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ARTICLE

Dynamic risk assessment: does a nearby breeding nest predator affect nest defence of its potential victim?

Alfréd Trnka · Tomáš Grim

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Abstract There is growing evidence that birds are able to discriminate different types of nest intruders and adjust their nest defence behaviour according to intruder dangerousness and distance from the nest (the dynamic risk assessment hypothesis). Here, we tested whether birds' decisions about nest defence may additionally be affected by an increasing familiarity with a particular nest predator. We tested nest defence responses of great reed warblers *Acrocephalus arundinaceus* to a nest predator, the little bittern *Ixobrychus minutus*. Great reed warbler nests located close ($\leq$7 m) to synchronously breeding little bitterns were "neighbour", other nests were "solitary". Great reed warbler specific aggression towards a little bittern dummy was much lower ($\sim$5-times) at neighbour than solitary nests. In contrast, generalised responses to a control innocuous intruder (the turtle dove, *Streptopelia turtur*) were statistically identical at neighbour and solitary nests. These patterns are in line with dynamic risk assessment hypothesis. We hypothesise that decreased great reed warbler aggression at neighbour nests also represents a specific behavioural adaptation to nesting in association with the little bittern. Little bitterns breeding closer to great reed warblers showed decreased risks of failure due to predation. However, further research is needed to experimentally test the causal links behind these patterns.

Keywords *Acrocephalus arundinaceus* · *Ixobrychus minutus* · Nest predation · Nesting association

Introduction

Perception of predation risk is an important factor influencing many aspects of behavioural decision-making in birds (Lima 2009). Decisions made about nest defence are considered to be crucial for birds' fitness (Montgomerie and Weatherhead 1988; Caro 2005). Active nest defence can markedly increase the chance of offspring survival, but it also entails high costs for defenders in terms of time and energy expenditure and injury or death caused by predators (Montgomerie and Weatherhead 1988). Moreover, nest defence behaviour may draw the attention of other predators and, paradoxically, increase the risk of nest predation (Krams et al. 2007; Grim 2008). Therefore, parents should take into account these costs when deciding whether and how intensively to defend their nest. If the nest intruder does not represent an immediate threat to the nest, it is more advantageous to nest owners to refrain from aggressive behaviour and instead stay hidden and monitor the intruder's activity around the nest (Kryštofková et al. 2011). Such behaviour enables birds to reduce the energy costs of unnecessary aggressive interactions and avoid attracting other nest predators (Polak 2013).

For parents to make the right decisions, the critical prerequisite is the recognition of a nest predator and the actual threat that it poses to the nest contents and adult birds (Curio et al. 1983; Caro 2005; Grim 2005). There is increasing evidence that birds are able to discriminate among different types of nest intruders, especially between nest predators and harmless

A. Trnka (✉)
Department of Biology, University of Trnava, Priemyselná 4,
918 43 Trnava, Slovakia
e-mail: atrnka@truni.sk

T. Grim
Department of Zoology and Laboratory of Ornithology, Palacký
University, 17. listopadu 50, 771 46 Olomouc, Czech Republic

animals, and adjust their nest defence behaviour according to their dangerousness and distance from the nest (dynamic risk assessment hypothesis; Kleindorfer et al. 2005; Kryštofková et al. 2011; Strnad et al. 2012). However, other ways in which birds may assess the immediate risk of nest predation are still little known. Previous studies have shown that the intensity of nest defence varies with the distance from the nests of avian predators, particularly sparrowhawks *Accipiter nisus* (Rytkönen and Soppela 1995), suggesting that birds may change their defence behaviour according to familiarity with the predator of adult birds. However, our literature search did not reveal any study of analogous familiarity effect for the predators of eggs and nestlings.

We investigated aggression of great reed warblers *Acrocephalus arundinaceus* towards a taxidermic dummy little bittern *Ixobrychus minutus* at great reed warbler nests with or without synchronously breeding little bitterns nearby. These two species often nest close together in our study site (as also seen in other localities, e.g., Samraoui et al. 2012). The great reed warbler (~30 g) is a highly aggressive passerine species that strongly attacks any intruders near its nest (Kleindorfer et al. 2005; Honza et al. 2010; Trnka and Prokop 2010, 2012). The little bittern, on the other hand, is a small (~150 g), secretive and very shy heron that predates nests of other birds nesting in reed habitats (Hudec 1994; Leisler and Schultze-Hagen 2011, p. 153). In our study area, it is responsible for about 18 % of great reed warbler nest failures (Trnka et al. 2010). Thus, great reed warblers should perceive little bitterns as a potential threat to their nests and show aggressive behaviour towards them.

Birds show two types of nest defence (Sealy et al. 1998). Generalised nest defence (or background aggression; Grim 2005) is directed towards any intruders near the nest and represents a general non-specific response to any disturbance caused by any animal near the owner's nest (Neudorf and Sealy 1992). Specific nest defence is directed specifically to particular enemies (brood parasites, predators, competitors) and adjusted to the specific risk they pose to the nest owners themselves or their progeny within the given ecological context (Ghalambor and Martin 2001). Based on dynamic risk assessment hypothesis (Kleindorfer et al. 2005), we predicted that (1) generalised nest defence by great reed warblers (i.e., aggression against non-specific intruder, the turtle dove *Streptopelia turtur*) will be independent of the presence or absence of a little bittern nest near the focal great reed warbler nest, whereas (2) specific nest defence against little bitterns will be significantly decreased when this heron breeds in the immediate vicinity of the focal great reed warbler nest.

Materials and methods

General field procedures

Fieldwork was carried out at a fishpond system near Štúrovo (47°51′N, 18°36′E, 115 m a.s.l.), south-western Slovakia, in May–July 2012 and 2013. For a detailed description of the study area, see Trnka and Prokop (2010). In the study years, the great reed warbler population consisted of 40–50 breeding pairs, while the little bittern breeding population comprised 15–20 pairs. All tested great reed warblers were marked with individually unique combinations of colour rings, and each individual/pair was tested only once (all tested nests were first broods, i.e. we did not test any replacement or second broods). Warblers were mist-netted during the incubation stage which enabled the sexing of each bird based on the presence/absence of a brood patch. Both great reed warblers and little bitterns breed here in narrow strips of reeds, *Phragmites australis*, surrounding the fishponds.

To locate great reed warbler and little bittern nests, we systematically searched the reedbeds and checked the vegetation at 4- to 5-day intervals. Distances between the nests were measured directly in the field with a tape measure (rounded to the nearest meter), and the position of each nest was determined with Garmin GPS. Altogether, we found 25 little bittern nests and 78 great reed warbler nests. Synchronised nests (i.e., when there was an overlap between nest building, egg laying, incubation or nestling stages of great reed warbler and little bittern) of one species located ≤7 m from nests of the other species were classified as "neighbour", other nests as "solitary" (Fig. 1). We used 7 m as a cut-off point because it represents the known average maximum distance at which great reed warblers in our study population aggressively protect their own nests, i.e. the majority of pairs in our study area defend their nests up to 7 m from their nest (A.T., personal observation). Importantly, our conclusions remained the same when we changed the cut-off point to 5 or 9 m distance (see "Results").

Dummy experiments

Overall, we took care to follow previously established standard protocols of experimental design and data analyses recommended for nest defence and enemy recognition studies (Neudorf and Sealy 1992; Sealy et al. 1998; Grim 2005, and references therein).

We tested great reed warbler responses to taxidermic dummies of the little bittern and the turtle dove as a control. The latter was chosen because it is a sympatric harmless species being neither a predator nor a brood parasite and does not compete with great reed warblers either for food or nest sites (Grim 2005). It is also similar in

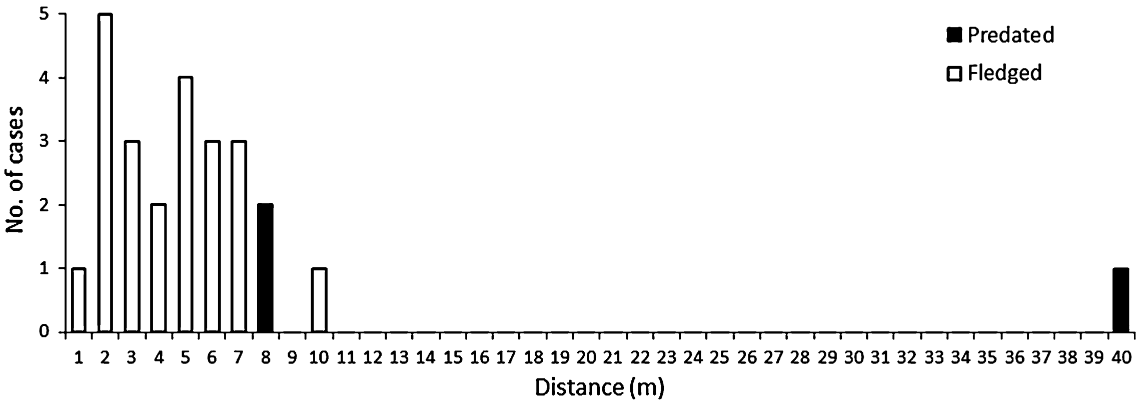

Fig. 1 Distribution of little bittern *Ixobrychus minutus* nests in relation to nearest synchronous neighbour great reed warbler *Acrocephalus arundinaceus* nest. See "Materials and methods" for definitions of terms

body size to the little bittern (Hudec 1994). Further, the use of the turtle dove in several previous studies of the same great reed warbler population confirmed that this is an appropriate control species (Trnka and Prokop 2012; Trnka and Grim 2013a).

For each experiment, we randomly chose 1 out of 2 specimens per dummy type. Using only one specimen per dummy type may have the advantage that it holds the stimulus constant; however, using different dummies ameliorates potential pseudo-replication and is therefore preferable (e.g. Sealy et al. 1998). Little bittern dummies were females; the turtle dove does not show sexual plumage dimorphism. The mounts were in life-like positions with folded wings and head pointing forward. Similarly to our previous work, we did not find any differences in great reed warbler responses to these specimen replicates in models where aggression was analysed per sex ("specimen" added to minimum adequate model: $F_{1,28} = 1.21$, $P = 0.28$) or per pair ($F_{1,28} = 1.21, P = 0.28$; see also Trnka and Prokop 2012; Trnka et al. 2012; Trnka and Grim 2013a). We reached the same conclusions when we added the specimen id predictor as a random (instead of fixed) effect and when we added it to the full (instead of minimal) model.

We adopted a sequential randomised presentation of dummies at great reed warbler nests (Sealy et al. 1998; Grim 2005). At our study site, great reed warblers show habituation during longer dummy presentations (Trnka et al. 2012), therefore we set the experiment length to the period before the habituation commences, i.e., to 1 min (as in all our previous studies, see above). A randomly chosen dummy was attached to reeds 0.5 m from the focal nest, facing the nest rim. Experiments started when the first parent arrived in the immediate vicinity of the nest and spotted the dummy. Experiments lasted for 5 min when great reed warblers did not physically attack the dummy. In cases of contact attacks, the experiment was terminated 1 min after the first contact attack (Trnka and Grim 2013a), and then the first dummy was removed. The other dummy was attached to the same place on the next day to avoid carry-over aggression. It was presented at the same time of day to avoid possible confounding time effects (Čapek et al. 2010). Observations were made by the first author from a hide placed ~5 m from the focal nest and double-checked by the other observer from a distance of ~10 m (see also Trnka and Grim 2013b). All experiments were conducted at monogamous nests (cf. Trnka and Prokop 2010) when nestlings were 8–10 days old. To minimise the influence of daytime and weather, all observations were made between 0700 and 1100 hours CET and under appropriate intermediate weather conditions (no rain or strong wind). None of the nests was depredated or abandoned within 2 days after the experiments were carried out.

We measured great reed warbler aggression as a continuous variable, i.e. the number of contact attacks per 1 min (other potential measures were excluded from reasons detailed in Trnka et al. 2012; Trnka and Grim 2013a). We did so separately for the female and male of each tested pair. However, considering that both parents were present at each tested nest and both sexes responded to dummy presentations, we also pooled responses from both sexes into one joint measure per pair. Most previous studies have also used this latter "per whole pair" approach (Grim 2005; Honza et al. 2010). Importantly, our conclusions were robust to the methodology (see also Trnka et al. 2012): when we assessed the birds' responses on a rough categorical scale as a presence or absence of contact attacks (see also Grim 2005; Honza et al. 2006; Grim et al. 2011), we reached the same conclusions (results not shown).

Statistical analyses

We tested whether great reed warbler responses to dummies were affected by potential confounding factors. Some potential confounders such as nesting stage (Campobello

Table 1 Responses to dummies (no. contact attacks per 1 min) of the little bittern *Ixobrychus minutus* and turtle dove *Streptopelia turtur* (control) by great reed warblers *Acrocephalus arundinaceus* with varying neighbourhood status, i.e., nearby (≤ 7 m) synchronous nests of bitterns either present or absent (see "Materials and methods")

Minimal adequate model	Per sex			Per pair		
	ddf	*F*	*P*	*ddf*	*F*	*P*
Status × dummy	120	36.63	<0.0001	57	19.16	<0.0001
Status	120	41.64	<0.0001	57	29.90	<0.0001
Dummy	120	62.40	<0.0001	57	33.21	<0.0001
Sex	120	16.22	<0.0001	–	–	–
Clutch size	120	5.96	0.02	57	4.25	0.04
Removed predictors						
FED	120	0.09	0.77	56	0.12	0.73
FED^2	119	3.29	0.07	55	3.05	0.09
Dummy × sex	117	0.64	0.43	–	–	–
Status × sex	116	0.39	0.54	–	–	–
Status × dummy × sex	115	2.07	0.15	–	–	–

Response in "per sex" model was aggressive response by females or males (unit of analysis = individual) whereas in "per pair" model the responses were pooled (unit of analysis = pair). Therefore the latter model cannot contain "sex" as a predictor. FED = first egg laying date. Results from GLMM with pair id as a random effect. *ddf* = denominator degrees of freedom. Nominator degrees of freedom = 1 in all cases

and Sealy 2010), daytime (Čapek et al. 2010), weather and mating status (Trnka and Prokop 2010) were avoided by experimental design. We statistically controlled for other potentially relevant factors that could not be avoided in this study design, namely first egg laying date (FED, continuous; including its squared term to test for non-linear seasonal patterns) and clutch size (continuous) as a surrogate of reproductive value (Campobello and Sealy 2010).

Main factors of interest were the following categorical predictors: dummy type (little bittern vs. turtle dove), neighbourhood status (solitary vs. neighbour) and parental sex (female vs. male). We included these fixed effects, all their interactions and potential confounders (FED, FED^2, clutch size) as predictors in a generalised linear mixed model (GLMM). Pair id was entered as a nominal random effect.

The response variable was the number of contact attacks (no. contact attacks per min). Poisson models showed considerable overdispersion ($\sim$3.2). Therefore, we used negative binomial models (Zuur et al. 2013) which dealt satisfactorily with overdispersion; overdispersion of data in final models: per sex = 0.83, per pair = 0.99 (Table 1).

We followed backward elimination of non-significant terms, starting with interactions (Grafen and Hails 2002). We checked the final (minimal adequate) model by adding the previously removed terms (one at a time) and found that none explained any significant variation. Test statistics and *P* values reported in "Results" for non-significant removed terms are from a sequential backward elimination procedure just before the particular term (being the least significant) was removed from the model. The minimal adequate model contained only significant predictors. We had specific a priori directional predictions, but the use of one-tailed tests in ecological studies is inappropriate (Lombardi and Hurlbert 2009). Therefore, all tests in the present study are two-tailed. Results are presented as mean ± SE. Some analyses were done in JMP 11.0.0 (SAS Institute, Cary, NC, USA). GLMMs were calculated in R (v.2.15.2; R Core Team 2012) using package glmmADMB (v.0.7.7; Fournier et al. 2012).

Results

At solitary great reed warbler nests, responses of pairs to the stuffed little bittern were the same as those to the control turtle dove (Table 1; Fig. 2). At neighbour nests, in contrast, great reed warbler responses to the little bittern were significantly reduced compared to the control (Table 1; Fig. 2). Responses to the control were virtually identical irrespective of the presence/absence of nearby active little bittern nests (Table 1; Fig. 2). Sex-specific responses did not differ interactively with either dummy or neighbourhood status (Table 1). Instead, males showed consistently lower aggression (9.1 ± 1.1) than females (14.0 ± 1.1) across dummies and neighbourhood status categories. Therefore, we pooled the female and male responses and present effect sizes per whole pair (Fig. 1). Most importantly, responses to little bittern versus control dummy strongly depended on neighbourhood status: both females and males responded to control turtle doves irrespective of neighbourhood status, but both sexes

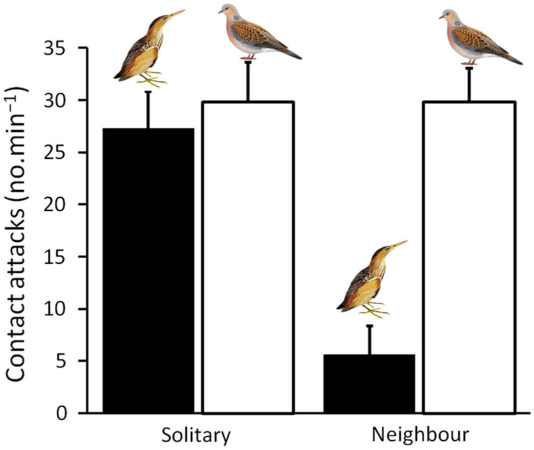

Fig. 2 Great reed warbler aggressive responses in relation to neighbourhood status [solitary = breeding far away (>7 m) from any synchronous little bittern nest; neighbour = breeding close (≤7 m) to a little bittern nest], and intruder taxidermic dummy type (*full bars* little bittern; *open bars* control turtle dove). Shown are means + SE (raw data). Little bittern versus turtle dove body size ratio of *inset figures* reflects this ratio of real dummies we used. The cut-off point of 7 m was based as a limit of aggressive "umbrella" around active great reed warbler nests because 7 m is an average maximum distance at which great reed warblers aggressively attack intruders near their nests (see "Materials and methods"). Patterns remained the same and statistically significant (Table 1) when limits of the protective umbrella were set to either 5 or 9 m from the focal great reed warbler nest

significantly decreased their responses to little bitterns when a real little bittern was breeding nearby (Table 1; Fig. 1). At the subset of neighbour nests where nest owners attacked the little bittern (6 of 14), the average rate of contact attacks was significantly lower than at solitary nests (where 17 of 18 attacked; neighbour: 13.2 ± 5.1, solitary: 28.9 ± 3.4, Welch's t test: $t_{9.8} = 2.57$, $P = 0.028$).

The distance between neighbour great reed warbler and little bittern nests did not correlate with any measure of great reed warbler aggression either for two sexes separately or for total aggression (r_s from −0.26 to −0.05, $n = 14$, P from 0.36 to 0.87). Similarly, breeding synchrony (great reed warbler FED minus its paired neighbour little bittern FED) did not correlate with aggression (number of contact attacks) against the little bittern dummy by female, male or whole pair (r_s from −0.21 to 0.06, $n = 14$, P from 0.47 to 0.84). Results (distance vs. aggression, breeding synchrony vs. aggression) did not change when we analysed only the specific aggression against the little bittern dummy (i.e., aggression to little bittern dummy minus aggression to control turtle dove dummy; following Grim 2005; r_s from 0.03 to 0.15, $n = 14$, P from 0.91 to 0.61).

When we changed the cut-off point between solitary and neighbour nests from 7 m to a more restrictive 5 m limit, we reached the same conclusions: neighbourhood status versus dummy type interaction remained significant in both the per sex model ($F_{1,120} = 22.53$, $P < 0.0001$) and the per pair model ($F_{1,57} = 10.82$, $P = 0.0017$). The results remained the same when we used a less restrictive 9 m limit instead: neighbourhood status versus dummy type interaction stayed significant in both the per sex model ($F_{1,120} = 47.66$, $P < 0.0001$) and the per pair model ($F_{1,57} = 28.24$, $P < 0.0001$).

Little bittern nests ($n = 25$) were located 1–40 m from a nearest synchronous great reed warbler nest (mean 6, median 5, SD 7.4; Fig. 1). Average first egg laying dates (FED; 1 = 1st May) were 32 ± 4 for little bitterns (range 5–58) and 28 ± 3 for great reed warblers (range 3–60). FED strongly positively correlated between little bittern and nearest great reed warbler nest ($r_s = 0.89$, $n = 25$, $P < 0.0001$). The more synchronous nests of the two species (i.e., the smaller difference between great reed warbler and little bittern FEDs) were also closer spatially ($r_s = 0.60$, $n = 25$, $P = 0.0015$). Exclusion of the most distant nest (40 m) did not change the conclusions ($r_s = 0.57$, $n = 24$, $P = 0.0035$).

Little bitterns showed very high breeding success: 88 % of 25 nests successfully produced young. The probability of little bitterns nesting successfully increased with decreasing distance to the nearest active great reed warbler nest (logistic regression: $\chi^2_1 = 9.29$, $P = 0.002$). Exclusion of the most distant nest (40 m) did not change the conclusions ($\chi^2_1 = 4.71$, $P = 0.029$). Thus, little bittern nests that successfully fledged were located significantly closer to great reed warbler nests (mean 4.4, median 4.5, range 1–10, $n = 22$) than those that failed due to predation (mean 18.5, median 8, range 8–40, $n = 3$). The probability of great reed warbler nesting successfully increased marginally significantly with decreasing distance to the nearest active little bittern nest (logistic regression: $\chi^2_1 = 4.36$, $P = 0.037$). However, this relationship was weak: after the exclusion of the most distantly paired nest (40 m) the statistical relationship disappeared (logistic regression: $\chi^2_1 = 1.37$, $P = 0.24$).

Discussion

Great reed warblers showed aggressive behaviour toward both little bitterns and control species near their nests in our study population. This is in line with findings of previous studies suggesting generally high anti-predator aggression in this species (Kleindorfer et al. 2005; Honza et al. 2010; Trnka and Prokop 2010; Trnka and Grim 2013a). However, while great reed warblers kept the generalised nest defence (i.e. aggression against the control turtle dove) at the same level across both neighbour and solitary nests, they dramatically decreased specific nest defence directed towards little bitterns at nests located close to synchronously breeding little bitterns. Specifically, the little bittern dummy was almost always attacked at solitary great reed warbler nests (94 % nests) but only at less than half of neighbour nests (43 % nests). However, not only the prevalence but also the rate of contact attacks was reduced when great reed warblers experienced little bitterns breeding close to their own nest. Importantly, these conclusions remained the same irrespective of how we analysed the data, i.e. (1) when we used continuous or categorical scale to quantify host responses in the same experiments, (2) whether we analysed the data separately for females and males or pooled their responses per whole pair, and (3) when we changed the cut-off point for neighbour versus solitary nests from 7 m to a more restrictive 5 m or less restrictive 9 m (see "Results").

Birds may pose innate knowledge about the risk of nest predation (Hobson et al. 1988; Veen et al. 2000), or they can learn this from experience (Conover 1987; Wiebe 2004). If nest predation risk assessment in the great reed warbler was innate with no learned fine-tuning, parents should respond to the little bittern dummy in the same way regardless of the presence or absence of little bittern nests near their own nests. However, strikingly non-random variation in great reed warbler nest defence at neighbour versus solitary nests suggests that nest defence behaviour of the great reed warbler has a learned component. We therefore assume that aggression of great reed warblers against little bitterns might be moulded by their previous experience with this heron (see also, e.g., Montgomerie and Weatherhead 1988; Rytkönen and Soppela 1995). It is natural to expect that great reed warblers nesting close to the nests of little bitterns have a higher chance of encountering them in their territories than warblers nesting further away. If such encounters did not lead to a real threat to the great reed warbler nests (note that little bitterns do not hunt near their nests; Hudec 1994), then great reed warbler parents could learn that little bitterns do not pose a direct threat to their nests. Thus, according to the life history theory, experienced great reed warblers should react less aggressively to little bitterns than inexperienced great reed warblers. This behaviour is in agreement with the predictions of the dynamic risk assessment hypothesis, according to which birds are capable of assessing the risk of nest predation and adjust their nest defence behaviour accordingly (Kleindorfer et al. 2005).

Another explanation for the patterns of decreased great reed warbler aggression at neighbour nests is that great reed warblers might simply become habituated to little bitterns occurring regularly in their territories. Under this scenario, great reed warblers would not actively assess the risk of nest predation. This hypothesis predicts a negative correlation between breeding synchrony and nest defence intensity (i.e. if the little bittern is in the great reed warbler territory for a short period, then great reed warblers should react more strongly than when the two species cohabit the same area for longer). However, we found no correlation between breeding synchrony and great reed warbler aggression against the little bittern dummy. Therefore, we hypothesise that the decision by birds whether and how intensively to defend their nests is affected not only by the dangerousness of predators and their distance from the nest (Kleindorfer et al. 2005; Kryštofková et al. 2011; Strnad et al. 2012) but birds may also decide to change their nest defence behaviour according to familiarity with the potential nest predator.

Finally, we propose a new hypothesis explaining differences in nest defence behaviour between great reed warblers nesting near little bitterns and those nesting solitary. In our study area, little bitterns showed clearly non-random spatio-temporal association with breeding great reed warblers: 84 % of 25 little bittern nests were located within 7 m from active great reed warbler nest, i.e., an average maximum distance at which great reed warblers aggressively protect their own nests as defined above (see "Materials and methods"). Spatially closer nests were also more synchronised. Although the little bittern, due to its secretive and shy habits, remains one of the least studied marsh-dwelling birds in Europe (Pardo-Cervera et al. 2010), other work also suggests its non-random breeding in the vicinity of great reed warbler nests (Samraoui et al. 2012). Such assemblages might result either from similar habitat preferences of the two species and/or limited nesting sites (Orians and Wilson 1964) or this association might have evolved specifically because it provides some direct benefits for one or both associates. The predator protection hypothesis suggests that birds associate with other species to gain protection from predators (Quinn and Ueta 2008). It is possible that little bitterns actively associate with highly aggressive great reed warblers because the latter species may inadvertently "help" the former as a sentinel by alerting to the approaching danger (Nuechterlein 1981) or as an active agent by attacking and driving the intruder away from its nest (Dyrcz et al. 1981). Such nesting association has already been reported for another congener, the least bittern *Ixobrychus exilis*, that associates with a colonially nesting passerine, the boat-tailed grackle *Quiscalus major* (Post and Seals 1993).

Overall, our findings are consistent with evidence from other studies supporting the active choice hypothesis (e.g. Post and Seals 1993; Richardson and Bolen 1999; Quinn et al. 2003). Pronounced homogeneity of reedbeds at our study site due to the strictly linear nature of the habitat (i.e., several metres long narrow strip) suggests that observed non-random spatio-temporal association of little bittern and great reed warbler nests was not only the result of similar habitat requirements of associate species but also that little bitterns actively associate with great reed warblers for some reason. Otherwise, it would be hard to explain another significant pattern we detected: the more spatially close neighbour nests of the two species were also more temporally synchronous. Such spatio-temporal correlation suggests that little bittern decisions where and when to breed are affected by the same kind of decisions on the part of great reed warblers.

However, that little bitterns nested non-randomly near great reed warbler nests does not yet support the predator protection hypothesis. Still, we find it unlikely that two species of vastly different body size as the little bittern and great reed warbler would prefer exactly the same kind of vegetation. Indeed, published data suggest that great reed warbler and little bittern have different preferences for vegetation structure (Amini Nasab et al. 2006). Instead, little bitterns may benefit from spatially consistently high generalised aggression by great reed warblers without paying the potential cost of having aggressive neighbours themselves (low specific aggression towards little bitterns). These patterns suggest that little bitterns actively and adaptively choose to breed near the highly aggressive great reed warblers.

However, not only little bitterns but also great reed warblers may benefit from such association. The evolutionary rationale is that it would be maladaptive for little bitterns to plunder nests of their protectors. Thus, the little bittern–great reed warbler nesting association might be reciprocally beneficial in terms of reduced nest predation for both associates (Campobello et al. 2012). As a result, reduced nest defence by great reed warblers at neighbour nests may be a specific behavioural adaptation to nesting in association with little bitterns. However, further research is needed to test this hypothesis.

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