We documented and experimentally tested the use of snake skins in construction of nests in a Great Reed Warbler *Acrocephalus arundinaceus* population in southwestern Slovakia. There was no difference in predation rates of artificial nests that did or did not contain sloughs. We suggest that snake skins in Great Reed Warbler nests may serve as a post-pairing signal revealing female parental quality.

**Keywords:** Grass Snake, post-pairing signal, predator-deterrence hypothesis, social mating system.

Parents of the majority of birds construct nests to provide protection for their eggs and chicks. The choice of suitable nest material is an important prerequisite for successful breeding (Hansell 2000). Nest material may either have structural and physical functions or play a signalling role in mate attraction or deterrence of potential predators (Brouwer & Komdeur 2004, Schuetz 2005, Igic *et al.* 2009, Mennerat *et al.* 2009). Among other materials, several bird species incorporate snake skins in their nests (Strecker 1926, Medlin & Risch 2006). Two main explanations have been proposed for this behaviour; birds may use snake skins to deter nest predators (Bolles 1890, Strecker 1926), or snake skin provides a soft and pliable nest-building material (Hansell 2000). However, reliable experimental evidence for the predator-deterrence hypothesis is provided only by Medlin and Risch (2006).

The Great Reed Warbler *Acrocephalus arundinaceus* is an open-nesting passerine in which females build conspicuous basket nests in *Phragmites* reeds over water. Although it is a well-studied European species, to our knowledge there is no published information on its use of snake skins as nesting material to date (Cramp 1992, but see Jelínek 2010). In the present study, we documented use of snake skins as nest material in a Great Reed Warbler population in Slovakia, and conduct two experiments to assess whether snake sloughs found in nests in our study area were preferred nesting material and whether they might play a predator-deterrent role. First, we manipulated the presence of real snake sloughs in the vicinity of Great Reed Warbler nests during their nest-building period. If sloughs are preferred by females, we expected to find them in the majority of these nests. Secondly, we assessed the predator-deterrent hypothesis by performing an experiment with abandoned Great Reed Warbler nests. If snake skins function as an anti-predatory material in Great Reed Warbler nests, we predicted that nests with sloughs would be predated less frequently than control nests.

**METHODS**

The study was conducted at fishponds near Štúrovo, southwestern Slovakia (47°51’N, 18°36’E, 115 m asl). The frequency of use of snake skin material was investigated in 2009. At the end of the breeding season we collected all completed Great Reed Warbler nests to inspect them for snake skins. As the Grass Snake *Natrix natrix* is the only species occurring in the study area, sloughs found in Great Reed Warbler nests were assumed to come only from this species.

The first experiment was performed between 10 May and 4 June 2010. During this period, we systematically searched for Great Reed Warbler nests at 3- to 5-day intervals to detect them during the nest-building period. We placed one 15-cm-long and 2-cm-wide piece of slough of the Corn Snake *Elaphe guttata* obtained from snake breeders and one tan cotton ribbon (as a control) of the same size and colour as Corn Snake skin at 20 cm distance from each found nest. The length of experimental skins was standardized on the basis of actual lengths of Grass Snake sloughs found in natural Great Reed Warbler nests in 2009 (mean ± se: 14.6 ± 0.85 cm, \( n = 28 \)). The nests were first checked 2 h after the experiment was started and thereafter once per day. Observations at a nest were terminated if both snake slough and ribbon were found in the nest structure, or if the nest was completed. The fate of each slough and ribbon and their positions in the nest were subsequently documented by analysing nest material of nests.

The second experiment started on 15 July 2010, at the end of the Great Reed Warbler breeding period. We used 60 abandoned or predated Great Reed Warbler
nests, each baited with three plasticine-filled mimic eggs. Twenty nests were fringed with a $25 \times 2 \text{ cm}$ piece of Corn Snake slough, 20 nests were fringed with cotton ribbon of the same size as the slough (control 1) and 20 nests had neither slough nor ribbon (control 2). Nest height, outer width and depth of the nest cup did not differ between the three types of nests (ANOVA, $F_{2,57} = 0.25$, 2.03 and 0.66, $P = 0.78$, 0.14 and 0.52, respectively). The nests were distributed alternately along a linear transect at the reed–water edge ($0.5$–$1 \text{ m}$ from open water) in the south part of the largest pond. The distance between neighbouring nests was $30 \text{ m}$. Each nest was attached with a green fine wire to the reed stems at a height of $1 \text{ m}$. Due to the high predation rate of artificial nests compared with natural Great Reed Warbler nests (Trnka et al. 2009), artificial nests were exposed for 7 days only. A nest was considered to have been predated if any of the mimic eggs were missing or appeared damaged. Predators were identified on the basis of peck marks left on the plasticine. The typical shape of marks allowed us to distinguish three categories of predators: large birds (large triangular bill marks), small birds (small triangular bill marks) and small mammals (incisor marks).

As nest success in this species may correlate positively with nest concealment and nest location (Hansson et al. 2000), we also measured the following nest-site characteristics for each artificial nest: number of all reed stems within a $0.5 \times 0.5 \text{ m}$ square with the nest in the centre, height and diameter of 10 randomly chosen stems in each square, and distance from the nest to the open reed–water edge.

Differences in means between groups were analysed by one-way analysis of variance (ANOVA). Differences in nest predation or in the use of snake skins between treatments were compared with Pearson’s chi-squared test ($\chi^2$). If at least one of the cells contained a value $\leq 5$, Fisher’s exact test was used. Bonferroni corrections were applied when the same data were tested more than once and the critical alpha value was adjusted accordingly. To test the effect of independent variables on nest predation (predated vs. not predated), we used multiple logistic regression. All statistical tests were two-tailed.

RESULTS

Grass Snake sloughs were found in $33.8\%$ of 68 natural nests collected in 2009. The skins were present only in the body of the nest, never in the lining. They were woven in with other nest material and looped over reed stems that support the nest. Experimental Corn Snake sloughs were used in $63.3\%$ of 49 nests tested during the nest-building period in 2010, whereas cotton ribbons were present in only $10.2\%$ of nests; this difference was statistically significant (Fisher’s exact test, $P < 0.001$). In all cases in which ribbons were used, snake skins were also used. These cases were excluded from subsequent analyses. The use of Corn Snake sloughs differed significantly between nests of different nest-building stages (Pearson’s $\chi^2 = 29.46$, df = 2, $P < 0.001$). Although no differences were found between just started and partially built nests (Fisher’s exact test, $P = 0.54$), snake skins were used markedly less frequently in the nests that were tested in the late stage of building (Fig. 1; Fisher’s exact tests, both $P < 0.001$, Bonferroni corrected alpha = 0.016).

Altogether, 18 (30%) of 60 artificial nests were predated during the 7-day exposure period of the second experiment. However, there were no differences in nest predation between the three types of nests (multiple logistic regression, Wald $\chi^2 = 3.35$, df = 2, $P = 0.19$; Fig. 2). Nest predation was not significantly influenced by microhabitat variables (density and height of reed stems and distance from water, Wald $\chi^2 = 2.90$, 2.91 and 0.03, $P = 0.09$, 0.09 and 0.87, respectively). Based on peck marks left on the plasticine content of eggs, 11 of 17 identified nest predators were large birds, and the others were small birds (four) and mammals (two).

DISCUSSION

Nearly one-third of Great Reed Warbler nests in our study area contained one or more pieces of Grass Snake sloughs. As far as we know, this is the first published study to document the use of snake skins in this species. This is somewhat surprising considering the long-term interest of scientists in this species (more than 90 papers...
on the Great Reed Warbler have appeared in the last two decades, *Web of Science*, January 2010). We suppose that this may result from either little attention paid to construction of Great Reed Warbler nests or from absence of snake sloughs in other studied localities. More speculatively, the use of this ‘atypical’ material in our study population may be innovative behaviour (Antczak et al. 2010). To elucidate this, however, other studies of different populations covering the distribution range of this species are needed.

The experiment with Corn Snake sloughs indicates that snake skins may be commonly used by Great Reed Warblers as a nest-building material in our study population. The majority of females that were tested in the early stages of nest building immediately detected and incorporated experimental skins into the nest structures. Furthermore, all sloughs found in nests during the first 2 h of the experiment were wet and woven in with other nest components, suggesting that females moistened them before their incorporation into the nest structure, as they do with other nest-building materials (Kluyver 1955). Such manipulation indicates a structural function of snake sloughs in Great Reed Warbler nests.

The nest predation experiment did not support the predator-deterrence hypothesis. Generalization of these findings is, however, limited by the use of experimental sloughs from an exotic snake species and other constraints of our experimental design including the placement of used nests by human observers. Because of these limitations and potential biases of nest experiments (e.g. Moore & Robinson 2004, Trnka et al. 2008), and our timing of the experiment when the main Great Reed Warbler nest predators might switch their hunting area or have functional shifts in diet, we cannot completely reject the predator-deterrence hypothesis based on this experiment (Strecker 1926, Medlin & Risch 2006). Further experiments with natural nests following general recommendations for experimental design (e.g. Hurlbert 1984) would be useful to test both assumptions in the future.

Finally, we propose a new explanation for why Great Reed Warblers use snake skins in their nests. Because snake sloughs are a relatively rare material in marsh habitats, we hypothesize that the ability of females to find them and incorporate into the nest structure may serve as a post-pairing signal revealing their parental quality (Soler et al. 1998, Schuetz 2005). A similar positive relationship between quality of parental care and nest size has already been found in this species (Avilés et al. 2009). Because the Great Reed Warbler is a facultatively polygynous species, and socially polygynous males are known to provide differential parental care to their females (Cramp 1992, Trnka & Prokop 2010), the hypothesis seems plausible in the context of the social mating system. The results of the first experiment may accord with this hypothesis, as snake skins were mainly incorporated early in the nest-building process when such a signal may be most effective in terms of female competition for harem status. We hope that this new perspective on the function of snake skins in bird nests will stimulate further research in this area.

We thank P. Procházka and M. Požgayová for helpful suggestions on early drafts of the manuscript. The comments of two referees and K. Tarvin substantially improved the manuscript. The study was supported by the Slovak Grant Agency for Science VEGA, project No. 1/0566/09.

**REFERENCES**


Received 4 November 2010; revision accepted 28 February 2011.

Associate Editor: Keith Tarvin.