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## Does egg colour affect predation rate on open passerine nests?

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**Abstract** The breeding success of many passerines is strongly reduced by egg predation. The adaptive significance of egg crypsis in open nesters is often taken for granted, but visually searching predators may first detect the nest or adult bird and not the eggs. Götmark predicted that selection should favour egg crypsis in the absence of conspicuous nests, whereas birds with conspicuous nests should have non-cryptic eggs. I compared the effect of egg colour treatment (white, blue, brown-spotted) on nest survival (1) among species characterized by different egg coloration, nest size and nest placement, and (2) between relatively well and poorly concealed nests within species. I used artificial nests ( $n=1,296$ ) and eggs mimicking (except in egg colour) those of the yellowhammer (*Emberiza citrinella*), blackcap (*Sylvia atricapilla*) and song thrush (*Turdus philomelos*). Concurrently, I monitored survival of real nests ( $n=1,106$ ). Nest survival differed among species, increased with nest concealment and throughout the breeding season, but was not significantly related to egg colour in any species. Nevertheless, the data for the yellowhammer suggest a trend in survival rates across the colour treatments. Brown eggs survived better than white eggs by 11% and 4% in 2 years, but this study had insufficient power to detect effects of this size. The results thus suggest that egg coloration in the song thrush and blackcap (shrub nesters) may be a neutral trait with regard to nest predation, whereas egg crypsis may be an anti-predation feature for the yellowhammer (ground/near-ground nester). The role of predation in the evolution of eggshell colour may vary not only between cavity and open nesters, but also across nest sites within the latter group.

**Keywords** Egg crypsis · Nest concealment · Nest predation · Nest site

### Introduction

Breeding success of most temperate-zone passerines is profoundly influenced by predation on eggs and nestlings (Ricklefs 1969; Martin 1995). Thus, nesting adaptations that reduce the predation rate are presumed to have great selective value (Ricklefs 1984). Eggs in open-cup nests (as opposed to cavity nests) are exposed to visually searching predators during laying and pauses during incubation, which together represent a significant part of the entire nesting cycle. Although the great diversity in eggshell colour patterns found even among closely related species or species that share similar nesting strategies remains to be explained, the adaptive significance of cryptic egg coloration is often taken for granted (Westmoreland and Kiltie 1996). Nevertheless, the evolution of eggshell colour patterns may also be influenced by factors other than predation risk (e.g. Götmark 1992 and references therein).

Egg crypsis is a likely explanation in ground-nesting birds, for which eggshell colour often provides camouflage and reduces nest predation (Tinbergen et al. 1962; Montevicchi 1976; Bertram and Burger 1981; Solís and de Lope 1995; Yahner and Mahan 1996; Lloyd et al. 2000), although some studies do not support this view (Janzen 1978; Jobin and Picman 1997). This adaptive explanation of egg colour is less obvious in shrub and canopy nesters (Götmark 1992). Lack (1958) brought attention to the puzzling occurrence of blue colour on some passerine eggs, which makes them conspicuous (to human eyes) on a dark nesting background. Lack (1958) and Oniki (1985) speculated that blue pigmentation may provide camouflage in the contrasting light environment of forest understoreys. Their adaptive explanation was not supported in an experiment by Götmark (1992), who came to conclusion that “blue eggs in the song thrush [*Turdus philomelos*] are not cryptic but may be selective-

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ly neutral or even maladaptive with regard to nest predation." Considering the marked spatiotemporal variation in the light environment of forest habitats, colour patterns may be relatively cryptic in some habitats, but relatively conspicuous in others (Endler 1993). Götmark (1992) stressed that his experiment was representative of coniferous forest with avian predators and suggested further studies in other habitats.

Visually oriented predators may locate nests by using cues other than egg colour, e.g. by observing parental activity (Martin et al. 2000). Nest predation is traditionally assumed to constrain the brightness of incubating birds (Wallace 1889; Martin and Badyaev 1996). However, several studies have shown that bright plumage (Stutchbury and Howlett 1995) or artificial bright colour at the nest (Haskell 1996; Miller 1999) did not increase the risk of predation on shrub nests. Alternatively, predators may search directly for conspicuous nests (Møller 1990; Cresswell 1997). Thus, nests and/or adults and not the eggs may be detected first by a predator. Götmark (1992) predicted that selection should favour egg crypsis in the absence of a conspicuous nests, whereas birds with conspicuous nests should have non-cryptic eggs (assuming a cost of pigmentation). Comparative data on non-passerine families with contrasting nesting strategies seems to partly support this view (Götmark 1993). However, the above prediction has not yet been tested with species that share a similar nesting strategy (e.g. passerines with open-cup nests in shrubs) but differ in nest conspicuousness/size and egg crypsis.

My aim in this study was to test the adaptive significance of egg colour with regard to the risk of nest predation in three species of open-cup nesting passerines: the yellowhammer (*Emberiza citrinella*), blackcap (*Sylvia atricapilla*) and song thrush. I used artificial nests and eggs that mimicked the natural models except in egg colour. Within each species I compared nest survival rates among three egg colour treatments: (1) white, considered to be the most conspicuous (as judged by the human eye) and possibly representing the least costly coloration for the female; (2) blue, similar to real eggs of the song thrush, and relatively conspicuous; (3) brown-spotted, similar to real eggs of the blackcap and yellowhammer, presumably cryptic. I adopted the randomized-block design to control for confounding environmental effects. As the method using artificial nests has many possible drawbacks (Major and Kendall 1996), I simultaneously conducted a validation experiment and recorded predation rates on active real nests (Weidinger, in press a).

In an attempt to test Götmark's (1992) hypothesis on the relationship between nest conspicuousness, egg crypsis and predation risk, I compared the effect of egg colour on the nest survival rate (1) among species characterized by different natural egg coloration, nest size and nest placement, i.e. nest conspicuousness, and (2) between relatively well and poorly concealed nests within each of these species. In the former case, I tested the species $\times$ colour interaction in a multi-species model; in the

latter case, I tested the concealment $\times$ colour interaction in separate-species models. I made the following predictions:

1. Egg colour should have no detectable effect on nest survival in the song thrush, i.e. in a species with conspicuous nests. This would provide support for Götmark's conclusion.
2. The validity of the first prediction should not depend on nest concealment. This seems relevant for species with conspicuous nests, which predators are likely to detect before detecting the eggs, regardless of nest cover.
3. White and blue eggs should reduce nest survival in the blackcap and yellowhammer, i.e. species with relatively less conspicuous nests (small or well hidden, respectively). This would suggest that in these species, the natural coloration of eggs is adaptive with regard to predation.
4. The anti-predator effect of cryptic egg coloration should increase with better nest concealment in the blackcap and yellowhammer.

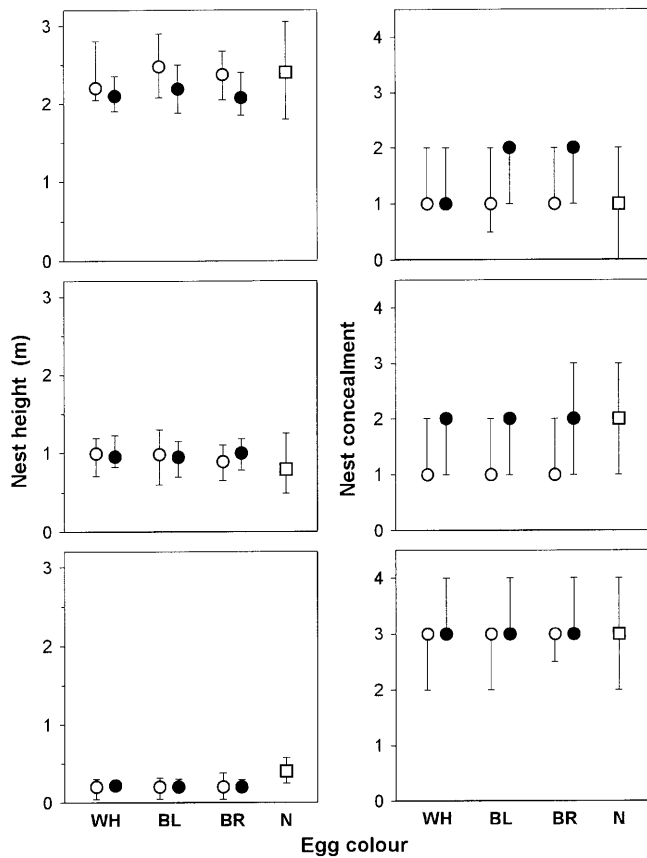
## Methods

### Study area

The study was conducted in a farmland area north of the village Luže (49°54' N, 16°2' E, 240–350 m above sea level) in Eastern Bohemia, Czech Republic, in 1998 and 1999. The landscape is a mosaic of arable land with remnants (2–25 ha) of deciduous woodland and settlements. The tree vegetation is dominated by ash (*Fraxinus excelsior*), poplar (*Populus nigra*), alder (*Alnus glutinosa*), oak (*Quercus petraea*), willow (*Salix* spp.) and elm (*Ulmus* spp.). The shrub layer is formed by elder (*Sambucus nigra*), bird-cherry (*Padus racemosa*) and blackthorn (*Prunus spinosa*). The herbaceous undergrowth is dominated by nettle (*Urtica dioica*). I performed the study on 24 plots (2–10 ha) located within an area of about 83 km<sup>2</sup>. Plots were selected to be representative of local woodland habitats in distinct habitat patches (woodlots or riparian belts) surrounded by arable land or grassland. The minimum distance between plots was 300 m, and the median nearest-neighbour distance was 750 m. With regard to assumed home range size in corvids (Cramp and Perrins 1994), spacing of the study plots was considered sufficient to reduce site-specific biases due to predation by a few, possibly specialized individuals (Söderström et al. 1998).

### Model species

I selected three model species that differ in nest placement (height aboveground, concealment by vegetation; Fig. 1), nest size and egg coloration. The yellowhammer (YH) has a medium-sized and thick-walled nest, placed on or close to the ground, well hidden in herbaceous vegetation; the eggs are with dark spots and hairlines on a light greyish-brown background. The blackcap (BC) builds a small and thin nest, placed typically in shrubs, 0.5–1.5 m aboveground, moderately concealed by vegetation; the eggs are variable in colour and pattern, with dark-brown or purplish blotches and spots on a light yellowish-white background. The song thrush (ST) has a conspicuous bulky nest, placed on shrubs or trees, 1.5–3 m aboveground, often little concealed by vegetation; eggs are light blue-green with sparse dark spots; egg colour contrasts with the yellowish nest cup made of rotten wood with no lining.



**Fig. 1** Height aboveground (m) and concealment (subjective score ranked from 0=low to 4=high) of artificial nests by species (*top-bottom* song thrush, blackcap, yellowhammer), egg colour treatment (WH white, BL blue, BR brown) and year (*open circles* 1998, *filled circles* 1999). The median and interquartile range are shown, all  $n=72$ . Characteristics of natural nests (N, years combined) are shown for comparison;  $n=298$ , 630 and 162 for song thrush, blackcap and yellowhammer, respectively. Differences among colour treatments within each species-year sample were non-significant (Kruskal-Wallis test, all  $P>0.05$ )

#### Artificial eggs and nests

I used artificial eggs turned out from hard plastic and painted with non-toxic outer paint (Latex; Teluria, Skrchov). Their size was equal ( $\pm 0.5$  mm) to the local mean dimensions of real eggs: 21.6 $\times$ 16.2 mm (YH), 19.6 $\times$ 14.7 mm (BC), 27.3 $\times$ 20.6 mm (ST). For each species, I used three egg colour treatments: white (WH), blue (BL), brown-spotted (BR). The natural coloration was represented by either BR (yellowhammer, blackcap) or BL (song thrush) treatments. Fresh eggs collected from abandoned clutches and eggshells were used as templates to mimic the natural coloration. According to the Kornerup and Wanscher (1967) notation, the blue treatment corresponded to the colour designated as 25(A-B)(5-6), the brown treatment corresponded to 5(B-C)2 (background) and 5F(3-6) (dark spots). I used four-egg clutches to approximate the mean clutch size observed in this area (Weidinger, in press b): 3.9 eggs (YH), 4.5 eggs (BC, ST). Eggs were attached to the nest by a thin wire so that they could be moved inside the cup, elevated or pulled out of the nest, but could not be removed, except by a strong predator. Tooth or beak marks left in the soft layer of paint were used to classify predators as bird or mammal. The artificial nests (Weidinger, in press a) consisted of a cup of appropriate size made of fine wire or perforated plastic. Natural material was used to form the outer walls (dry grass, dry leaves, moss, twigs) and nest

cup (fine dry grass, rough flax fibres, sawdust mash) to mimic the real nests. No part of the artificial structure was visible. The outer diameter of the nest, inner diameter of the cup, nest height and cup depth (all dimensions in cm) of artificial nests were: YH (13, 6.5, 5, 4), BC (9, 5.5, 4.5, 3.5), ST (16, 11, 8, 6). Artificial nests and eggs were characterized by unnatural scent. This fact, however, does not invalidate comparisons among treatments, because the artificial materials used (wire, plastic, paint) were identical.

#### Experimental design and field procedures

I used a randomized-block design with 24 blocks (=study plots) of 27 treatments. The treatments had a  $3^3$  factorial structure: colour (WH, BL, BR) $\times$ species (YH, BC, ST) $\times$ season (early=May, middle=June, late=July). Each treatment was represented by one nest per block, resulting in 648 nests per year. The experiment was repeated on the same study plots in 2 consecutive years.

Nine nests representing all possible colour $\times$ species combinations were simultaneously placed on each study plot for one trial. I set up the three seasonal trials on 30 April–3 May, 25–28 May and 24–27 June (1998) and 27–30 April, 27–30 May and 27 June–1 July (1999). Nests were placed each time at different arbitrarily selected sites (see below) within each study plot and were removed between trials. All nests were exposed for 15 days, which was close to the mean duration of the egg stage of the real nests (16 days in YH and BC, 17 days in ST), and were checked on the 5th, 10th and 15th day. A nest was considered depredated when at least one egg was damaged, pulled out of the nest, missing or buried in nest lining. Spacing of artificial nests was irregular depending on the presence of suitable nesting substrate and the location of active natural nests. Before placing an artificial nest, I ensured, as far as possible, that no natural nest was active within a radius of about 10 m. The distance between neighbouring artificial nests was about 50 m, the minimum distance was 30 m in a few cases. I placed artificial nests in sites resembling those occupied by natural nests of the model species. I tried to keep nest substrate, height aboveground and nest concealment similar for all colour treatments within each species in a particular block and trial (Fig. 1). I did not use any nest markers in the field.

Field work was conducted from about 0800 hours to sunset, but all successive visits to an individual nest were approximately ( $\pm 2$  h) at the same time of day. The following nest site characteristics were recorded on the last visit to a nest: species of nest-bearing plant; height of nest aboveground (m); nest concealment category (subjective score ranked from 0=low to 4=high), obtained as a sum of horizontal and overhead concealment (each ranked 0–2). To simplify the analysis, and because overall concealment differed markedly among species (Fig. 1), I categorized nest concealment within each species as relatively good (score 4 in YH, scores 2–4 in BC and ST) or poor (the remaining scores).

#### Control data and potential predators

Two types of control data were collected in a validation experiment (Weidinger, in press a) conducted simultaneously with the present study. (1) I validated the use of artificially constructed nests by monitoring survival of artificial clutches placed in used natural nests left in their original position (total  $n=103$ , 421 and 185 for YH, BC and ST, respectively). (2) I monitored survival of active natural nests found on the study plots (total  $n=162$ , 639 and 305 for YH, BC and ST, respectively). Survival rates of natural nests beyond the egg stage were estimated by the Mayfield method (Hensler 1985) and were compared with survival rates of artificial nests. The occurrence of potential avian predators (corvids) was recorded visually throughout the breeding season. The abundance of small mammals was estimated by snap-trapping in the second half of August (24 plots $\times$ 2 transects $\times$ 30 traps $\times$ 1 night=1,440 trap-nights per year).

## Data analysis

The experiment was analysed separately for the 2 years because many uncontrolled factors may differ dramatically between breeding seasons. I used two types of response variable: (1) nest survival over the 15-day exposure time (binary response coded 0–1), and (2) the number of 5-day intervals survived (ordinal response coded 0–3). Factor effects on either type of response variable were examined by fitting generalized linear models with logit link and binomial or multinomial ordinal distribution, respectively. Analyses of the two response variables led to essentially the same results, hence only those based on the ordinal response are presented.

Nest height and concealment were covariates not controlled by the experiment and were partially redundant with the factor “species” (Fig. 1). The nest concealment score was also positively correlated with the factor “season” in the blackcap (Spearman  $r_{s,214}=0.30$  and 0.52 in 1998 and 1999, respectively; both  $P<0.001$ ) and song thrush ( $r_{s,214}=0.39$  and 0.34, both  $P<0.001$ ), and a similar tendency was found in the yellowhammer ( $r_{s,214}=0.05$  and 0.20,  $P=0.474$  and 0.004, respectively). Hence, I examined two categories of model: (1) a multi-species model that included effects of colour, species, season and random block, and (2) separate-species models that included effects of colour, season and concealment (covariate); the random block effect was not included because of unbalanced sample size and empty cells in the data table.

An appropriate sampling unit in predation studies is the individual predator. Given the spacing and size of the study plots, each plot in this study likely represented only one pair of avian predators (corvids) but many individual small mammals (the home ranges of which are less than the plot area). Although each treatment (combination of colour, species and season) was represented by only one nest per study plot, the three seasonal trials (though nests were placed in different sites each time) may represent potential pseudoreplication. To check for this, I also performed analyses on data pooled across trials, thus reducing  $n$  from 648 to 216 measurements per year (Table 1).

To evaluate the effect size (=differences among colour treatments) in the above models, I examined 0.95 confidence intervals on the logistic regression coefficients for BR versus WH and BL versus WH colour treatments. To quantify the effect size in a simple comparison of nest survival rates between two treatments, I estimated the exact 0.95 confidence interval on the difference be-

tween two proportions using StatXact (Cytel 1997). Given the sample size available per colour treatment ( $n=72$  for each species,  $n=216$  in pooled sample), type I error rate=0.05, power=0.80, and assuming a survival rate of 50% in one of the treatments, the minimum effect size detectable in a two-tailed  $\chi^2_1$  test was estimated at 24% (within-species comparison) or 14% (pooled sample comparison). Equivalently, the power to detect a difference of 20% (40 vs 60%) would be 0.61 (within species) or 0.98 (pooled sample).

## Results

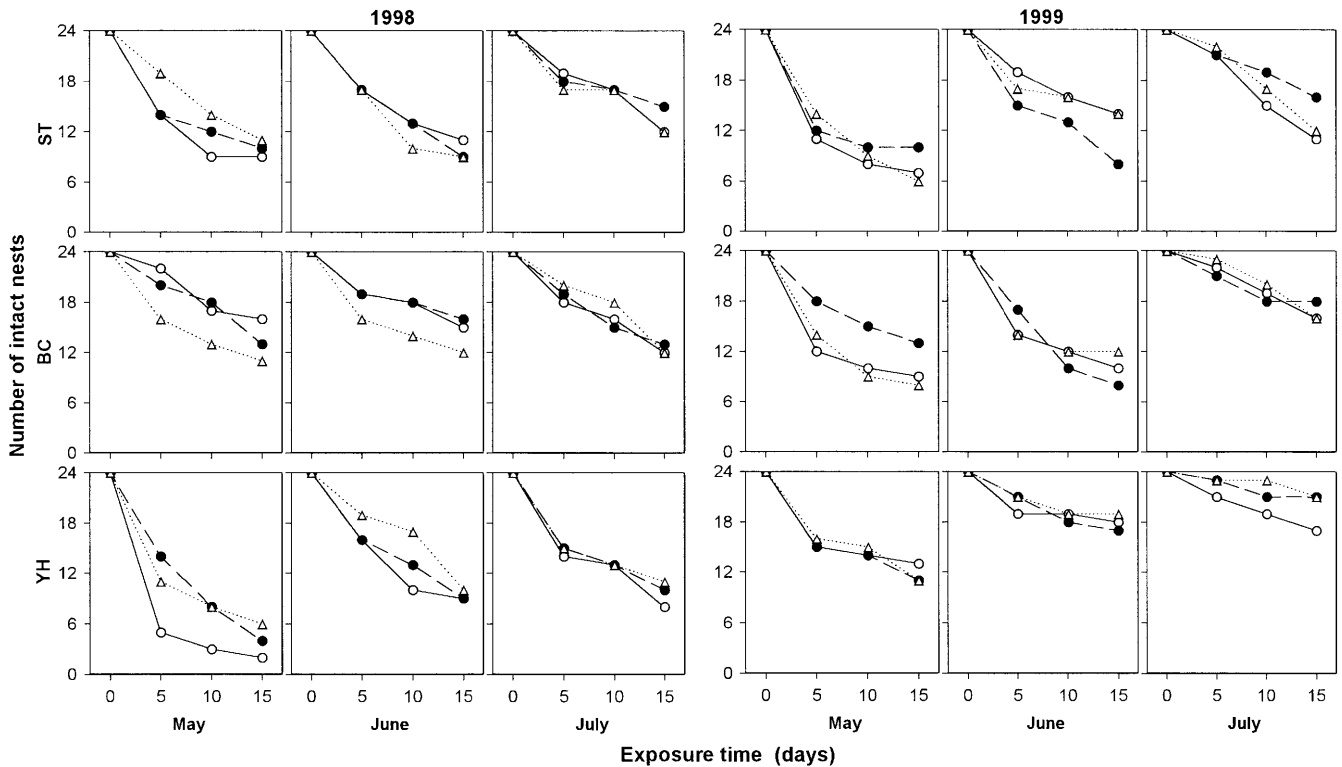
Contrary to expectation, no significant main effect (all  $P>0.3$ ) or interactions with other factors (all  $P>0.1$ ) of colour treatment were found (Table 1). Analysis of data pooled across trials led to similar conclusions (Table 1). The nest survival rates for the WH, BL and BR treatment were similar: 44, 46 and 44% in 1998; 53, 57 and 55% in 1999 (all  $n=216$ ). The odds-ratios estimated by the models for BR versus WH and BL versus WH treatments were close to 1 (0.99–1.12). The main effects of species and season were significant in both years (Table 1). In 1998, the nest survival rate was lower in YH (32%) than in BC (56%) or ST (45%). The opposite was found in 1999: the nest survival rate in YH was higher (68%) than in BC (51%) or ST (45%, all  $n=216$ ). Nest survival rates generally increased from the May through June to July trials: 38, 46 and 49% in 1998; 41, 56 and 68% in 1999 (all  $n=216$ ). Nevertheless, in both years, the pattern of seasonal variation differed across species (significant species $\times$ season interaction). In 1998, the nest survival rate increased markedly in YH but remained approximately stable in ST and BC (Fig. 2). The differences were less pronounced in 1999 when all species showed an increasing trend.

**Table 1** Generalized linear models (logit link, ordinal response) of factor effects on nest survival. The response variable represented: *Individual nests* the number of 5-day intervals (0–3) survived by an individual nest; *Pooled across trials* the total number of nests (0–3) that survived in the three trials. The explanatory factors were egg colour (white, blue, brown), species (yellowhammer, blackcap, song thrush), time of breeding season (May, June, July) and study plot (=random block). Given for each factor or in-

teraction of factors is the likelihood-ratio  $\chi^2$  value (=increase in deviance when the term is removed from the model). *Italicized* are terms included in the reduced model that was selected by the best-possible-subset method based on the likelihood-ratio statistic (all  $P<0.05$ ). Logistic regression coefficients ( $b$ =log odds-ratios) with a standard error (SE) are shown for brown and blue colour treatments vs the white treatment (=reference category)

Effect	df	Individual nests ( $n=648$ )		Pooled across trials ( $n=216$ )	
		1998	1999	1998	1999
(1) Colour	2	1.48	1.92	0.34	0.48
(2) Species	2	<i>35.51***</i>	<i>28.30***</i>	<i>30.49***</i>	<i>30.18***</i>
(3) Season (trial)	2	<i>11.75**</i>	<i>65.38***</i>		
(4) Study plot	23	<i>53.32***</i>	<i>98.97***</i>	<i>56.06***</i>	<i>79.59***</i>
1 $\times$ 2	4	7.12	1.49	4.54	0.44
1 $\times$ 3	4	1.22	4.94		
2 $\times$ 3	4	<i>13.33**</i>	<i>11.04*</i>		
1 $\times$ 2 $\times$ 3	8	8.49	4.36		
Colour (brown)	<i>b</i>	–0.0030	0.0506	–0.0468	0.0085
SE	0.1071	0.1215	0.1824	0.1850	
Colour (blue)	<i>b</i>	0.1171	0.1109	0.1090	0.1076
SE	0.1080	0.1215	0.1827	0.1850	

\* $P<0.05$ ; \*\* $P<0.01$ ; \*\*\* $P<0.001$



**Fig. 2** Survival of artificial nests by species (YH yellowhammer, BC blackcap, ST song thrush), time of breeding season and egg colour treatment (open circles white, filled circles blue, triangles brown)

**Table 2** Generalized linear models (logit link) of factor effects on the number of 5-day intervals survived by an individual nest (ordinal response coded 0–3). The explanatory factors were egg colour (white, blue, brown), time of breeding season (May, June, July) and nest concealment (two categories). Total  $n=216$  nests per species and year. For other explanations see Table 1

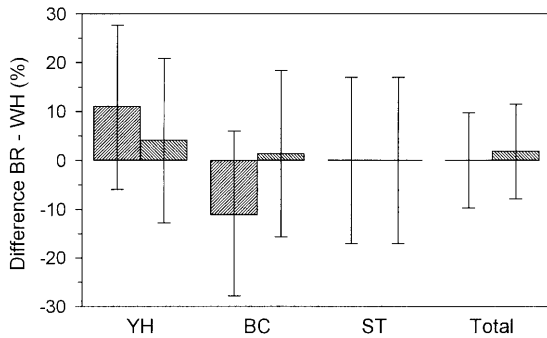
Effect	df	Yellowhammer		Blackcap		Song thrush	
		1998	1999	1998	1999	1998	1999
(1) Colour	2	0.15	1.57	2.81	3.13	0.54	0.04
(2) Season (trial)	2	4.83 <sup>+</sup>	8.58 <sup>*</sup>	2.04	12.00 <sup>**</sup>	0.86	10.06 <sup>**</sup>
(3) Concealment	1	7.34 <sup>**</sup>	9.33 <sup>**</sup>	8.02 <sup>**</sup>	1.20	3.57 <sup>+</sup>	1.39
1×2	4	2.16	1.96	1.57	0.94	3.33	4.73
1×3	2	0.73	0.38	2.37	1.80	2.29	1.12
2×3	2	0.91	2.23	0.46	0.59	9.48 <sup>**</sup>	1.05
Colour (brown)	<i>b</i>	0.0654	0.2341	-0.3183	-0.0201	-0.1024	0.0382
	SE	0.2789	0.2601	0.1919	0.2081	0.1973	0.1860
Colour (blue)	<i>b</i>	0.0578	0.0415	0.1932	0.3431	-0.0515	-0.0254
	SE	0.2654	0.2664	0.1995	0.2155	-0.1984	0.1887

<sup>+</sup> $P<0.1$ ; <sup>\*</sup> $P<0.05$ ; <sup>\*\*</sup> $P<0.01$

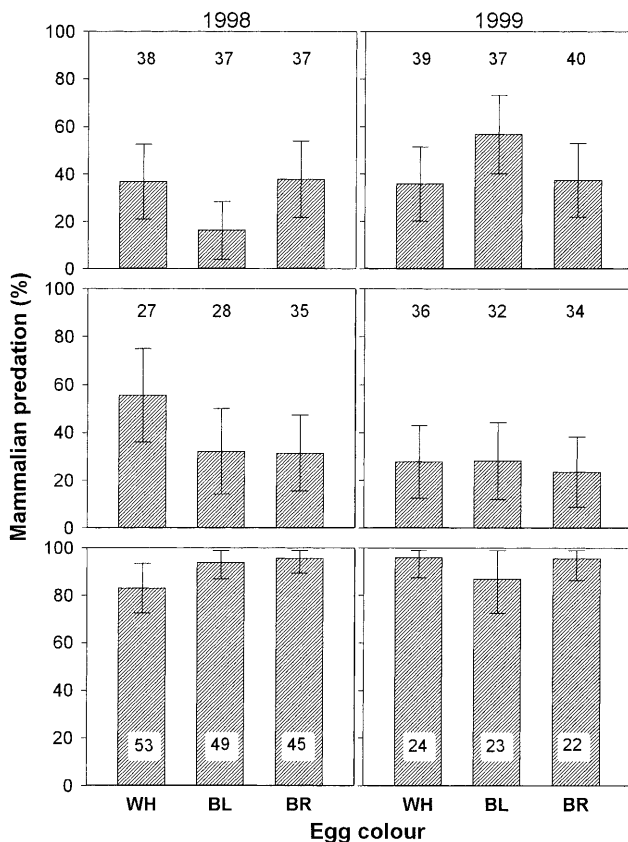
The separate-species models (Table 2) supported the findings based on multi-species models. Again, no significant effects of colour, colour×season or colour×concealment interactions were found. The nest survival rate generally increased throughout the season and with increasing nest concealment. Due to a positive correlation between these two factors (see Methods), only one of them remained significant after controlling for the other (with exception of model for YH).

Differences in nest survival rate (=effect size) between WH and BR (the most versus the least conspicuous) colour treatments within each species-year sample and in samples pooled across species were of both directions and their absolute size ranged from 0 to 11% (all  $P>0.05$ ; Fig. 3).

Marks left on artificial eggs permitted discrimination between avian and mammalian predators in 85% of nests and an uncertain discrimination in an additional 12% of nests ( $n=657$  predated nests). There was no consistent relationship between egg colour and type of predator in any year (Fig. 4). The pattern of variation among colour treatments differed across species in 1998 (significant colour×species interaction; Table 3). The relative contribution of mammals (mainly small rodents) to overall predation differed markedly among species: mammals were responsible for most predation events on the yellowhammer (91 and 93% in 1998 and 1999, respectively) but for less than half predation events on the blackcap (39%, 27%) and song thrush (30%, 43%) (see Fig. 4 for sample sizes). Mammalian predation was relatively

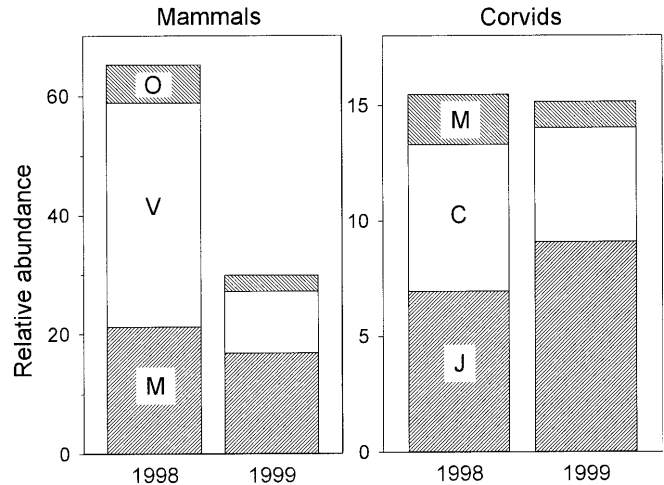


**Fig. 3** Differences (with exact 0.95 confidence interval) in survival rates between brown (*BR*,  $n=72$ ) and white (*WH*,  $n=72$ ) egg colour treatment in yellowhammer (*YH*) blackcap (*BC*), song thrush (*ST*) and the total sample (pooled across species). The two bars for each species represent 1998 and 1999, respectively



**Fig. 4** Proportion (with approximate 0.95 confidence interval) of all predation events ( $n$  shown with bars) that were attributable to mammals by species (*top–bottom* song thrush, blackcap, yellowhammer) and egg colour treatment (*WH* white, *BL* blue, *BR* brown) of artificial nests

more important during the last trial in 1998 (57, 50 and 66% in May, June and July, respectively;  $n=131$ , 108 and 110) and a similar, though not significant, seasonal trend was found in 1999. The abundance of corvids on the study plots was similar in both years, whereas that of small mammals, in particular the bank vole (*Clethriono-*



**Fig. 5** Relative abundance of potential nest predators on the study plots. Mammals: numbers captured per 100 trap-nights (1440 trap-nights per year); *M* wood mouse (*Apodemus sylvaticus*) and yellow-necked mouse (*A. flavicollis*); *V* bank vole (*Clethrionomys glareolus*); *O* other species, mainly common vole (*Microtus arvalis*). Corvids: frequency of occurrence per 100 plot-visits (528 plot-visits per year); *J* jay (*Garrulus glandarius*); *C* hooded crow (*Corvus corone cornix*); *M* magpie (*Pica pica*). Data from Weidinger (in press a)

**Table 3** Generalized linear models (logit link) of factor effects on type of nest predator (coded 0=birds or 1=mammals). The explanatory factors were egg colour (white, blue, brown), species (yellowhammer, blackcap, song thrush) and time of breeding season (May, June, July). For other explanations see Table 1; sample size is shown in Fig. 4

Effect	<i>df</i>	1998	1999
(1) Colour	2	1.03	0.14
(2) Species	2	126.76***	79.16***
(3) Season	2	5.97+	0.96
1×2	4	11.94*	4.82
1×3	4	4.79	2.66
2×3	4	5.59	1.01
Colour (brown)	<i>b</i>	0.1804	-0.1160
	SE	0.2378	0.3193
Colour (blue)	<i>b</i>	-0.2325	0.0247
	SE	0.2300	0.2670

+ $P<0.1$ ; \* $P<0.05$ ; \*\*\* $P<0.001$

*mys glareolus*), decreased markedly between 1998 and 1999 (Fig. 5; Weidinger, in press a).

## Discussion

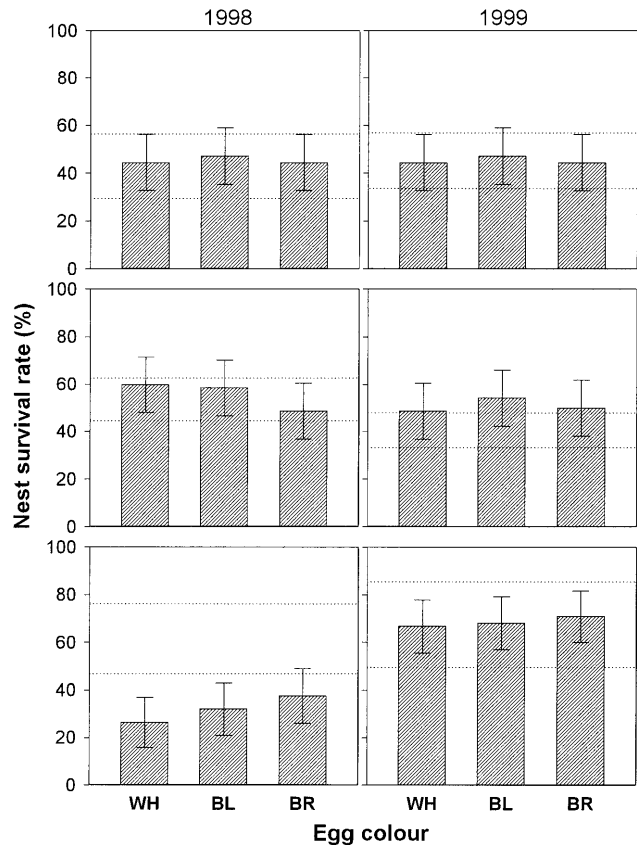
With regard to the tested predictions, the experimental results were consistent across the two annual replicates as well as for two types of response variable. No significant effect of egg colour on nest survival was found. Contrary to expectation, neither the species×colour interaction in a multi-species model, nor the concealment×colour interaction in separate-species models were detected. The results thus suggest that predation risk is not related to egg colour and that this does not vary among species character-

ized by different nest conspicuousness, or with nest concealment within individual species.

These findings are consistent with predictions (1) and (2) and support Götmark's (1992) conclusion that egg coloration in the song thrush may be a neutral trait with regard to nest predation. The present and Götmark's study differed in habitat (deciduous vs coniferous woodland), including the predator communities, experimental design (randomized blocks vs completely randomized), artificial material (plastic vs quail eggs) and duration (two vs one breeding season). The common conclusions of both studies are thus unlikely to be influenced by local or other methodological factors, suggesting instead validity over a range of environments.

Predictions (3) and (4) were not supported. I hypothesized that egg coloration in the blackcap and yellowhammer is cryptic, and hence adaptive with regard to nest predation. The data contradict this conventional view, and suggest a similar explanation (i.e. neutral trait) as in the song thrush. This finding was rather surprising, because the real eggs as well as their artificial mimics were well camouflaged in the nests (as judged by human eye), whereas the artificial clutches of white or blue eggs were conspicuous against the dark nest background. Blackcap nests are small and thin (often transparent from below) and represent a much smaller visual target than song thrush nests. Nevertheless, predators likely detect these small nests before detecting the eggs, regardless of variation in overall nest concealment. Møller (1990) has shown that even intraspecific variation in nest size may influence predation risk in the blackbird (*T. merula*). The size of artificial nests has also been shown to influence discovery (Sieving and Willson 1998).

Different explanations may be applicable to the yellowhammer. The nests of this species are larger than those of the blackcap but well camouflaged, often embedded in dense herbaceous vegetation near the ground. According to Götmark (1992, 1993), cryptic eggs should be favoured by selection in the absence of conspicuous nests. The apparent failure to support the adaptive explanation could be due to the prevalence of mammalian predation (>90% of predation events; Fig. 5), which is less likely to be influenced by egg colour. The experimental setup was relevant to predators that rely on vision when foraging, but the field work coincided with the peak phase of the rodent population cycle. Given the high nest encounter probability, mammalian predation on YH nests may have represented a stochastic event not dependent on egg colour (this study) or nest characteristics (Weidinger, in press a). Hence, any possible effect of colour-selective avian predation on YH nests, which would be detectable in other years, may have been cancelled out by non-selective mammalian predation. This explanation is unlikely to be true for the blackcap and song thrush, where mammals were responsible for <40% of predation events. Moreover, the contribution of mammals to overall predation rates was roughly proportional across the egg colour treatments in all model species (Fig. 4, Table 3; see Yahner and Mahan 1996, for opposite results).



**Fig. 6** Survival rates (with approximate 0.95 confidence interval) of artificial nests over the 15-day exposure period by species (top–bottom: song thrush, blackcap, yellowhammer) and egg colour treatment (WH white, BL blue, BR brown); all  $n=72$ . The horizontal dotted lines indicate the approximate 0.95 confidence interval on survival rates of active natural nests estimated by the Mayfield method for the 15-day egg stage;  $n$  (1998)=63, 175 and 60 nests for song thrush, blackcap and yellowhammer, respectively;  $n$  (1999)=84, 242 and 43 nests

Though not significant, the data for the yellowhammer (contrary to the other species) still suggest a trend in survival rates across the colour treatments (BR>BL>WH; Fig. 6). Brown eggs survived better than white eggs by 11% (1998) and 4% (1999) (Fig. 3). Such differences in nest survival may be of biological significance (Ricklefs 1984), but my study had insufficient power to detect an effect of this size at the conventional 0.05 level of statistical significance (see Methods for power estimates and Fig. 3 for confidence intervals on effect size). If real, the observed pattern would suggest egg crypsis in the yellowhammer.

The validation study (Weidinger, in press a) showed that artificial nests accurately reflected mean survival rates as well as seasonal trends and interspecific differences in survival of the real nests in some subsets of data, but the pattern was not consistent across species and between years (see also Wilson et al. 1998). The largest discrepancy was the low survival of artificial yellowhammer nests in 1998 (Fig. 6), the year with an extreme-

ly high abundance of rodents (Fig. 5). However, my goal was to evaluate the relative effect of different egg colour treatments on nest survival, rather than measuring actual nest success. In contrast to previous studies, I used artificial eggs of natural size instead of real eggs of unnatural size (e.g. quail or hen eggs; see Haskell 1995 for a discussion of possible egg size effects), which seems more relevant to visually oriented predators. Eggs of any type had to be painted and thus became "artificial", but plastic eggs allowed discrimination between avian and mammalian predators. Hence, I assume that the conclusions of this study were not influenced by potential biases associated with the realism of the experimental apparatus. Nevertheless, the results of this and similar studies should be interpreted with caution: avian colour vision differs from that of humans (e.g. the perception of ultraviolet light; Hunt et al. 1997) and perception of colour patterns may interact with habitat-specific light environments (Endler 1993; Marchetti 1993).

In conclusion, nest survival in this study differed among species, increased with nest concealment and throughout the breeding season, but was not significantly related to egg coloration in any species. Tentative conclusion could be that in shrub-nesting birds, nests are located by predators using cues other than egg coloration (Götmark 1992; song thrush and blackcap in this study) or the plumage brightness of nest-attending birds (Stutchbury and Howlett 1995; Haskell 1996; Miller 1999), regardless of nest size/conspicuousness. Although egg colour per se (after experimental removal of the nest effect) was shown to influence predation risk (Götmark 1992), in the presence of even relatively inconspicuous nests (blackcap in this study), egg coloration likely represents a neutral trait with regard to nest predation. Only one study (Westmoreland and Best 1986) has provided compelling experimental evidence for the adaptive value of cryptic egg coloration in shrub-nesting species. In ground-nesting birds with well-camouflaged nests or eggs laid directly on the ground, cryptic egg coloration could be explained as an adaptive anti-predator strategy (Montevicchi 1976; Solís and de Lope 1995; Yahner and Mahan 1996; Lloyd et al. 2000). This study provided partial support for egg crypsis in the near-ground-nesting yellowhammer, but further testing is needed.

For visually oriented predators, the major distinction between ground and shrub/canopy nests is that the former can be observed only from above, whereas the latter can be viewed from all directions. Because eggs in open-cup nests are visible only at some angle from above the nest, eggs (as compared to nests) are relatively more exposed in ground nests than in off-ground nests. Life history traits in birds covary with the intensity of nest predation, which differs markedly among nest sites, being generally less for ground nesters than off-ground nesters in woodland habitats (Martin 1995; Martin and Badyaev 1996). The available evidence suggests that the extent to which predators use egg coloration as a cue for locating nests may also differ between ground- and off-ground-nesting birds. This implies that the role of predation as a

selective force in the evolution of eggshell colour patterns varies not only between cavity-nesting birds and open nesters (Lack 1968) but also across nesting sites within the latter group.

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