

# NEST SITE PREFERENCE AND NEST SUCCESS IN BLACKCAPS *SYLVIA ATRICAPILLA* IN POLAND

## PREFERENCIA DE NIDIFICACIÓN Y ÉXITO REPRODUCTOR DE LA CURRUCA CAPIROTADA *SYLVIA ATRICAPILLA* EN POLONIA

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**SUMMARY.**—*Nest site preference and nest success in blackcaps Sylvia atricapilla in Poland.*

Predation is reported to be the main cause of nest failure in songbirds and selection of safer nest sites is thus an important determinant of breeding success. We studied the effect of nest site location: in bramble, elder or hornbeam, on breeding success as well as selection of different nest sites in the blackcap *Sylvia atricapilla*, a species whose nests are heavily preyed upon both by rodents and corvids. We found that breeding success differs between nest site types, with higher levels of predation of nests built in elder or hornbeam than of those in bramble. We also found that blackcaps select bramble when it is available within the nesting territory. Nests in bramble were better concealed than those in elder or hornbeam. Since nest height above the ground did not differ according to the plant species used, nest concealment was probably the main factor affecting blackcap nest survival.

*Key words:* blackcap, breeding success, nest site preferences, *Sylvia atricapilla*.

**RESUMEN.**—*Preferencia de nidificación y éxito reproductor de la curruca capirotada Sylvia atricapilla en Polonia.*

Se ha registrado que la predación es la mayor causa del fallo reproductor en los Paseriformes y en consecuencia, la elección de un lugar seguro es un factor muy importante que va a determinar el éxito. Estudiamos el efecto de la localización del nido (en zarzas, saúcos y carpes) en el éxito reproductor, así como las preferencias del adulto a los diferentes lugares de nidificación en la curruca capirotada *Sylvia atricapilla*, una especie que sufre una fuerte depredación por roedores y córvidos. Encontramos que: (i) el éxito reproductor difiere entre los lugares de localización del nido, siendo los niveles de predación más elevados en los nidos construidos en saúcos y carpes que en los ubicados en zarzas; (ii) las curru-cas prefieren nidificar en zarzas cuando este tipo de ubicación está disponible en el territorio de la

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pareja reproductora. También encontramos que los nidos en zarzas estuvieron más escondidos que los localizados en saúcos y carpes. Ya que la altura al suelo de los nidos no difiere en los saúcos y carpes, el ocultamiento de los nidos fue probablemente el principal factor que afecta a la supervivencia de las currucas.

*Palabras clave:* curruca capirotada, éxito reproductor, preferencias de nidificación, *Sylvia atricapilla*.

## INTRODUCTION

Predation is reported to be the main cause of nest failure in songbirds (Martin, 1992; Ricklefs, 2000). Nest site location and concealment from predators thus play an important role in nest survival (Martin, 1993; Caro, 2005; Remeš, 2005a). Nest site location is associated with vulnerability to particular sets of predators. For example, nests close to the ground are more often depredated by rodents and other mammals, while avian predators mostly detect those located higher up on trees and bushes (Remeš, 2005b). Nest location is also linked to nest accessibility. Dense thorny bushes may prevent both intended and incidental intrusions in the case of low-nesting species (Collias, 1964; Lazo and Anabalon, 1991; Hatchwell *et al.*, 1999), which might otherwise result in nest predation as well as nest damage by animals that pass by. Leaf cover is also considered to affect predation rate, especially in small birds, such as warblers, whose abilities to defend a nest are limited. One such species is the blackcap *Sylvia atricapilla*. Schaefer (2004) showed that blackcap parents do not defend their nests against most predation attempts. In addition, poorly concealed nests are more easily revealed to visually orientated predators by parental activity around the nest (e.g. McLean, *et al.*, 1986; Cresswell, 1997; Martin *et al.*, 2000; Muchai and du Plessis, 2005).

Among warblers, the blackcap suffers from high predation rates (Bairlein *et al.*, 1980). Nests are heavily preyed upon by both

rodents and corvids (Weidinger 2002) and only 30% escape predation (Weidinger, 2000; Remeš, 2003a, 2003b). Although the blackcap occupies a broad range of habitats and nest-sites (Glutz von Blotzheim and Bauer, 1991; Weidinger, 2000; Schaefer and Barkow, 2004), the majority of nests in our study location were built in bramble *Rubus* sp., in elder *Sambucus nigra* shrubs or in hornbeam *Carpinus* sp. brushwood. Whereas nests in elder and hornbeam were easy to find using active searching and visual inspection of breeding territories, those in bramble were much more difficult to locate. Large, dense, thorny, bramble patches with dense leaf cover often make nests invisible to, and unapproachable by, humans and possibly other visually oriented nest predators. They thus seem to offer much safer nest sites than either elder or hornbeam brushwood.

We here compare blackcap breeding performance at different types of nest sites and analyse potential nest site characteristics that may account for differences in nesting success. We also investigate whether blackcaps select potentially safer nest sites preferentially when building nests.

## METHODS

The blackcap is a small, migratory songbird that is widespread in Europe, where it breeds in habitats that offer dense tree and shrub vegetation (Cramp, 1992). It builds a thin-walled, open-cup nest of 10 cm diameter and 5 cm depth in the shrub and herbaceous

layers of lowland floodplain or humid deciduous forests (Storch, 1998). Incubation lasts 12 days and nestlings stay in the nest for another 12 days, but they are able to leave the nest when 9 days old.

The study was conducted in 2008 and 2009, in deciduous and mixed forests surrounding the “Czeszewski Las” (17° 31' E, 52° 09' N) reserve in Central Poland. The forest is dominated by oak *Quercus* sp., ash *Fraxinus* sp., hornbeam *Carpinus betulus*, alder *Alnus* sp. and elder *Sambucus nigra*. Hornbeam brushwood and birch *Betula pendula* predominate in parts of the forest parts that have been severely altered by Scots pine *Pinus sylvestris* silviculture. Blackcaps in this location build their nests mainly in elder, hornbeam brushwood or bramble. We determined blackcap territories by mapping the most peripheral song-posts of singing males from the onset of breeding season, when territorial behaviour was strongest. Singing males were observed for approximately one hour per observation and most territories were visited more than once before mapping territory boundaries. The outer song-posts were marked with a piece of string. Where territories were adjacent, the males sang mostly on the territory boundary nearest to the neighbouring male's territory. In such cases we assessed territory extent by using blackcap song playback from the opposite direction. We began playback at about 50 m from a singing male, this being the diameter of the largest blackcap territories reported by Cramp (1992). If the male did not react we reduced the distance progressively, each time by 10 m, until the territory owner responded aggressively. Playback was conducted at intervals of at least one hour, to prevent males from becoming habituated. The territory was then mapped as a circle of the estimated diameter.

We searched for nests from mid April to mid July, by careful inspection of potential nest sites within mapped territories. We tried

to search each territory at intervals no longer than 10 days until the nest was found. In the cases of larger bramble patches, which are difficult to examine in their entirety due to their impenetrability, we used playback to assess the probable nest location: once a functional nest is completed males usually abandon outlying song-posts, resulting in a contraction in territory size around the nest (Cramp, 1992). We recorded the stage at which a nest was found under one of five categories:

- (i) Egg laying stage (eggs cold and clutch incomplete).
- (ii) Early incubation (warm eggs that sink to the bottom of a cup of water).
- (iii) Late incubation (warm eggs that float).
- (iv) Nestlings 1-4 days old (naked).
- (v) Nestlings 5-8 days-old (more or less covered with feathers).

Nests were checked every 3-5 days until they were depredated or the nestlings fledged. The last inspection of successful nests was when nestlings were 8 days old, since older nestlings are likely to explode from the nest when disturbed. A nest was considered as successful if at least one nestling survived until 8 days old. Nest success was evaluated using the Mayfield method (Mayfield, 1961, 1975; Hensler, 1985; Jehle *et al.*, 2004). To obtain an estimate of nest success (NS) over the entire nesting period, the daily survival rate (DSR) was raised to the power equivalent to the mean number of days in the nesting period (in our case 24: 16 days for eggs and 8 for nestlings):  $NS = (DSR)^{24}$ . DSR was calculated as:  $DSR = 1 - \text{no. of failed nests} / \text{no. of exposure days}$ . Apparent nest success (0/1) was used in the GLM model.

The following nest site characteristics were recorded: species of nest-bearing plant; height of nest above ground (cm) and nest concealment as the percentage of the nest bowl obscured by foliage. Nest height was pre-

cisely measured with a tape from the ground to the bottom of the nest, to the nearest cm. Nest vertical and horizontal concealment were estimated by observing the nest from distances of 1 m, vertically above the nest and in the four cardinal directions at the nest level. These five estimates were averaged to obtain a single percentage for a nest (Remeš, 2005a). Estimates were done to the nearest 10%. A 13 cm diameter mirror mounted on a telescopic pole was used to estimate concealment, especially from above, of nests that were sited too high for direct inspection. We also recorded clutch size and approximate laying date. The precise laying date was unknown for the subset of nests that were found as complete clutches and lost to predators before hatching. Instead of excluding such nests from analyses, we used approximate laying date, as we assumed that a few days difference in laying date is less important than the information on which stage of the breeding season the eggs in a given nest were laid. Therefore we divided the breeding season (from mid April to mid July) into nine 10-day periods, to which all nests were assigned. The nests found during laying were described to the period in which they were located. When a nest with a complete clutch was found, we waited until hatching and then calculated the period to which it should be assigned. The risk of incorrect assignment of nests that suffered predation before hatching was minimised by water-testing one egg from each clutch. If the egg sank, indicating recent laying, we assigned the clutch to the period in which the nest was found. If it floated, indicating more advanced embryo development, the clutch was assigned to the preceding period.

To analyse nest site selection we analysed birds' choices within the subset of territories in which more than one nest site type was available to the territory owners. We also noted the actual nest site and the occurrence of alternative nest sites present within a given breeding territory for all breeding pairs

(1/0 value). In addition, we assessed the abundance of potential nest-supporting plants within a territory. This was practically impossible to do precisely so we distinguished 3 categories of abundance:

1. A single clump present.
2. Several clumps present.
3. Most of the territory covered by the plant.

We also investigated whether pairs that lost their nests due to predation chose the same or a different nest-supporting plant when re-nesting. We assumed a new nest found within a territory after a nest failure to be a replacement nest built by the territory owners.

### *Statistics*

CONTRAST analysis (CONTRAST software, Hines and Sauer, 1989) was used to compare nest survival in different nest site types or between the first and later clutches. The program serves primarily for the analysis of survival rates and has been used in other studies to compare daily nest survival rates (e.g. Martin and Joron, 2003). The Contrast user manual provided by the program authors gives further details.

A Generalised Linear Model (GLM) was used to assess the effect of nest site, laying date, clutch size (a potential indicator of parental condition) and study year on black-cap nest success. The GLM model used assumed a logistic link function and a binomial distribution of the dependent variable (nest success = 1 or 0 per nest), with site and year as factors and laying date and clutch size as covariates.

Differences between nest sites in nest concealment and nest height of above the ground was tested using a t test for independent samples.

A MANOVA test was conducted with nest concealment and height as dependent variables and nest site as a factor, to explore whether nest concealment and height were involved in the differences in nest success between nest site types.

The effect of the abundance of nest-supporting plants within a territory on nest success was analysed using the Kruskal-Wallis Test. Nest site selection by blackcaps was tested with a Binominal Test. The Chi-squared test was used to analyse the effect of year on nest site selection.

The analyses were conducted with SPSS 16 software (SPSS Inc., Chicago, IL, U.S.A.) and the CONTRAST program (Hines and Sauer, 1989).

## RESULTS

### 1. Nest success in different types of nest site (bramble, elder and hornbeam)

In total we found 42 nests in elder, 27 in hornbeam brushwood and 32 in bramble. Some nests were also found in nettle *Urtica dioica*, the fern *Athyrium filix-femina* and hawthorn *Crataegus* sp. but too few to merit inclusion in this study. Nest predation was the only cause of reproductive failure that we observed and no instances of nest desertion were noted. A few eggs did not hatch but these never exceeded a single egg in a given clutch and non-hatching did not account for the outcome of any nests. Some nestlings died, probably due to starvation during periods of heavy rain, but again only single nestlings per affected nest were involved.

The Mayfield nest success (NS) calculated from the DSR of all analysed blackcap nests ( $n = 101$ ) was 0.28. However, when calculated separately for different types of nest sites, it was more than twice as high for nests built in bramble (NS = 0.49,  $n = 32$ ) than for nests located in elder (NS = 0.20,  $n = 42$ ) or

hornbeam brushwood (NS = 0.21,  $n = 27$ ). Comparison by CONTRAST revealed that nest survival of nests in hornbeam and elder was similar (difference in DSR = 0.0026,  $\chi^2 = 0.024$ ,  $df = 1$ ,  $p = 0.878$ ) indicating comparable predation rates at these two types of nest sites. Thus, in our further analyses we combined nests in hornbeam and elder into one category (elder + hornbeam) with NS = 0.21. The nest success of pairs breeding in bramble and elder + hornbeam is shown in figure 1. The difference in NS between the two nest sites types was highly significant (CONTRAST analysis: difference in DSR = 0.0321,  $\chi^2 = 7.995$ ,  $df = 1$ ,  $p = 0.005$ ). This difference remained significant when we calculated nest success separately for first clutches (CONTRAST analysis: difference in DSR = 0.318,  $\chi^2 = 4.053$ ,  $df = 1$ ,  $p = 0.04$ )

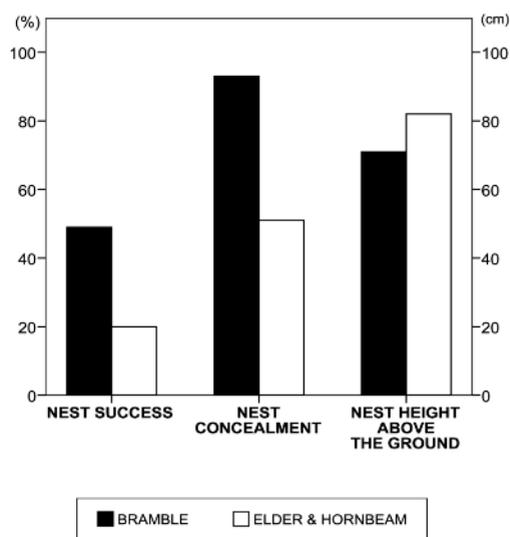


FIG. 1.—Nest success, nest concealment and nest height above the ground for nests located in bramble (■,  $n = 32$ ) and elder/hornbeam (□,  $n = 69$ ). [Exito de nidificación, ocultamiento y altura del nido desde el suelo para nidos localizados en zarzas (■,  $n = 32$ ) y saúcos, y carpes (□,  $n = 69$ ).]

and subsequent nesting attempts (CONTRAST analysis: difference in DSR = 0.398,  $\chi^2 = 4.929$ ,  $df = 1$ ,  $p = 0.03$ ). There were also no significant differences in nest success in analysed nest site types between years, both for bramble (CONTRAST analysis: difference in DSR = 0.0015,  $\chi^2 = 0.009$ ,  $df = 1$ ,  $p = 0.925$ ) and hornbeam + elder (CONTRAST analysis: difference in DSR = 0.0032,  $\chi^2 = 0.038$ ,  $df = 1$ ,  $p = 0.845$ ).

Most nests were found during the egg laying or incubation period (88%). The high proportion of nests found at those stages resulted from the relatively frequent monitoring and careful inspection of studied territories. There were no significant differences between the two nest site types (bramble vs. hornbeam + elder) in relation to the nesting stage (egg laying, early incubation, late incubation, nestlings 1-4 days-old, nestlings 5-8 days-old) of the nests that were found ( $\chi^2 = 0.644$ ,  $df = 4$ ,  $p = 0.958$ ). Thus, we did not include the nesting stage variable in our subsequent analyses.

Finally, we analysed whether the laying date, clutch size and the year influenced nest success. The GLM model showed that nest success was significantly different between the two nest site types (Wald  $\chi^2 = 8.56$ ,  $df = 1$ ,  $p = 0.003$ ) while the effects of laying date, clutch size and year were not significant (Wald  $\chi^2 = 0.441$ ,  $df = 1$ ,  $p = 0.507$ , Wald  $\chi^2 = 0.014$ ,  $df = 1$ ,  $p = 0.906$  and Wald  $\chi^2 = 0.275$ ,  $df = 1$ ,  $p = 0.6$ , respectively).

All these results indicate that bramble is generally a safer nest site for blackcaps than elder or hornbeam brushwood.

## 2. Nest site characteristics affecting nest success

Nests located in bramble were much better concealed than those in elder or hornbeam (table 1 and figure 1) and the difference in concealment was highly significant ( $t = 10.59$ ,

$p < 0.001$ ,  $n_1 = 32$  nests in bramble,  $n_2 = 69$  nests in elder and hornbeam).

The average height of the nest above the ground in bramble was slightly lower than in elder and hornbeam (table 1 and figure 1) but this difference was not significant ( $t = -0.99$ ,  $p = 0.32$ ,  $n_1 = 32$  nests in bramble,  $n_2 = 69$  nests in elder and hornbeam). A MANOVA test revealed that nest concealment significantly affected nest success in blackcaps ( $F = 112.14$ ,  $df = 1$ ,  $p < 0.001$ ) while the effect of nest height was insignificant ( $F = 0.985$ ,  $df = 1$ ,  $p = 323$ ).

We also analysed the effect of the abundance of the nest supporting plant within a territory on nest success. We found that the abundance of bramble within a territory had a significant effect on the nest success of the territory owner (Kruskal-Wallis Test:  $H = 14.79$ ,  $df = 1$ ,  $p < 0.001$ ,  $n = 32$ ). Most cases of predation of nests built in bramble took place in territories that contained only a single bramble patch (69% of the total amount of predation in bramble). Nest success was significantly higher in territories that were almost entirely covered by bramble than in those containing only one bramble patch (CONTRAST analysis: difference in DSR = 0.727,  $\chi^2 = 7.33$ ,  $df = 1$ ,  $p = 0.007$ ). In contrast, the effect of the abundance of elder + hornbeam brushwood within a territory on nest success was not significant (Kruskal-Wallis Test:  $H = 1.53$ ,  $df = 1$ ,  $p = 0.216$ ,  $n = 68$ ). Nest survival was similar in territories with one elder or hornbeam patch and those largely covered by elder or hornbeam brushwood (CONTRAST analysis: difference in DSR = 0.0073,  $\chi^2 = 0.129$ ,  $df = 1$ ,  $p = 0.719$ ).

There was no significant difference in the average abundance of the nest supporting plant within a territory between the two nest site types (Kruskal-Wallis Test:  $H = 0.026$ ,  $df = 1$ ,  $p = 0.871$ ,  $n = 101$ ). Detailed characteristics of the variables analysed for different nest site types in sections 1 and 2 above are given in table 1.

TABLE 1

Characteristics and comparison of variables analysed in different nest site types (bramble and elder/hornbeam).  
 [Características y comparación de las variables analizadas en los diferentes tipos de nido (zarzas y saucos + carpes).]

VARIABLE	NEST SITE TYPE										DIFFERENCE	SIG.
	BRAMBLE					ELDER & HORNBEAM						
	Mean	Min - Max	SE	n		Mean	Min - Max	SE	n			
Nest success (Mayfield)	0.49	n. a.	0.0078	32		0.21	n. a.	0.0082	69		$\chi^2 = 7.995$	<b>p = 0.005</b>
Nest concealment (%)	93	40 - 100	2.5885	32		51	20 - 90	2.4331	69		t = 10.59	<b>p &lt; 0.001</b>
Nest height from ground (cm)	75.7	16 - 162	7.1573	32		99.4	16 - 280	6.4678	69		t = -0.99	p = 0.32
Estimated laying date	3.1	1 - 9	0.3358	32		3.7	1 - 9	0.2437	69		F = 1.2	p = 0.275
Clutch size	4.7	2 - 6	0.1462	32		4.6	3 - 6	0.0778	69		F = 0.11	p = 0.738
Nest stage (when found)	2.1	1 - 5	0.1924	32		2.1	1 - 5	0.1449	69		$\chi^2 = 0.644$	p = 0.958
Nest-supporting plant abundance	2.1	1 - 3	0.1485	32		2	1 - 3	0.0968	69		H = 0.026	p = 0.871

### 3. Nest site preferences in the blackcap

Both types of potential nest site (bramble and elder + hornbeam) were available in 19 of the 101 territories studied. Within this sample, 84% of pairs (16 out of 19) nested in bramble. The difference between the number of blackcaps that chose bramble and those that nested in elder or hornbeam was highly significant (Binomial Test:  $p = 0.004$ ). Although the relative abundance of both nest site types varied to some degree between the territories (some contained more bramble patches while others more elder + hornbeam patches), the difference was not significant (Kruskal-Wallis Test:  $H = 0.164$ ,  $df = 1$ ,  $p = 0.685$ ,  $n = 19$ ) and bramble did not dominate. This shows that blackcaps select bramble when both nest site types are available (figure 2). This pattern was consistent in both years of our study as

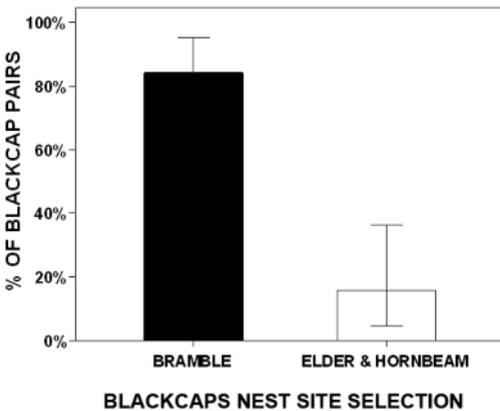


FIG. 2.—Blackcap nest site preferences in territories offering bramble and/or elder/hornbeam ( $n = 19$ ). ■: % of pairs that nested in bramble; □: % of pairs that nested in elder or hornbeam. Error bars = 95% CI.

[Preferencia de nidificación de la curruca capirotada en territorios con zarzas, saúcos y/o carpas ( $n = 19$ ). ■: % de parejas que construyen su nido en zarzas; □: % de parejas que construyen su nido en saúcos y carpas. Barras de error = 95% de CI.]

we did not find any effect of year on nest site selection ( $\chi^2 = 0.11$ ,  $df = 1$ ,  $p = 0.737$ ).

When analysing all nesting attempts in the study ( $n = 101$ ), elder or hornbeam brushwood was present as an alternative nest site in 50% (16 out of 32) of the territories in which blackcaps built their nests on bramble. In contrast, bramble was recorded in only 4% (3 out of 69) of territories in which blackcaps nested in elder or hornbeam. This was highly significant ( $\chi^2 = 29.83$ ,  $df = 1$ ,  $p < 0.001$ ) and suggests that blackcaps nest in elder or hornbeam mainly where bramble is not available.

Using data on the first nests and re-nesting attempts of 42 pairs, we also tested whether predation influenced the choice of nest-supporting plant when re-nesting. We obtained nest replacement data for 11 pairs in which the depredated nest was in bramble and 31 pairs in which the depredated nest was in elder or hornbeam. Most pairs (86%) re-nested in the same type of nest site, although only if there was another patch of the same plant species available within a territory. Only four out of 31 pairs that first nested in elder or hornbeam, and two out of 11 that first nested in bramble, changed the nest-supporting plant when re-nesting. In all these cases there was no alternative patch of the plant that had borne the first nest within a territory, so that the change of the nest site seemed obligatory. This observation suggests that blackcaps in general do not tend to change nest site type after a nest failure. However, none of the pairs that previously nested in elder or hornbeam had bramble as an alternative when choosing a site for a replacement nest. Thus, this subset of pairs gives no information on whether the birds tend to change the nest site type after a nest failure. In contrast, elder or hornbeam were present in all 11 territories in which replacement nesters had first nested in bramble. Nine of these pairs re-nested in bramble. Two pairs that chose elder had no other bramble patch within a territory. This shows that blackcaps do not switch their tendency

to nest in the generally safer bramble despite a recent experience of predation in this type of nest site and the presence of other nest-supporting plant types nearby.

Our results clearly suggest that blackcaps selected bramble over elder and hornbeam as a nest site and used these less concealing plants only when bramble was not present within their breeding territories.

## DISCUSSION

The survival of blackcap nests located in bramble was over twice as high as those sited in elder or hornbeam brushwood. This effect was independent of the year of the study and of variables, such as laying date and clutch size, that are potentially linked to parental condition. The nests in bramble were better concealed and this was probably the main factor affecting nest survival, since nest height above the ground was not significantly different between nest-site plant species. Our results support earlier findings that nest concealment increases nest survival (e.g. Martin, 1992, 1993; Hoi - Leitner *et al.*, 1995; but see Baláz *et al.*, 2007). Nests that are well hidden in dense vegetation are relatively safe from visually searching avian predators (Bairlein *et al.*, 1980, Santos and Tellería, 1991, Schaefer, 2002) and suffer lower levels of predation (Weidinger, 2004). Concealment was a significant predictor of nest survival in 16 of 20 studies in which birds were the predominant nest predators (reviewed by Clark and Nudds, 1991). Corvids are thought to be the main predators of blackcap nests – they accounted for about 50% of total predation on artificial nests (Weidinger, 2002; Remeš, 2005b) and for 65% on real videotaped nests (Schaefer, 2004). Another benefit of nesting in dense vegetation may result from the muffling of nestling begging calls, since the amplitude of such calls has been shown to increase predation, particularly by avian

predators (e.g. McDonald *et al.*, 2009). Moreover, concealment may affect not only the probability of nest survival but also the survival probability of the incubating parents (Wiebe and Martin, 1998). This is very likely in the blackcap since incubating birds usually stay on the nest until the last moment when a predator appears (Schaefer, 2004). Predators may use multiple visual cues to locate nests (Santisteban *et al.*, 2002), for example watching parental provisioning behaviour (e.g. Martin *et al.*, 2000), so building the nest in a large bramble patch allows parents to approach it under cover, thus minimising the risk of revealing its location. Our study supports this possibility since blackcap breeding success was significantly higher in territories that were almost entirely covered by bramble.

Our observations of parental provisioning indicated that locating the nest by following the parents was impossible in larger bramble patches since the birds disappeared under the leaves about 2 m from the nest. In contrast, we were able to track the majority of nestling-feeding parents right up to the nest when this was located in elder or hornbeam brushwood. The dense leaf cover offered by bramble seems not only to increase nest crypsis (reviewed by Newton, 1998) but also could mask nestling begging calls and parental activity around the nest. All these benefits of concealment may be of particular importance in the blackcap, as adult birds do not defend their nests against a predator (Schaefer, 2004). The antipredator strategy of blackcaps seems to rely mainly on nest camouflage. Bramble, with its dense leaf cover, has also been described as a favoured nest site for species as diverse as the Long-tailed tit *Aegithalos caudatus* (Hatchwell *et al.*, 1999), Grey Partridge *Perdix perdix*, Red-legged Partridge *Alectoris rufa* (Rands, 1988) and Superb Fairy-wren *Malurus cyaneus* (Nias, 1986). *Rubus* sp. seems to provide nesting birds with advantages lacking at

other nest sites, the most obvious and well studied of these being nest concealment. However, the inaccessibility of nests placed in thorny shrubs may also be important. Irrespective of the kind of the protection, higher bramble abundance within a territory translated into higher nest success in our study. Similar results were obtained by Nias and Ford (1992) for the superb fairy-wren.

Nest height above the ground did not affect nest success in the present study, as also found by Remeš (2005b), perhaps because this factor did not significantly differ between the two nest site types.

Significantly higher nest success in bramble than elder or hornbeam should result in blackcaps preferentially selecting the first type of nest site. Our results support this prediction: when both plant types were present within a territory, blackcaps selected bramble preferentially. Only 3 out of 19 blackcap nests were built on other shrubs in the vicinity of *Rubus* bushes. In 2 of these 3 cases there was a single patch of bramble containing an already depredated blackcap nest, which probably belonged to the territory owners. This may explain why replacement nests were in different nest sites, as blackcaps and other species rarely re-nest in the same place after nest failure (Chalfoun and Martin, 2010). Although our study demonstrated that blackcaps did not change their preference to nest in generally safer bramble despite recent experience of predation at this type of nest site, in the above two particular cases a new nest site had to involve a different nest-bearing plant species due to the lack of another bramble patch within a territory. The fact that a single experience of predation did not make the number of birds in our study abandon nesting in bramble, where another patch was available, suggests that birds may be able to associate the incidence of past predation events with the nest site type. Blackcaps may also select more concealed/less accessible nest sites because during incubation they feel

less stressed than in exposed nests. Another possibility is that blackcaps look for high nest concealment more in response to the risk of common cuckoo *Cuculus canorus* parasitism than the risk of predation. The cuckoo is well known to parasite blackcaps nests (e.g. Honza *et al.*, 2004) and searches for nests visually, as do avian predators. Thus, nests sited to avoid cuckoo parasitism may benefit in addition from reduced predation. Bramble has also been described as a preferred nesting site of the blackcap by Carbonell and Tellería (1998a, 1998b) and as an advantageous nest site which results in low predation by Schaefer (2002). The greater number of nests located in elder and hornbeam than in bramble (69 v. 32) in our study location resulted from limited bramble patch availability and the difficulty in finding nests in bramble, rather than any blackcap preference for nesting in elder or hornbeam.

The differences in nest success between the nest site types detected in our study may explain variation in blackcap nesting success in other studies. This is most often about 30% (Weidinger, 2000, 2002, 2007; Remeš, 2003a; Schaefer, 2004), but values ranging from 15.5% to 52-59% have been reported (Remeš, 2003b; Baláz *et al.*, 2007). Dissimilarity in nest site types and variation in nest-bearing plant type availability between these studies may account to some degree for the observed discrepancies.

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