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Smaller Eastern Olivaceous Warbler *Hippolais pallida elaeica* nests suffer less predation than larger ones

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Abstract. The "costs of predation" hypothesis predicts that larger nests are more likely to be predated than smaller ones. However, nest size has not been found to be related to predation probability within any species. This study evaluated the "costs of predation" hypothesis in the Olivaceous Warbler during 2001–2003 in northwestern Bulgaria. Successful nests were significantly smaller and denser than those that were predated. Nest size decreased significantly during the course of the breeding season and increased with nest height. The relationship between nest size and the likelihood of predation was still significant even when the effects of laying date and nest height were controlled. Nest size was negatively related to fledging success even when only successful nests were considered. This finding is contrary to the prediction of the "sexual display" hypothesis, which states that nest size is positively related to fledging success, and suggests that nest size may signal phenotypic quality through the ability in this species to build a small but compact nest. It seems that both natural selection and sexual selection have led to the evolution of small nests in the Olivaceous Warbler. This is the most likely reason why the difference in nest-size between predated and non-predated nests was apparent, even in unmanipulated settings.

Key words: Olivaceous Warbler, *Hippolais pallida*, nest size, breeding, nest predation, fledgling success

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INTRODUCTION

Avian nests are special constructions in which eggs and young develop (Soler et al. 1998b). Nest building has been viewed as a result of natural selection, and the nest has been considered an evolutionary compromise between benefits such as protection from adverse environmental conditions during incubation and early nestling stage, reduction in the energetic cost of incubation (Walsberg & King 1978, Sciurine & Kern 1980, Kern 1984), and costs such as energy expended in nest-building and predation risk (Slagsvold 1984, 1989, Lima 1987). Recently researchers have focused on nest-building and nest-size as sexually selected traits (Palomino et al. 1998, Soler et al. 1998a, 1998b, Soler et al. 2001, Fargallo et al. 2004).

Several non-exclusive hypotheses have been proposed to explain variation of nest size in birds. One of them, the "costs of predation" hypothesis, proposes that risk of predation is one of the most important constraints on nest-size (Collias & Collias 1984, Slagsvold 1989). Nest predation is considered the main selective force for the evolution of life history traits in birds as it accounts for 80% of nest losses on average (Martin 1992, 1993a). Thus natural selection should favour life history traits that reduce the negative effects of nest predation given the importance of reproductive success to fitness (Martin 1993b). Nest conspicuousness is related to risk of nest predation (Lack 1954), because larger nests are easier to detect for predators searching visually than smaller ones. Thus large nests appear to suffer more from predation than small nests (Snow 1978). Building larger nests also may impose risk of adult predation during nest-building phase (Collias & Collias 1984) as a large nest requires more trips by the building bird which can potentially attract attention of predators. However, predation rate in

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several studies on individual species did not differ in relation to nest size (Pikula, 1979, Slagsvold 1982, 1989, Soler et al. 1995, Palomino et al. 1998). Soler et al. (1998a) stated that although this cost of predation as a constraint of nest-size is logical, intraspecific variation in nest-size is not related to the risk of nest predation. Møller (1990) argued that it may not be possible to find a significant effect of nest predation on nest-size in an entirely observational study because the quality of the nest-site *per se* and/or bird quality may mask the effect of nest size on nest predation. Individuals building large nests are supposed to be better quality birds which may choose territories of superior quality containing more and better secured nest-sites. Furthermore, more experienced breeders may be better able to defend their nests from predators. Thus the positive relationship of nest size and bird quality and/or nest site quality and ultimately breeding success may hide the expected positive correlation of nest size and predation probability. In experiments with real Blackbird *Turdus merula* nests containing artificial eggs, Møller (1990) found that smaller experimental nests suffered significantly less predation than larger ones. However, in the same study, active Blackbird nests did not differ in size in relation to the probability of predation. Thus, the "costs of predation" hypothesis for variation in nest size has not been supported by observational data within any species.

In this paper, I studied nest-size variation in a small open-nesting passerine species with poorly known breeding biology (Cramp 1992), the Eastern Olivaceous Warbler *Hippolais pallida elaeica*, in a population in northwestern Bulgaria. The aim of this study was to evaluate the "costs of predation" hypothesis for variation in nest size. Accordingly, predated nests were predicted to be larger than those that escaped predation. The difference in nest size between predated and non-predated nests was considered in relation to nest height, laying date, clutch-size, hatching success and fledging success.

METHODS

The study was conducted during 2001–2003 in northwestern Bulgaria. The study area included 3 villages: Zlatia (43°46′N, 23°30′E), Gorni Tsibar (43°48′N, 23°32′E) and Ignatovo (43°46′N, 23°28′E). In northwestern Bulgaria, Olivaceous Warblers breed only within the boundaries of human settlements, and build their nests from 0.45 to 7.5 m above the ground, in shrubs, bushes, tall herbs, broadleaved and coniferous trees (own data). There is no agreement regarding the contribution of male in nest building in the Olivaceous Warbler (Cramp 1992). Males arrive earlier on the breeding grounds and often choose the nest-site by building more or less developed platforms of nest material, but females may choose another site later. In Egypt, males are recorded to build the entire nest alone, though this was not observed in other studies (Cramp 1992). Others state that females build most of the nest, while males may have variable, less important contribution (Dementiev & Gladkov 1954, Pashkovski 1965, Lebedeva 1993, A. Bachvarova unpubl., Author's data). It is likely that male contribution to nest building may indicate its future parental investment (Palomino et al. 1998).

Nests were searched for systematically within territories from mid May to late July, and were visited every 2–7 days after discovery in order to record breeding parameters such as laying dates, clutch size, number of chicks hatched and number of chicks fledged. Each nest was classified as successful (producing at least 1 fledgling) or unsuccessful (complete nesting failure) according to the outcome of the breeding attempt. Nest-size measurements were done as soon as the chicks fledged or the nest was predated. The height above the ground of most nests was also measured. Predated nests which were noticeably damaged were not included in the analyses.

Nest volume and nest cup volume were calculated according to the formula:

$$\text{Volume} = 4/3 \times \Pi \times a^2 \times b \times z,$$

where: a — smallest radius, b — largest radius, z — fraction of an ellipsoid = ½ for cup-shaped nests (Soler et al. 1998b).

The difference in nest volume and cup volume gave material volume (Soler et al. 1998b).

For most nests, mass was also recorded. For these nests, the density of the nest wall was calculated as the ratio nest mass/material volume (Palomino et al. 1998).

Nest volume was used as a measure of nest size in the analyses. The density of the nest wall served as an index of the compactness of the nest. Hatching success was defined as the number of chicks hatched controlling for clutch-size and fledging success — the number of chicks fledged, controlling for the number of chicks hatched.

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Only nests that were either successful or were depredated were included in this study as the study only concerned failures to predators. Thus the sample size comprised 59 nests for which nest-size measurements were available. However, sample sizes may vary slightly from analysis to analysis as data on some variables which were correlated to nest-size was not available for all nests.

Nest volume, nest mass and laying date were normally distributed. Nest height was not normally distributed, but after a log transformation, a normal distribution was achieved. Clutch size could not be normalized and was therefore used in non-parametric procedures.

Statistical analyses were performed using SPSS. 11.0. All tests are two-tailed. Means are reported with their standard deviations.

RESULTS

Of 59 nests used in this study, 20 (33.9%) were predated and 39 (66.1%) escaped predation and produced at least one fledgling. The great majority of losses to predation occurred at the egg stage (17 of 20, 85%).

Nest volume of Olivaceous Warbler nests varied from 64.3 to 175.9 cm³. The coefficient of variation was 20.3%. Predated and non-predated nests differed significantly in nest volume ($F_{1,53}$ = 7.54, p = 0.008). The effects of year ($F_{2,53}$ = 2.15, p = 0.13) and the interaction success x year ($F_{2,53}$ = 2.883, p = 0.065) were not significant. Successful nests were significantly smaller than unsuccessful ones (112.0 ± 21.03 vs. 128.4 ± 25.78 cm³). Nest volume was significantly and negatively correlated with the density of the nest wall (r = -0.68, p < 0.0001, n = 56). The density of nest wall similarly differed significantly between successful and unsuccessful nests (Mann-Whitney U-test, U = 162, p = 0.002). Successful nests were not only smaller but had denser walls, i.e. more mass per unit nest material volume. A MANOVA model including the two components of the nest wall density, i.e. material volume and nest mass as dependents and breeding outcome as a factor, showed that only the material volume differed significantly between successful and unsuccessful nests ($F_{1,54}$ = 7.87, p = 0.007). Nest mass was unrelated to the probability of predation ($F_{1,54}$ = 2.39, p = 0.13). Thus, differences in nest wall density between successful and unsuccessful nests were mainly due to variation in material volume.

Table 1. Multiple linear regression model of laying date, nest height and final success on nest volume.

Variable	B ± SE	β-weights	t	p
(Constant)	159.294 ± 14.325		11.120	0.000
Laying date	-0.793 ± 0.274	-0.351	-2.900	0.006
Nest height	9.969 ± 4.657	0.261	2.141	0.037
Success	-14.422 ± 6.217	-0.284	-2.320	0.024

A multiple linear regression model (Table 1) including laying date, nest height and success as independent variables and nest volume as a dependent was significant ($F_{3,50}$ = 6.64, p = 0.001, R^2 = 0.29). All the three factors were significant

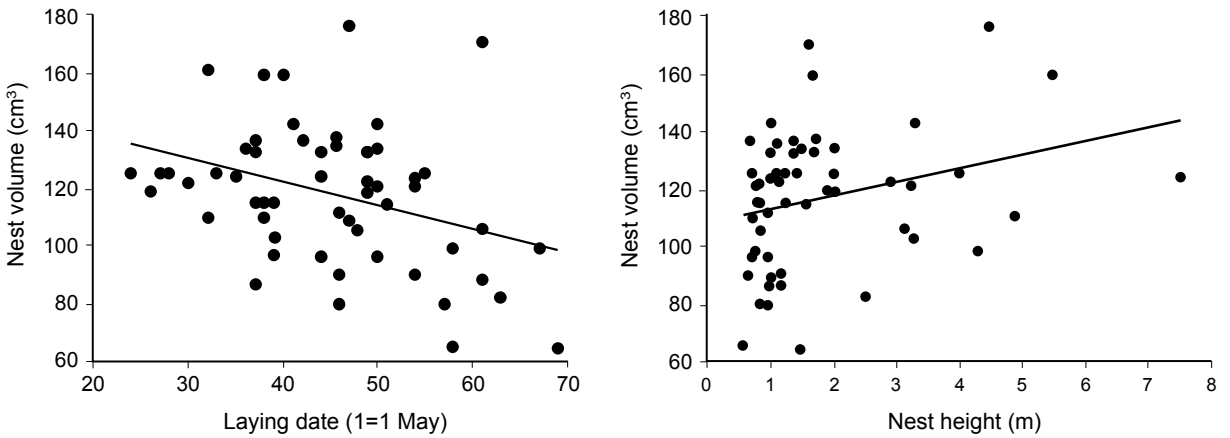


Fig.1. Relationships of nest volume with laying date (r = -0.362, p = 0.006, n = 56) and nest height (for log-transformed height: r = 0.336, p = 0.011, n = 57)

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and together explained 28.5% of variance in nest volume. Nest volume decreased with laying date and increased with nest height (Fig. 1). Nest height and laying date were not correlated (r = -0.076, p = 0.59, n = 54). Thus, nest volume differed significantly between successful and unsuccessful nests, even when laying date and nest height were controlled.

The probability of final success was unrelated to nest height and laying date (MANOVA, Pillai's trace = 0.016, F = 0.54, p = 0.59).

Clutch size was unrelated to nest volume (r_s = 0.17, p = 0.25, n = 49). It decreased significantly with laying date (r_s = -0.612, p < 0.0001, n = 49) but did not differ significantly between successful and unsuccessful nests (Mann-Whitney U-test, U = 202.5, p = 0.26). Hatching success was unrelated to nest size when either all nests with complete clutches were included irrespective of nest fate (Partial r = -0.06, p = 0.69, n = 46) or when predated nests were excluded (Partial r = 0.151, p = 0.37, n = 35). However, fledging success was significantly correlated with nest-size when all the nests irrespective of outcome were included (r = -0.61, p < 0.0001, n = 35). Moreover, considering only nests which produced at least 1 fledgling, nest volume was still significantly related to fledging success (Partial r = -0.347, p = 0.044, n = 32). Thus, smaller nests were associated with increased fledgling production. Fledging success was not related to laying date when either all nests were included (Partial r = -0.14, p = 0.32, n = 48) or when predated nests were excluded (r = 0.04, p = 0.82, n = 32).

Considering successful nests only, the number of fledglings was significantly and negatively correlated with nest height (Partial r = -0.36, p = 0.04, n = 31).

DISCUSSION

Nestling activity may cause expansion of the nest cup and/or nest volume (Palomino et al. 1998). Because nests that failed did not experience deformation due to nestling activity (most were predated at the egg stage) and successful ones were measured after nestlings fledged, the results would be biased to systematically greater nest-size for successful nests. However, nest volume was greater for unsuccessful nests, i.e. the reverse of what should be expected and therefore a possible bias due to nestling activity is excluded.

This study demonstrated differential nest size in relation to the probability of nest predation in Olivaceous Warblers, and provided support for "cost of predation" hypothesis. According to the prediction, nests that escaped predation were significantly smaller in size than predated ones, which suggests that there is a directional selection for small nest size in this species. This is the first study that demonstrated such a difference for real nests in unmanipulated settings at the intraspecific level. On the other hand, the difference in nest size between successful and unsuccessful nests could be due to some other factors correlated with both nest size and the probability of predation. The importance of laying date, nest height and fledgling success (as a correlate of individual quality) is discussed below.

Seasonal effects

Predation pressure may be stochastic or follow a seasonal pattern (Filliater et al. 1994, Burhans et al. 2002). If nest size decreases during the course of the breeding season, and predation rate also does so, the relationship between nest size and the probability of predation could simply reflect the seasonal decrease of both nest size and predation pressure. Nest volume decreased significantly with laying date but there was no indication, that predation pressure followed any seasonal pattern, as successful and unsuccessful nests did not differ in relation to laying dates. Therefore, seasonal patterns cannot explain the relationship of predation and nest-size.

Nest height

The risk of predation is related to nest height in some species (e.g. Jakober & Stauber 1981, Antonov & Atanasova 2002). The higher Olivaceous Warblers built the nest above ground, the larger the nest volume became. If predation pressure was increased for higher nests, then this might explain the positive association of nest size and predation probability. However, predation risk did not show any relationship with nest height as predated and non-predated nests did not differ in nest height, which makes such a possibility unlikely.

When the nest height and laying date were controlled, nest volume still differed significantly between predated and non-predated nests, indicating that selection for nest size works at any nest heights during any time of the breeding season. However, some other nest site and/or microhabitat variables potentially correlated with predation risk and nest size, not measured in this study, could be the primary cause for the relationship of nest size and breeding outcome.

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Individual quality

As both sexes participate in nest building (see Methods), nest-size variation may have a sexual selection component (Soler et al. 1998a, 1998b). Fledging success (the most important fitness correlate) was negatively related to nest volume, and this relationship persisted even when only nests that produced at least one fledgling were considered. Thus, smaller nests, which were in addition less likely to be predated, may be built by high quality individuals. This finding is contrary to the prediction of "sexual display" hypothesis (Palomino et al. 1998, Soler et al. 1998b) that nest size should be positively related with fledging success because only individuals in good condition are supposed to build large nests, as nest building is costly in terms of energy expenditure and predation risk (Zahavi 1987, Soler et al. 1998b). Thus, individuals building large nests should also be better parents and nest size may be considered as an indicator of the readiness of the builder(s) to invest in reproduction (Soler et al. 1998b). In the Olivaceous Warbler, however, nests may signal phenotypic quality of the builder through different characteristics. Successful nests were not only smaller but were also more compactly built as the analysis of density of nest wall showed. Building nests as compact as possible, i.e. concentrating a given amount of nest material in as little nest volume as possible, is likely a relatively difficult and demanding task which mainly experienced builders may accomplish. Given a constant mass of nest material, smaller nests are perhaps tighter and more resistant to destruction. Thus, the ability to build a small and compact nest may be a signal of quality of the building bird in this species. One nest site variable, nest height, was negatively related to fledging success (only non-predated nests considered) and positively related to nest-size. It seems that experienced birds build smaller and more compact nests nearer the ground, and enjoy reduced predation and higher fledging success. The fact that the relationship of nest size and predation risk was evident without controlling for bird quality and/or nest-site quality could be because natural selection and sexual selection both work in the same direction, i.e. towards smaller nest size.

Nest volume in Olivaceous Warblers varied dramatically compared with intraspecific variation in nest size found in other passerines (A. Møller, pers. comm.). There was still much unexplained variation (78.5%) even after the effects of laying date, clutch size and success were controlled. Nest placement in Olivaceous Warblers was very variable, and nests differed greatly in the degree to which they were supported from below, and in the number of branches participating in nest attachment (own unpubl. data). "Nest support hypothesis" (Collias & Collias 1984) predicts that nests having more support from below should be smaller than those with less support. Thus, it is possible that much of the residual variation in nest size might be explained by variation in nest support. However, data on nest support are unavailable in this study.

In conclusion, I found that larger Olivaceous Warbler nests were more likely to be predated than smaller ones in unmanipulated setting, suggesting a directional selection for smaller nest size. This might be because both natural selection (through nest predation) and sexual selection (small nests likely signal better parental quality) might have selected for small nest size. Future studies, experimentally manipulating nest-size and with proper control of nest site characteristics, would be valuable, to show if smaller nests are predated less often due to their size *per se*.

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STRESZCZENIE

[Czy wielkość gniazd wpływa na poziom drapieżnictwa gniazdowego u zaganiacza bladego?]

Celem pracy była ocena stopnia drapieżnictwa w zależności od wielkości gniazd u zaganiacza bladego. W założeniu przewidywano, że na ataki drapieżników narażone będą częściej duże gniazda niż małe. Wielkość gniazd zarówno tych, które splądrowały drapieżniki jak i tych, które pozostały nietknięte, porównywano w relacji z: wysokością na jakiej wisiało gniazdo, datą złożenia jaj oraz ich liczbą, liczbą piskląt wyklutych oraz podlotów.

Badania na 59 gniazdach przeprowadzono w latach 2001–2003 w płn-zach. Bułgarii. Stwierdzono, że około 40% z nich zostało zniszczonych przez drapieżniki, w większości na etapie złożonych jaj, a pozostałe 60% było nietknięte i opuściło je przynajmniej jedno pisklę.

Badania potwierdziły prawdziwość hipotezy — wykazały, że gniazda małe, o masywniejszych ścianach były znacznie rzadziej niszczone przez drapieżniki. Wielkość gniazd w trakcie sezonu lęgowego zmniejszała się, rosła natomiast wraz z wysokością na jakiej były umieszczcane. Zależność między wielkością gniazda i drapieżnictwem była stwierdzana również wtedy, gdy analizowano wyłącznie dane z gniazd, z których wyszło przynajmniej 1 pisklę.

Wśród zaganiaczy bladych najwięcej podlotów pochodziło z małych, gęsto i precyzyjnie skonstruowanych gniazd, bardziej odpornych na zniszczenie. A zatem takie gniazda mogłoby wskazywać na fenotypy najlepiej przystosowane, co przeczy hipotezie „sexual display", która zakłada pozytywną korelację pomiędzy wielkością gniazda a liczbą podlotów.

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