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Nest Concealment and Nest Defence by Two Passerines: Effect of Protective Nesting Association

Marcin Polak

Department of Nature Conservation, Institute of Biology and Biochemistry, Maria Curie-Skłodowska University, Akademicka 19, 20-033 Lublin, Poland. Tel: + 48-081-537-59-71. E-mail: mpolak@hektor.umcs.lublin.pl

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Selection of favourable micro-habitat conditions at nest-sites and nest defence can be important anti-predatory strategies in open-cup nesting birds. In response to nest predation risks, some species of birds appear to form protective nesting associations in which both may gain benefits due to mutual warning and nest defence. Despite the many studies assessing the impact of various factors on nest defence and nest placement, how interactions between species while breeding can modify these strategies is still poorly understood. Here I evaluate whether nesting associations in two species influence nest defence intensity and nest-site selection. An observational approach was used to analyse the defensive behaviours of the Barred Warbler *Sylvia nisoria* and Red-backed Shrike *Lanius collurio* in an agricultural landscape in eastern Poland. Association was determined by the position of the nest with respect to that of the associated species (by the nest of one species being within the breeding territory of the other). Nest defence behaviour of these two passerines was assessed as their response to a human intruder near an active brood. This study showed that the nest size and visibility were similar in nest-sites of pairs nesting in association and in spatial isolation. Barred Warblers nesting within shrike breeding territories strongly defended their nests. Warblers breeding alone displayed a lower level of defence than birds nested in association. Shrikes not nesting with warblers were significantly more aggressive than those breeding in the protective nesting association. I suggest that shrikes tried to compensate for the lack of assistance by warblers in joint nest defence and were forced to invest more into defending their own nests. This research suggests that positive interactions within the heterospecific network of relations in ecosystems may be one of the factors responsible for diversifying the intensity of avian nest defence.

Key words: Positive interaction, Antipredator response, Nest defence, Protective nesting association, *Lanius collurio*, *Sylvia nisoria*.

BACKGROUND

During the reproductive period, birds caring for their offspring are frequently exposed to potential predators that may threaten their broods directly or indirectly (Martin and Martin 2001; Quinn et al. 2003). Nest predation causes nest failure in many species (Lima 2009; Wang and Hung 2019) and many species of birds select dense vegetation for nesting and actively defend their nests against potential predators (Caro 1978). Having detected a nest predator near the nest, the parent birds have to decide whether to defend the nest (Lima 2009; Klvaňová et al. 2011).

Defensive responses are very diverse and depend on the size and type of predator (Stenhouse et al. 2005; Templeton et al. 2005), parental sex (Klvaňová et al. 2011), distance from the nest (Kryštofková et al. 2011), time of the breeding season (Morrell et al.

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2016), vegetation density (Mérő and Žuljević 2017), personality (Vrublevska et al. 2014), and number and age of offspring (Caro 1978; Regelmann and Curio 1983). A crucial factor influencing antipredatory behaviour is where the parents decide to reproduce (Kleindorfer et al. 2005). Some avian species select large and dense shrubs for their nest sites (Goławski and Mitrus 2008). Many researchers pointed to thorny bushes as preferred sites for open-cup nesting passerines (Tryjanowski et al. 2000, Goławski and Mitrus 2014). Choosing this bush type can have an adaptation significance, since it reduces the possibility that the potential predators penetrate the inner bush and destroy broods. The choice of an appropriate nesting location is important for nesting success (Quinn et al. 2003; Forsman et al. 2008). One important biotic parameter informing this decision is the presence of other species (Krams and Krama 2002). When choosing a nest-site, birds may favour or avoid nesting near nests of other species (Martin and Martin 2001).

A high risk of predation can lead to the formation of associations, even with potential competitors, the members of which jointly defend their nests (Quinn and Ueta 2008). Despite the many studies examining the impact of various factors on avian nest defence, few have examined how interactions between species modify nest defence behaviours (Campobello et al. 2015). Larger groups of birds tend to be more effective at defending their breeding sites against predators (Krams and Krama 2002; Krams et al. 2009). An individual or pair responding alone stands little chance against a raptor, but when defending as part of heterospecific group, the risk can be reduced or diluted. On the other hand, there are also potential costs associated with nest defence, including direct mortality or injury caused by a predator, and reduction in the time and energy available for other essential activities (Quinn and Ueta 2008).

Here I examine the effect of joint nest defence behaviour when two unrelated species nest near one another. The Barred Warbler *Sylvia nisoria* and Red-backed Shrike *Lanius collurio* have different behaviours and nesting patterns, but they often nest relatively near each other. Even though both species are open-cup nesting passerines, their behaviours and life strategies differ from those of the majority of small birds that nest in shrubs and small trees (Kuźniak et al. 2001). Both of them have a variety of antipredator defences (Goławski 2007). Both actively defend their broods and are aggressive toward predators, including large mammals and humans (Tryjanowski and Goławski 2004; Goławski and Mitrus 2008; Polak 2013). Because the shrike often perches high and can see over a wide area, while the warbler forages near the ground, they may potentially inform one another of predators in different locations. Thus, when one species responds to a predator, that response may inform the other species, setting the stage for potential cooperation (Isenmann and Fradet 1995). Red-backed Shrikes and Barred Warblers can actively choose the neighbourhood in which they are to breed, forming heterospecific protective nesting associations (Polak 2012 2015). Nesting near each other incurs benefits because it offers better protection from predators (Neuschulz 1988; Goławski 2007; Polak 2014).

Both species arrive at the breeding grounds at roughly the same time, but Barred Warblers start nesting earlier (Polak 2015). Nearly half of the shrikes from the local population nest near warbler nests, and the other half nests away from warbler nests (Polak 2014). Shrikes benefit from this through better protection from predators and a higher reproductive success (Neuschulz 1988; Goławski 2007; Polak 2014). Experiments using stuffed models have shown that Barred Warblers and Red-backed Shrikes tolerate each other near their nests (Polak 2016).

The objective of this research was to analyse the influence of protective nesting association on nest concealment and the intensity of nest defence of the Barred Warbler and Red-backed Shrike. This research focuses on the following detailed questions: (1) Does the distance between focal and heterospecific associations affect the choice of nest site? I predicted that due to the lack of protective umbrella the birds nesting alone should build nests well hidden in dense vegetation, in contrast to birds that selected breeding in protective nesting association. (2) Can the creation of a protective nesting association modify the defensive effort? I predicted that both species would decrease the intensity their nest defence when nesting together because each benefit from the behaviour of the other. One possible scenario is that shrikes that choose to nest outside warbler territories would be forced to behave more aggressively to defend their broods. This would enable them to compensate for the lack of assistance in nest protection on the part of the associated species. (3) Does brood size affect the intensity of nest defence behaviour? (4) Are there differences between sexes in the birds' defense roles?

MATERIALS AND METHODS

Study area

The study was conducted at two locations (river valley and farmland) in central and eastern Poland. The 2010–2011 surveys were carried out in the Middle Vistula Valley near the village of Stężyca (51°34'N, 21°48'E; 76–84 ha), central Poland (Polak 2012), whereas the 2012–2014 surveys were conducted in farmland in the Roztocze region near the village of Żurawnica (50°38'N, 22°58'E; 106 ha), eastern Poland (Polak and Filipiuk 2014). The same methodology was applied in both plots.

Nest visits

From beginning of May to mid-July, the plots were surveyed regularly every few days to discover as many Red-backed Shrike and Barred Warbler territories and nests as possible. The numbers of surveys in the various years were as follows: 2010 = 14, 2011 = 18, 2012 = 17, 2013 = 15, 2014 = 13. The survey was conducted for 77 days total. I took pictures of bird behaviour and movements. Territories of both species are described and mapped in Polak and Filipiuk (2014). 60 Barred Warblers were caught using mistnets and playback and individually marked with coloured rings. In the river valley, the density of shrikes varied from 3.4 to 4.5 pairs (territories)/10 ha and that of warblers from 2.2 to 3.2 pairs (territories)/10 ha (Polak 2012). In the farmland plot, the density of Red-backed Shrikes varied from 3.0 to 3.1 pairs/10 ha and that of Barred Warblers was 1.9 pairs/10 ha (Polak and Filipiuk 2014). Maps were drawn for each breeding season to show the distribution and range of the breeding territories of the two species. The boundaries of breeding territories were delineated using the minimal convex polygon method, in which a territory was taken to be the smallest such polygon, determined from the spatially extreme points plotted on the map where birds were observed in a given territory (Kenward 1987). Shrike territory size varied from 0.03 to 1.09 ha (mean = 0.3 ± 0.2) and warbler territory size varied from 0.03 to 0.83 ha (mean = 0.4 ± 0.2; Polak and Filipiuk 2014). About half of the studied pairs of both species nested within nesting territories of the other species (in association) (Polak 2014). Data were gathered on 98 shrike broods and 44 warbler broods. The basic method of locating nests was a 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. Nests were inspected from the beginning May to mid-July at intervals of 2–10 days in order to establish basic reproductive parameters (for shrike: mean = 3.8 ± 1.4 visits, range 1–7; for warbler: mean = 3.8 ± 1.3 visits, range 1–7). Nests were checked at any time of the day in calm dry weather.

Nest-site parameters

The distance between the lower edge of the nest and the ground was measured with a tape accurate to 10 cm. The height of bushes above ground were measured with a measuring 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. 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 (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.

Nest defence behaviour

Defensive behaviour was assessed as the response to a human intruder near an active nest (following Stenhouse et al. 2005). I measured defence by beginning at a distance of 50 m from the nest; when I began noting behavioural response, and I slowly walked directly to the nest, which I then checked. To reduce the impact of nest visits on predation risk and avian behaviour, the length of period during nest visits was restricted to a minimum, especially at the incubation stage. The score was ranked according to the degree of perceived risk: 0 – no response; 1 – weak reaction, bird responds slightly, but does not approach and does not fly in the direction of the observer, the alarm reaction included repetitive alarm calling, bill clattering, tail movements and characteristic display behaviours; 2 – bird responds intensively, approaching and flying in the direction of the observer, the alarm reaction included repetitive alarm calling, bill clattering, tail movements and characteristic display behaviours (following Goławski and Mitrus 2008). As I noted scores I also noted the sex of the individual responding to my presence.

Defence comparisons were made during the nestling period only (Polak 2016). For further analyses, the most aggressive responses among all the reactions of each individual during all nest visits were taken into consideration. At least two days passed for any nest to be tested again, and only those nests with at least two tests were included in the analysis. Only one nesting attempt was used for each pair, and replacement clutches were not analysed. In this study the replacement clutch was defined as the late nest found in the same territory after the first brood failed. Thus, the final sample size for nest defence analyses was 49 shrike nests and 23 warbler nests.

Statistical analyses

Median and quartiles of each nest-site characteristics were calculated for micro-habitats localised in territories of both species nesting in association and in spatial isolation. The differences between these two groups were analysed using the Mann-Whitney test with the Bonferroni correction. 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, 0.05 were treated as statistically significant. I used generalised linear models (GLZ) with a log-link function and normal distribution error to test the effects of sex, number of hatchlings and type of association on the brood defence in both species. The defense score was the dependent variable in this model. Number of hatchlings as a continuous predictor and sex and type of association (position of nest with respect to the associate) were included as categorical factors. All calculations were made in STATISTICA 12.0 for Windows software (StatSoft Inc. 2014).

RESULTS

Nest concealment

In this study, on 98 nests occupied by shrikes, 41 nests were located within and 57 nests outside of warbler territories. 23 of the 44 warbler nests were within shrike territories. In both species there were no statistically differences with regard to nest-site characteristics among pairs nesting alone and in association (Table 1 and Table 2). The following parameters: shrub height, nest height above ground, nest size and nest visibility were similar in pairs breeding within the boundaries of associate species and in areas situated beyond the breeding territories of associate species.

Nest defence behaviour

Analysed factors had statistically significant effects on the intensity of nest defence (Table 3), but only two of them were statistically significant in this model: number of hatchlings and nesting in protective association. The intensity of nest defence was significantly influenced by number of hatchlings: larger broods had higher values than smaller. Defence

Table 1. The comparative statistics and Mann-Whitney test results for nest-site parameters (median and quartile range) of Red-backed Shrikes in pairs breeding beyond the breeding territories of associate species (Barred Warbler –) and in areas situated within the boundaries of associate species (Barred Warbler +)

Variable	Barred Warbler –			Barred Warbler +			*Z*	*p*
	Median	Quartile	*n*	Median	Quartile	*n*		
Shrub height (cm)	260	220–330	57	280	230-340	41	-0.46	0.65
Above ground height (cm)	120	100–150	57	140	100-170	41	-1.12	0.26
Nest diameter (cm)	14	13–15	57	14	13-15	41	-0.98	0.33
Nest height (cm)	11	10–12	57	11	10-12	41	-0.51	0.61
Nest visibility	7	5–14	46	7.5	5-11.5	36	-0.09	0.93

Table 2. The comparative statistics and Mann-Whitney test results for nest-site parameters (median and quartile range) of Barred Warblers in pairs breeding beyond the breeding territories of associate species (Red-backed Shrike –) and in areas situated within the boundaries of associate species (Red-backed Shrike +)

Variable	Red-backed Shrike –			Red-backed Shrike +			*Z*	*p*
	Median	Quartile	*n*	Median	Quartile	*n*		
Shrub height (cm)	240	215–280	21	240	190–280	23	0.67	0.50
Above ground height (cm)	90	70–115	21	80	60–110	23	0.61	0.54
Nest diameter (cm)	12	11–13	21	12	11–12	23	0.61	0.54
Nest height (cm)	9	7–9	21	9	8–10	23	-0.90	0.37
Nest visibility	5	4–5	19	5	4–6	17	-0.51	0.61

scores of warblers in associations were greater than those of alone warblers (Fig. 1). Shrike pairs nesting in a protective association were less aggressive than those nesting independently (Fig. 2). Sexes showed similar defensive behaviours in both species.

DISCUSSION

The nest-site characteristics of Red-backed Shrikes and Barred Warblers breeding alone and in protective nesting associations were similar in this study. This applies in particular to nest visibility, which were almost identical in these two groups of birds. Nest placement in shrubs by parents is supposed to be non-random and adaptive with regard to the risk of predation (Goławski and Mitrus 2008; Polak 2014). Contrary to expectation, this study showed that the choice of nesting strategy (alone vs. in heterospecific association) had no effect on micro-habitat nest parameters.

This study showed that the birds may use dynamic nest defence strategy to adjust their reaction to the human intruder. These results should be interpreted with caution, because the reaction of birds to humans may be different than their response to real predators (especially corvids), and the number of visits to the nest can affect the level of avian aggression aggression during next inspections. The warblers that nested in

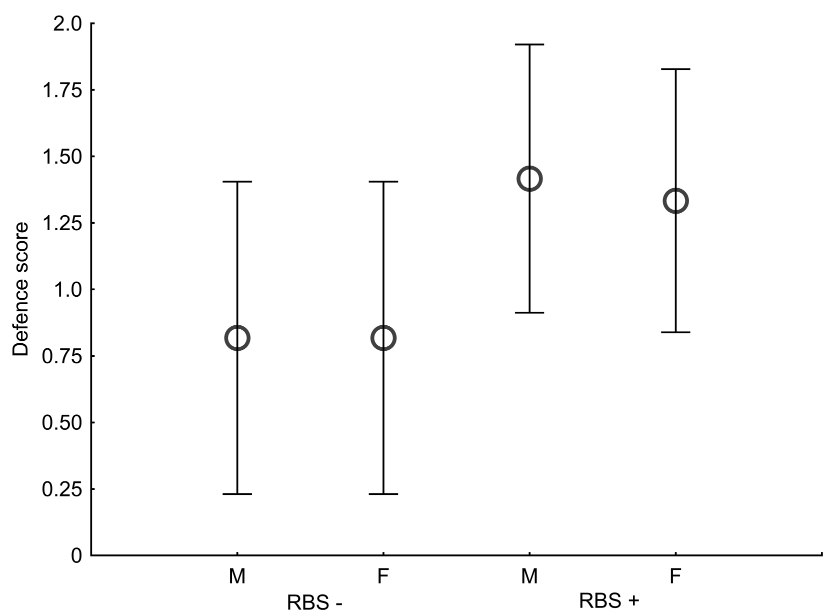

Fig. 1. Mean (± 95% confidence intervals) defence score of male (M) and female (F) Barred Warblers in relation to interspecific territory overlapping. (RBS –) – pairs breeding in areas beyond the breeding territories of the associated species (Red–backed Shrike); (RBS +) – pairs breeding within the boundaries of the associated species.

Table 3. Results of generalised linear models (GLZ) showing factors affecting the defence score of Red-backed Shrikes and Barred Warblers

Parameters	Estimate	SE	Wald	*p*-value
Red-backed Shrike (*n* = 98)				
Intercept	-0.20	0.18	1.18	0.28
Number of fledglings	0.07	0.037	3.843	0.05
Sex	-0.03	0.06	0.33	0.57
Type of association	0.22	0.07	10.11	0.00
Barred Warbler (*n* = 46)				
Intercept	-0.94	0.56	2.88	0.09
Number of fledglings	0.23	0.11	4.03	0.04
Sex	0.04	0.10	0.20	0.66
Type of association	-0.23	0.11	-4.64	0.03

close proximity to the accompanying species displayed the most intense defence responses. Barred Warblers nesting outside shrike territories were less aggressive. Previous research shows that only half the population of Red-backed Shrikes nested in a protective nesting association (Polak 2012 2014). This may have resulted from different behavioural, demographic and ecological factors as macro- and micro-habitat preferences, level of aggression, phenology, density, distributions of suitable nest sites and other unknown reasons (Polak 2012). Those earlier observations showed that the habitat niches of both species overlapped to a large extent, which may have led to competition for nest sites (Polak and Filipuk 2014). As shrikes may suffer negative consequences as a result of nesting close to warblers, their decisions about where to build their nests may be informed by such a trade-off. It is possible that Red-backed Shrikes may decide to nest together with warblers, but because of the potential costs, they choose only those warblers that defend their nests most vigorously against both avian brood parasites and predators. The present research has also shown that shrikes nesting beyond warbler territories exhibit a higher level of defence than those choosing to nest in association with the Barred Warbler. It is possible that birds that do not cooperate with the associated species are deprived of its assistance in early warning and chasing predators away and are forced to invest more in defending their own nests. Barred Warblers and Red-backed Shrikes arrived at their breeding grounds at a similar time (Polak 2015), but the analysis nesting chronology showed that in this protective nesting association shrikes join warblers, because Barred Warblers began laying eggs earlier than Red-backed Shrikes in the nests on the study plots.

However, individual variation in the nest defense behavior may be associated with the other factors: parental sex (Klvaňová et al. 2011), distance from the nest (Kryštofková et al. 2011), time of the breeding season (Morrell et al. 2016), vegetation density (Mérő and Žuljević 2017), personality (Vrublevska et al. 2014) and brood value (Regelmann and Curio 1983). The defensive behaviour might change in response to the type and size of the predator (Templeton et al. 2005). In this study the larger broods tended to be defended more intensely than the smaller broods. These results could support the "value of offspring hypothesis" (Clutton-Brock 1991), which predicts that the parents adjust their investment and increase their response to maximise their reproductive success (Klvaňová et al. 2011).

Here, the presented results indicate no differences between sexes in defensive behaviour in the Red-backed Shrike and Barred Warbler. Males of various avian species defended their broods with greater intensity than females (Klvaňová et al. 2011; Kryštofková et al. 2011). In general, males may take greater risks than females because they have elevated testosterone levels and maintain honest signalling to competitors. However, no difference (Ibáñez-Álamo and Soler 2017) or the opposite pattern (Trnka and

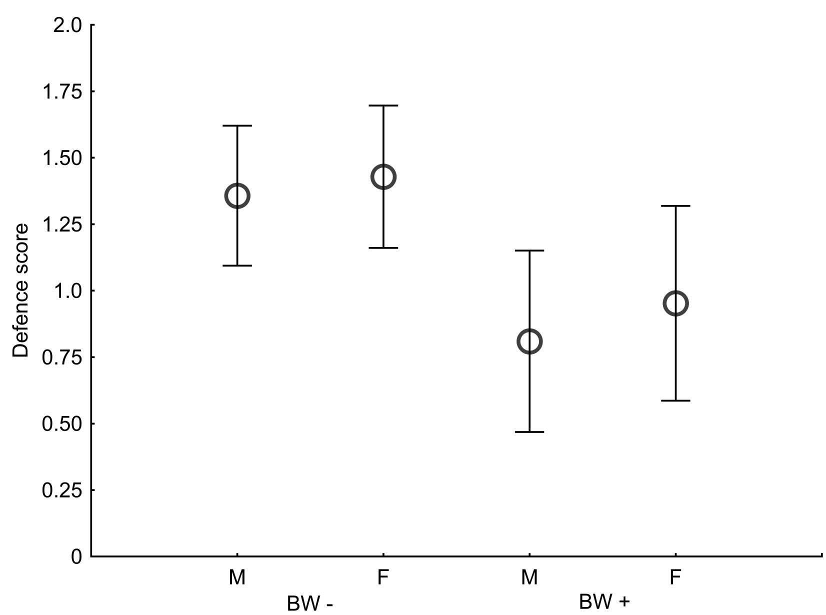

Fig. 2. Mean (± 95% confidence intervals) defence score of male (M) and female (F) Red-backed Shrikes in relation to interspecific territory overlapping. (BW –) – pairs breeding in areas beyond the breeding territories of the associated species (Barred Warbler); (BW +) – pairs breeding within the boundaries of associate species.

Prokop 2010) have also been observed. The difference between males and females responses can be explained by several possible explanations, including confidence of parenthood, mating system and status, level of testosterone, renesting potential and parental investment of the partner (Požágayová et al. 2009; Trnka and Grim 2013; Mérő and Žuljević 2017). Here, due to the lack of significant differences between male and female parental investment, both sexes displayed similar nesting defence behaviours, as found in other studies (Tryjanowski and Goławski 2004; Polak 2013).

CONCLUSIONS

In conclusion, the present study indicates that interactions within the heterospecific network of relations in ecosystems may be one of the factors responsible for diversifying the intensity of nest defence in avian populations. Warblers nesting outside the shrike's territories displayed a lower level of defence than birds nested in close proximity to the associated species. The shrikes nesting outside the warbler territories displayed a higher level of defence. This research expands our knowledge in a field that is so far poorly explored by behavioural ecologists and attempts to address the question of how positive interactions between different species can modify the antipredator strategies of birds that form a protective nesting association.

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