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## Nest concealment and parental behaviour interact in affecting nest survival in the blackcap (*Sylvia atricapilla*): an experimental evaluation of the parental compensation hypothesis

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**Abstract** Nest concealment varies strongly within populations of many species. Although some studies have revealed the beneficial effects of concealment in mitigating predation pressure on nests, other studies were unable to find similar effects. One potential reason for the mixed results is that parental behaviour may compensate for the effects of nest cover, and specifically designed experimental studies are needed to reveal this compensation. I studied the effects of concealment on the probability of nest survival in the blackcap (*Sylvia atricapilla*), by experimentally manipulating the degree of nest-foilage cover. There was a significant effect of the treatment depending on nest type and the phase of nesting. Whereas there was no effect of concealment on nest survival in natural nests, there was a positive effect in real nests baited with plasticine clutches (i.e. without parental activity). Parents probably behaviourally compensated for poor concealment in natural nests (nest guarding, defence). In line with this, there was no effect of concealment on nest survival during incubation, whereas there was probably a positive effect in the nestling phase. Parents spent more time on the nest during incubation (80%) than during the care of nestlings (40%) and, consequently, had more opportunities to compensate for poor cover. In general, we cannot use single measures of behaviours or states (nest concealment) as an indication of predation risk because of the capacity for compensation in other behaviours.

**Keywords** Predation · Nest-site selection · Nest defence · Nest concealment

### Introduction

Nest predation is the main source of nest mortality in small passerines (Ricklefs 1969). Consequently, bird parents are expected to select a safe nest site to avoid destruction of their nests by predators. A well-concealed site is an obvious option, because foliage cover reduces the transmission of auditory, visual, and olfactory cues from the nest to potential predators (Martin 1993). Thus, well-concealed nests should have higher survival prospects compared to poorly concealed ones. However, both beneficial and no effects of concealment have been regularly found in studies looking at the effects of nest cover on nest survival (e.g. Willson and Gende 2000; Jakober and Stauber 2002; review in Martin 1992a). Reasons for the mixed results are at least threefold. First, a diverse community of predators may depredate nests with different cover at a similar rate, and different predators may select for different degree of nest concealment (Clark and Nudds 1991; Martin and Joron 2003; Remeš 2005). Second, almost all studies made to date examine natural variation in nest concealment that may be selectively neutral (there are only three experimental studies: Howlett and Stutchbury 1996; Stokes and Boersma 1998; Peak 2003). Third, parental behaviour at the nest may lead to complex relationships between nest concealment and survival (Weidinger 2002).

Parent birds often defend their nests by attacking and distracting potential predators (Montgomerie and Weatherhead 1988). However, other parental behaviours (e.g. feeding) attract predators to the nest and increase the probability of its depredation (Martin et al. 2000a, 2000b; Tewksbury et al. 2002). Both these sets of behaviours may interact with nest concealment (Weidinger 2002). Although parents may compensate for poor nest concealment and nest conspicuousness by nest defence, they may, conversely, reveal poorly concealed nests to visually orientated predators by their activity around the nest (McLean et al. 1986; Cresswell 1997a; Martin et al. 2000b). Thus the relationships between parental behaviour, nest cover, and survival may be complex and differ among species (Murphy et al. 1997; Flaspohler et al. 2000; Weidinger 2002).

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One fruitful approach to studying the effect of nest cover on the survival prospects of nests and its interaction with parental behaviour is to compare natural nests with parental activity and artificial clutches without parents (Cresswell 1997a; Weidinger 2002). There are three likely outcomes with respect to nest concealment: (1) no effect of concealment in both artificial and natural nests: nest cover is a selectively neutral trait and parental behaviour does not interact with it. (2) A positive effect of concealment in both artificial and natural nests: nest cover has beneficial effects, again no interaction. (3) A positive effect of concealment in artificial nests but no effect in natural nests: nest concealment has favourable effects, but parents are able to compensate for poor cover (the parental compensation hypothesis).

There have been major reservations about the approaches using artificial nests in avian ecology (Burke et al. 2004; Moore and Robinson 2004; Thompson and Burhans 2004). However, these reservations concern studies that assume that predation rates are the same on both natural and artificial nests, which is obviously not true (review in Moore and Robinson 2004). The experimental approach described above does not make similar assumptions. Different patterns of predation on natural versus artificial clutches are assumed and are, in fact, the object of this study. Since the absence of parents on artificial nests is the essence of the approach, the only possible methodological bias could be introduced by the type of artificial nests and clutches used, which was minimised in this study (see Discussion).

In this work, I studied nest survival in relation to nest concealment in the blackcap (*Sylvia atricapilla*). I manipulated nest cover and followed the effects of this manipulation on the probability of nest depredation. To reveal whether parental behaviour compensates for poor nest cover, I compared the effects of concealment on nest survival between natural and artificial clutches. I also analysed the effects of concealment on nest survival separately for the incubation and nestling phases. These phases differ strongly in the fraction of time parents spend on the nest, which could have important consequences for the potential of parents to defend their nest and distract predators from its vicinity.

## Methods

The blackcap is a small (ca. 20 g), insectivorous, migratory passerine building its thin-walled, open-cup nests in the shrub and herbaceous layers of mature forests, about 1 m high. It breeds from late April until July and its nesting success is about 30% (Weidinger 2000; Remeš 2003a, 2003b). I conducted this study during two seasons (2000, 2001) on two study plots (total area 30 ha, 150 m apart) in a deciduous forest near Grygov, eastern Czech Republic (49°31'N, 17°19'E, 205 m a.s.l.). The forest was dominated by oak (*Quercus* spp.), ash (*Fraxinus excelsior*), lime (*Tilia* spp.), bird cherry (*Prunus padus*), and elder (*Sambucus nigra*). Blackcaps built their nests primarily in bird cherry, elder (height of both shrubs ca. 3–6 m) and nettle (*Urtica dioica*, height increasing with the season up to ca. 2 m).

I searched nests from late April to early July by careful inspection of shrubs and herbaceous vegetation. Shrubs formed a loose patchwork with open space, and their cover was 30–70% depending on location. In every nest found, I determined its height above the ground, clutch/brood size and its age. I also estimated the degree of concealment of each nest visually as a percentage of the nest bowl obscured by foliage (10% increment). I estimated horizontal and vertical concealment 1 m from a nest in the four cardinal directions and 1 m above a nest, and averaged these five estimates to obtain a single percentage for a nest. Nests were most often built near the edge of a supporting shrub/herb, and vegetation cover within 1 m was critical for nest visibility even from a greater distance. I subsequently monitored the nest at 3-day intervals until fledging or predation. The majority of nest losses in this study were caused by depredation (97%, losses not due to predation were excluded from the analyses). Typically, the whole contents of a nest disappeared, sometimes leaving remnants of egg shells.

In approximately half the nests, I removed a part of foliage concealment by cutting twigs and leaves and removing them from the vicinity of a nest. For the experiment, I used every other nest found. In the vicinity of control nests, I spent an equivalent amount of time to that needed for the foliage removal at experimental nests (ca. 3 min). I estimated concealment of every nest when it was found and when baited with plasticine eggs. To judge the effectiveness of the foliage-removal treatment, I estimated concealment of experimental nests also immediately after the foliage removal.

I baited blackcap nests with 4 brown plasticine eggs (clutch size in this population averages 4.7 eggs) of similar colour and size to natural eggs (20×15 mm). The time between fledging/failure of a nest and its baiting was  $7.2 \pm 3.5$  days (mean  $\pm$  SD,  $n=109$ ). Each plasticine egg was mounted on a thin wire anchored to the nest cup to prevent its removal. Clutches were monitored and removed after 14 days exposure (in the blackcap, incubation lasts 11 days, the nestling phase 9 days). A predation event was recorded if any of the four plasticine eggs was marked by a potential predator. There was no relationship between the fate of a natural nest and the same nest later on when baited with a plasticine clutch ( $\chi^2=0.03$ ,  $df=1$ ,  $P=0.871$ ,  $n=109$ ).

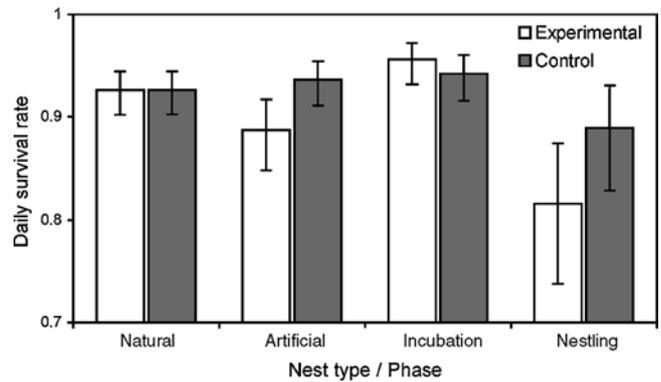
I quantified the time parents spent on the nest by counting nest visits when at least one parent was present on the nest (events) and total nest visits (trials). I did this for every nest separately for incubation and the nestling phase, and analysed it in a binomial model with the events/trials response variable (i.e. binomial proportion; the phase of the nest cycle was treated as a within-subject factor in GEE analysis in proc GENMOD of SAS). First visits were excluded.

I evaluated nest survival using the Mayfield method (Mayfield 1975), as implemented in a multivariate framework by Aebischer (1999). I analysed the effects of the experimental removal of concealment (experimental vs control nests) on the probability of survival in natural nests compared to artificial nests (by looking at the interaction between these terms). For natural nests, I compared

the effects of the removal between the incubation and the nestling phases (again by looking at the interaction term). In both these analyses, I controlled for nest height [ $\log_{10}$ -transformed, median=0.48 m (range 0.1–2.2 m)], season [date of the first egg in natural nests, 7 May (22 April to 24 June); date of the initiation of the experiment in artificial clutches, 2 June (4 May to 6 July)], and year. Initially, all two-way interactions of these factors were included and those that were non-significant were eliminated in a stepwise manner. Since natural and artificial clutches were studied in the same nests, and similarly, incubation and the nestling phase of the breeding cycle took place within the same nest, these factors were treated as within-subject factors in repeated-measures analyses. Both focal interactions were significant. Thus I analysed the effects of the cover-removal treatment separately for natural and artificial nests, and in natural nests also separately for incubation and the nestling period. Sample sizes in individual analyses vary because of missing data in some cells; for example, when a nest was depredated during incubation, it was no longer available for the nestling-phase analysis. All tests were two-tailed with  $\alpha=0.05$ , and were done in SAS (SAS Institute 2000).

## Results

The total number of nests was 124, of which 55 were experimental and 69 control. The concealment of nests before the foliage removal was  $87.0 \pm 14.8\%$  (mean  $\pm$  SD) in experimental and  $79.8 \pm 19.7\%$  in control nests, and decreased to  $33.5 \pm 12.3\%$  in experimental nests immediately after the experimental removal. The concealment of nests when they were baited with artificial clutches was  $29.9 \pm 15.9\%$  in experimental and  $76.5 \pm 20.9\%$  in control nests. This shows that the experimental treatment was highly effective in decreasing foliage concealment in experimental nests. A slight decrease of concealment on both control and experimental nests with artificial clutches compared to the natural situation can be ascribed to the desiccation of vegetation.



**Fig. 1** Probability of nest survival (over 1 day) separated for different types of nests and phases of the nesting cycle. Least squares means and their 95% confidence intervals from the analyses reported in Results. Note that the *y*-axis begins at 0.7

Daily survival rate of natural nests was  $0.926 \pm 0.007$  (mean  $\pm$  SE,  $n=124$ ), and in artificial clutches it was  $0.915 \pm 0.009$  ( $n=109$ ). When nest survival was analysed in all nests together, there was a significant interaction between the nest type (natural vs artificial) and the experimental treatment (control vs experimental). In natural nests, there was also a significant interaction between the phase of the nesting cycle (incubation vs nestling) and the treatment (Table 1). This shows that the effects of the experimental removal of nest cover differed between: (a) natural and artificial nests, and (b) incubation and the nestling phase of the breeding cycle in natural nests. Thus, I analysed the effects of the removal treatment on the probability of nest survival separately for natural and artificial nests, and also for incubation and the nestling phase in natural nests. The removal of concealment had a significant negative effect on nest survival in artificial clutches ( $\chi^2=6.27$ ,  $P=0.012$ ,  $n=109$ ) and, though not significant, a negative effect during the nestling phase in natural nests ( $\chi^2=3.08$ ,  $P=0.079$ ,  $n=64$ ). In contrast, there was no effect in natural nests across both nesting phases ( $\chi^2 < 0.01$ ,  $P=0.991$ ,  $n=115$ ) and during incubation ( $\chi^2=0.90$ ,  $P=0.344$ ,  $n=107$ ; Fig. 1).  $\chi^2$  statistic here is an LR statistic for type 3 analysis in proc GENMOD of SAS.

**Table 1** Generalised linear models (binomial error distribution, logit link) of the probability of nest survival in relation to selected factors for: (1) all nests ( $n=124$ ) and (2) only natural nests ( $n=115$ ).  $\chi^2$  statistic is a score statistic for type 3 GEE analysis in proc GENMOD of SAS. Focal interactions showing whether the effect of the treatment is differential with respect to the nest type and/or the phase of the nesting cycle are given in **bold**. Within-subject effects are given in *italics*; “na” denotes the factors/interactions not applicable in the particular analysis

Factor	All nests		Natural nests	
	$\chi^2$	<i>P</i>	$\chi^2$	<i>P</i>
Treatment (experimental $\times$ control)	4.07	0.044	0.57	0.449
<i>Nest type</i> (natural $\times$ artificial)	2.28	0.131	na	na
<i>Phase of the nesting cycle</i> (incubation $\times$ nestling)	na	na	15.92	<0.001
Nest height	2.35	0.125	8.48	0.004
Season	1.73	0.189	0.32	0.572
Year	0.18	0.674	12.37	<0.001
<b>Treatment</b> * <i>Nest type</i>	4.24	0.039	na	na
<b>Treatment</b> * <i>Phase of the nesting cycle</i>	na	na	4.06	0.044
<i>Nest type</i> *Year	14.40	<0.001	na	na

Parents spent more time on their nest during incubation compared to the nestling phase ( $\chi^2=21.85$ ,  $P<0.001$ ,  $n=107$ ). The probability of being on the nest was 78.7% (72.2–84.0%) during incubation and 41.5% (31.8–51.9%) in the nestling phase (LS means with 95% CIs).

## Discussion

### The parental compensation hypothesis

Parental activity on the nest seems to be a critical component interacting with nest cover and exerting beneficial effects on nest survival in the blackcap (but see Weidinger 2002). There was a strong positive effect of concealment on nest survival in artificial clutches without parental activity, whereas in natural clutches with parents present there was no effect. Poorly concealed nests were clearly more vulnerable to nest predation, and poor concealment must have been compensated for by the parents on natural nests (Cresswell 1997a). In line with this, no effect of nest cover on survival during incubation contrasted with a tendency for a positive influence during the nestling phase. This again demonstrates the important role of parental behaviour. Parents spent significantly more time during the day on the nest when incubating compared to the care for nestlings (ca. 80% vs 40%). Consequently, they had more opportunities to avert the risk of predation.

Active nest defence is effective in many passerine species (Martin 1992b), and in the blackcap it includes alarm calls, predator mobbing, injury feigning and distraction displays (Cramp 1992; Bures and Pavel 2003; V. Remeš, personal observations). Blackcaps are able to vigorously attack the brood parasitic common cuckoo (*Cuculus canorus*), including strong contact attacks (Røskaft et al. 2002; Grim 2005; V. Remeš, personal observations). Moreover, there is experimental evidence that they can attack in a contact manner a dummy of the hooded crow (*Corvus cornix*; T. Grim, personal communication). However, blackcaps seem to engage little in direct nest defence against a predator directly on the nest (Bures and Pavel 2003; Schaefer 2004), and it seems improbable that they are able to avert destruction of the nest once it has been discovered by a large predator (Schaefer 2004). Thus, although the evidence is mixed, defensive actions probably take place before the nest is discovered by a predator, i.e. at a greater distance from the nest.

### Possible mechanisms of parental compensation

In a small bird like the blackcap, the most effective active nest defence seems to be: (a) actions aimed at decreasing the conspicuousness of the nest to searching predators, and/or (b) preventive actions taken at a distance from the nest aimed at luring potential predators away from the nest (e.g. injury feigning and distraction displays). First, parents may have decreased activity around, and the number of approaches to, poorly concealed nests to escape the attention

of wandering predators (Martin et al. 2000b). Second, they may also have invested more time and energy in the guarding of poorly concealed nests that are more vulnerable to depredation. In both these cases, there could be time costs. More time invested in nest guarding and lower activity at the nest would mean, for example, lower feeding effort with negative effects on the young. Moreover, nest defence may be more effective on poorly concealed nests, because there may be a trade-off between nest cover and the ability of parents on the nest to detect an approaching predator and take effective mitigating action (Götmark et al. 1995; Koivula and Rönkä 1998; Wiebe and Martin 1998). Monitoring the spatial activity of radio-tagged parents and the number of approaches to the nest would be useful in testing these alternatives: do parents spend more time in the vicinity of poorly concealed nests? Do they reduce the number of approaches to the nest (during both incubation and feeding)? Do they have longer reaction distances in response to an intruder on poorly concealed nests?

Given that blackcaps are able to strongly attack an enemy at the nest (see above), it is possible that they are able to directly defend the nest at least against small predators (e.g. rodents; Schaefer 2004, see also Schaefer 2002) or predators that are not able to prey on them. In such cases, at least two mechanisms could lead to higher intensity of defence on poorly concealed nests (McLean et al. 1986; Kleindorfer et al. 2003). First, there is a higher probability that a poorly concealed nest had already been discovered by an approaching predator, and consequently it pays to defend it strongly. Second, parents of well-concealed nests may rely more on the inconspicuousness of their nest and avoid loud nest defence that may attract predators or brood parasites (McLean et al. 1986; Gill et al. 1997; see also Burhans 2000; Burhans and Thompson 2001). A useful approach to test this prediction would be experimentation with potential predators (both large and small) in a vicinity of nests differing in concealment and at a range of distances from the nests.

More time invested in nest guarding, lower activity on the nest, and higher vigour of nest defence could all lead to reduced survival and condition of both adults and young on poorly concealed nests. Proximate mechanisms involved would be diverse. More time invested in nest guarding trades off against self-maintenance (Martin 1992b; Komdeur and Kats 1999). Vigorous nest defence may be correlated with higher energy output, physiological stress, and mortality risks (Montgomerie and Weatherhead 1988). Moreover, poorly concealed nests are more often discovered by potential predators (see the results with artificial clutches), which can require more frequent nest defence. Reduced activity around the nest could lead to low feeding rates with resulting negative impacts on the performance of young. Parents may also transfer at least part of the time and energy costs of nest guarding/defence to their young, e.g. by decreasing feeding rates, with the same result. Thus, in future studies it will be important to simultaneously monitor general performance (survival, condition, growth, health) of both adults and nestlings.

### Alternative explanations and potential methodological bias

A major alternative explanation for the results of this study is the potentially different composition of the predator fauna robbing natural and artificial clutches. This could be caused by: (a) a methodological bias or (b) parental behaviour, in which case the cause would be regarded as natural.

Inspection of the bill and tooth marks on plasticine eggs revealed that major predators in this system are birds [jay (*Garrulus glandarius*) and woodpeckers (*Picoides* spp.)] and small mammals [most probably mice (*Apodemus* spp.) and bank vole (*Clethrionomys glareolus*), Remeš 2005]. However, artificial nests and eggs may bias the composition of the predator fauna compared to the natural situation (Rangen et al. 2000; Maier and DeGraaf 2001; Thompson and Burhans 2004). Since I used natural blackcap nests in their original position, the most probable bias introduced by the use of plasticine eggs is an overestimation of the depredation by olfactorily orientated rodents. They may be attracted by the odour of the plasticine (Rangen et al. 2000; but see Cresswell 1997b) or may more easily penetrate plasticine eggs as compared to real eggs (Maier and DeGraaf 2001). However, this would make my test of the parental compensation hypothesis conservative. If olfactorily orientated rodents were overrepresented as predators in artificial clutches, there should be no relationship between nest cover and success (see Remeš 2005). This prediction goes against that made by the parental compensation hypothesis, which predicts that there should be a positive effect of nest concealment in artificial nests (see above). Alternatively, overrepresentation of rodents as predators of artificial clutches may be offset by underrepresentation of the olfactorily orientated pine marten (*Martes martes*), which appears to be an important predator of natural nests in similar habitats (K. Weidinger, personal communication). Moreover, I used natural blackcap nests, which are much better than the generally discredited wicker nests (e.g. Davison and Bollinger 2000), and results obtained by the comparison of artificial with natural clutches were validated on natural nests by comparing incubation with the period of care for the young.

Artificial nests may be found by predators according to their visibility, which may result in the positive effect of nest concealment on nest survival. In contrast, predators may locate natural nests predominately by cuing on parental behaviour (e.g. feeding), which would lead to the absence of any concealment effect. The feasibility of this alternative, if at work at all, would depend on the details of the foraging behaviour of potential predators, which is generally not known. However, two lines of evidence suggest that this alternative was not responsible for the pattern detected in this study. First, indirect evidence indicates that predators of the blackcap search for nests actively or find them randomly instead of observing adults (Schaefer 2004). Second, validation on natural nests points in the same direction. There was no effect of concealment on nest survival during incubation with low parental activity, whereas there was a

positive, though not significant, effect during care for the young, when parental activity is high. Parental activity here means the number of approaches to the nest, which could be used by predators to locate nests, and which in small songbirds is generally lower during incubation than during care for the young (Martin et al. 2000b).

Although the alternative explanation outlined above cannot be automatically ruled out, the arguments and the evidence presented indicate that active behavioural compensation for poor concealment by parents was the more probable causal mechanism behind the findings of this study.

### Conclusions

Given that here behavioural compensation for poor nest cover was the major mechanism and provided it is costly, it pays parents to choose well-covered nest sites. From this point of view, it would be wrong to conclude that there is no selection on nest concealment, and similarly that predation is a random process (as evidenced by artificial clutches). However, such conclusions were often made based on the finding that there is no effect of nest cover on the probability of nest depredation in natural nests (e.g. Filliater et al. 1994; Howlett and Stutchbury 1996; Willson and Gende 2000). Moreover, many studies showed that birds select nest sites differentially with respect to some features (vegetative cover, support plant species etc.) but that later on these features do not affect the probability of nest depredation. They often concluded that birds selected a particular nest-site feature for other reasons than reducing predation (Braden 1999; Bisson and Stutchbury 2000). However, predation can still be the causal agent because the selected features may disengage parents from the need to invest in costly compensation. Conclusions regarding the randomness of nest predation, the absence of selection on concealment or the irrelevance of predation in driving nest-site selection may often have originated from basing conclusions on observed patterns without analysing the processes behind them (see also Schmidt and Whelan 1999).

To sum up, the effects of the experimental manipulation of nest concealment on the probability of nest survival in the blackcap separated for natural and artificial nests, and for incubation and nestling care, suggest that parents behaviourally compensated for poor nest cover. Species systematically differ according to their life-history in their likelihood to take risks in nest defence (Ghalambor and Martin 2001). This may partly explain why researchers in the past have obtained varied and conflicting results concerning the relationship between the degree of nest concealment and survival. My results also demonstrate that the absence of positive effects of nest cover on nest survival does not automatically mean a lack of natural selection on higher nest concealment. Generally, we cannot use single measures of behaviours or states (here nest concealment) as an indication of predation risk because of the capacity for compensation in other behaviours (see also Cotton et al. 2004).

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