest defence was not observed for Red-backed Shrikes in this study, nevertheless, we could expect a similar increase of warning and aggression intensity against potential predators by their higher breeding pair density (Tryjanowski & Golawski 2004). However, it is important to consider possible observer bias as a reason for the high breeding productivity in Gribskov. Ekberg *et al.* (2011) argued that targeted monitoring is important for obtaining accurate data on the number of fledglings and showed that more pairs were found with improved monitoring efficiency. While this may explain differences between targeted project sites and the Denmark-wide Citizen Science data, it cannot explain the differences between sites with targeted monitoring projects, like Gribskov and Rørvig.

In order to estimate the required productivity for maintaining a stable population, post-fledging survival rates are important to consider (Hušek *et al.* 2010). In this study, all pairs with ringed nestlings were successful in producing fledglings and had a high young survival of 0.73 (se = 0.07) over the study period, which can be used as an indication for their post-fledging survival. Other studies calculated lower post-fledging survival rates, between 0.48 and 0.62 (Baláž 2007, Hušek *et al.* 2010). Certainly, the results in this study are not representative for the entire Danish population, rather for a local population in Northern Zealand, mainly Gribskov. Therefore, further studies are needed on a larger scale.

4.3. Survival rate and behavioural activity during the post-fledging period

Our data on the previously under-studied post-fledging period (Anders & Marshall 2005, Cox *et al.* 2014) revealed linked pattern in survival and behaviour of young Red-backed Shrikes. The characteristics of mark-resighting models without known fate do not allow to date mortality events with a high accuracy (Cooch 2008), but our results showed the highest mortality during the few days of transition from nestling to fledgling and first days in their natal territories. This pattern is also found in studies on the Great Grey Shrike (*Lanius excubitor*, Yosef 1993) and other passerines (Yackel *et al*. 2006), particularly in species with short nestling periods (Cooch 2008, Cox *et al*. 2014). The increasing apparent survival rate of young Red-backed Shrikes could be explained by the decrease in vulnerability to predation, bad weather and starvation due to their increasing behavioural activity and gradual independence from parental care. This study reveals a significant increase in the activity of the fledglings, especially in more independent behavioural traits, such as flying and hunting. Comparable behavioural studies have only been conducted on Woodchat Shrikes (*Lanius senator*), a closely related species with similar ecology but more southern distribution, and showed similar results (Marcum & Yosef 1998, Nikolov & Hristova 2007). Higher behavioural activity can mostly be explained by the progression in growth of their flight feathers, which is completed three to four weeks after hatching (Cramp & Perrins 1993, Nikolov & Hristova 2007). This study showed that Red-backed Shrikes can start self-feeding already one week after fledging, four days earlier than described by Cramp & Perrins (1993). Despites these early successful hunting attempts, they still depend on parental care until they fully learn the hunting techniques as well as develop their hooked bill and tomial tooth (Cramp & Perrins 1993, Nikolov & Hristova 2007). Extended post-fledging parental care is costly, but for passerines with short nestling periods, like the Red-backed Shrike (Cramp & Perrins 1993), it is substantially increasing young survival during the most vulnerable period (Grüebler & Naef-Daenzer 2010).

Two weeks after fledging, the Red-backed Shrikes started to spread out over 200 metres away from the nest and mix with fledglings from other families. At a similar age, Woodchat Shrikes also show increasing intra- and interspecific interactions, including with non-family members (Nikolov & Hristova 2007). Other studies on Red-backed Shrikes only showed an increasing overlap in the territories of adults (Fornasari *et al*. 1994, Marcum & Yosef 1998) and that fledglings start to disperse further away from the nest-site (Cramp & Perrins 1993, Olsson 1995). This dispersal could be a response to the predation pressure in their natal territories (Yosef 1993), first post-fledgling exploration movements (Baker 1993) or a response to the decrease in male territory defence which allows fledglings to mix between families and in some cases even leads to shared parental care (Fornasari *et al*. 1994).

5. Conclusion

This study revealed that especially forest clearings and to a certain degree also other heterogenous, extensively managed open habitats have positive effects on the breeding distribution, success and productivity of Red-backed Shrikes. Breeding productivity also differs between study areas, indicating the importance of potential core areas, like Gribskov, Hulsig Hede or Mols Bjerge in Denmark. Further studies should investigate these core areas and their importance as a potential population source. The low mean breeding productivity across Denmark emphasises the need for further studies including data on complete nest losses and the post-fledging survival on a larger scale (Cox *et al*. 2014). To fully understand what affects their breeding performance also other potential factors, like weather conditions and predation risk, needs to be considered over their entire annual life cycle (Tøttrup *et al*. 2012, Jørgensen *et al*. 2013, Bech *et al*. 2020). In this study, both the fledglings' behavioural activity and survival rate increased gradually during the post-fledging period. The higher activity of fledglings indicates their decreasing dependency on parental care, which explains the increasing survival rate. Also, changes in their spatial pattern and social interactions are closely linked to behavioural changes. It is important to further understand and describe complex behavioural changes during the post-fledging period to understand the post-fledging survival better, which is directly linked to the breeding productivity (Anders & Marshall 2005, Nikolov & Hristova 2007).

Pikkulepinkäisen (*Lanius collurio*) lisääntymisbiologia: levinneisyys, lisääntyminen ja lentopoikasvaiheen eloonjääminen Tanskassa

Maatalouden tehostaminen ja elinympäristöjen heikentyminen Euroopassa ovat 1900-luvulta lähtien vähentäneet avoimiin maisemiin sopeutuneiden lintujen, kuten pikkulepinkäisen (*Lanius collurio*), populaatioita. Niiden tehokas suojelu edellyttää kuitenkin tietoa lajin lisääntymisestä. Tässä tutkimuksessa keskityimme erityisesti siihen, mitkä tekijät vaikuttavat pikkulepinkäisen pesintään liittyviin muuttujiin, kuten levinneisyyteen, suorituskykyyn, sekä pesinnänjälkeiseen eloonjäämiseen ja käyttäytymiseen. Keskityimme erityisesti lentopoikasvaiheeseen, sillä vaikka se on tärkeä vaihe lisääntymisen kannalta, sitä ei ole tutkittua paljoa. Tutkimusaineistomme koostui eri elinympäristötyypeissä pesivistä pareista, ja sen havainnot perustuivat koko Tanskan kattavaan kansalaistieteelliseen aineistoon. Lisäksi aineistoa täydennettiin Pohjois-Sjellannin ja Pohjois-Jyllannin paikallisprojektien tiedoilla. Pikkulepinkäispareja löydettiin merkittävästi vähemmän maatalousympäristöistä ja toisaalta enemmän metsäisistä, osittain luonnontilaisista avoimista ja synantrooppisista (ns. ihmisen luomista) elinympäristöistä. Metsissä pesivien parien tuottavuus oli huomattavasti korkeampi kuin maatalouympäristöissä tai osittain luonnontilaisissa avoimissa elinympäristöissä pesivien parien tarkastelujaksolla 2000–2021. Joissakin tutkimuskohteissa poikasia syntyi huomattavasti keskimääräistä enemmän, mikä viittaa siihen, että alueet ovat pesinnän ydinalueita. Keskimääräinen poikastuottavuus on ollut vakaa Tanskassa kahden viime vuosikymmen ajan: 2.3 poikasta paria kohden. Rengastettujen poikasten eloonjäämistodennäköisyys parani lentopoikasvaiheen jälkeisenä aikana, johtuen todennäköisesti niiden aktiivisemman ja itsenäisemmän käyttäytymisen lisääntymisestä. Tässä tutkimuksessa havaittu suhteellisen alhainen poikastuottavuus vaatii kuitenkin lisätutkimusta ja tarkempaa aineistoa mahdollisista toissijaisista elinympäristöistä (esim. maatalousalueet), jotta saamme paremman kokonaiskuvan elinympäristöjen vaikutuksesta pikkulepinkäispopulaatioiden vaihteluihin.

Acknowledgements. We are grateful for the financial support from the Scientific Committee at Dansk Ornitologisk Forening (DOF), which made the fieldwork possible. Citizen Science data is an important part of this study and therefore we also need to thank every volunteer, who entered records of breeding Red-backed Shrikes on DOFbasen. Further thanks go to Morten Bentzon Hansen for the opportunity to use netfugl.dk as a platform to call for Citizen Science effort, as well as to Daniel Palm Eskildsen for providing us with the breeding locations of Red-backed Shrikes from the Danish Breeding Bird Atlas.

References

Anders, A. D., & Marshall, M. R. 2005: Increasing the accuracy of productivity and survival estimates in assessing landbird population status. — Conservation Biology 19(1): 66–74. https://doi.org/10.1111/j.1523-1739.2005.00543.x

Baker, R. R. 1993. The function of post-fledging exploration: a pilot study of species of passerines ringed in Britain. — Ornis Scandinavica 24: 71–79. https://doi.org/10.2307/3676413

Bakx, T. R., Lindström, Å., Ram, D., Pettersson, L. B., Smith, H. G., van Loon, E. E., & Caplat, P. 2020: Farmland birds occupying forest clear-cuts respond to both local and landscape features. — Forest Ecology and Management 478: 118519. https://doi.org/10.1016/j.foreco.2020.118519

Baláž, M. 2007: On the breeding biology of the Red-backed Shrike (*Lanius collurio*) in the windbreaks of sw slovakia. — Acta Zoologica Universitatis Comenianae, 47(1): 35–39.

Bech, J., Graubæk, P., Larsen, P. E., Strange, K.-E. & Valeur, B. 2020: Rødrygget Tornskade på Rørvighalvøen 1973–2020. Bestandsudvikling og målrettet naturpleje. (In Danish)

Bouget, C., & Duelli, P. 2004: The effects of windthrow on forest insect communities: a literature review. — Biological Conservation 118(3): 281–299. https://doi.org/10.1016/j.biocon.2003.09.009

Bowler, D., Richter, R. L., Eskildsen, D., Kamp, J., Moshøj, C. M., Reif, J., Strebel, N., Trautmann, S. & Voříšek, P. 2021: Geographic variation in the population trends of common breeding birds across central Europe. — Basic and Applied Ecology 56: 72–84. https://doi.org/10.1016/j.baae.2021.07.004

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(2): 160–167. https://doi.org/10.1080/00063650709461471

Cooch, E. 2008: Program MARK, A gentle introduction. Available at http://www.phidot.org/software/mark/docs/book

Corine Land Cover (CLC) 2012: CLC Version 2020_20u1. — Copernicus Land Monitoring Service, European Environment Agency (EEA). Available at http://land.copernicus.eu/pan-european/corine-land-cover/clc-2012/view. Accessed 1.9.2021.

Cox, W. A., Thompson III, F. R., Cox, A. S., & Faaborg, J. 2014: Post-fledging survival in passerine birds and the value of post-fledging studies to conservation. — The Journal of Wildlife Management 78(2): 183–193. https://doi.org/10.1002/jwmg.670

Cramp, S. & Perrins, C.M. (eds) 1993: The Birds of the Western Palearctic. Vol. 7. — Oxford University Press, Oxford.

DOF 2020: DOFbasen. Available at https://dofbasen.dk/observationer. Accessed 15.9.2020.

Donald, P. F., Green, R. E., & Heath, M. F. 2001: Agricultural intensification and the collapse of Europe's farmland bird populations. — Proceedings of the Royal Society of London. Series B: Biological Sciences 268(1462): 25–29. https://doi.org/10.1098/rspb.2000.1325

Ekberg, P., Petersen, T. L., Jørgensen, P. S. & Tøttrup, A. P. 2011: The breeing population of Red-backed Shrike *Lanius collurio* in Gribskov, Denmark. — Dansk Ornilogisk Foreningen Tidsskrift 105: 179–182.

Esri Inc. 2021: ArcGIS Desktop 10.6.1: ArcMap and ArcCatalog. — Available at https://www.esri.com. Accessed 1.9.2021.

European Union (EU) 2009: Directive 2009/147/EC on the conservation of wild birds.

Fornasari, L., Bottoni, L., Sacchi, N., & Massa, R. 1994: Home range overlapping and socio-sexual relationships in the Red-backed Shrike *Lanius collurio*. — Ethology Ecology & Evolution 6(2): 169–177. https://doi.org/10.1080/08927014.1994.9522992

Geertsma, M., van Berkel, H., & Esselink, H. 2000: Are high fitness values sufficient to maintain a Dutch population of the Red-backed Shrike (*Lanius collurio*). — Ring 22(1): 79–88.

Golawski, A., & Golawska, S. 2008: Habitat preference in territories of the Red-backed Shrike *Lanius collurio* and their food richness in an extensive agriculture landscape. — Acta Zoologica Academiae Scientiarum Hungaricae 54(1): 89–97.

Goławski, A., & Meissner, W. 2008: The influence of territory characteristics and food supply on the breeding performance of the Red-backed Shrike (*Lanius collurio*) in an extensively farmed region of eastern Poland. — Ecological Research 23(2): 347–353. https://doi.org/10.1007/s11284-007-0383-y

Greenwood, J. J. 2007: Citizens, science and bird conservation. — Journal of Ornithology 148(1): 77–124. https://doi.org/10.1007/s10336-007-0239-9

Grell, M. B. 1998: Fuglenes Danmark: de danske fugles udbredelse, tæthed, bestandsforhold og udviklingstendenser 1971–1996 baseret på resultaterne oaf Dansk Ornitologisk Forenings landsdækkende kortlægning i 1993–96. Gads forlag. (In Danish)

Heldbjerg, H., & Fox, T. 2008: Long-term population declines in Danish trans-Saharan migrant birds. — Bird Study 55(3): 267–279. https://doi.org/10.1080/00063650809461532

Hemerik, L., Geertsma, M., Waasdorp, S., Middelveld, R. P., van Kleef, H., & Klok, C. 2015: Survival, reproduction, and immigration explain the dynamics of a local Red-backed Shrike population in the Netherlands. — Journal of Ornithology 156(1): 35–46. https://doi.org/10.1007/s10336-014-1120-2

Horvath, R., Farkas, R., & Yosef, R. 2000: Nesting ecology of the Red-backed Shrike (*Lanius collurio*) in northeastern Hungary. — Ring 22(1): 127–132.

Hušek, J., Weidinger, K., Adamík, P., & Slagsvold, T. 2012: Impact of nesting mortality on avian breeding phenology: a case study on the Red-backed Shrike (*Lanius collurio*). — PLOS ONE 7(8): 1–9.

Hušek, J., Weidinger, K., Adamík, P., Hlavatý, L., Holáň, V., & Sviečka, J. 2010: Analysing large-scale temporal variability in passerine nest survival using sparse data: a case study on Red-backed Shrike *Lanius collurio*. — Acta Ornithologica 45(1): 43–49. https://doi.org/10.3161/000164510X516074

Jakober, H., & Stauber, W. 1987: Dispersionsprozesse in einer Neuntöter-Population. — Beih. Veröffentlichungen Naturschutz Landschaftspflege Baden-Württemberg, 48: 119–130. (In German)

Jørgensen, P. S., Tøttrup, A. P., Rahbek, C., & Geertsma, M. 2013: Effects of summer weather on reproductive success of the Red-backed Shrike (*Lanius collurio*). — Bird Study 60(1): 1–10. https://doi.org/10.1080/00063657.2012.724051

Keller, V., Herrando, S., Voríšek, P., Franch, M., Kipson, M., Milanesi, P., Marti, D., Anton, M., Klvanová, A., Kalyakin, M. V., Bauer, H.-G. & Foppen, R. P. B. 2020: European breeding bird atlas 2: Distribution, abundance and change. — Lynx Edicions/European Bird Census Council (EBCC): Barcelona (967 pp.).

Krebs, J. R., Wilson, J. D., Bradbury, R. B., & Siriwardena, G. M. 1999: The second silent spring? — Nature 400(6745): 611–612. https://doi.org/10.1038/23127

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.

Kuźniak, S. 1991: Breeding ecology of the Red-backed Shrike *Lanius collurio* in the Wielkopolska region (Western Poland). — Acta Ornithologica 2(26): 67–83.

Latus, C., Schultz, A., & Kujawa, K. 2004: Occurrence of the Red-backed Shrike (*Lanius collurio*) depends on natural factors and mode of land use in the Quillow catchment, Germany. — Biological Letters 41(2): 87–93.

Marcum, H. & Yosef, R. 1998: A comparison of life history parameters of five Laniidae species. — International Centre for Birdwatching in Eilat Technicial Publication 7: 92–101.

Matyjasiak, P. 1995: Breeding ecology of the Red-backed Shrike (*Lanius collurio*) in Poland. — Proceedings of The Western Foundation of Vertebrate Zoology 6: 228–234.

Morelli, F., Mróz, E., Pruscini, F., Santolini, R., Goławski, A., & Tryjanowski, P. 2016: Habitat structure, breeding stage and sex affect hunting success of breeding Red-backed Shrike (*Lanius collurio*). — Ethology Ecology & Evolution 28(2): 136–147. https://doi.org/10.1080/03949370.2015.1022907

Morelli, F., Santolini, R., & Sisti, D. 2012: Breeding habitat of Red-backed Shrike *Lanius collurio* on farmland hilly areas of Central Italy: is functional heterogeneity one important key? — Ethology Ecology & Evolution 24(2): 127–139. https://doi.org/10.1080/03949370.2011.635696

Nikolov, B. P., & Hristova, I. P. 2007: Time-activity budgets of juvenile woodchat Shrikes *Lanius senator* during the post-fledging period. — Ardea 95(2): 235–241. https://doi.org/10.5253/078.095.0206

Olsson, V. 1995: The Red-backed Shrike *Lanius collurio* in southeastern Sweden: breeding biology. — Ornis Svecica 5(3–4): 101–110. https://doi.org/10.34080/os.v5.23012

Overballe-Petersen, M. V., Raulund-Rasmussen, K., Buttenschøn, R. M., & Bradshaw, R. H. 2014: The forest Gribskov, Denmark: lessons from the past qualify contemporary conservation, restoration and forest management. — Biodiversity and Conservation 23(1): 23–37. https://doi.org/10.1007/s10531-013-0582-5

Pedersen, L., Geertsma, M., & Tøttrup, A. P. 2012: Prey diversity is affected by climate and differs between age classes in the Red-backed Shrike (*Lanius collurio*). — Ornis Fennica 89(2): 99.

Pedersen, L., Jackson, K., Thorup, K., & Tøttrup, A. P. 2018a: Full-year tracking suggests endogenous control of migration timing in a long-distance migratory songbird. — Behavioral Ecology and Sociobiology 72(8): 1–10. https://doi.org/10.1007/s00265-018-2553-z

Pedersen, L., Schnedler-Meyer, N. A., Ekberg, P., & Tøttrup, A. P. 2018b: Effects of forest management practices in clearings on breeding performance of the Red-backed Shrike (*Lanius collurio*). — Ornis Fennica 95(4).

R Core Team 2021: R: A language and environment for statistical computing. — R Foundation for Statistical Computing, Vienna, Austria. Available at https://www.R-project.org. Accessed 1.9.2021.

Roos, S. 2002: Functional response, seasonal decline and landscape differences in nest predation risk. — Oecologia 133(4): 608–615. https://www.jstor.org/stable/4223461

Schmidt, K. A., Rush, S. A., & Ostfeld, R. S. 2008: Wood thrush nest success and post-fledging survival across a temporal pulse of small mammal abundance in an oak forest. — Journal of Animal Ecology 77(4): 830–837. https://doi.org/10.1111/j.1365-2656.2008.01378.x

Söderström, B. 2001: Seasonal change in Red-backed Shrike *Lanius collurio* territory quality-the role of nest predation. — Ibis 143(3): 561–571. https://doi.org/10.1111/j.1474-919X.2001.tb04883.x

Söderström, B., & Karlsson, H. 2011: Increased reproductive performance of Red-backed Shrikes *Lanius collurio* in forest clear-cuts. — Journal of Ornithology 152(2): 313–318. https://doi.org/10.1007/s10336-010-0587-8

Stoate, C., Boatman, N. D., Borralho, R. J., Carvalho, C. R., De Snoo, G. R., & Eden, P. 2001: Ecological impacts of arable intensification in Europe. — Journal of Environmental Management 63(4): 337–365. https://doi.org/10.1006/jema.2001.0473

Svendsen, J. K., Sell, H., Bøcher, P. K., & Svenning, J. C. 2015: Habitat and nest site preferences of Red-backed Shrike (*Lanius collurio*) in western Denmark. — Ornis Fennica 92(2): 63–75.

Tellería, J. L. 2018: Distribution of the Red-backed Shrike *Lanius collurio* at its western range boundary: patterns and conservation prospects. — Ardeola 65(2): 221–232. https://doi.org/10.13157/arla.65.2.2018.ra2

Titeux, N., Dufrene, M., Radoux, J., Hirzel, A. H., & Defourny, P. 2007 Fitness-related parameters improve presence-only distribution modelling for conservation practice: the case of the Red-backed Shrike. — Biological Conservation 138(1–2): 207–223. https://doi.org/10.1016/j.biocon.2007.04.019

Tøttrup, A. P., Klaassen, R. H. G., Kristensen, M. W., Strandberg, R., Vardanis, Y., Lindström, Å., Rahbek, C., Alerstam, T. & Thorup, K. 2012: Drought in Africa caused delayed arrival of European songbirds. — Science 338(6112): 1307–1307. https://doi.org/10.1126/science.1227548

Tøttrup, A. P., Pedersen, L., Onrubia, A., Klaassen, R. H., & Thorup, K. 2017: Migration of red-backed Shrikes from the Iberian Peninsula: optimal or sub-optimal detour? — Journal of Avian Biology 48(1): 149–154. https://doi.org/10.5441/001/1.32m2335q

Tryjanowski, P., & Goławski, A. (2004). Sex differences in nest defence by the red-backed shrike Lanius collurio: effects of offspring age, brood size, and stage of breeding season. Journal of Ethology 22(1): 13–16. https://doi.org/10.1007/s10164-003-0096-9

Tryjanowski, P., Goławski, A., Kuźniak, S., Mokwa, T., & Antczak, M. 2007: Disperse or stay? Exceptionally high breeding-site infidelity in the Red-backed Shrike *Lanius collurio*. — Ardea 95(2): 316–320. https://doi.org/10.5253/078.095.0214

Tryjanowski, P., Hartel, T., Báldi, A., Szymański, P., Tobolka, M., Herzon, I., Golawski, A., Konvička, M., Hromada, M., Jerzak, L., Kujawa, K., Lenda, M., Orlowski, G., Panek, M., Skórka, P., Sparks, T., Tworek, S., Wuczyński, A. & Żmihorski, M. 2011: Conservation of farmland birds faces different challenges in Western and Central-Eastern Europe. — Acta Ornithologica 46(1): 1–12. https://doi.org/10.3161/000164511X589857

Tryjanowski, P., Sparks, T. H., & Crick, H. Q. (2006). Brief report Red-backed Shrike (*Lanius collurio*) nest performance in a declining British population: a comparison with a stable population in Poland. Ornis Fennica 83: 181–186.

Van den Burg, A., Nijssen, M., Geertsma, M., Waasdorp, S. & Van Nieuwenhuyse, D. (2011). De grauwe klauwier — ambassadeur voor natuurherstel. KNNV Uitgeverij.

Vanhinsbergh, D., & Evans, A. (2002). Habitat associations of the Red-backed Shrike (*Lanius collurio*) in Carinthia, Austria. Journal für Ornithologie 143(4): 405–415. https://doi.org/10.1046/j.1439-0361.2002.02040.x

Vikstrøm, T., & Moshøj, C. M. (2020). Fugleatlas: de danske ynglefugles udbredelse 2014–2017. Dansk Ornitologisk Forening.

White G. C. (2021). MARK Version 9.0: Mark and Recapture Parameter Estimation. — Department of Fish, Wildlife and Conservation Biology, Colorado State University, USA. Available at https://www.cnr.colostate.edu/~gwhite/mark/mark.htm. Accessed 1.9.2021.

Wiklund, C. G., & Andersson, M. (1994). Natural selection of colony size in a passerine bird. — Journal of Animal Ecology 63(4): 765–774. https://www.jstor.org/stable/5254

Yackel Adams, A. A., Skagen, S. K., & Savidge, J. A. (2006). Modeling post-fledging survival of lark buntings in response to ecological and biological factors. Ecology 87(1): 178–188. https://doi.org/10.1890/04-1922

Yosef, R. (1993). Effects of Little Owl predation on Northern Shrike postfledging success. — The Auk 110(2): 396–398. https://www.jstor.org/stable/4088571

Yosef, R., International Shrike Working Group (ISWG) & Christie, D. A. (2020). Red-backed Shrike (*Lanius collurio*). — In Del Hoyo, J., Elliott, A., Sargatal, J., Christie, D. A. & De Juana, E. (eds) Birds of the World. Cornell Laboratory of Ornithology.

Online supplementary material

Supplementary material available in the online version of the article includes Tables S1–S13 and Figures S1–S2.