

# Comparative breeding ecology, nest survival, and agonistic behaviour between the Barred Warbler and the Red-backed Shrike

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**Abstract** The majority of studies have demonstrated that the Barred Warbler *Sylvia nisoria* (BW) and the Red-backed Shrike *Lanius collurio* (RBS), where they occur sympatrically in central Europe, inhabit similar niches and are not averse to nesting in each other's vicinity. The present work compares the reproductive parameters, nest survival, and behavioural interactions between these two ecologically similar species. The study was carried out in eastern Poland in two types of habitat: a river valley and farmland. Inter-habitat analysis showed both species to have similar reproductive parameters, although nest survival of the RBS was greater in farmland than in the river valley. Interspecific comparison revealed that the BW built smaller nests, laid fewer and smaller eggs than the RBS, but the production of offspring was similar in both species. In comparison to the other populations from Europe, both the BW and RBS in eastern Poland experienced good breeding parameters, and this is likely to be related to the region's extensive agriculture management and abundant food resources. The main factor reducing breeding success in both species was the plundering of their broods by raptors. Analysis using the MARK program indicated that habitat parameters significantly affected brood survival in the RBS to a relatively constant extent throughout the season. While habitat factors were less decisive in BWs, the fate of this species' broods was strongly dependent on the phase of the reproductive cycle, and its nests were least

likely to survive in the middle of the breeding season. The level of aggression between the BW and RBS was low, as demonstrated by experiments with stuffed models; this was a factor in favour of their nesting in close proximity to one another.

**Keywords** Species co-existence · Protective nesting association · Positive interactions · Nest survival

## Zusammenfassung

### Vergleichende Brutbiologie, Nesterfolg und agonistisches Verhalten zwischen Sperbergrasmücken und Neuntöttern

Die meisten Studien zeigten, dass Sperbergrasmücken *Sylvia nisoria* (BW; engl.: Barred Warbler) und Neuntötter *Lanius collurio* (RBS; engl.: Red-backed Shrike), wo sie in Mitteleuropa sympatrisch auftreten, ähnliche ökologische Nischen besetzen und beim Nisten die gegenseitige Nähe nicht scheuen. Die vorliegende Arbeit vergleicht die fortpflanzungsbezogenen Parameter, den Nesterfolg und das Interaktionsverhalten zwischen diesen beiden ökologisch ähnlichen Arten. Die Untersuchung wurde in zwei Lebensraumtypen in Ostpolen durchgeführt: in einem Flusstal und auf Landwirtschaftsflächen. Im Vergleich der Lebensräume zeigten beide Arten ähnliche Fortpflanzungsparameter, obgleich der Nesterfolg beim RBS auf den Landwirtschaftsflächen höher war als im Flusstal. Der interspezifische Vergleich zeigte, dass BW kleinere Nester bauten und weniger und kleinere Eier legten als RBS, die Produktion an Nachkommen war bei beiden Arten aber ähnlich. Im Vergleich mit den anderen europäischen Populationen wiesen BW und RBS aus Ostpolen gute Brutparameter auf, was vermutlich mit extensivem

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Landwirtschaftsmanagement und reichlicher Nahrungsverfügbarkeit zusammenhängt. Der Hauptfaktor, der bei beiden Arten zur Abnahme des Bruterfolges führte, war Brutraub durch Greifvögel. Analysen mit dem Programm MARK deuteten darauf hin, dass Habitatparameter den Bruterfolg beim RBS über die Brutsaison hinweg in relativ konstantem Maße beeinflussten. Während Habitatfaktoren beim BW weniger entscheidend waren, hing das Schicksal der Brut dieser Art stark von der Phase des Fortpflanzungszyklus ab, und ihre Nester hatten zur Mitte der Brutsaison die geringsten Überlebenschancen. Das Ausmaß der Aggression zwischen BW und RBS war niedrig, wie Experimente mit präparierten Attrappen zeigten; dieser Faktor begünstigt das Nisten der beiden Arten in gegenseitiger Nähe.

## Introduction

In Europe, population declines of many farmland avian species have been attributed to decreased reproductive success resulting from habitat loss, fragmentation, and management intensification (Tryjanowski et al. 2011). Practical recommendations for declining bird species are often based solely on species occurrences or population trends (Szymkowiak et al. 2014). However, researchers can gain a better understanding of the factors that influence avian demography and reproduction to answer questions about variation across habitats and regions and to recommend more effective conservation tools. There is little knowledge on the influence of time- and environmental-dependent factors on breeding ecology in general and nest survival in particular (Fisher and Wiebe 2006). This kind of information is important for management because nest survival is a particularly influential component of the annual cycle of many bird populations (Walker et al. 2005). Novel analytical tools have now been developed that allow nest survival to vary with time or other habitat covariates (White and Burnham 1999). Previous studies have shown that habitat characteristics may have important effects on avian reproductive success (Goławski and Mitrus 2008; Musilová et al. 2014). Different habitats often support specific predator communities, and patterns in nest survival are presumably driven by variation in the risk of predation (Fisher and Wiebe 2006). Nest survival might change in a linear or quadratic fashion over the season coincident with increases in vegetation cover for nest concealment and different patterns of predator activities (Wilson et al. 2007). Parents may defend nests more vigorously in the nestling period, because their reproductive value increases with age (Smith and Wilson 2010).

European regions differ significantly in their agriculture characteristics. The farmland environment in Central-Eastern Europe is generally more extensive than in Western Europe and the majority of farmland bird studies in Western Europe have been performed on small, declining populations (Tryjanowski et al. 2011). So far, strong and stable Central-Eastern Europe populations of farmland species have not been studied sufficiently (Szymanski and Antczak 2013; Szymkowiak et al. 2014). In this study, I investigated the breeding ecology of two farmland, shrub-breeder species—the Red-backed Shrike *Lanius collurio* (hereafter, RBS) and the Barred Warbler *Sylvia nisoria* (hereafter, BW) in eastern Poland. BW is a little-known and secretive warbler and we have poor knowledge about the breeding ecology of this passerine (Orłowski et al. 2015). Both species still have high protection status in Europe and they are listed in Annex 1 of the Birds Directive on the conservation of wild birds (Directive 2009/147/EC). In Western Europe the main threat for RBS and BW is the progressive reduction of habitat availability due to the destruction or deterioration of farmland habitats (Hollander et al. 2011). By contrast, in Central-Eastern Europe, where extensive agriculture practices and strong farmland bird populations remain, inappropriate or changing management of production are the key issues (Tryjanowski et al. 2011; Orłowski et al. 2015). The life history theory aims to discover the factors that determine heterospecific and conspecific variation in breeding parameters. We should expect that ecologically similar species can have similar reproductive traits due to their evolutionary history, and such comparative studies should be useful in characterizing reproductive patterns and determining factors affecting differences in life history (Schaefer et al. 2004).

The aggressive behaviour of the RBS has been intensively studied in recent years (Strnad et al. 2012; Němec and Fuchs 2014). This species leads a predatory lifestyle and is capable of stealing the eggs and nestlings of other passerines and even of preying on fledglings and adult birds (Kuźniak and Tryjanowski 2003). For this reason many small birds avoid nesting in close proximity to RBS; this includes warblers of the genus *Sylvia*. The exception to this rule is the largest European warbler species—the BW, which has no fear of the RBS and frequently nests in the latter's territories in central Europe (Kuźniak et al. 2001; Goławski 2007a). Earlier studies showed that in their breeding territories both species quickly detect approaching raptors intent on plundering their nests; once the danger has been perceived, both sexes defend their nests with great determination (Polak 2013). Observations have shown that where RBS and BW nest near one another they may join forces to defend their broods.

The latest comparative studies confirm that the two species have similar habitat requirements; this can lead to competition between them, however (Neuschulz 1988; Polak 2012). Both BW and RBS choose a well-insolated mosaic of open, scrubby terrain with high densities of the invertebrates that are the mainstay of their diet (Cramp 1992; Goławski 2007b). In central Europe the two species usually colonize two quite distinct types of habitat: sub-optimal—open farmland, and optimal—meadows and pastures in river valleys (Cramp 1992; Cramp and Perrins 1993). Both species achieve higher densities in the latter rather than in the former habitats (Polak and Filipiuk 2014). However, it has been shown recently that their habitat niches do not overlap entirely: subtle differences in their selectivity of habitats have been observed (Polak 2012). Moreover, the later laying RBS may use the BW as a source of social information about the quality of nesting habitats (Morelli and Tryjanowski 2015; Polak 2015). In this context, therefore, it would be interesting to discover the real nature of the relationship between the BW and RBS: is communal nesting a straightforward consequence of their similar habitat preferences, or does one species actively select the neighbourhood of the other for the sake of cooperation and joint defence of their broods against predators? Comparison of breeding success in BW and RBS nesting in close proximity to one another has shown that pairs nesting in overlapping territories benefit from enhanced breeding success (Neuschulz 1988; Goławski 2007a; Polak 2012).

In the present study I compared the basic breeding parameters of the two species between a habitat with a greater (river valley) and smaller (farmland) density and different structure of vegetation. Breeding territories and shrubs containing nests were distributed more evenly in the river valley than in the farmland, where the birds nested in isolated clumps of vegetation (Polak 2012; Polak and Filipiuk 2014). On the one hand, we should expect superior reproductive parameters (clutch size, egg size, breeding success) in the river valley, since this is the birds' optimal habitat. On the other, the diverse habitat structure and the higher density of nests may significantly modify predatory pressure on BW and RBS broods; moreover, nest survival may differ significantly between the two types of environment. The initial hypothesis was that the same selective factors governing the daily nest survival should be acting on birds that utilize similar, partly overlapping ecological niches, i.e. those which have similar habitat requirements and nutritional demands. To test it, I analysed the influence of habitat factors and timing of breeding on nest survival with the aid of the MARK software program. Both species actively defend their broods and behave aggressively towards predators, including large mammals and even humans (Tryjanowski and Goławski 2004; Goławski and

Mitrus 2008). In light of the results of these studies, I expected that nest survival would increase throughout the nesting period, but as a result of intensification of nest defence. Another aim of this work was to assess the level of aggression towards conspecifics and other heterospecifics inhabiting the study area.

## Methods

### Reproductive data

The fieldwork took place on two study plots in eastern Poland. From 2009 to 2011, observations were carried out near the village of Stężycza (N51°34'; E21°48') in the Middle Vistula River valley (Polak 2012). During 2012–2014, I also carried out observations on a 106-ha study plot in farmland near the village of Żurawnica (N50°38'; E22°58') in the central Roztocze region (Polak and Filipiuk 2014). The number of breeding pairs/territories of both species was defined using the combined version of the cartographic method (Tomiałojć 1980). From May to July the plots were surveyed regularly every few days. The numbers of surveys in the various years were as follows: 2009 = 9, 2010 = 14, 2011 = 18, 2012 = 17, 2013 = 15, and 2014 = 13. During each field visit the aim of the visual and auditory observations was to discover as many RBS and BW territories and nests as possible. The birds' movements and territorial behaviour were recorded on orthophotographs. The birds in some territories were individually marked with coloured rings. The density of RBS varied from 3.0 to 4.5 pairs (territories)/10 ha, while that of BW ranged from 1.9 to 3.2 pairs (territories)/10 ha (Polak 2012; Polak and Filipiuk 2014). The basic method of locating nests was the systematic search of all potential breeding sites in the shrubs growing on the study plots. The position of each nest was marked on an orthophotograph and the exact coordinates were entered on a GPS receiver. The distance between the lower edge of the nest and the ground was measured with a tape accurate to 10 cm. Nest diameter was measured (to the nearest 1 cm) as the maximum horizontal distance between the most extreme edges of the nest by using a measuring tape. Similarly, nest height was estimated as the maximum vertical distance between the most extreme edges of the nest. Nests were inspected every few days from May to July in order to establish basic reproductive parameters: egg-laying date, clutch size, hatching date, number of nestlings. The length and width of the eggs were measured with callipers to an accuracy of 0.1 mm. Egg volume was calculated according to Surmacki et al. (2006) using the following equation:  $\text{volume} = 0.5322 \times \text{length} \times (\text{width})^2$ . The nest was considered as replacement clutch when clutch failure occurred in

a territory and the second brood was initiated later by parents in close surroundings. In this research replacement clutches were not analysed. Data from 129 RBS nests and 56 BW nests were thus worked up. The degree of concealment of the nests was assessed as their visibility at a distance of 1 m and at a height of 1.6 m above the ground (Holway 1991; Goławski and Mitrus 2008). Nest concealment was evaluated from the four main points of the compass on a scale from 1 to 5, where 1 = 0–20 % visibility, 2 = 21–40 % etc. In all cases, nest concealment was evaluated in May and June once all the leaves on the shrubs were fully developed. The visibility index was calculated by summing the measurements from all four directions. If a brood was depredated, I attempted to determine the cause and to record all traces left by the predator. Three categories of predators were distinguished on the basis of the traces they left at the nest: large mammals, small mammals, and birds. If there were no eggs or shell remnants in the nest, the brood was assumed to have been depredated by a bird. If there were remnants of eggshells in the nest, but the nest itself remained intact, the brood was assumed to have been depredated by a small mammal. The research showed that mammals generally left shell fragments in or on the nest cup, indicating that they consumed the eggs in the nest. Birds, on the other hand, appeared to eat eggs away from the nest site and most tried to remove the egg from the nest (Boulton and Cassey 2006; Goławski and Mitrus 2008). A nest depredated by a large mammal had usually been pulled down, the nest structure was no longer intact, and the vegetation around the nest had been trampled on.

### Experiments with decoys

The field experiment examined whether the type of decoy affected the behavioural response of warblers and shrikes by comparing their reaction to conspecific and heterospecific species. If BW and RBS do indeed actively select each other's neighbourhood in their breeding territories, we can assume that, because of the lower level of competition and the only partial overlap of habitat niches, the level of aggression between them should be lower than between individuals of one species (complete overlap of niches). In order to check this out, I placed stuffed models of the BW and RBS near some nests of both species. In addition, I checked the reactions of the relevant pairs to a species that could potentially plunder their nests (a stuffed Great Grey Shrike *Lanius excubitor*—hereafter, GGS), and also to a control species (a stuffed Lesser Whitethroat *Sylvia curruca*—hereafter, LW).

The behavioural tests were conducted in May, June, and July of 2012 and 2013. To measure aggression against an intruder I presented stuffed LW, BW, RBS, and GGS

models. All these species were present on the study plot. Only seven tested BWs were colour-ringed and I cannot rule out the possibility that I tested the same individuals again in the second breeding season. Even so, I consider this unlikely, as in each season I worked in different parts of the study plot. Moreover, it was found that BW and RBS populations in central Europe have a low breeding philopatry (Neuschulz 1988; Tryjanowski et al. 2007). The decoys were placed in a natural perching posture, without using any luring mechanism such as playback or movement. All the tests were performed in an area with low vegetation so that they were easily detectable by birds. The presentation of the four different model species was randomised. The location of the models in relation to the nests was the same in the four treatments. I presented the four models to parents of 17 RBS and 12 BW broods. All the experiments took place during the nestling period, because previous tests had indicated that the aggression response was very low during the incubation period in both species (Polak M, unpublished data). The trials were undertaken at different times of the day from morning to evening in calm and dry weather. The presentations were always separated by >20 min. Before conducting the experiments, I measured the lengths of nearby trunks and branches, which allowed me to accurately determine a bird's approach distances. The models were mounted on a stick at the same height of 1.2 m above the ground. They were placed at the same distance (5 m) from the two species' nests, because nest defence is well known to decrease in intensity with distance from the brood (Kryštofková et al. 2011). The decoys were installed when no bird was nearby so as to minimize any potential disturbance effects. During each session the birds' behaviour was recorded by a single researcher. I observed and evaluated the behaviour of the adult shrikes and warblers from a hide. Both parents were recorded at the same time. Each trial consisted of 15 min of continuous focal sampling of behaviour. Generally, the nest defence behaviour of each bird was measured using three different variables: aggression score, duration of alarm reaction, and minimum distance to the model. The aggression score was categorized separately for males and females on a scale from 0 to 7. The rank values of mobbing behaviour were assigned according to its increasing degree of risk: 0—no response to the model; 1—bird mobs from a distance of at least 10 m without alarm calls; 2—calling bird from a distance of at least 10 m; 3—no alarm calls, bird mobs from a distance of up to 10 m; 4—calling bird close to the model (<10 m), but does not fly in the direction of the model; 5—bird mobs intensively and flies to the model, but does not attack; 6—bird attacks decoy, but without contact; 7—bird attacks model with contact. Further analyses looked at the most extreme aggressive



response from all reactions performed by each individual during 15 min of a trial. The definition of alarm reaction included repetitive alarm calling, bill clattering, tail movements, and characteristic display behaviours (Cramp 1992; Cramp and Perrins 1993).

### Statistical analysis

I used STATISTICA 6.0 for Windows software (Statsoft Inc., 2001) and MARK version 8.0 (White and Burnham 1999) for comparing breeding parameters between species and habitats. Nests were considered successful when at least one juvenile fledged. Hatchability was defined as the ratio of the number of hatched nestlings to the number of eggs laid. The number of fledglings/breeding pairs was defined as the number of young reaching 12–14 days of age in all the broods examined in the population studied, and the number of fledglings/successful pairs was defined as the number of young reaching 12–14 days of age in successful pairs (when at least one young bird had survived to 12–14 days old).

I used the nest survival module in MARK (Rotella et al. 2004) to compare nest survival models and to obtain estimates of daily nest survival. All the analyses performed in MARK included live broods and nests lost only as a result of predation. Dates were scaled so that 1 was the date when the first nest was found. I thus defined a 43-day nesting season beginning on 23 May and ending on 4 July for BW and a 47-day nesting season beginning on 21 May and ending on 6 July for RBS. This season respectively comprised 42 and 46 daily intervals for which the daily survival rate was estimated. I selected the best predictive models using Akaike's information criterion corrected for a small sample size ( $AIC_c$ ; Burnham and Anderson 2002), which allowed multiple working hypotheses to be evaluated simultaneously. I used the same methods for each species but conducted the analyses separately. The list of candidate models was based on combinations of factors that I assumed a priori might affect BW and RBS nest survival. I compared the model support using  $AIC_c$  and evaluated the strength of evidence for each model using normalized weights  $w_i$ . I followed the convention that the model with the lowest  $AIC_c$  represented the best compromise between goodness-of-fit and model complexity, and that models with  $\Delta AIC_c$  (the difference between the  $AIC_c$  for a particular model and that of the best model)  $< 2$  fitted almost as well as the most parsimonious model (Whittingham et al. 2006). Because the candidate model set contained a mix of models with linear and quadratic terms, as well as interactions, I was unable to use model averaging in the interpretation of parameter estimates. The first set of models considered the influence of habitat and vegetation parameters. I constructed models of nest survival that incorporated combinations of three individual covariates (nest visibility, nest height above ground, type of

habitat—river valley vs. farmland), and compared them to the null model of constant survival rate  $S$  (.). I hypothesized that the better concealed nests (greater vegetation cover) would have a greater chance of survival than the more exposed nests (Gołowski and Mitrus 2008). Earlier experimental work in the same study areas had shown that artificial nests situated low above the ground were subject to the lowest level of predation (Polak 2014) and I predicted that nests located close to the ground should be less exposed to predation. Recent research has indicated that the type of habitat significantly affects the degree of predation pressure (Báldi 2004; Brzeziński et al. 2010); accordingly, I hypothesized that the level of predation on natural nests should be higher in the river valley than in the farmland owing to the higher density of corvids in this type of habitat (Polak 2014). The reproductive period is a critical one for many organisms, and the decision of when to initiate breeding is of crucial significance where the adaptation of individuals is concerned (Lewis et al. 2012). In the temperate climate zone, migratory birds usually have only a short time window for breeding, and these individuals are under strong pressure from the passage of time (Tøttrup et al. 2012). I predicted that variation in daily nest survival would be related to temporal variation within a season and the highest survival rates would be achieved by birds that nested earlier than average (Lewis et al. 2012). The daily survival rate of many altricial species varies in relation to nest age and may decline owing to the greater frequency of visits by parents when feeding nestlings. However, my previous research indicated that during the late nestling period both BWs and RBSs vigorously defend their nests and behave aggressively towards predators (Polak 2013), and that in this reproductive phase nest survival should increase as a consequence of intensified nest defence. Therefore, linear time trends could not reflect a bimodal pattern of nest survival (Dinsmore et al. 2002) and I fitted quadratic time and age–nest trend models that allowed daily nest survival to follow a curvilinear pattern. Nest age and day of season can be difficult to separate when nests are initiated synchronously, but since with the RBS most nests were initiated across the season, I included both variables in the models. As suggested by Dinsmore et al. (2002), all were unstandardised, because the unstandardised covariates did not affect numerical optimization, and the logit link function was adopted.

When analysing data from decoy experiments I compared the responses elicited during the four treatments of heterospecific and conspecific models at the warbler and shrike nests by using repeated measures analysis of variance (ANOVA), with the type of presentation and sex of parents as the independent factors, and aggression score, length of alarm reaction, and minimum distance to the model as the dependent variables. Means are expressed  $\pm$ SD and all tests are two-tailed.

## Results

### Reproductive parameters

BW were observed to build smaller nests than the RBS. Nest diameter varied between species but not between habitats (two-way ANOVA, species  $F_{1,181} = 104.28$ ,  $P < 0.001$ , habitat  $F_{1,181} = 0.66$ ,  $P = 0.42$ , interaction  $F_{1,181} = 1.03$ ,  $P = 0.31$ , Table 1). Similarly, differences in nest height between shrikes and warblers were significant but not between habitats (species  $F_{1,181} = 216.49$ ,  $P < 0.001$ , habitat  $F_{1,181} = 0.55$ ,  $P = 0.46$ , interaction  $F_{1,181} = 2.26$ ,  $P = 0.13$ ). For the BW, the clutch size ranged between four and six and the modal clutch was five ( $n = 49$ , CV = 10 %). The average number of eggs in a clutch in the RBS population was  $5.5 \pm 0.7$  ( $n = 106$ , range 3–7, CV = 12 %) and the modal clutch was six (49 % of total). The clutch size was similar between habitats but BW laid significantly smaller clutches than RBS (species  $F_{1,151} = 14.62$ ,  $P < 0.001$ , habitat  $F_{1,151} = 1.44$ ,  $P = 0.23$ , interaction  $F_{1,151} = 0.05$ ,  $P = 0.82$ ). There was a significant decline in clutch size with laying data for both the BW (standardized data: Pearson's correlation;  $r = -0.30$ ,  $P < 0.05$ ,  $n = 48$ , raw data:  $r = -0.34$ ,  $P < 0.05$ ,  $n = 48$ ) and RBS (standardized data: Pearson's correlation;  $r = -0.23$ ,  $P < 0.05$ ,  $n = 106$ , raw data:  $r = -0.16$ ,  $P = 0.09$ ,  $n = 106$ ). For the BW, a total of 186 different eggs were measured from 38 different nests and for RBS, 533 eggs from 102 nests. There was a significant effect of species but not of habitat on egg length (species  $F_{1,715} = 33.84$ ,  $P < 0.001$ , habitat  $F_{1,715} = 3.59$ ,  $P = 0.06$ , interaction  $F_{1,715} = 0.54$ ,  $P = 0.46$ ), egg breadth (species  $F_{1,715} = 344.77$ ,  $P < 0.001$ , habitat  $F_{1,715} = 1.82$ ,  $P = 0.18$ , interaction  $F_{1,715} = 0.03$ ,  $P = 0.85$ ) and egg volume (species  $F_{1,715} = 248.55$ ,  $P < 0.001$ , habitat  $F_{1,715} = 3.65$ ,  $P = 0.06$ , interaction  $F_{1,715} = 0.01$ ,  $P = 0.91$ ). The populations studied were characterised by good hatching

success, reaching 98 % among BW and 97 % among RBS ( $n = 34$  and 61 complete broods respectively). Although the BW laid smaller clutches than the RBS, the number of fledglings per pair (species  $F_{1,173} = 0.34$ ,  $P = 0.56$ , habitat  $F_{1,173} = 0.01$ ,  $P = 0.91$ , interaction  $F_{1,173} = 0.35$ ,  $P = 0.56$ ) and the number of fledglings per successful pair (species  $F_{1,79} = 2.28$ ,  $P = 0.13$ , habitat  $F_{1,79} = 0.57$ ,  $P = 0.45$ , interaction  $F_{1,79} = 0.02$ ,  $P = 0.90$ ) was similar between species and habitats. Among broods that were completely destroyed, brood predation was the main cause of nest failure in both passerines (69 % for BW; chi-squared test;  $\chi^2 = 212.12$ ,  $P < 0.001$ , and 71 % for RBS;  $\chi^2 = 232.52$ ,  $P < 0.001$ , respectively). Brood losses in RBS nests were depredated by birds (30; 59 %;  $\chi^2 = 67.60$ ,  $P < 0.001$ ), small mammals (3; 6 %), large mammals (6; 12 %), and unknown predators (12; 23 %). The corresponding figures for BW are birds (10; 53 %;  $\chi^2 = 50.64$ ,  $P < 0.001$ ), small mammals (1; 5 %), large mammals (3; 16 %), and unknown (5; 26 %). Besides predation, an important cause of nest failure was brood desertion by parents (19 % for BW and 22 % for RBS, respectively). Other reasons were weather (4 and 0 %, respectively), death of parents (0 and 2 %), brood parasitism by European cuckoo *Cuculus canorus* (0 and 2 %), and unknown (8 and 3 %).

### Factors affecting daily nest survival rate

The constant model estimated the Mayfield daily nest survival probability during the breeding season at 0.967 (95 % CI 0.949–0.979) for BW and 0.971 (95 % CI 0.961–0.978) for RBS. The top models for BW included quadratic and linear terms for both covariates: time of season and age of nest (Table 2). Daily nest survival rates of BW nests gradually declined until mid-season, and then rose gradually to a peak at the end of the reproductive period (Fig. 1a). Models including type of habitat, nest visibility, and nest height had lower AIC<sub>c</sub> values than the

**Table 1** Reproductive parameters (mean  $\pm$  SD) of the Barred Warbler and Red-backed Shrike in eastern Poland between 2009 and 2014

Parameter	Barred Warbler		Red-backed Shrike	
	River valley	Farmland	River valley	Farmland
Nest diameter (cm)	11.8 $\pm$ 1.3 (31)	11.8 $\pm$ 0.9 (25)	13.9 $\pm$ 1.7 (63)	14.3 $\pm$ 1.3 (66)
Nest height (cm)	8.8 $\pm$ 1.7 (31)	8.6 $\pm$ 1.1 (25)	10.7 $\pm$ 2.0 (63)	11.3 $\pm$ 1.7 (66)
Clutch size	5.1 $\pm$ 0.5 (27)	5.0 $\pm$ 0.5 (22)	5.6 $\pm$ 0.5 (52)	5.4 $\pm$ 0.7 (54)
Egg length (mm)	21.2 $\pm$ 0.9 (110)	20.8 $\pm$ 0.9 (76)	21.6 $\pm$ 1.0 (284)	21.5 $\pm$ 1.0 (249)
Egg breadth (mm)	15.7 $\pm$ 0.4 (110)	15.6 $\pm$ 0.4 (76)	16.5 $\pm$ 0.5 (284)	16.4 $\pm$ 0.5 (249)
Egg volume (cm <sup>3</sup> )	2.8 $\pm$ 0.2 (110)	2.7 $\pm$ 0.2 (76)	3.1 $\pm$ 0.3 (284)	3.1 $\pm$ 0.3 (249)
Fledglings/pair	2.5 $\pm$ 2.4 (31)	2.3 $\pm$ 2.3 (23)	2.1 $\pm$ 2.6 (62)	2.3 $\pm$ 2.5 (61)
Fledglings/successful pair	4.6 $\pm$ 0.7 (16)	4.3 $\pm$ 0.9 (12)	4.9 $\pm$ 1.2 (26)	4.8 $\pm$ 1.3 (29)

Sample sizes are in parentheses

**Table 2** Top candidate models predicting nest survival of Barred Warblers and Red-backed Shrikes in eastern Poland

Candidate model	<i>K</i>	AIC <sub>c</sub>	ΔAIC <sub>c</sub>	W <sub>i</sub>
Barred Warbler ( <i>n</i> = 45 nests)				
S (TIME + TIME <sup>2</sup> )	3	93.64	0.00	0.484
S (TIME + TIME <sup>2</sup> + AGE <sup>2</sup> )	4	95.44	1.80	0.196
S (TIME + TIME <sup>2</sup> + AGE)	4	95.59	1.95	0.183
S (TIME + TIME <sup>2</sup> + AGE + AGE <sup>2</sup> )	5	96.41	2.77	0.121
S (AGE + AGE <sup>2</sup> )	3	101.86	8.22	0.008
S (TIME <sup>2</sup> + AGE + AGE <sup>2</sup> )	4	103.72	10.08	0.003
S (TIME + AGE + AGE <sup>2</sup> )	4	103.87	10.22	0.003
S (.)	1	105.07	11.42	0.002
Red-backed Shrike ( <i>n</i> = 104 nests)				
S (HABITAT)	2	253.06	0.00	0.312
S (HABITAT + VISIBILITY)	3	254.69	1.63	0.138
S (.)	1	254.94	1.88	0.122

The number of parameters (*k*), Akaike’s information criterion with small-sample bias adjustment (AIC<sub>c</sub>), the difference between the lowest AIC<sub>c</sub> and AIC<sub>ci</sub> (ΔAIC<sub>c</sub>), and the model weight (*w<sub>i</sub>*) are shown

null model. Habitat parameters significantly affected brood survival among RBS to a relatively constant extent throughout the season (Fig. 1b), and models incorporating the type of habitat and nest visibility index ranked the highest. These two covariates had the highest cumulative AIC<sub>c</sub> weights (Table 2). Daily nest survival rates decreased with increasing nest visibility index ( $\beta = -0.014$ , 95 % CI  $-0.079$  to  $0.050$ ). Nest survival was lower in the river valley (0.962, 95 % CI 0.945–0.973) than in farmland (0.978, 95 % CI 0.966–0.989). Models with time trends on shrike nest survival received less support and had lower AIC<sub>c</sub> values than the null model.

**Intra- and inter-specific aggression**

In both species, aggression differed in response to the different models (repeated measures ANOVA,  $F_{4, 224} = 14.12$ ,  $P < 0.001$ , Figs. 2, 3). RBSs displayed aggressive reactions in relation to the BW, RB, and GGS models but none against the LW model. BWs behaved aggressively towards the BW and GGS models, but not the RBS and LW models. Using aggression scores as an index of aggressiveness, RBSs were more aggressive than BWs ( $F_{4, 224} = 9.99$ ,  $P < 0.005$ ). Male RBSs were more aggressive than females ( $F_{1,134} = 4.38$ ,  $P < 0.05$ ), but there were no sex-related differences in the aggression score for BWs ( $F_{1,94} = 0.13$ ,  $P = 0.72$ ). The duration of the reaction time was significantly influenced by the dummy treatment ( $F_{4, 224} = 14.12$ ,  $P < 0.001$ ). There were no species differences in reaction time to any of the four different models ( $F_{4, 224} = 1.34$ ,  $P = 0.25$ ). There were no sex-related differences in the duration of the reaction time in either RBS ( $F_{1,134} = 0.25$ ,  $P = 0.62$ ) or BW ( $F_{1,94} = 0.17$ ,  $P = 0.68$ ). The minimal distance was not significantly influenced by the dummy treatment ( $F_{4, 224} = 0.93$ ,  $P = 0.42$ ). In response to all the models, there were no

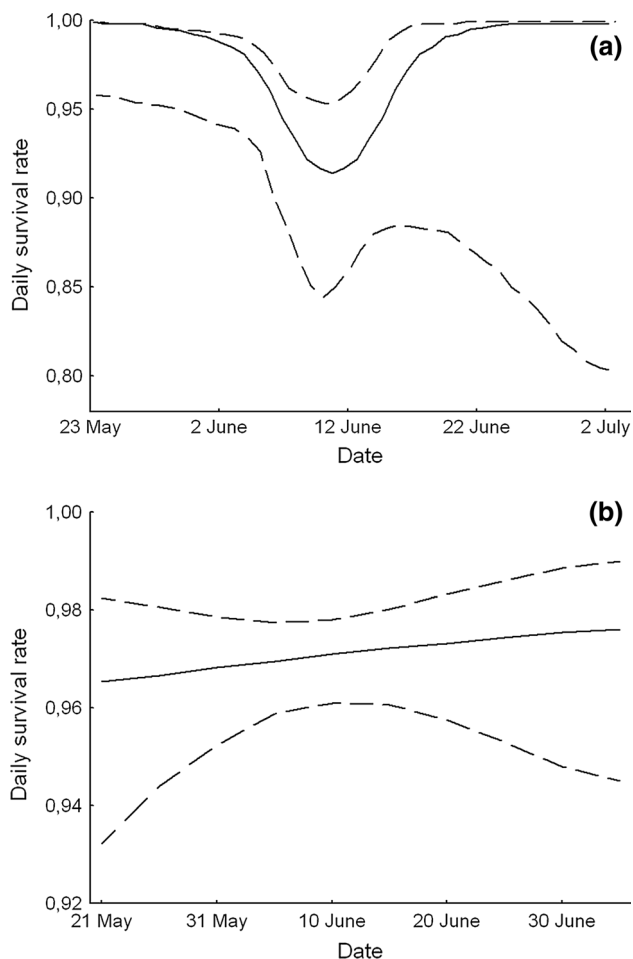
differences in the approach distance between the two species ( $F_{4,224} = 1.34$ ,  $P = 0.25$ ). Female BWs reacted at a much shorter distance than males ( $F_{1,94} = 6.04$ ,  $P < 0.05$ ). However, there were no sex-related differences in approach distance for RBS ( $F_{1,134} = 0.01$ ,  $P = 0.98$ ).

**Discussion**

**Reproductive characteristics**

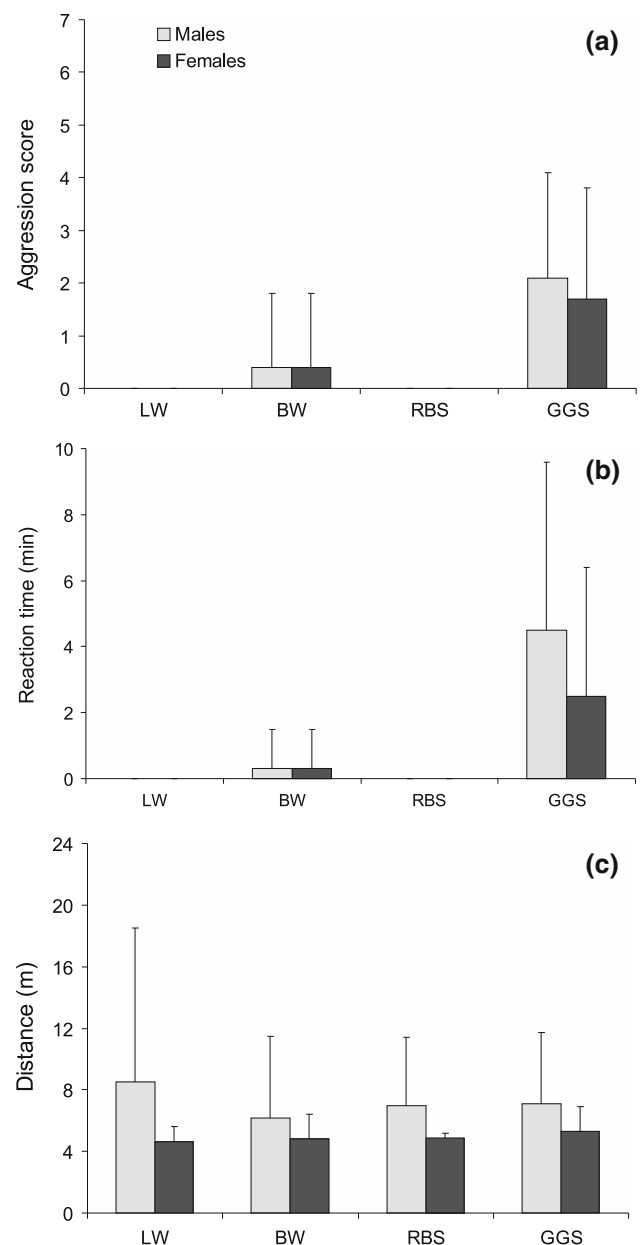
Some authors suggested that the BW is a hedgerow specialist (Szymanski and Antczak 2013; Orłowski et al. 2015). However, our earlier observations showed that the densities of BW are higher in river valleys than in farmland landscapes and this species prefers continuous patches of bush habitats over hedgerows (Polak 2012; Polak and Filipiuk 2014; Bažant M. unpublished data). The main hypothesis was that the breeding parameters were higher in river valleys as the optimal habitat than in fragmented farmland. However, in contrast to the initial expectations, the present study showed that the reproductive performance (clutch size, egg volume, and number of fledglings) of the BW and RBS populations inhabiting continuous and linear habitats were similar. Our present and earlier studies (Kuźniak 1991; Golawski 2006; Polak 2012) show that so far, local populations of two farmland species in Poland are dense and have high breeding parameters. Tryjanowski et al. (2007) suggested that highly nomadic local populations are part of a metapopulation and in each season shrikes have abundant possibilities to settle in different habitats.

Several studies have documented that nest predation was the major cause of reproductive failure in RBS and BW



**Fig. 1** Model averaged estimates of daily nest survival in eastern Poland, 2009–2014, for Barred Warbler (a) and Red-backed Shrike (b) showing effect of time of breeding. *Solid lines* represent daily survival rate estimated using beta parameters from the best-fit model. *Dashed lines* represent upper and lower 95 % confidence intervals for the estimated daily survival rate

(Neuschulz 1988; Kuźniak 1991; Gołowski 2006). These findings showed that daily nest survival of the RBS was higher in farmland than in the river valley. Very probably this was due to the larger densities of corvids in the river valley (Polak 2014). This study confirmed that it was mainly birds rather than mammals that were responsible for the brood losses in the two species (Kuźniak 1991; Söderström et al. 1998). Recent studies have shown that RBSs and BWs actively defend their broods and behave aggressively towards predators, including avian raptors, large mammals, and even humans (Tryjanowski and Gołowski 2004; Strnad et al. 2012; Němec and Fuchs 2014). However, the present comparative study demonstrated that nest concealment is more important than intensive nest defence and the more open nests of RBS were more often plundered by predators than well-hidden BW broods. This fate did not befall the BW, as the nests of

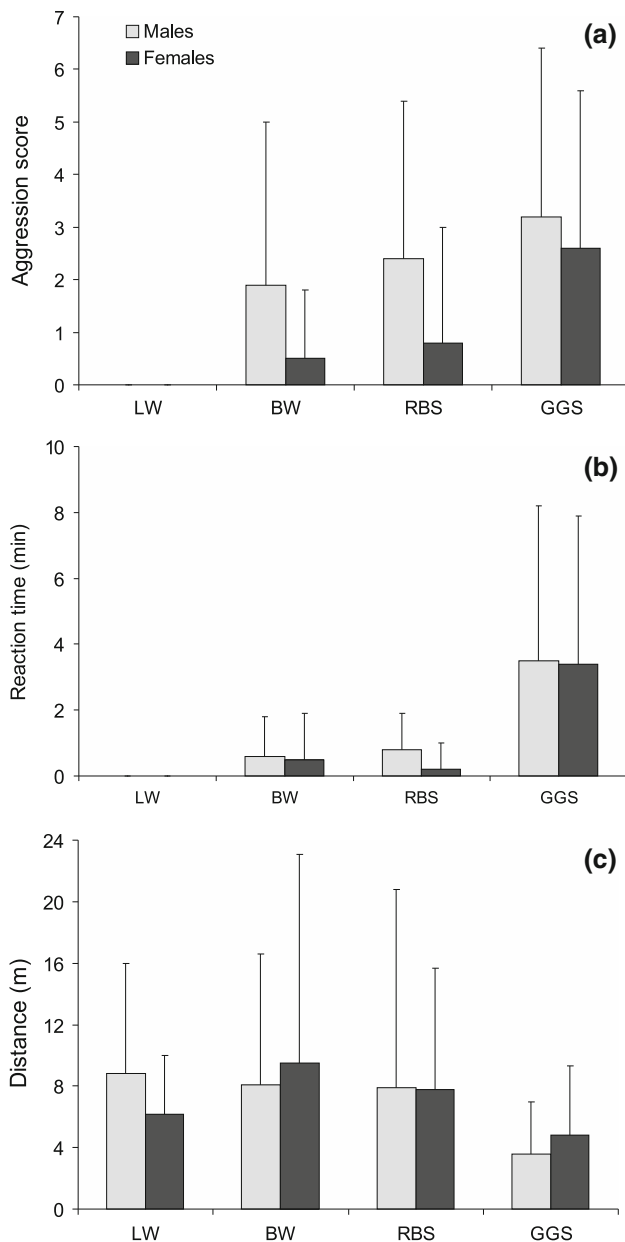


**Fig. 2** Mean ( $\pm$ SD) aggression score (a), reaction time (b), and closest distance (c) of male and female Barred Warblers (BW) in response to the different dummy type. *RBS* Red-backed Shrike, *GGs* Great Grey Shrike, *LW* Lesser Whitethroat

this species, unlike RBS, were well concealed within the lower shrub zone. The nests of RBS were built higher up and were more exposed in the upper parts of low-growing shrubs (Polak 2012). Nest concealment can inhibit transmission of visual, chemical, or auditory cues to predators and there are numerous studies demonstrating the positive effects of concealment on nest survival (Musilová et al. 2004; Gołowski and Mitrus 2008).

Comparative analysis of the reproductive parameters of the two species showed that BW built smaller nests and





**Fig. 3** Mean (±SD) aggression score (a), reaction time (b), and closest distance (c) of male and female Red-backed Shrikes (RBS) in response to the different dummy type. *BW* Barred Warbler, *GGS* Great Grey Shrike, *LW* Lesser Whitethroat

laid fewer and smaller eggs than RBS, even though the ultimate production of offspring was similar in both. Overall breeding parameters reported from studied populations of both species were slightly better than those recorded in others part of Europe. Mean clutch sizes of BWs in eastern Poland were larger (5.0–5.1) than those recorded in Ukraine (4.8) (Knysh 2005), Sweden (4.8) (Hedenström and Åkesson 1991), and western Poland (4.7) (Kuźniak et al. 2001) and similar to the records obtained in northern Germany (5.0) (Neuschulz 1981) and Russia

(4.8–5.0) (Payevsky et al. 2003). Dimensions of BW eggs reported in this study (20.8–21.2 mm × 15.6–15.7 mm) were slightly larger than noted by Kuźniak et al. (2001) as well as Knysh (2005), where the mean measurements were 20.9 × 15.8 mm and 20.8 × 15.6 mm, respectively. The hatching success noted in the BW studied population (98 %) was higher than that obtained in other studies: 91 % in Sweden (Hedenström and Åkesson 1991) and 94 % in Germany (Neuschulz 1981). The average number of young (4.3–4.6) leaving the nest form successful broods in the BW study population was slightly higher than in Ukraine (3.9) (Knysh 2005), western Poland (4.4) (Kuźniak et al. 2001), and Germany (4.5) (Neuschulz 1988). In this study, the average clutch size (5.4–5.6) in the RBS was larger from results obtained in other European populations (4.3–5.2, Kuźniak 1991; Horvath et al. 2000; Šimek 2001). The mean number of fledglings per successful pair (5.4–5.6) noted in the presented study fall into high values in comparison to other studies: 4.5–4.7 (Kuźniak 1991; Golawski 2006; Müller et al. 2005). The high breeding parameters recorded from these populations were probably due to extensive management and abundant food resources. In some regions in eastern Poland we still have bird-friendly farming management that can support relatively strong avian populations inhabiting agriculture landscapes.

**Factors affecting nest survival rate**

Analysis with the aid of the MARK program showed that although the two species inhabited the same ecological niche, different selection pressures operated on their reproductive success. The daily survival rate of the RBS was apparently more sensitive to variation in habitat conditions, and degradation and loss of habitats due to recent changes in agricultural practices could have negatively affected the productivity of RBS (Kuźniak and Tryjanowski 2003). The results presented here reveal that nest survival of BW was strongly affected by the timing of breeding. The daily survival rate of the RBS was relatively stable throughout the reproductive period. This is in agreement with other studies (Müller et al. 2005; Golawski 2006) where shrikes had similar brood losses rates during the different stages of breeding season. The fate of the RBS broods was determined primarily by environmental parameters, i.e. habitat type and degree of nest concealment within the surrounding vegetation. The daily survival rate of RBS nests (0.971) obtained in the present study was similar to the values reported in other studies (0.964–0.984) in Hungary, Germany, and the Czech Republic (Hušek et al. 2010). In BWs, factors related to nesting dates were of greater significance. As the breeding season progressed, the daily survival rate of BWs gradually decreased, reaching its lowest level halfway through the

season but picking up again towards the end of the season. An earlier study had shown that even though the breeding periods of most BWs and RBS' overlapped, slight differences in nesting phenology were discernible (Polak 2015). Since the BW departed from the breeding grounds earlier than the RBS, the pressure of passing time was greater on broods of the former than of the latter. On average, the clutch initiation date in this BW population was 7 days earlier than in the RBS (Polak 2015), and their broods were better synchronized.

The heightened survival rate of warbler broods at the nestling stage could have been due to the development dense, low vegetation that may have decreased detection of nests by predators (Rader et al. 2007; Wilson et al. 2007). Another possible explanation is greater intensity of behaviour associated with nest defence (Hałupka and Hałupka 1997; Polak 2013). During the egg incubation stage birds behave more secretively in the neighbourhood of their nests and rarely show signs of alarm towards predators turning up nearby. However, during the nestling period parents actively defend their broods (Smith and Wilson 2010). There is increasing evidence that as a nest ages and its relative value increases, adult birds can increase their investments by defending them more aggressively (Pavel and Bureš 2001; Tryjanowski and Goławski 2004; Segura and Reboreda 2012). The reproductive window of BWs is extremely short; it is likely that their re-nesting potential is lower throughout the season and their current breeding attempt is of maximum value from the start, and that limited opportunities to repeat clutches in warblers could cause an increase in parental investment of their current brood (Pavel and Bureš 2001; Hollander et al. 2008). The increase in survival rate with increasing nest age could also be due to the fact that predators find more vulnerable nests early in the breeding period and broods that remain active are less detectable by predators (Martin et al. 2000; Dinsmore et al. 2002).

### Intra- and inter-specific agonistic behaviour

The results of behavioural tests with stuffed models were in line with my initial expectations and showed that aggressive behaviour between BW and RBS was not as intensive as between conspecifics. In general, the shrikes, especially the males, were more aggressive near their nests towards intruders than the warblers. The RBS male was more involved in nest defence. Most authors demonstrated higher intensity of mobbing in nest defence in males than in females in various bird species, possibly caused by elevated levels of testosterone (Pavel and Bureš 2001; Kryštofková et al. 2011; Strnad et al. 2012). During the experiments neither BW nor RBS behaved aggressively towards the stuffed LW, which was an interesting result because RBS can hunt on smaller sylviid species (Kuźniak and Tryjanowski 2003; Polak M.,

unpublished data). BWs behaved the most aggressively towards the stuffed GGS, a potential predator and threat to young warblers. Aggressive reactions were also observed with respect to conspecifics, but in accordance with my initial expectations, BW tolerated the presence of RBS near their nests. This has been confirmed by observations of other pairs during a six-year field study (M. Polak—unpublished data). Despite the close proximity of BW and RBS nests, sometimes even in the same shrub, no aggression whatsoever was recorded on the part of the BW towards the RBS. The simplest explanation for why BW do not mob RBS is that warblers assess them as dangerous to themselves. However, this is in conflict with this study where warblers mobbed much bigger GGS models. An alternative explanation is that warblers assess them as not competitive/dangerous birds. By contrast, the RBS pairs tested in the experiments reacted aggressively towards three species. In response to the BW model tested, shrikes tended to give only alarm calls. Their response was the most violent towards GGS, less strong with respect to conspecifics and the mildest vis-à-vis the BW. This is in agreement with a previous study (Strnad et al. 2012; Němec and Fuchs 2014) where shrikes demonstrated the ability to discriminate between particular animal species and tried to respond adequately to a threat. Discrimination among different types of intruders seems to be advantageous for individuals, because this enables unnecessary aggressive interactions to be reduced in order to minimise the energy costs of defence during the breeding period (Tryjanowski and Goławski 2004; Kryštofková et al. 2011). These results may indicate that despite the similar ecological requirements and the consequent competition for resources, BW and RBS tolerate each other's presence near their nests, displaying at most a low level of aggression towards the other species.

### Conclusion

In summary, this study has shown that: (1) both species have similar breeding parameters in the two types of habitat investigated here; (2) BWs constructed smaller nests, and laid fewer and smaller eggs than RBSs, although the ultimate production of offspring was similar in both species; (3) in comparison to the other populations from Europe, BWs and RBSs in eastern Poland experienced good breeding parameters and this is likely to be related to the extensive agriculture management and abundant food resources; (4) habitat parameters had a greater effect on daily survival rate in RBS than in BW; (5) nest survival in BWs was strongly dependent on breeding cycle phase—nests in the middle of the breeding season were the least likely to survive; and (6) the level of mutual aggression between the BW and the RBS was low and may well have contributed to the nesting of one species near the other.

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## References

- Báldi A (2004) Predation of artificial nests in a marshland: site and visibility effects. *Ornis Hung* 14:27–30
- Boulton RL, Cassey P (2006) An inexpensive method for identifying predators of passerine nests using tethered artificial eggs. *New Zeal J Ecol* 30:377–385
- Brzeziński M, Żmihorski M, Barkowska M (2010) Spatio-temporal variation in predation on artificial ground nests: a 12-year experiment. *Ann Zool Fenn* 47:173–183
- Burnham KP, Anderson DR (2002) Model selection and multimodel inference. Springer, Heidelberg
- Cramp S (1992) Handbook of the birds of Europe, the Middle east and North Africa. In: The birds of the western Palearctic, vol VI: warblers. Oxford University Press, Oxford
- Cramp S, Perrins CM (1993) Handbook of the birds of Europe, the Middle east and North Africa. In: The birds of the western Palearctic vol VII: flycatchers to shrikes. Oxford University Press, Oxford
- Dinsmore SJ, White GC, Knopf FL (2002) Advanced techniques for modelling avian nest survival. *Ecology* 83:3476–3488
- Fisher RJ, Wiebe KL (2006) Nest site attributes and temporal patterns of northern flicker nest loss: effects of predation and competition. *Oecologia* 147:744–753
- Goławski A (2006) Breeding biology of the Red-backed Shrike *Lanius collurio* in the extensive agricultural landscape of eastern Poland. *Orn Pol* 47:1–10
- Goławski A (2007a) Does the Red-backed Shrike (*Lanius collurio* L.) benefit from nesting in the association with the Barred Warbler (*Sylvia nisoria* Bechst.)? *Pol J Ecol* 55:601–604
- Goławski A (2007b) Seasonal and annual changes in the diet of the Red-backed Shrike *Lanius collurio* in farmland of eastern Poland. *Bel J Zool* 137:215–218
- Goławski A, Mitrus C (2008) What is more important: nest-site concealment or aggressive behaviour? A case study of the Red-backed Shrike, *Lanius collurio*. *Folia Zool* 57:403–410
- Hałupka K, Hałupka L (1997) The influence of reproductive season stage on nest defense by meadow pipits (*Anthus pratensis*). *Ethol Ecol Evol* 9:89–98
- Hedenström A, Åkesson S (1991) Notes on the breeding biology of the Barred Warbler *Sylvia nisoria* at Ottenby, Sweden. *Ornis Svec* 1:57–58
- Hollander FA, Van Overveld T, Tokka I, Matthysen E (2008) Personality and nest defense in the great tit (*Parus major*). *Ethology* 114:405–412
- Hollander FA, van Dyck H, San Martin G, Titeux N (2011) Maladaptive habitat selection of a migratory passerine bird in a human-modified landscape. *PLoS One* 9:e25703
- Holway DA (1991) Nest-site selection and the importance of nest concealment in the Black-throated Blue Warbler. *Condor* 93:575–581
- Horvath R, Farkas R, Yosef R (2000) Nesting ecology of Red-backed Shrike (*Lanius collurio*) in northeastern Hungary. *Ring* 22:127–132
- Hušek J, Weidinger K, Adamik P, Hlavaty L, Holář 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 Ornithol* 45:43–49
- Knysh NP (2005) Present situation of the Barred Warbler in Ukraine and its biology according to researches in Sumy region. *Berkut* 14:99–110
- Kryštofková M, Haas M, Exnerová A (2011) Nest defence in Blackbirds *Turdus merula*: effect of predator distance and parental sex. *Acta Ornithol* 46:55–63
- Kuźniak S (1991) Breeding ecology of the Red-backed Shrike *Lanius collurio* in the Wielkopolska region (W Poland). *Acta Ornithol* 26:67–83
- Kuźniak S, Tryjanowski P (2003) Red-backed shrike. Wydawnictwo LKP, Świebodzin (in Polish)
- Kuźniak S, Bednorz J, Tryjanowski P (2001) Spatial and temporal relations between the Barred Warbler *Sylvia nisoria* and the Red-backed Shrike *Lanius collurio* in the Wielkopolska region (W Poland). *Acta Ornithol* 36:129–133
- Lewis S, Nussey DH, Wood AG, Croxall JP, Phillips RA (2012) Intrinsic determinants of a population trend in timing of breeding in the wandering albatross. *Oikos* 121:2061–2071
- Martin TE, Scott J, Menge C (2000) Nest predation increases with parental activity: separating nest site and parental activity. *Proc R Soc Lond B* 267:2287–2293
- Morelli F, Tryjanowski P (2015) No species is an island: testing the effects of biotic interactions on models of avian niche occupation. *Ecol Evol* 5:759–768
- 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. *Popul Ecol* 143:37–50
- Musilová Z, Musil P, Zouhar J, Poláková S (2014) Nest survival in the Reed Bunting *Emberiza schoeniclus* in fragmented wetland habitats: the effect of nest-site selection. *Ornis Fennica* 91:138–148
- Němec M, Fuchs R (2014) Nest defense of the Red-backed Shrike *Lanius collurio* against five corvid species. *Acta Ethol* 17:149–154
- Neuschulz F (1981) The biology of a population of Barred Warblers (*Sylvia nisoria*) in North Germany. *J Orn* 122:231–257
- Neuschulz F (1988) Zur Synökie von Sperbergrasmücke *Sylvia nisoria* (Bechst., 1975) und Neuntöter *Lanius collurio* (L., 1758). *Luchow-Dannenberger Orn. Jber.* 234
- Orłowski G, Wuczyński A, Karg J (2015) Effect of brood age on nestling diet and prey composition in a hedgerow specialist bird, the Barred Warbler *Sylvia nisoria*. *PLoS One* 10:e0131100
- Pavel V, Bureš S (2001) Offspring age and nest defence: test of feedback hypothesis in the meadow pipit. *Anim Behav* 61:297–303
- Payevsky V, Vysotsky V, Zelenova N (2003) Extinction of a Barred Warbler *Sylvia nisoria* population in Eastern Baltic: long-term monitoring, demography, and biometry. *Avian Ecol Behav* 11:89–105
- Polak M (2012) Habitat preferences of the sympatric Barred Warbler (*Sylvia nisoria*) and the Red-backed Shrike (*Lanius collurio*) breeding in central Poland. *Ann Zool Fenn* 49:355–363
- Polak M (2013) Comparison of nest defence behaviour between two associate passerines. *J Ethol* 31:1–7

- Polak M (2014) Protective nesting association between the Barred Warbler *Sylvia nisoria* and the Red-backed Shrike *Lanius collurio*: an experiment using artificial and natural nests. *Ecol Res* 29:949–957
- Polak M (2015) Variation in the nesting phenology of two positively interacting passerines. *Avian Biol Res* 8:97–103
- Polak M, Filipiuk M (2014) Habitat preferences of the Barred Warbler *Sylvia nisoria* and the Red-backed Shrike *Lanius collurio* in the Middle Roztocze region. *Orn Pol* 55:22–23 (in Polish)
- Rader MJ, Brennan LA, Hernández F, Silvy NJ, Wu B (2007) Nest-site selection and nest survival of northern bobwhite in southern Texas. *Wilson J Ornithol* 119:392–399
- Rotella JJ, Dinsmore SJ, Shaffer TL (2004) Modelling nest-survival data: a comparison of recently developed methods that can be implemented in MARK and SAS. *Anim Biodiv Conserv* 27:187–205
- Schaefer HC, Eshiamwata GW, Munyekenye FB, Böhning-Gaese K (2004) Life-history of two African *Sylvia* warblers: low annual fecundity and long post-fledging care. *Ibis* 146:427–437
- Segura LN, Reboresda JC (2012) Nest survival rates of Red-crested Cardinals increase with nest age in south-temperate forests of Argentina. *J Field Ornithol* 83:343–350
- Smith PA, Wilson S (2010) Intraspecific patterns in shorebird nest survival are related to nest age and defence behaviour. *Oecologia* 163:613–624
- Söderström B, Pärt T, Rydén J (1998) Different nest predator faunas and nest predation risk on ground and shrub nests at forest ecotones: an experiment and a review. *Oecologia* 117:108–118
- Statsoft Statsoft Inc. (2001) Statistica for Windows (data analysis system). Version 6.0. StatSoft Inc., Tulsa
- Šimek J (2001) Patterns of breeding fidelity in the Red-backed Shrike (*Lanius collurio*). *Orn Fenn* 78:61–71
- Strnad M, Němec M, Veselý P, Fuchs R (2012) Red-backed Shrikes (*Lanius collurio*) adjust the mobbing intensity, but not mobbing frequency, by assessing the potential threat to themselves from different predators. *Ornis Fenn* 89:206–215
- Surmacki A, Kuczyński L, Tryjanowski P (2006) Eggshell patterning in the Red-backed Shrike *Lanius collurio*: relation to egg size and potential function. *Acta Ornithol* 41:145–151
- Szymański P, Antczak M (2013) Structural heterogeneity of linear habitats positively affects Barred Warbler *Sylvia nisoria*, Common Whitethroat *Sylvia communis* and Lesser Whitethroat *Sylvia curruca* in farmland of Western Poland. *Bird Study* 60:484–490
- Szymkowiak J, Skierczyński M, Kuczyński L (2014) Are buntings good indicators of agricultural intensity? *Agr Ecosyst Environ* 188:192–197
- Tomiałojć L (1980) The combined version of the mapping method. *Not Orn* 21:33–54 (in Polish)
- Tøttrup AP, Klaassen RHG, Kristensen MW, Strandberg R, Vardanis Y, Lindström Å, Rahbek C, Alerstam T, Thorup K (2012) Drought in Africa caused delayed arrival of European songbirds. *Science* 338:1307
- 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. *J Ethol* 22:13–16
- 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* 95:316–320
- Tryjanowski P, Hartel T, Báldi A, Szymański P, Tobółka M, Herzon I, Goławski A, Konvička M, Hromada M, Jerzak L, Kujawa K, Lenda M, Orłowski G, Panek M, Skórka P, Sparks TH, Tworek S, Wuczyński A, Žmihorski M (2011) Conservation of farmland birds faces different challenges in Western and Central-Eastern Europe. *Acta Ornithol* 46:1–12
- Walker J, Lindberg MS, MacCluskie MC, Petrus MJ, Sedinger JS (2005) Nest survival of scaup and other ducks in the boreal forest of Alaska. *J Wildl Manag* 69:582–591
- White GC, Burnham KP (1999) Program MARK: survival estimation from populations of marked animals. *Bird Study* 46:120–138
- Whittingham MJ, Stephens PA, Bradbury RB, Freckleton RP (2006) Why do we still use stepwise modelling in ecology and behaviour? *J Anim Ecol* 75:1182–1189
- Wilson S, Martin K, Hannon SJ (2007) Nest survival patterns in willow ptarmigan: influence of time, nesting stage, and female characteristics. *Condor* 109:377–388