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## Protective nesting association between the Barred Warbler *Sylvia nisoria* and the Red-backed Shrike *Lanius collurio*: an experiment using artificial and natural nests

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**Abstract** The pressure of predators may significantly affects the distribution pattern of nesting birds. Some individuals may reduce the risk of predation by nesting near other species with an aggressive nest defence. In the present study I tested the predator protection hypothesis using experimental (artificial nests) and observational (real nests) approaches on two ecologically similar passerine birds—the Barred Warbler *Sylvia nisoria* and the Red-backed Shrike *Lanius collurio*. Studies have been conducted in eastern Poland in two types of habitat: river valley and farmland. The main predators of natural and artificial nests were birds, and to a lesser extent, also mammals. I found wide variation level of predation of both types of nests in different years. Nest survival rate of artificial nests was significantly lower in the farmland than in the river valley and in natural nests I observed reverse pattern. According to the predictions of the predator protection hypothesis the survival rates of the natural and artificial nests were significantly higher in territories of individuals breeding in the protective nesting association. This type of interspecific positive interaction between two associate species can be classified as facultative mutualism.

**Keywords** Cooperative breeding · Facultative mutualism · Predation · Species interactions

### Introduction

The wide diversity of ecological interactions between species can be compressed into three large groups: negative (minus), neutral (zero) and positive (plus)

(Bronstein 1994). Positive interactions are ubiquitous in natural communities (Herre et al. 1999), although it is now widely recognized that they have been relatively ignored by researchers who focused almost exclusively on competition and predation (Bronstein 2009). In recent years cooperation and helping between unrelated individuals is one of the key topics in evolutionary biology (Quinn and Ueta 2008; Bshary and Bronstein 2011). A model example of positive interaction is the formation of protective nesting association (Bogliani et al. 1999; Richardson and Bolen 1999). In their attempts to minimise nest predation, animals actively seek out individuals of an accompanying species nesting nearby (Blanco and Tella 1997; Bang et al. 2005). In the world of animals such species interactions have been described primarily among birds, but they have also been observed between birds and social insects, and even reptiles (Haemig 2001). The mechanism and causes underlying the formation of breeding associations are not completely understood and continue to arouse controversy among behavioural ecologists (see review: Quinn and Ueta 2008). Despite the rich descriptive literature on the subject of protective breeding associations, experimental studies of them are still rare (Haemig 2001). Within a protective nesting association one or more species benefit directly from the protective umbrella afforded by another species (Norrdahl et al. 1995). In birds, breeding associations are usually formed between an aggressive species, often an owl or a raptor, and a less aggressive species, frequently a passerine, which takes advantage of the defensive behaviour of the protecting species and builds its nests close by (Blomqvist and Elander 1988; Ebbinge and Spaans 2002). The less aggressive species thus enhances its adaptation through higher breeding success, which is achieved as a result of protection from nest predators (Halme et al. 2004). On the other hand, the principal costs that species “protected” by an aggressive neighbour incur are that their broods may be plundered or

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that they themselves may fall victim to that neighbour (Covas et al. 2004).

An interesting phenomenon, yet far less frequent and thus rarely studied, is the formation of associations by species from the same systematic groups, in which there is no great disproportion in body size, preying method or intensity of aggressive behaviour (Clark and Robertson 1979; Isenmann and Fradet 1995; Richardson and Bolen 1999). In the present study I chose two ecologically similar passerines—the Red-backed Shrike *Lanius collurio* (henceforth: RBS) and the Barred Warbler *Sylvia nisoria* (henceforth: BW)—in order to assess the potential advantages of their nesting together. A number of studies have shown that, where they breed sympatrically in central and eastern Europe, these two species have no aversion to breeding close to one another and inhabit similar environments (Nankinov and Darakchiev 1979; Neuschulz 1988; Polak 2012). Both species vigorously defend their nests and behave aggressively towards predators (Glutz von Blotzheim and Bauer 1991; Cramp and Perrins 1993). Some researchers are of the opinion that any breeding association between these two species is due solely to their similar habitat preferences and that relations between them are neutral; birds nesting in proximity to each other gain no advantage from this (Gotzman 1965; Kuźniak et al. 2001). In contrast, other authors point out that, in accordance with the predator protection hypothesis, birds actively choose the neighbourhood in which they are to breed, because they benefit from this through better protection from predators and a higher reproductive success (Cramp 1992; Cramp and Perrins 1993; Isenmann and Fradet 1995). This was recently confirmed by Goławski (2007), who provided evidence that RBSs nesting in close proximity to BWs achieved greater breeding success, and also by Neuschulz (1988), who demonstrated that BWs inhabiting territories occupied by RBSs were also reproductively more successful. But because of the limited range, negative breeding population trend and rarity of BWs in many areas, a comparative study of populations of the two species during the same period of time and in the same area has yet to be done (Goławski 2007). Such a study would determine whether these interactions are based on commensalism or mutualism (Isenmann and Fradet 1995).

The main objective of the present work was to perform an experiment to test the predator protection hypothesis in these two species using artificial and natural clutches. It was assumed that if the protective umbrella was functioning effectively, the artificial nests should have the greatest chance of survival in sites occupied by both BWs and RBSs, a lesser chance in areas inhabited exclusively by one or the other species, and the least chance of survival in the control nests situated beyond the breeding territories of either species. I also assessed the extent to which habitat parameters modified the activity patterns of raptors in the two habitat types. In view of their methodological

limitations, experiments with artificial nests are criticised by many researchers, because the results do not always reflect the real level of predation on natural broods (Mazgajski and Rejt 2005; Brzeziński et al. 2010). In order to assess the predation pressure on natural clutches, I collected information on the biology and breeding success of the RBS and BW. This enabled to compare the reproductive success of birds nesting within the territories of the associate species and outside them.

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## Materials and methods

### Study area

The field work was carried out on two study plots in eastern Poland. In 2009–2011 observations were carried out near the village of Stężycza (N 51°34'; E 21°48') in the Middle Vistula River valley. This plot, 76 ha in area (84 ha in 2010), was a well-insolated, dry pasture. Because of the reduced grazing by cattle and horses in recent years, succession to shrubby vegetation, especially the Hawthorns *Crataegus sp.*, was rapid. To the east the plot was bounded by an ox-bow lake, to the west by the River Vistula. There were small patches of willow-poplar riverine woodland *Salici-populetum*. The studies on this plot embraced a mosaic of four main habitats: open terrain (42.8 %), shrubs and bushes (29.4 %), trees (19.7 %) and water (8.1 %; Polak 2012). In 2012–2013 I also carried out observations on a study plot 106 ha in area in the farmland near the village of Żurawnica (N50°38'; E22°58') in the central Roztocze region. The component typical of the deforested hills there consists of long, narrow strip fields, separated by high balks. The main crops in this plot were cereals. The studies on this plot embraced a mosaic of six main habitats: fields (65.9 %), fallow land (22.3 %), bushes (6.4 %), trees (3.1 %), roads (2.2 %) and buildings (0.1 %; Polak and Filipiuk 2014).

### Study species

BW is a small passerine from the family *Sylviidae*, weighing 22–27 g, whose range is restricted to central and eastern Europe. It builds very well hidden nests in the shape of a basket of plant materials and animal hair. There is usually one brood per year in BW, however two broods per year were reported in Georgia (Cramp 1992). A brood usually contains 5 eggs. BW winters in central and eastern Africa (Cramp 1992). RBS is a passerine species widely distributed in the Western Palearctic. This species is normally single-brooded, but in case of first brood failure, replacement clutches are laid regularly. This species builds open cup nests on various bushes and trees. The nests are bulky structures made of plant stems and roots and sometimes containing man-made materials. Four to seven eggs are laid and are

incubated for 14 days. RBS is a trans-continental migrant wintering in southern Africa (Cramp and Perrins 1993).

#### Natural nests

The observations on both plots were carried out using the same methodology. 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. During each field visit the aim of the visual and auditory observations was to discover as many RBS and BW territories 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, and BW oscillated between 1.9 and 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 bushes and shrubs growing on the study plots. The position of each nest was marked on an orthophotograph and the exact coordinates were entered on the GPS receiver. The height of the shrubs and the distance between the lower edge of the nest and the ground were measured with a tape accurate to 10 cm. 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. If a brood was depredated, I attempted to determine the cause and to record all traces left by the predator. For each season maps were drawn to show the distribution and range of the breeding territories of the two species. The boundaries of breeding territories were delineated using the method of minimal polygons, in which a territory was taken to be the smallest convex polygon, determined from the spatially extreme points plotted on the map where birds were observed in a given territory (Kenward 1987). The size of BW and RBS's breeding territories on the study plots varied from 0.03 to 1.09 ha (Polak and Filipiuk 2014). According to Goławski (2007) the all analyses performed in the present work included nests lost only as a result of predation. Replacement clutches were not analysed. Data from 98 RBS nests to 44 BW nests were thus worked up. During the incubation period the clutches were defined as being successful when eggs had survived to up to hatching period. Hatchability was defined as the ratio of the number of hatched nestlings to the number of eggs laid. Pairs that succeeded to produce at least one fledging were recorded as successful. Reproductive success was calculated as the ratio of successful broods to the total number of broods found. The number of fledglings/breeding pairs was defined as the number of young reaching 12–14 days of age in all

examined broods in the studied population 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 had survived to 12–14 days old). 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 has shown that mammals generally left shell fragments in or on the nest cup, indicating eggs were eaten in the nest, and the birds 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. The degree of concealment of 82 RBS nests and 36 BW nests was assessed as their visibility at a distance of 1 metre 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.

#### Artificial nest experiment

In order to assess the degree of nest predation in particular years and the efficacy of the protective umbrella around the nests of the two target species, experiments were carried out in 2010–2013 using 362 artificial nests imitating natural clutches (Batáry and Báldi 2005). For this purpose I used commercial nests normally sold to bird breeders. Made from natural, withered plant fibres, the nests were basket-shaped and had the following dimensions: depth = 5 cm, internal diameter = 10 cm, external diameter = 12 cm, height = 7 cm. These dimensions lie within the natural range of variability of the nests of the target species on the study area (MP, unpublished data). The artificial broods were placed within shrubs ca 60–80 m distant from one another. They were deployed in such a way as to evenly cover most of the study plot; the coverage varied from ca 80 % (2013) to 100 % (2011–2012). These nests were placed at an average height of  $118.5 \pm 44.6$  cm (range 20–240 cm) and in nest shrubs of average height  $299.8 \pm 97.3$  cm (range 90–650 cm); these parameters lie within the normal range of variability in the populations under scrutiny (Polak 2012). The nests were attached to the branches with thin wire (Báldi and Batáry 2005). Each nest contained one, commercial Quail's egg,

and one egg made from white plasticine. This latter egg was used to identify the kind of predator, since the traces left by mammalian predators differ from those left by birds. The plasticine egg was permanently fixed to the nest with thin wire so that a predator could not remove it easily (Stuart-Smith and Hades 2003). The average dimensions of the plasticine egg (length = 20 mm, width = 15 mm) corresponded to those of the two species in the target populations (MP, unpublished data). Both eggs were left in the nests for 14 days, the period corresponding to the length of the incubation period in the RBS and BW (Cramp 1992; Cramp and Perrins 1993). The exposure time of these artificial clutches was synchronised with the peak laying period in the two target species. This was from 31 May to 14 June in 2010, from 30 May to 13 June in 2011 and 2012 and from 28 May to 11 June in 2013. After the elapse of 14 days, all the artificial nests were inspected. Broods were deemed to have been depredated if the Quail's egg was missing or damaged and if there were bill, tooth or claw marks on the plasticine egg. Three categories of predator were distinguished on the basis of these traces: large mammals, small mammals and birds. If the Quail's egg was missing and there were triangular bill marks on the plasticine egg, the predator was assumed to have been a bird. If the broken shell of the Quail's egg was in the nest and the plasticine egg showed small tooth marks, the predator will have been a small mammal; if the tooth marks were large and the nest structure was destroyed, then it must have been a large mammal. In 35 % of artificial nests, where the teeth marks left by mammals on plasticine eggs were recorded, I found the remains of shell Quail eggs. In contrast, only in 3 % of broods, where the bill marks were identified, I observed the shell fragments, and in the remaining nests Quail's eggs were brought away from the nest site.

#### Statistical analysis

The logistic regression model was used to analyse which factors had a significant influence on the survival of artificial and natural clutches. The fate of a natural/artificial clutch, i.e. success (1) or loss (0), was selected as the dependent variable, whereas year, type of habitat (river valley vs. farmland), position of the nest with respect to the associate species (present or absent within the boundaries of RBS and/or BW breeding territory),

height of the nesting shrub and height of the nest above the ground were the independent variables. The chi-squared test with Yates's correction (reproductive success and hatchability) and the t test (clutch size, number of nestlings in all nests, number of fledglings in nests with success) were used to compare the breeding biology parameters between birds nesting within the territories of associate species and beyond such territories. Mean values are given together with the standard deviation  $\pm$  SD. The STATISTICA 6.0 package was used for the statistical calculations (Statsoft Inc. 2001). A two-tailed critical area was assumed in the tests, and results in which the probability of committing a type I error was equal to or less than 0.5 were treated as statistically significant.

## Results

### Survival rate of artificial nests

123 (44 %) of the 362 artificial nests were depredated by predators. Brood losses showed great variation regarding site and time. In both habitats the main predators were birds (Table 1). The logistic regression model showed that four of the five variables significantly affected the survival of the artificial nests: year, type of habitat, position of the nest with respect to the associate species and height of the nest above the ground (Wald = 56.348;  $P < 0.001$ ; Table 2). The most losses were recorded in 2012 (58 %;  $n = 126$  nests) and the least in 2011 (12 %;  $n = 88$ ). In the other years, losses due to predators were at the average level: 2010 (39 %;  $n = 65$ ), 2013 (34 %;  $n = 83$ ). The artificial nests survived better in the river valley (28 % losses;  $n = 214$ ) than in the farmland (43 % losses;  $n = 148$ ). In both study plots nests located close to the ground were less exposed to predation (Fig. 1a). In addition, survival rate of artificial nests in both plots depended on whether they were located within or beyond the boundaries of breeding territories of the two target species (Fig. 1b). Artificial nests situated within the territories of both RBS and BW were subject to the lowest level of predation (24 %;  $n = 136$ ). Losses were higher in nests located exclusively in RBS (28 %;  $n = 71$ ) or BW (35 %;  $n = 46$ ) territories and were the highest in the control nests sited outside the breeding territories of either species (51 %;  $n = 109$ ).

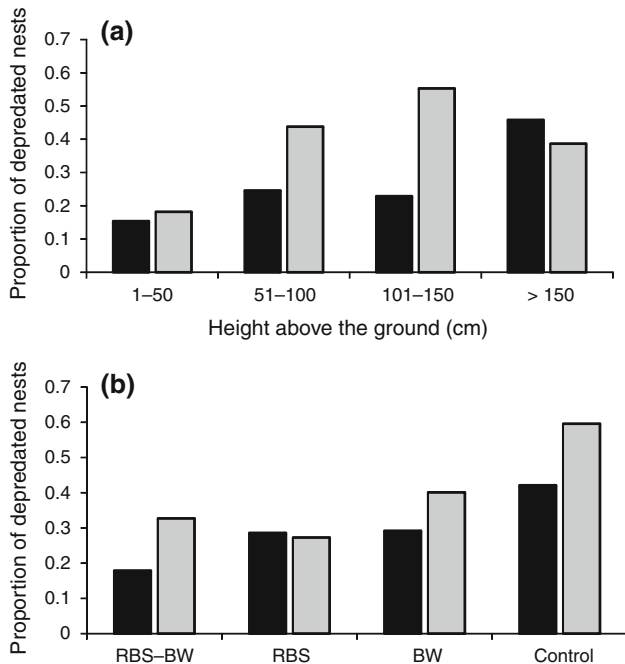
**Table 1** Percentage of artificial and the Red-backed Shrike's (RBS) and the Barred Warbler's (BW) natural nests depredated in the incubation period by the various predator classes in two different habitats

Habitat	Type of nest	Sample size of all nests	Birds (%)	Large mammals (%)	Small mammals (%)	Unknown (%)
River valley	Artificial	214	42 (70)	11 (18)	1 (2)	5 (10)
	RBS	56	21 (84)	1 (4)	–	3 (12)
	BW	28	6 (100)	–	–	–
Farmland	Artificial	148	36 (57)	2 (3)	14 (22)	11 (18)
	RBS	28	8 (80)	–	2 (20)	–
	BW	16	2 (67)	–	1 (33)	–

**Table 2** The factors affecting survival of artificial nests ( $n = 362$ ; logistic regression model)

Variable	Estimate	SE	Wald statistic	Odds ratio (95 % CI)	<i>P</i>
Constant	-2.71	0.64	18.05	0.07 (0.02–0.23)	<0.001
Year	-1.26	0.26	24.08	0.28 (0.17–0.47)	<0.001
Habitat type	3.49	0.63	30.85	32.7 (9.51–112.6)	<0.001
Position of the nest with respect to the associate	-0.34	0.10	12.24	0.71 (0.59–0.86)	<0.001
Height of the nest above the ground	0.01	0.003	5.17	1.00 (1.00–1.01)	<0.05

For each parameter its *B* estimate with standard error (SE), Wald statistic, odds ratio (change in probability of nest survival/probability of nest depredation) with 95 % confidence interval (CI) and *P* value are given. Only significant parameters are shown



**Fig. 1** Predation rate of artificial nests placed in different heights above the ground (a) and in relation to position of the artificial nest with respect to the associate species (b). RS–BW sites occupied by both BWs (Barred Warblers) and RBSs (Red-backed Shrikes), RBS places inhabited exclusively by RBSs, BW areas inhabited exclusively by BWs, Control areas situated beyond the breeding territories of either species. Black bars farmland, grey bars river valley

#### Survival rate of natural nests during the egg incubation period

The level of clutch losses due to predation during the incubation of eggs in RBS was 45 % ( $n = 56$ ) in the river valley and 24 % ( $n = 42$ ) in the farmland. This rate was generally lower in BW: 21 % clutches ( $n = 28$ ) lost in the river valley and just 19 % ( $n = 16$ ) in the farmland. The concealment index of nests in vegetation was  $5.1 \pm 1.5$  (range 4–11;  $n = 36$ ) in BW, whereas in RBS it was higher and covered a wider range of values, i.e. from 4 to 20 (mean =  $9.2 \pm 4.9$ ;  $n = 82$ ). It is evident from a comparison of these indices that BW hid their nests much better than RBS did (*t* test,  $t = -4.9$ ,  $df = 116$ ;  $P < 0.001$ ). Clutch losses in RBS nests were depredated by birds—29 (83 %), small mammals—2 (6 %), large mammals—1 (3 %) and unknown preda-

tors—3 (9 %). The corresponding figures for BW are birds—8 (89 %) and small mammals—1 (11 %; Table 1). The logistic regression model showed that two of the five variables had a significant effect on the level of clutch losses in RBS: year and position of the nest with respect to the associate species (Wald = 17.598;  $P < 0.005$ ; Table 3). In contrast, none of the analysed variables were significantly responsible for clutch survival in BW (all parameters:  $P > 0.44$ ). The rate of clutch losses during egg incubation in RBS differed widely from year to year, varying from 13 % (2011;  $n = 16$ ) to 69 % (2009;  $n = 16$ ), but in BW was more stable and varied from 11 % (2011;  $n = 9$ ) to 27 % (2010;  $n = 11$ ). RBSs nesting within BW territories suffered half as many brood losses due to predation (22 %;  $n = 41$ ) as RBSs nesting outside BW territories (46 %;  $n = 57$ ).

#### Breeding parameters of natural nest localised in different position to the associate species

41 of the 98 RBS broods were located within BW territories. RBSs nesting near BWs had a higher reproductive success (66 %;  $n = 41$ ) than their conspecifics nesting outside BW territories (44 %;  $n = 57$ ; Table 4). Moreover, the number of chicks produced in RBS nests located in close proximity to the associate species was significantly higher than in those located outside areas inhabited by BWs. The other reproductive parameters analysed were similar. More than half of the breeding pairs of BW (52 %;  $n = 44$ ) in the study plots nested within RBS territories. Reproductively, these pairs were significantly more successful (70 %;  $n = 23$ ) than their counterparts nesting in areas where RBSs did not do so (43 %;  $n = 21$ ). Analysis of the remaining breeding parameters did not reveal any statistically significant differences.

## Discussion

On both study plots almost half the population of RBSs and BWs nested in breeding associations. Birds choosing the near neighbourhood of the associate species benefited in that they had a higher breeding success, and thus a greater production of fledglings, than those pairs that

**Table 3** The factors affecting predation of Red-backed Shrike's (RBS) nests during the incubation period ( $n = 98$ ; logistic regression model)

Variable	Estimate	SE	Wald statistic	Odds ratio (95 % CI)	<i>P</i>
Constant	2.53	0.88	8.35	12.52 (2.21–71.15)	< 0.005
Year	−0.57	0.18	10.24	0.57 (0.40–0.81)	< 0.005
Position of the nest with respect to the associate	−1.06	0.49	4.70	0.35 (0.13–0.92)	< 0.05

For each parameter its *B* estimate with standard error (SE), Wald statistic, odds ratio (change in probability of nest survival/probability of nest depredation) with 95 % confidence interval (CI) and *P* value are given. Only significant parameters are shown

**Table 4** The comparison of reproductive parameters (mean  $\pm$  SD and sample size in brackets) of Red-backed Shrike's (RBS) and Barred Warbler's (BW) pairs breeding within the boundaries of associate species (+) and in areas situated beyond the breeding territories of associate species (−)

Reproductive parameters	RBS nests			BW nests		
	BW +	BW −	<i>P</i> value	RS +	RS −	<i>P</i> value
Clutch size	5.5 $\pm$ 0.6 (31)	5.6 $\pm$ 0.6 (49)	0.64*	4.9 $\pm$ 0.4 (17)	5.2 $\pm$ 0.5 (21)	0.07*
Hatchability	96 % (27)	93 % (30)	0.88**	97 % (14)	95 % (15)	0.94**
Number of fledglings/breeding pairs	3.2 $\pm$ 2.6 (41)	2.1 $\pm$ 2.6 (56)	< 0.05*	3.2 $\pm$ 2.1 (23)	2.0 $\pm$ 2.5 (21)	0.11*
Number of fledglings/successful pairs	4.9 $\pm$ 1.4 (27)	5.0 $\pm$ 1.0 (24)	0.83*	4.3 $\pm$ 1.0 (17)	4.8 $\pm$ 0.8 (9)	0.22*
Reproductive success	66 % (41)	44 % (57)	< 0.05**	70 % (23)	43 % (21)	< 0.05**

Differences between broods were tested using t test (\*) and chi-square tests with Yates correction (\*\*)

nested outside the breeding territories of the protective species. This is in agreement with the results obtained by researchers in other populations of the two target species (Neuschulz 1988; Goławski 2007). Even though RBSs and BWs are small passerines, they differ in their behaviour and appearance from most other small birds nesting in shrubs and bushes in Western Palearctic (Cramp 1992; Cramp and Perrins 1993). Recent studies have shown that they actively defend their broods and behave aggressively towards predators, including large mammals and even humans (Tryjanowski and Goławski 2004; Goławski and Mitrus 2008). With its powerful beak and strong legs, RBS is itself a predator of small vertebrates (Cramp and Perrins 1993). Some authors point out that some features of the appearance of adult male BWs, like the barred plumage on the breast and the intensively yellow iris and the black pupil, are a form of cuckoo–hawk mimicry and may be helpful in scaring off other animals (Welbergen and Davies 2011; Leisler and Schulze-Hagen 2013). An experiment with stuffed Hooded Crows *Corvus cornix* showed that BWs and RBSs chase away, sometimes communally, this kind of predator from their breeding sites (Polak 2013). Once the stuffed Crows were noticed, these aggressive passerines emitted alarm calls, which attracted conspecifics and heterospecifics to the site. The higher breeding success of birds nesting in a protective nesting association is due to the possibility of using their neighbour's aggressive anti-predator behaviour, which effectively defends broods against threats (Blomqvist and Elander 1988; Bogliani et al. 1999; van Kleef et al. 2007). Moreover, the two species may cooperate in that RBSs, usually perching at the top of bushes, can spot a predator approaching over open terrain, while BWs, searching for invertebrates within the vegetation, can discover any

danger threatening from within the bushes (Isenmann and Fradet 1995). The rapid detection of a predator raises the chances of effectively chasing it away from the breeding site (Clark and Robertson 1979; Blanco and Tella 1997).

However, the higher reproductive success of RBSs and BWs nested in association do not have to be explained only by the predator protection hypothesis, because this may be modified by other parameters as variation in food resources and habitat conditions. An alternative explanation of the observed pattern is the possibility that one of the two chooses appropriate sites in the breeding areas where there is less predation and/or rich foraging to be had, while the other species joins up with the first one, deriving benefits from such cooperation. Recent studies indicate that birds from a different species, sometimes even competing for the same resources, or from the same species, may be utilised as a source of information about habitat quality, predation risk and available food resources (Nocera et al. 2009). Such social information obtained from heterospecifics may be more valuable and more up-to-date, since under the same ecological conditions they may make slightly different use of the available resources (Forsman et al. 2008). Nest survival may be lower in areas with diminished food availability because breeding songbirds must spend more time foraging and less time defending their nests (Dunn et al. 2010). Be that as it may, the data on the survival rate of the artificial nests presented in this paper provide compelling evidence for accepting the predator protection hypothesis is the fundamental reason underlying this behaviour. The experiment confirmed the existence of a protective umbrella around the RBS and BW nests, since the artificial nests located in territories inhabited by both species survived best, while

those situated outside such territories fared worst. In this context it would be interesting to ask why all the birds in the populations studied did not nest in a protective nesting association. This could be due to a compromise between the benefits and costs of nesting jointly in the same patches of habitat (Richardson and Bolen 1999). Earlier observations in the same study plots (Polak 2012) indicated that the ecological niches of the two species largely overlap, which may give rise to competition for breeding sites (Martin and Martin 2001). Competition for similar food resources is less likely, since the two species forage in separate microhabitats (Gotzman 1965).

This study has shown that birds were responsible for most clutch losses in both species. This accords with the results of other studies done on various RBS populations (Goławski and Mitrus 2008), since in farmland, a high level of brood losses is related to the high density and activity of corvids (Brzeziński et al. 2010). Even though no exact data were gathered as to which species ravaged the artificial and natural nests, it is highly probable that the most frequent predators were the Hooded Crow and Jay *Garrulus glandarius* among the birds, the Fox *Vulpes vulpes*, Pine Marten *Martes martes* and Cat *Felis silvestris* among the large mammals, and the Wood/Yellow-necked Mouse *Apodemus sylvaticus/flavicollis* and Hazel Dormouse *Muscardinus avellanarius* among the small mammals (Weidinger 2009).

Recent research has shown that an important factor in the considerable differentiation in the level of brood losses from year to year is the number of victims (mainly small mammals) or other food sources for predators, the availability of which may vary strongly and be modified by environmental conditions (Ebbing and Spaans 2002; van Kleef et al. 2007; Brzeziński et al. 2010; Żmihorski et al. 2010). In the present study I noted substantial season-to-season fluctuations in the level of brood losses from the artificial nests and RBS broods. The aggressive behaviour against predator and better concealment of BW nests were most probably the reasons why the survival rate of incubated eggs in this species was higher than in RBS; this rate remained at a relatively constant, low level throughout the study period. A number of studies have shown that an interaction between both tactics of defence, i. e. aggression and degree of concealment of a nest in vegetation is one of the most important factors determining the risk of predation by other birds, especially corvids (Holway 1991; Batáry and Báldi 2005; Goławski and Mitrus 2008). The high rate of survival of BW clutches during their incubation was very probably why none of the environmental parameters analysed here affected the success of BW to any significant extent.

As in other studies of this kind, the type of habitat significantly affected the degree of predation pressure (Báldi 2004; Brzeziński et al. 2010). The level of clutch losses due to predation in the artificial nests was decidedly higher in the farmland than in the river valley, whereas the situation was reversed in the case of

natural nests. This higher level of predation on natural clutches in the river valley is a surprising result. In the fragmented farmland the breeding sites of both species tend to be clustered, which is not the case in river valleys; in the former landscape, therefore, it should be easier for predators to find nests (edge effect, Báldi and Batáry 2005; Wegge et al. 2012). The reason for this apparent discrepancy could be the high density of Hooded Crows in the river valley, which were never sighted on the farmland study plot (MP, unpublished data). The higher level of predation on natural nests in the river valley than in the farmland might be partly due to the higher density of trees in this type of habitat, because previous findings have shown that nest predation in open habitats increases close to lookouts for corvids, i. e. single trees, groups of trees or forest edges, and the higher detectability of parents feeding nestlings (review in: Söderström et al. 1998). The experiment with the artificial clutches showed that those located higher up in the shrubs were exposed to the greatest predation pressure. This will probably have been due to the activities of corvids, which cannot get so easily at clutches situated low over the ground (Żmihorski et al. 2010).

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## Conclusions

This study has shown that BWs and RBSs nesting in close proximity to one another achieve higher reproductive success. Both species were able to effectively defend their breeding sites against predators and benefit from this association; one can classify this type of interspecific positive interaction as facultative mutualism (Lyons 2014). The experiment with the artificial nests shows that a protective umbrella exists around the breeding sites of the two species.

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