ARTICLE

Why do grebes cover their nests? Laboratory and field tests of two alternative hypotheses

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Abstract Egg predation is a common feature influencing the reproductive success of open nesting birds. Evolutionary pressure therefore favours building cryptic, inconspicuous nests. However, these antipredatory pressures may be in conflict with thermoregulatory constraints, which select for dry nest material maintaining optimum temperature inside a nest cup during the absence of incubating parents. Here we examined possible trade-offs between nest crypsis and thermoregulation in Little Grebes (*Tachybaptus ruficollis*), which lay their eggs in floating nests built from wet plant material. As this species regularly covers its eggs with nest material, we experimentally examined (1) the rates of egg predation on covered and uncovered artificial nests and (2) possible thermoregulatory costs from nest covering by comparing temperature and relative humidity changes inside the nest cup. Results revealed that covering clutches is beneficial in terms of deterring predators, because uncovered eggs were more vulnerable to predation. Moreover, covering clutches also had thermoregulatory benefits because the mean temperature and relative humidity inside nest cups covered by dry or wet materials were significantly higher for covered compared to uncovered treatments. Covering clutches in Little Grebes therefore does not pose thermoregulatory costs.

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Introduction

Nest building has been a typical feature of the biology of birds since their origin and has had a key role in shaping the relationship in bird reproduction between parents and offspring (Hansell 2000). The sole function of nest building is maintaining conditions for developing embryos or young, and/or protecting the eggs during incubation (Montgomerie and Weatherhead 1988; Healy et al. 2008).

Because nest predation is a major factor influencing breeding success of open-nesting birds (Ricklefs 1969; Martin 1992), there should be selective pressures for birds to make nests less vulnerable to predation. Parent birds can actively defend nests against nest predators (Montgomerie and Weatherhead 1988) or make the nest visually cryptic (Kreisinger and Albrecht 2008; Opermanis 2004) thereby reducing nest predation rates (Cresswell 1997). Accordingly, thermoregulatory constraints should select for nest construction that influences temperature inside the nest (Franklin 1995; Szentirmai et al. 2005; Mayer et al. 2009).

Nest crypsis (cryptic colouration of parents or eggshells, or a specific type of nest construction) has been considered an effective anti-predation strategy (Collias and Collias 1984; Collias 1997; Hansell 2000). Nests may contain non-structural cryptic material (Hansell 1996; Schuetz 2005), can be placed in less visible microhabitats (Martin 1992, 1993; Clark and Shutler 1999; Flaspohler et al. 2000; Martin et al. 2000; Albrecht and Klvaňa 2004; Weidinger 2004; Colombelli-Negrel and Kleindorfer 2009) or clutches in the nests can be covered by nest material or down (Mickelson 1975; Summers and Hockey 1981; Götmark

and Ahlund 1984; Salonen and Penttinen 1988; White and Kennedy 1997; Kreisinger and Albrecht 2008).

It has been proposed that, in some birds, covering clutches evolved through antagonistic coevolution between sexes (Valera et al. 1997; Low 2004), but the majority of research shows evidence that clutch covering reduces nest predation and thus was selected by natural selection. For example, chickadees, titmice, and other parids that cover their eggs with nest material during the day prior to incubation may significantly reduce the danger of egg destruction by House Wrens (*Troglodytes aedon*) (White and Kennedy 1997). Vacca and Handel (1988) showed that uncovered nests of Cackling Canada Geese (*Branta canadensis minima*) suffered almost twice the rate of predation as nests in which eggs were left covered with goose down. Similarly, Salonen and Penttinen (1988) found that uncovered clutches of Great Crested Grebes (*Podiceps cristatus*) were more vulnerable to predation by crows.

Although these examples clearly show that nest covering is beneficial in terms of reducing the risk of predation, costs associated with covering clutches are almost unknown. The aim of this study was to test whether clutch covering by parents reduces nest predation (nest predation hypothesis) and how clutch covering influences thermoregulation (thermoregulation hypothesis) in Little Grebes, a non-passerine bird that constructs floating nests of plant material concealed among reeds on the surface of the water. Both parents incubate the eggs and regularly cover them up with wet nest material when they leave their nest. When incubating, the cover is removed (Cramp and Simmons 1977; Glutz von Blotzheim et al. 1987).

We predicted that (1) clutches covered by nest material make eggs less visible to visual predators compared to open, uncovered clutches. However, because wet nest materials (especially wet down) cause more rapid egg cooling rates (Hilton et al. 2004), covering clutches in Little Grebes may pose serious thermoregulation costs. We therefore predicted that (2) cooling rates of air inside the nest cup would be more rapid when clutches are covered with wet nest material compared to open nests or nests experimentally covered by dry material. The relative humidity, in contrast, is expected to be higher under conditions with covered compared to uncovered clutches.

Methods

Collecting nest materials

The nests of Little Grebes were sought systematically at the beginning of June 2008 in various fishponds in western Slovakia. Immediately after chick hatching, ten nests were collected and stored in PVC bags. Similarly, covering materials from six active nests were cautiously removed and maintained individually in PVC sacks. To minimize disturbance of nests, remaining clutches were covered by nest material directly from the side of the nests. Fresh-weight of nests (range: 5.2–8.0 kg, mean = 6.44, SE = 0.58, N = 10) and nest coverings (range: 23.13–38.25 g, mean = 31.66, SE = 1.99, N = 6) was subsequently recorded in a laboratory. Nest covers were then dried (all were exposed for 48 h at 60°C) and weighed on an electronic balance (range: 4.47–6.16 g, mean = 5.42, SE = 0.19, N = 6).

Because the main part of nests of Little Grebes floats under the water surface, it seems unlikely that these parts directly contribute to thermoregulation or visual properties of eggs in the nests. Moreover, the weight of nests was highly variable, mainly depending on water depth (A. Trnka and P. Prokop, unpublished data). To standardise the amount of nest material in all experiments, we used only 1 kg of wet material removed from upper parts of each collected nest (N = 10). This nest material (used later in the artificial nests experiment) is in close contact with incubated eggs, thus most appropriate for examining its role in thermal and visual protection of eggs.

Laboratory experiment

The laboratory experiment was conducted between 23 and 27 June 2008. The 1-kg masses of nest material (upper parts of nests, see above) from ten Little Grebe nests were placed into plastic mesh bags (mesh diameter 25 cm). Artificial nests with moulded nest cups of the same internal diameter and depth were maintained for 48 h under laboratory conditions with standard temperature of 30°C. To simulate real climatic conditions inside a nest cup, five unfertilized Quail *Coturnix coturnix* eggs were placed in the center of each artificial nest. The eggs were stored wrapped in polythene at 4°C during the 5-day period of experiments; the wrapping minimised water loss from the eggs. Prior to cooling-rate experiments, eggs were warmed in a poultry incubator for ~1 h to a constant 37 ± 1°C following Hilton et al. (2004). The thermocouples placed at the bottom of the nest cup and connected to datalogger (hygrochron DS1923) connected to a laptop computer, enabling real-time temperature display.

A complete set of nesting material with eggs was placed in the refrigerator with standard air temperature (8°C). As nest material cooled, the temperature and relative humidity inside the nest cup were measured every 2 min for a 74-min cooling period.

The same eggs and nests were used in three experimental treatments: uncovered eggs (control), eggs covered by wet nest material (experiment 1) and eggs covered by dry experimental material (experiment 2). One-way

ANOVA did not find any differences in mean length ($F_{4,40} = 1.72$, $P = 0.11$), width ($F_{4,40} = 0.92$, $P = 0.52$) or mass ($F_{4,40} = 0.93$, $P = 0.51$) of Quail eggs between the three treatments.

Nest covering was standardised according to weights found under natural conditions; wet and dry nest coverings weighed 31.70 g (SE = 0.27, $N = 10$) and 5.40 g (SE = 0.21, $N = 10$) respectively.

Field experiment

The field experiment was conducted at the end of the breeding season at ponds near Trnava, SW Slovakia (48°21′N, 17°33′E), where visually oriented avian predators (especially marsh harriers, *Circus aeruginosus*) cause the majority of nest losses. Five ponds extend over an area of about 60 ha and are surrounded by large areas of water and terrestrial reed beds containing common reed (*Phragmites australis*) and reed mace (*Typha angustifolia* and *T. latifolia*). The ponds have a stable water level during the breeding period due to management in this protected area. Artificial nests ($N = 30$, 10 for each of three treatments) for the field experiment were constructed similarly to the nests used for the laboratory experiment. The 1-kg masses of nest material were placed on polystyrene panels (40 × 40 cm) and fixed to the surrounding vegetation (mainly to stems of reed mace, *T. angustifolia*). Based on realistic densities and distances between nests of Little Grebes in our study area (0.14–0.30/ha, Trnka 1999), 15 artificial nests (5 for each of the three trials) were placed in each of two ponds. Each artificial nest was baited with five fresh Quail eggs; only white eggs that visually resemble eggs of Little Grebe were selected. The nests were distributed alternately along linear transects at the reed-water edge (0–5 m from open water). The distance between neighbouring nests was 15 m.

Experiments using artificial nests increase natural nest densities, which may draw predators and lead to an artificial increase in predation rates (Hoi and Winkler 1994; Schmidt and Whelan 1999). However, we assumed that densities enhanced by artificial nests in our study did not alter nest predation rates significantly, since experiments based on much larger differences in other ground-nesting birds, such as ducks, show no consistent effect of nest densities on nest predation (Ackerman et al. 2004). Furthermore, we controlled for these confounding factors by starting the experiment after the peak of breeding activity and by respecting natural nest densities (see above) of Little Grebes in our study area (Trnka 1999). Artificial nests were set up on 2 July 2008 and exposed for 4 days only, due to high predation rate observed during first inspection on 6 July 2008. A nest was considered predated if any of the eggs were missing or appeared damaged.

Statistical analyses

Repeated measures ANOVA (with treatment as categorical predictor) was used because the sample of nests was exposed to the same conditions in turn, which means that the measurement of the dependent variable is repeated. Using a standard ANOVA in this case is not appropriate because it fails to model the correlation between the repeated measures. Our procedure followed similar design of Hilton et al. (2004). Field data were compared by Fisher's exact test because the expected values in some cells of a contigency table were below 5 (Agresti 1992).

Results

Laboratory experiment

Repeat-measures ANOVA revealed an effect of treatment on mean temperature inside the nest cup among three types of the nests ($F_{2,108} = 11.83$, $P < 0.001$). Figure 1 shows that the mean temperature was highest in nests covered by wet or dry nest material, while the mean temperature of uncovered nests was lowest. Somewhat unexpectedly, the effect of individual nests also significantly influenced results ($F_{9,972} = 150.22$, $P < 0.001$).

Mean relative humidity inside nest cup was highest in nests covered by wet material, followed by nests covered by dry material. Open nests had lowest relative humidity (repeat-measures ANOVA, $F_{2,108} = 406.84$, $P < 0.001$, Fig. 2). Relative humidity significantly differed among individual nests ($F_{9,972} = 316.42$, $P < 0.001$).
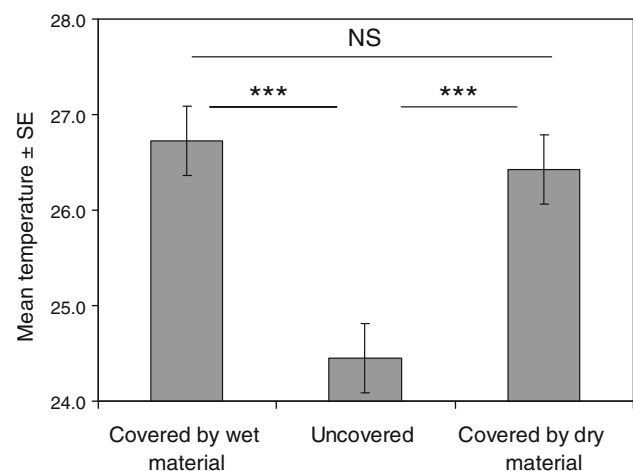

Fig. 1 Differences in mean temperature inside a nest cup (°C) among three types of nests. *P* values are based on Tukey post hoc comparison of mean (***P < 0.001, *NS* not significant)
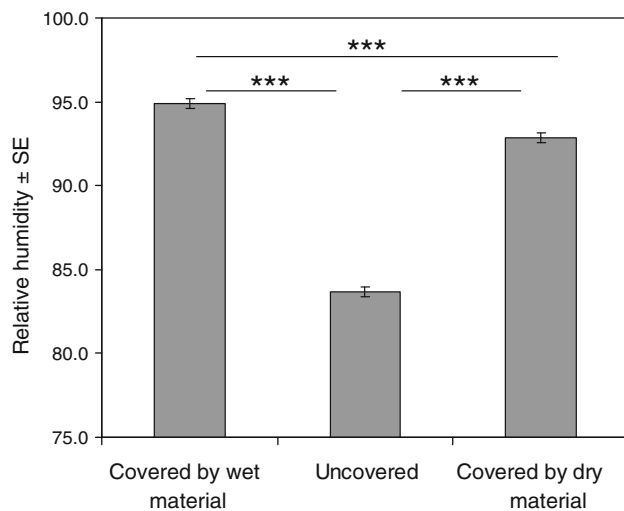
Fig. 2 Differences in mean relative humidity inside a nest cup (%) among three types of nests. *P* values are based on Tukey post hoc comparison of means (***$P < 0.001$)

Field experiment

Most of the open nests were predated (7 of 10) during 4 days of exposure. In contrast, nests concealed by wet (1 of 10) or dry material (1 of 10) were predated least and at an identical frequency. We therefore pooled data from the latter two groups of concealed nests and compared nest predation with open nests. The difference between covered and uncovered nests was significant (Fisher's exact test, $P = 0.002$), favouring a lower rate of nest predation of covered nests.

Discussion

Our data showed that covering clutches with nest material in Little Grebes is beneficial in terms of deterring visual predators as well as maintaining optimum temperature and humidity conditions for eggs inside a nest cup. Results of this study are based on both laboratory and field experiments and, as far as we are aware, no study examined these hypotheses simultaneously in a single species up to date. Two hypotheses were explicitly tested.

First, the thermoregulation hypothesis states that cooling rates of air inside a nest cup will be more rapid when clutches are covered by wet nest material. This hypothesis was not supported. Our study showed that covering clutches with wet material is most probably beneficial for developing embryos because cooling rates of air inside the nest cup were lower in the presence of covering material. Dry material showed similar thermoregulatory properties as wet material. In contrast, nest cups in open nests had the

lowest mean temperature. At first glance, these results look surprising because previous research has shown that wet material is associated with higher egg cooling rates (Hilton et al. 2004). However, Hilton et al. (2004) tested materials used for nest construction by terrestrial birds, not water-birds. We suggest that covering nests with wet material may have similar (although not the exactly the same) thermoregulatory benefits as burying eggs in the mounds of decaying vegetation by megapodes (Megapodiidae) (Jones et al. 1995). Saprogenic processes caused by bacterial activity in such an incubation environment result in increasing temperature which is beneficial for maintaining the appropriate temperature for incubated eggs. Additionally, the water body might also have a microclimatic function because the water temperature is more stable over the course of the day than the air temperature. Thus, the microclimate in natural nests of grebes may have more stable properties than samples of nests measured under laboratory conditions. Water temperature might influence the thermoregulatory properties of nest cups under natural conditions. In turn, an association between covering eggs by parents and water temperature needs to be examined.

Interpretation of these results may be partially limited because the temperature was measured inside the nest cup only, rather than directly on the egg surface (Hilton et al. 2004) or with a thermistor embedded in the eggs (Szentirmai et al. 2005), which seem to be more powerful approaches than measuring temperature changes of the air in the vicinity of the eggs. However, it is generally known that egg temperature depends on the surrounding environment and therefore changes in the air temperature immediately surrounding the eggs should predict also egg cooling rates. Moreover, the cooling rate of the eggs may be influenced by other variables such as the number of eggs in the nest, their dimensions, thickness and porosity of eggshells, and nesting stage. Thus, we are confident that our measures provide a close to realistic view of thermoregulatory processes in the nest.

An alternative possibility for nest building behaviour is that clutch covering may regulate incubation temperatures (Mayer et al. 2009). This explanation seems less likely, however, because Little Grebes breed in shady habitats unexposed to direct sunlight (Cramp and Simmons 1977).

Second, the predation hypothesis states that open nests suffer greater predation risk. This hypothesis was fully supported by the field experiment with artificial nests; open nests were more vulnerable to predation compared to nests covered by dry or wet nest material. We suggest that Marsh Harriers in particular are responsible for egg losses, because waterbirds (Underhill-Day 1985), as well as their eggs (Kreisinger and Albrecht 2008), are known to be important parts of their diet. However, Eurasian

Coots (*Fulica atra*) are also suspected of egg crushing. They are known to be aggressive toward other birds especially during breeding season (Cave et al. 1989) and to destroy eggs intentionally (A. Trnka, pers. obs.). Moreover, the species was highly abundant in our study area. Thus, our results extend current knowledge regarding the adaptive significance of covering clutches by birds and agree with research conducted on other bird species (Götmark and Ahlund 1984; Salonen and Penttinen 1988; Vacca and Handel 1988; White and Kennedy 1997; Kreisinger and Albrecht 2008). The importance of covering clutches is particularly significant for grebes, whose eggs are especially conspicuous within the first few days after egg laying (the colour changes from white to brown). Hence, the eggs of Little Grebes probably do not serve a cryptic function (see Kilner 2006). Similarly, the white colour of the eggs does not influence egg predation rates on artificial nests of the closely related Great Crested Grebes (Salonen and Penttinen 1988). In agreement with Götmark (1993) we suggest that evolutionary pressures in this species particularly favour overall nest crypsis, but not egg crypsis.

Future research should be focused on egg covering behaviour under natural conditions as well as on measuring thermal conditions of covered and uncovered clutches using real Little Grebe's eggs. Regarding the former, it is questionable whether grebes always cover their clutches or whether this behaviour is restricted to the presence of a predator. For example, White-fronted Plovers (*Charadrius marginatus*) cover their eggs only when incubation is interrupted by an approaching human, but not before other interruptions in incubation (Summers and Hockey 1981). In this case, it would be suggested that covering eggs primarily evolved as an antipredator strategy. Primary selective forces responsible for clutch covering in grebes therefore require more direct observations (e.g. measuring relationships between clutch covering behaviour and predator abundance) and experiments in the field. Regarding the latter focus of future research, we cannot rule out the possibility that thermoregulatory properties of Little Grebes' eggs are different than terrestrial birds such as quails. Furthermore, cooling rates should be compared inside eggs or at least on the egg surface (e.g. Hilton et al. 2004; Szentirmai et al. 2005). Examining thermoregulatory relationships using the above described way in the laboratory and field conditions would shed more light on a possible evolutionary origin of clutch covering by grebes.

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