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Coping with nest predation risk in a species-rich bird community inhabiting a Siberian wetland

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Abstract. Birds protect their nests against predators in various ways. In addition to active defence, they can hide their nests or use the protection of other species breeding nearby that actively defend the nests. Studies evaluating these strategies simultaneously are rare, especially from areas unaltered by humans. Nest predation risks were studied in a wetland bird community at Lake Baikal, Russia. The community contained several species actively defending their nests, although most were “passive defenders”. Such tactics as active defence, concealed nesting, neighbourhood nesting and coloniality were tested for their effects on predation risk. The main predators were birds, particularly carrion crows (*Corvus corone*). Analysis of 193 nests using multimodel inference based on Akaike’s information criterion suggests the most successful tactic was active nest defence, although most birds applying this tactic build open (uncovered) nests. Passive defenders effectively reduced this risk by nest concealment and/or breeding near active defenders. Opposing patterns were found for active versus passive defenders near the most successful breeder but also a potential nest predator, the Mongolian gull (*Larus mongolicus*). Conservation implications emphasize support for large aggregations of active nest defenders, vegetation cover providing good nest shelter, and sufficient area of interior habitat reducing edge effects.

Key words: anti-predator behaviour, breeding success, colonial breeding, Lake Baikal, nest concealment, protective umbrella hypothesis, waterbirds

Introduction

Nest predation is a key phenomenon determining breeding performance in birds (e.g. Skutch 1949, Lack 1966, Caro 2005, Lima 2009). Moreover, it is a major force in the evolution of avian life-history associated with such breeding traits as nest construction (Gill 2007), clutch size, number of brood, and caring for young (Martin 1995). Breeding birds have a significant capacity to assess and respond, over ecological time, to changes in the risk of predation to both themselves and their eggs or nestlings (Larsen & Grunnetjern 1997, Albrecht & Klvaňa 2004, Caro 2005, Lima 2009, Dassow et al. 2012).

Various anti-predator behaviours of particular ground-nesting species have been found to reduce predation risk in individual bird species and under different circumstances. These include avoiding areas with high predation risk (Norrdahl & Korpimäki 1998, Tryjanowski et al. 2002), aggressiveness toward nest predators (Elliot 1985), placing nests in dense

vegetation and thus enhancing nest concealment (Guyn & Clark 1997, Albrecht & Klvaňa 2004), clumping in colonies (Götmark & Andersson 1984, Šálek & Šmilauer 2002), and breeding in close proximity to “umbrella species” with active nest defence (Dwernychuk & Boag 1972a, Quinn & Ueta 2008).

Active nest defence against predators and nest concealment have been regarded as the essential adaptations of ground-nesting species to increase nesting safety in habitats threatened by predators (Lima 2009). In addition, various poor nest defenders as ducks (Dwernychuk & Boag 1972a, Götmark & Åhlund 1988), grebes (Burger & Gochfeld 1995), waders (Bub 1957, Nankinov 1978, Dyrce et al. 1981, Larsen & Grunnetjern 1997), and passerines (Eriksson & Götmark 1982) have been found to prefer breeding in close proximity to other birds, such as gulls, raptors and waders, which actively repel avian predators and thus provide reliable nest protection (reviewed by

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Quinn & Ueta 2008). These associations seemed to be particularly important in open habitats, such as tundra, wetlands and grasslands (Quinn & Ueta 2008). Surprisingly, it is not uncommon for such umbrella species as gulls also to be predators of other nests in the colonies (Dwernychuk & Boag 1972a, Larsen & Grundetjern 1997, Götmark 1989). Thus, decision making in these cases can be perceived as a trade-off between benefits gained from nest protection and costs ensuing from predation risk by protector species (Götmark 1989, Larsen & Grundetjern 1997, Quinn & Ueta 2008).

Nesting in large aggregations or in proximity to active nest defenders may be also accompanied by higher nest predation risk because some predators from a colony's surroundings can be attracted to areas with higher concentrations of nests. This phenomenon is described as the hypothesis of density dependent predation (Göransson et al. 1975, Andersson & Wiklund 1978, Larivière & Messier 1998). Andersson & Wiklund (1978) showed experimentally that such nesting in aggregations can be advantageous only if accompanied by active defence against predators. Without such defence, nesting is rather maladaptive and provides a clumped food resource to predators. Therefore, silent and cryptic nesting separately from other nests could potentially be beneficial for non-active nest defenders if predators preferably visit colonies in their area having limited abilities to defend themselves (e.g. small, loose colonies).

Different tactics are in use simultaneously and are easily studied worldwide within diverse bird communities inhabiting such open habitats as marshlands and tundra (e.g. Brunton 1997, Larsen & Grundetjern 1997, Götmark & Åhlund 1988, Caro 2005). Different species thus face various trade-offs in deciding upon how to optimize nest protection and reduce the risks of egg depredation. For example, nest crypsis is highly efficient for solitarily nesting mallards (*Anas platyrhynchos*) (Albrecht & Klvaňa 2004) while common eiders (*Somateria mollissima*) rely on nest attendance rather than on nest concealment (Bolduc et al. 2005). However, it is not clear how efficient are these tactics in diverse communities with colonies formed by active nest defenders potentially attractive for nest predators. Furthermore, there has been an absence of studies comparing anti-predator effectiveness of such tactics as nest concealment and active nest defence within the same areas. In particular, little is known about whether nest concealment of poor nest defenders with cryptic nesting (such as ducks or some shorebirds) is a more

or less effective anti-predator tactic than nest defence of openly nesting active defenders (e.g. gulls, terns or lapwings). Moreover, numerous studies provide inconsistent results and interpretations as to whether the proximity of poor defenders to conspicuously breeding active nest defenders (whether or not they are potential nest predators) positively affects nesting success compared to separate nesting.

Although anti-predator tactics have evolved in natural communities, most recent studies are nevertheless based upon data collected in anthropogenic areas (e.g. Larivière & Messier 1998, Albrecht & Klvaňa 2004, but see Larsen & Grundetjern 1997) and thus come from human-altered communities (e.g. with impoverished habitat and species diversity, artificial densities of some introduced species, and/or modified structure and numbers of predators). Knowledge of predation risks in native communities is particularly important, however, for understanding those issues involved in communities modified by human activities within a cultural landscape, including managed wetland and grassland nature reserves.

The present study analysed nest success of birds within a diverse bird community in a native Siberian wetland at Lake Baikal, Russia. We tested 1) whether active nest defenders reduced probability of nest predation; 2) whether placing nests into dense vegetation (i.e. nest concealment) increased nest survival; 3) how

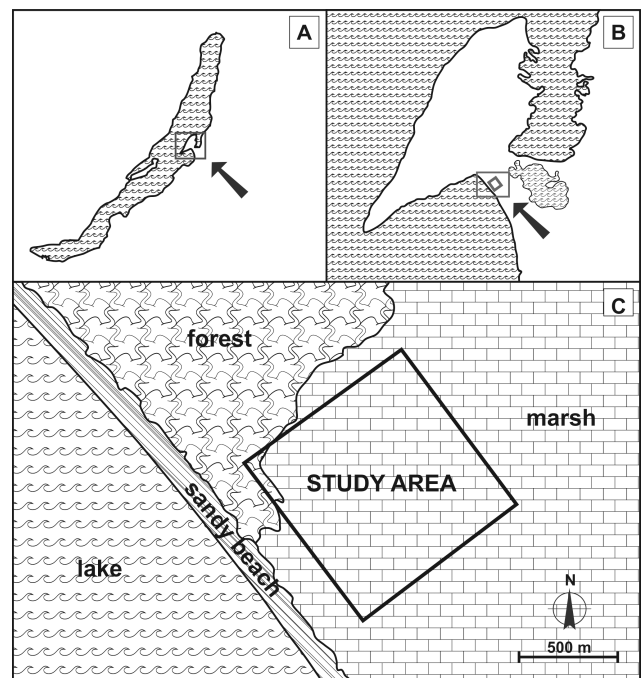


Fig. 1. Location of the study area on the isthmus of the Svjatoj Nos Peninsula, Lake Baikal, Russia. A) Lake Baikal, B) Isthmus of the Svjatoj Nos Peninsula, C) Position towards the coast and forest.

clumping of aggressive nest defenders affect nest survival; 4) how efficient is using proximity to nests of aggressive defenders for successful breeding. The role of Mongolian gull (*Larus mongolicus*) which can be simultaneously a nest predator was particularly interesting in this context. Finally, we examined 5) whether nest predation is influenced by the proximity of the forest edge, from where a majority of predators penetrates. The effectiveness of anti-predator tactics was compared within the community, and it was investigated whether or when their combinations play a role. The study offers some recommendations for conservation management of species-rich avian communities inhabiting open wetlands.

Material and Methods

Study area

The research was conducted on the isthmus of the Svjatoj Nos Peninsula (Fig. 1), Lake Baikal, Russia, one of the key areas for wetland bird breeding in a wider region around Lake Baikal (Mlíkovský et al. 2002, Mlíkovský 2009). The isthmus of the Svjatoj Nos Peninsula, with an area of approximately 300 km², is covered mostly by a continuous mosaic of various open wetland habitats. The study area of approximately 1.4 km² is situated on the south-west edge of marshlands (53°33' N, 108°56' E) in order to include a gradient from the edge of a pine forest (taiga) to deep water with floating islands of vegetation. The habitats were formed by various plant associations (with diverse vegetation height of 5–50 cm) with dominant bog-bean (*Menyanthes trifoliata*) cover, sedges (*Carex* spp.) and mosses (for more details, see Mlíkovský & Stýblo 1992 and Šálek 2013). The taiga and shore of Lake Baikal near the study area provide excellent refuge for common generalist predators of bird nests, such as carrion crows (*Corvus corone*), ravens (*Corvus corax*) and red foxes (*Vulpes vulpes*) (see below).

Data collection

All fieldwork took place between 4 June and 12 July 2013. The basic study area of 1 × 1 km was subdivided into 12 bands (each with a width of about 85 m), recorded by GPS coordinates for easy location in the field. Three additional bands were subsequently added after primary inspection of the breeding grounds in the early season in order to take in more nesting attempts of various species within gull colonies, a typical phenomenon of the local wetland. All bands were surveyed carefully, repeatedly, and in random order by a team of 3–6 people to locate and measure bird

nests. “Band trips” included slow walking with a span of up to 10 m between adjacent observers in shallower sections while inflatable boats were used to reach vegetation patches on deep water with floating islands. Nests were located by direct detection in vegetation or via parents indicating nest presence. All observers’ movements were tracked using GPS devices. For all those nests found, including those already depredated or hatched, GPS positions were stored using waypoint averaging which facilitated recording the location with the highest possible accuracy (usually < 3 m). Species determination was made according to the presence of an adult bird, the colouration and size of eggs or eggshell remains, or, in the case of some duck species, feathers from the nest lining. Some of the nests remained unidentified (in particular, duck nests depredated in early incubation stages), and these nests were assigned to the corresponding genus (e.g. *Aythya* sp., *Anas* sp.). Prior to any manipulation at the nest, a photo of each nest was taken vertically from a height of 1 m to estimate nest concealment. While moving around the nest and manipulating the eggs, extreme care was taken to reduce handling time and impact on the surrounding vegetation in order to minimize predation risk caused by observers (Dwernychuk & Boag 1972a, b).

To assess the date of incubation start, the floating method was used (van Paassen et al. 1984, Mabee et al. 2006). The nests were checked after 10–15 days (during “band trips” or in separate inspections, if necessary) to determine nest fates. Nests were considered as successfully hatched when sufficient amounts of very small eggshell fragments were present in the nest cup linings (Green et al. 1987, Šálek & Šmilauer 2002, Mabee et al. 2006). The remaining nests, including those found with eggshell remains and those without any eggs before the expected hatching date, were considered as depredated.

To specify the anti-predation behaviour of each species, the behaviour of birds in the area was monitored and compared with findings from the literature. Based on 327 records of aggressive interactions between nesting birds and potential avian nest predators, five regular active nest defenders were identified: the common tern (*Sterna hirundo*) with 103 aggressive interactions, northern lapwing (*Vanellus vanellus*; n = 95), black-headed gull (*Chroicocephalus ridibundus*; n = 69), Eurasian curlew (*Numenius arquata*; n = 48), and Mongolian gull (n = 12). These species also repeatedly attacked approaching human observers. This list is in good agreement with previous findings from elsewhere (Cramp & Simmons 1983, Burger &

Gochfeld 1988, Montgomerie & Weatherhead 1988). The species most attacked were the carrion crow ($n = 188$ aggressive interactions) and Mongolian gull ($n = 83$), which should thus be considered as potentially important nest predators. To specify the range of real nest predators more thoroughly, photo-traps were installed in 20 artificial nests baited with hen eggs or with dummy lapwing eggs. The predators encountered were again mostly carrion crows and Mongolian gulls. In addition, the common gull (*Larus canus*) and red fox, the only mammalian predator, were detected.

Data analysis

For estimates of nest success, we applied the apparent method (Weidinger 2003). Thus, we scored each nest as successful, if at least one egg hatched, or unsuccessful, if the nest had been depredated before hatching. Given the team's intensive nest searching effort throughout the season, good visibility of open habitats, and conspicuousness of most nests, the success rate for finding nests was very high. Taking into account the incubation stage of all nests found as active (including those excluded from final analysis due to their abandonment or remaining active after completion of fieldwork), only 11 of 108 nests (10.2 %) with a known date of incubation start were shown to have been overlooked after one band trip while only four nests (3.7 %) so appeared after two trips. In addition, most of these nests had been overlooked at the laying stage when the parent birds were off the nests. Since it can be assumed that only a small number of nests were overlooked, we consider usage the apparent method instead of Mayfield method (Mayfield 1961) reasonable in this study (Weidinger 2003). Hence, the group of "successful" nests include also nests, which suffered partial egg loss. Although we suppose that partial predation may be widespread phenomenon in the study area (e.g. because carrion crows were observed carrying away individual gull eggs from gull colonies, own observations), we recorded only few direct evidences of partial predation (3 % of nests included into analysis). This did not allow us to provide a detailed analysis of predictors of partial predation. Nests which were abandoned before hatching or which were active (at least the first egg had been laid) even after completion of fieldwork were excluded from the analysis of their nest fates. Using the apparent method for estimates of nest success, it was possible to include into the analysis those nests found as inactive ($n = 102$, i.e. 52 % of all nests), without which the analysis would have been incomplete and possibly inappropriately biased.

Breeding species were sorted into three groups according to their anti-predator strategies (listed in Table 1). One group, called "active nest defenders", consisted of species which actively attack approaching nest predators but do not themselves threaten the nests of other species. These are the black-headed gull, common tern, Eurasian curlew and northern lapwing. The Mongolian gull was singled out in the specific category "potential nest predator", as it also depredates other nests. The last group, called "passive nest defenders", includes species which do not actively repel predators. These three distinct groups were analysed in separate models to reveal predictors that influence nest predation risk.

For each nest, the nearest active nest of an active nest defender and the nearest active nest of the Mongolian gull were included as two predictors of nest predation risk. In addition, the numbers of all active nests of both active and passive nest defenders (as a measure of nest density dependence) as well as the numbers of all active Mongolian gull nests (as a measure of the concentration of this specific nest predator) within a radius of 50 m were included as two additional possible predictors. The simplified rule with the arbitrary distance of 50 m was adopted based on previous experimental findings that at least some nest defending species, such as lapwings, respond to predators approaching at such a distance (e.g. Elliot 1985). In selecting the nearest nests and the nest numbers within a 50 m radius, only those nests were included which were considered active for at least one day during the expected lifetime of the nests for which the calculation was made (the "minimum one-day overlap" rule). The minimum one-day overlap rule was applied also to nests found inactive and for which the clutch's initiation date was unknown. In such cases, either the date of clutch initiation was approximated as the corresponding median date for other nests from the same species (synchronized gulls) or (for other species) egg laying was assumed to have started immediately after the last inspection of the site. In such cases, the expected lifetime of the nest was limited to one day.

Based on clearly detectable gradients across the marshland in moisture and distance from the beach as well as forest edge (Fig. 1), from which most potential nest predators can penetrate, inhomogeneous intensity of predation pressure was assumed in the study area. Based on this fact and given the relatively simple geometry of these gradients approximately corresponding to the cardinal points, the coordinates (latitude and longitude) of all nests were included as

transparent proxy predictors of nest predation risk to account for potential associated effects. Proportions of open water relative to other habitats in a network of squares 25 × 25 m across the study area was related to latitude (X) and longitude (Y) (Spearman rank correlation $r_s = 0.45$ and $r_s = -0.66$ for X and Y coordinates, respectively, both $P < 0.001$). Similarly, distance of nests to beach line was strongly related to the coordinates ($r_s = 0.53$ and $r_s = 0.61$ for X and Y, respectively, both $P < 0.001$) as well as distance of nests to forest edge did so ($r_s = 0.64$ and $r_s = -0.78$ for X and Y, respectively, both $P < 0.001$). All distance measurements were carried out using project layers in the ArcGis 10 (ESRI, CA, USA) environment. Nest concealment was estimated as the proportion (%) of the nest construction hidden by vegetation when viewed from above. All estimates were done by a single investigator (MS) from a photo taken by an observer immediately after the nest had been found. However, due to overall vegetation growth, concealment of nests was significantly correlated with Julian date when the photo was taken ($r_s = 0.34$, $P < 0.001$). Thus, we additionally analyzed seasonal pattern in nest success using generalized linear

model with binomial response variable (successful or depredated) (GLM_{binom}) on the subset of nests in which the date of incubation start was known. To analyse probability of nest predation, the most parsimonious models were found using a multi-model inference approach based on Akaike's information criterion corrected for small sample size (AICc) (Burnham & Anderson 2002). The program R, version 3.1.1 (R Development Core Team 2014) with package MuMIn (Bartoń 2014) was used for computing the models. Two sets of generalized linear models for binomial distribution were computed, separately for active and passive defenders. In both cases, global models (GLM_{binom}) included all those predictors listed in Table 2. In total, 129 *a priori* models in each set were computed. The best candidate models were considered to be those with $\Delta AICc \leq 2$, but only those models which did not contain uninformative predictors were considered (Arnold 2010). To enable inference and ecological interpretation, even for those predictors not included into the most parsimonious models, for each of the included predictors cumulative Akaike's weights were additionally computed across the full model set as a measure of relative variable importance

Table 1. Species breeding in the area, predation risk strategy, number of nests found, mean (± SD) percentage nest cover.

Species	Strategy ^a	% in strategy	Number	Nest cover ^b	SD
Mongolian gull (<i>Larus mongolicus</i>)	1	100	44	3.1	0.88
Black-headed gull (<i>Chroicocephalus ridibundus</i>)	2	70	59	1.6	0.37
Common tern (<i>Sterna hirundo</i>)	2	13	11	5.0	1.44
Northern lapwing (<i>Vanellus vanellus</i>)	2	10	8	0.1	0.12
Eurasian curlew (<i>Numenius arquata</i>)	2	7	6	0.0	0.00
Unidentified duck	3	34	22	12.9	3.21
Tufted duck (<i>Aythya fuligula</i>)	3	26	17	35.3	5.71
Mallard (<i>Anas platyrhynchos</i>)	3	8	5	23.0	13.08
Red-necked grebe (<i>Podiceps grisegena</i>)	3	6	4	1.3	1.08
Wood sandpiper (<i>Tringa glareola</i>)	3	5	3	60.0	18.86
Pintail (<i>Anas acuta</i>)	3	3	2	0.0	0.00
Long-toed stint (<i>Calidris subminuta</i>)	3	3	2	35.0	10.61
Horned grebe (<i>Podiceps auritus</i>)	3	3	2	7.5	1.77
Ruff (<i>Philomachus pugnax</i>)	3	3	2	25.0	3.54
Shoveller (<i>Anas clypeata</i>)	3	1.5	1	50.0	0.00
Teal (<i>Anas crecca</i>)	3	1.5	1	10.0	0.00
Pochard (<i>Aythya ferina</i>)	3	1.5	1	10.0	0.00
Black-necked diver (<i>Gavia arctica</i>)	3	1.5	1	70.0	0.00
Unidentified grebe	3	1.5	1	20.0	0.00
Baillon's crane (<i>Porzana pusilla</i>)	3	1.5	1	100.0	0.00

^a 1 = potential nest predator, 2 = active nest defender, 3 = passive nest defender. ^b Nest cover is expressed as percentage of the nest construction hidden by vegetation when viewed from above.

Table 2. Predictors included into the analysis of nest predation risk.

Acronym	Variable content
Xc	Longitude
Yc	Latitude
nNests	Number of nests of species other than Mongolian gull in a radius of up to 50 m
Distactive	Distance to the nearest nest of an active defender
nMong	Number of Mongolian gull nests in a radius of up to 50 m
Distmong	Distance to the nearest Mongolian gull nest
Concealment	Percentage of nest covered by vegetation, from vertical view

Table 3. The most parsimonious models (in bold) explaining nest predation risk for active and passive nest defenders.

Model	K ^a	AICc ^b	ΔAICc ^c	ω _i ^d	% explained variation
Active defenders					
Distmong^c + Xc + Yc	4	91.1	0	0.062	19.22
Yc	2	91.5	0.4	0.051	14.57
nNests	2	93.5	2.36	0.019	12.65
Passive defenders					
Concealment + Distmong + nNests	4	77.1	0	0.113	23.9
Concealment + Distmong	3	77.5	0.33	0.096	21.0
Distactive + Concealment + Yc	4	80.5	3.41	0.021	20.1

^a Total number of estimated regression parameters, including intercept. ^b Akaike's information criterion adjusted for small sample sizes.

^c Difference in AICc relative to the top model. ^d Akaike weight. ^e Predictors are defined in Table 2.

($\sum \omega_i$) (e.g. Marchetti et al. 2004, Tipton et al. 2008). This can be particularly important (Arnold 2010) inasmuch as some predictors were intercorrelated.

For mutual comparisons of the mortality rates among strategies, Tukey's multiple comparisons test was computed using the package multcomp in R (Hothorn et al. 2014). Because only 1 of the 44 Mongolian gull nests was depredated, the tactic represented by the Mongolian gull was used only for comparison of predation rates among the three anti-predator strategies and subsequent analysis was conducted only for active and passive defenders.

Results

Structure of the community

The analysed dataset consisted of 193 nests from 20 bird taxa including 18 identified species (Table 1). A major part of the community (59 nests, 30.6 % of all nests) was composed of the active nest defender the black-headed gull, followed by the potential nest predator Mongolian gull (44 nests, 22.8 %). Among active nest defenders, there were three other less abundant species, namely the common tern, northern lapwing and Eurasian curlew (25 nests, 13.0 %). Passive defenders made up a more diverse part of

the bird community (14 species in total) and were dominated by ducks. The tufted duck (*Aythya fuligula*) was the most common passive defender (17 nests, 8.8 %), followed by the remaining identified ducks: mallards, pintails (*Anas acuta*), shovellers (*Anas clypeata*), teals (*Anas crecca*) and pochards (*Aythya ferina*) in total of 11 nests (5.7 %). Twenty-one duck nests remained unidentified (10.9 %). The other eight species categorized as passive nest defenders had 1-4 nests (8.3 % in total). Within the sum of nests, the proportions of passive nest defenders, active nest defenders (other than Mongolian gull) and the potential nest predator Mongolian gull, respectively, came to 33.7 %, 43.5 % and 22.8 %.

Nest predation rates and the most parsimonious models

We recorded 57 depredation events (29.5 % of all nests). The Mongolian gull potential nest predators were most successful in terms of nest survival probability, as only one of 44 monitored nests (2.3 %) was depredated. With 25 depredated nests (29.8 % of 84 nests), active nest defenders suffered from higher nest predation compared to Mongolian gulls (the difference being marginally non-significant, Tukey's

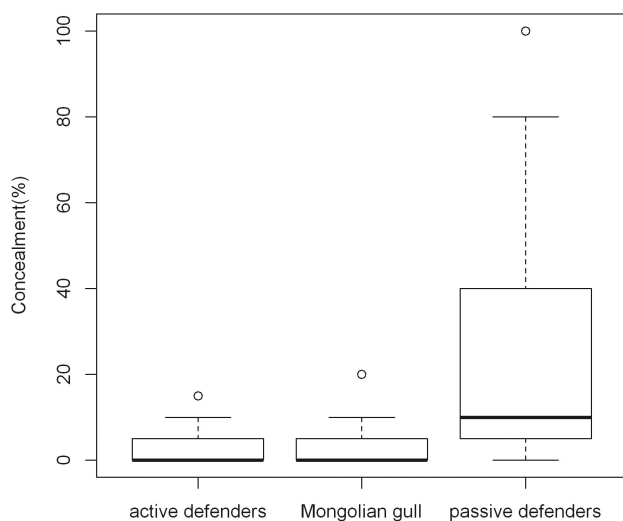


Fig. 2. Variation in nest concealment for three breeding strategies in a community of birds at the Svjatoj Nos marshland in 2013. Dark line: median, boxes: lower and upper quartiles, whiskers: 10 % and 90 % quantiles, circles: outliers.

test; $P = 0.053$). Among passive nest defenders, almost one-half of nests failed due to predation (31 nests, i.e. 47.7 % of 65 nests). This was significantly higher than for either Mongolian gulls or active nest defenders (Tukey's test; $P < 0.001$ and $P = 0.009$, respectively).

The most parsimonious models explaining nest predation risk for active and passive nest defenders were selected; for each of the two strategies, two models achieved $\Delta AICc < 2$ (Table 3). As shown, the strategies markedly differed in the most important predictors which appeared in the models. As only a

Table 4. Relative importance of predictors, expressed by sums of weights.

Predictor ^b	Strategy ^a	
	Active ^c	Passive ^c
Distmong	0.47	0.87
Concealment	0.43	0.97
nNests	0.40	0.48
Distactive	0.28	0.32
Yc	0.87	0.32
nMong	0.34	0.25
Xc	0.5	0.37

^a Relative importance values indicate cumulative Akaike's weights ($\sum \omega_i$). ^b Predictors are defined in Table 2. ^c Strategy 1 = passive defenders; strategy 2 = active defenders.

single Mongolian gull nest was depredated, it would be pointless to analyse the effects of predictors responsible for nest predation risk in this strategy.

The most parsimonious model for active nest defenders included both coordinates and distance to the nearest Mongolian gull nest (Table 3). In this model, latitude ($P = 0.001$, estimate = -675.5 , SE = 207.9), and longitude ($P = 0.042$, estimate = 274.2, SE = 134.90) significantly contributed to explaining nest predation risk, thereby indicating lower predation risk further from the edge of marshlands. The third variable in the best model, distance to the nearest Mongolian gull nest, remained marginally non-significant ($P = 0.052$, estimate = 0.006, SE = 0.0032) and with a negative trend (i.e. increased predation risk near the nests). The second candidate model contains only one predictor: latitude ($P < 0.001$, estimate = -302.27 , SE = 85.36).

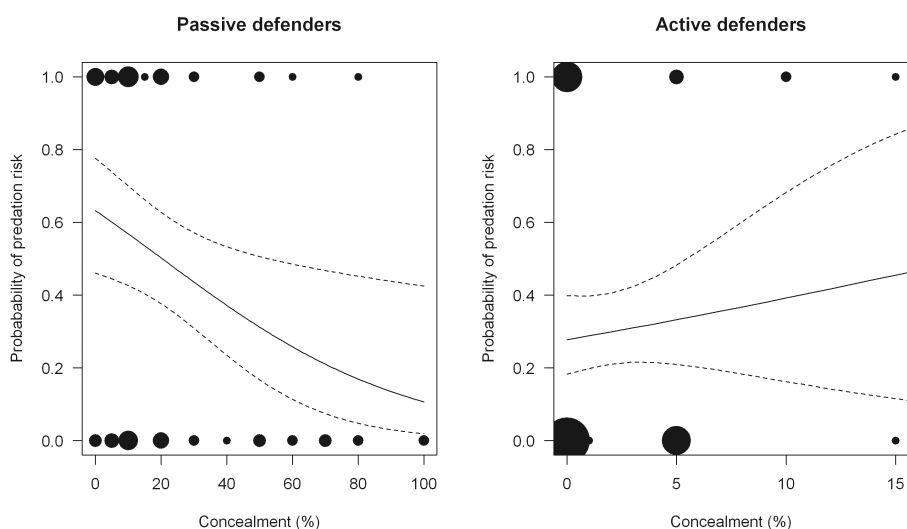


Fig. 3. Predicted probability of nest predation based on logistic regression with binary dependent variable (successfully hatched vs. depredated) for passive and active nest defenders in relation to nest concealment in the community of birds at the Svjatoj Nos marshland in 2013. Size of data points reflects sample sizes at each concealment category (from 1 to 41). Dashed line indicates 95 % confidence interval.

For passive nest defenders, the most parsimonious model (Table 3) included positive effects of nest concealment ($P < 0.001$, estimate = 0.039, SE = 0.0140), distance to the nearest Mongolian gull nest ($P = 0.012$, estimate = -0.004, SE = 0.0015), and a non-significant positive effect from the number of neighbouring nests ($P = 0.160$, estimate = 0.042, SE = 0.030). The second candidate model included only positive effects of nest concealment and the distance to the nearest Mongolian gull nest (both $P < 0.001$).

Predictors of nest predation

Nest concealment broadly differed between passive nest defenders and the two remaining strategies (Fig. 2). Passive defenders ranged broadly (between 0 % and 100 %) in the extents to which they concealed their nests (median 10 % of nest cover), and this had a strong effect on probability of nest survival ($\sum \omega_i = 0.97$, Fig. 3). In contrast, most nests of active nest defenders were entirely unconcealed (range 0-15 %, median = 0 % of nest cover) and the importance of this predictor for nest success among active defenders was markedly lower ($\sum \omega_i = 0.43$). Although this is a statistically non-significant finding, the trend toward surprisingly lower probability of nest survival with higher nest concealment is nevertheless worthy of note.

Because nest concealment significantly arised within season ($r_s = 0.34$, $P < 0.001$), we separately modeled overall seasonal pattern of nest success, indicating possible seasonal trends in predation pressure. Whereas the fixed effects of nesting strategy (active versus passive nest defense) and timing of clutch initiation were non-significant (GLM_{binom}: both $\chi^2 < 1.4$ and $P > 0.24$), the interaction of nesting strategy and timing of clutch initiation was highly significant ($\chi^2 = 7.7$, $P < 0.001$). This refers to opposite seasonal trends in predation rates in passive and active nest defenders; in active defenders the probability of nest survival during the season significantly decreased (estimate = -0.09, SE = 0.036, $P = 0.005$) while in passive nest defenders non-significantly increased (estimate = 0.036, SE = 0.031, $P = 0.250$).

Neighbourhood with nests of the Mongolian gull, a potential nest predator, showed effects for both active and passive nest defenders. For both strategies, the distance to the nearest Mongolian gull nest (“Distmong” in Table 4) was more important than was the number of Mongolian gull nests within a radius of up to 50 meters (“nMong”, this predictor did not appear in any of the best models). However, the importance of the distance to the nearest Mongolian

gull nest was much lower for active nest defenders than for passive defenders ($\sum \omega_i = 0.47$ versus 0.87, respectively).

Neighbourhood with other species

The cumulative weights of the two predictors representing this attribute, i.e. the number of all nests within a radius of up to 50 m and the distance to the nearest nest of an active nest defender (“nNests” and “Distactive”, respectively, in Table 4), showed patterns clearly opposite those indicated by analogous predictors based exclusively on Mongolian gull nests. These predictors did not appear in the best candidate models, however, thus indicating their notably lower importance. The number of nests within a radius of up to 50 m was found to be more important ($\sum \omega_i = 0.40$ for active and 0.48 for passive defenders) than the distance to the nearest nest of an active nest defender ($\sum \omega_i = 0.28$ for active and 0.32 for passive defenders). Moreover, the effects of both predictors seemed to be positive (even though not very strong) for active as well as passive defenders.

Coordinates

Latitude (Yc) was the strongest predictor of nest success in the group of active defenders ($\sum \omega_i = 0.87$), for which longitude (Xc) also was of considerable importance ($\sum \omega_i = 0.50$). Neither of the coordinates seemed to be highly important, however, for passive defenders ($\sum \omega_i = 0.32$ for Yc, $\sum \omega_i = 0.37$ for Xc).

Discussion

Significant differences in probability of nest survival were found among the three anti-predator strategies of marshland birds. The nests of Mongolian gulls, which displayed one strategy, survived better than did the nests of the other birds pursuing the two remaining strategies (active nest defenders and passive nest defenders), thus indicating that “being a great gull” was definitely the most advantageous nesting strategy in the area. It is probable that active nest defence combined with large body size and colonial breeding led to successful intimidation of a wide range of potential nest predators including birds and mammals. Nests of active defenders had generally lower probability of nest predation than did those of passive defenders. This suggests that active nest defence can itself be a very effective anti-predator strategy. However, the effectiveness of individual anti-predator tactics practiced by active and passive defenders strongly differed. In particular, nest concealment itself as well as its influence on nest predation risk greatly

differed between these two strategies. First, whereas the nests of active defenders remained generally unconcealed and with only modest variation, the nests of passive defenders showed notably high variation in concealment. This difference probably resulted in the finding of no obvious effect of nest concealment for active defenders while concealment played a particularly important role in reducing nest predation among passive defenders. In the literature, we can find results both supporting (e.g. Dwernychuk & Boag 1972b, Brouwer & Spaans 1994, Guyn & Clark 1997, Traylor et al. 2004, Albrecht & Klvaňa 2004) and refuting (e.g. Crabtree et al. 1989, Colwell 1992, Vickery et al. 1992, Grant et al. 1999, Yerkes 2000, Thyen & Exo 2005, MacDonald & Bolton 2008a) the idea that there should be a positive effect of nest concealment on probability of nest survival in ground-nesting birds. In contrast to the results presented here, some studies regarding such passive nest defenders as ducks (Yerkes 2000) and Wilson's phalarope (*Phalaropus tricolor*) (Colwell 1992) found no support for the effect of nest concealment on nest survival or found a positive effect in an active nest defender (the herring gull *Larus argentatus*; Brouwer & Spaans 1994).

A probable explanation for these ambiguous results regarding the effect of nest concealment may consist in the different structures of predator communities among those areas studied (MacDonald & Bolton 2008a). Nest concealment can be particularly important where visually orientated avian predators play a key role (Brouwer & Spaans 1994, Traylor et al. 2004). If mammalian predators with olfactory orientation prevail, however, nest concealment is of much less or no importance (Crabtree et al. 1989, Vickery et al. 1992). Moreover, Crabtree et al. (1989) showed that for areas with strong mammalian predation pressure only the visibility of nests as viewed from the ground has a negative effect on nest success (as opposed to visibility from 30°, 60° and 90° above the ground). Our additional results in the forms of direct observations, pictures taken by photo-traps, and collected remains of depredated eggs or adults (the authors' unpublished data) suggest that the carrion crow and possibly also Mongolian gull (discussed below) were the dominant nest predators within the study area. The red fox, which also was confirmed to be a nest predator within the studied area, probably sought food mostly near the forest edge. An analysis of food remains at one fox den located next to the study area over two years (2013 and 2014) showed that the prevalent foraging habitats for foxes were forests and marshland edges.

For example, the mallard, which regularly nests at the transition between forest and marshlands, was the only duck species determined in the food remains (the authors' unpublished data).

Because nest concealment significantly increased during the breeding season, it is also important to discuss whether the clutches initiated later in the season could not be less prone to predation for other reason than just nest concealment. For example abundance of other food resources for predators later in the season may reduce predation pressure on nests (Pienkowski 1984, Dinsmore et al. 2002, MacDonald & Bolton 2008b). However, as we found, seasonal increase in probability of nest predation in active nests defenders (which do not conceal their nests) is in contradiction with this assumption suggesting that the opposite trend for passive nest defenders (preferably masking their nests in vegetation) toward reduced nest predation risk is very probably associated with seasonal increase of vegetation cover.

Proximity to a Mongolian gull nest reduced probability of nest survival of active nest defenders, such as black-headed gulls and common terns. A clearly different and contrasting pattern was detected for passive nest defenders, such as ducks, for which proximity to Mongolian gull nests was one of the positive predictors explaining nest success. It can be supposed that whereas ducks are cryptic while incubating and thoroughly cover their eggs during incubation recesses (Kreisinger & Albrecht 2008), the nests of active defenders remained almost permanently visible and thus both Mongolian gulls and other predators required much less effort to find and depredate their eggs. It can be supposed, therefore, that Mongolian gulls did not actively seek duck nests and also that such intruding predators as carrion crows, which regularly prospected colonies of black-headed gulls and common terns and then took away captured eggs (own observations), had limited time to find and depredate hidden nests. That would be particularly true when the intruders were under attack by Mongolian gulls defending their own territories. Although there is no direct evidence that the Mongolian gulls also depredated the real nests at the study site, these gulls were recorded intensively robbing eggs from unprotected nests of startled great cormorants (*Phalacrocorax carbo*) near the study site on islands in the Čivyrkujskij Bay (the authors' unpublished data). Mongolian gulls were therefore probably able easily to overcome the defences of other active defenders nearby and fortuitously to capture eggs from their conspicuous nests (Verbeek 1988).

Only weak support was obtained for the effect of nest density on nest predation risk. For example, the distance to the nearest Mongolian gull nest was more important than the number of Mongolian gull nests within a radius of up to 50 meters (as an indicator of nest density). Admittedly, the number of all nests in a radius of up to 50 m was found to be more important than the distance to the nearest nest of an active nest defender, but the relative importance of both variables was rather small. Moreover, the number of surrounding nests was found to be a good predictor of nest survival probability in the best model only for passive defenders, although its effect was statistically non-significant. Opposing trends probably influenced this ambiguous result. Although on the one hand better protection within larger and/or denser nesting colonies can be expected (Götmark & Andersson 1984, Elliot 1985), on the other hand these colonies may attract more predators (Andersson & Wiklund 1978, Larivière & Messier 1998). Moreover, the active defence of smaller species such as the black-headed gull and northern lapwing may be sufficiently effective only when sufficient number of individuals cooperate (Elliot 1985). Those colonies appearing in the area during 2013 were rather small and sparse, and so these might not have provided adequate anti-predator protection.

Coordinates, and especially latitude, contributed significantly to explaining the variation in nest predation risk for active nest defenders. However, latitude was strongly correlated with distance from the marshland edge, which is itself also associated with water depth (increasing depth from the edge to marshland interior). This might suggest that predators (in particular terrestrial mammals) penetrating into the swamp from adjacent forests very easily reached nests situated closer to marshland edges. The risks arising from this possible edge effect (Skórka et al. 2014) points up the importance of size in designing protected areas to effectively support breeding species inhabiting internal habitats such as open wetlands (Arnold et al. 2007). To some extent, however, the latitudinal effect may be locally conditioned, as it was associated with the positions of large colonies of gulls, situated more to the south within the study site, and predation risk might therefore be lower there than in more northern sections with generally lower numbers of active nest defenders.

It is evident that the presence of the most successful nesting species, the Mongolian gull, significantly affected the results obtained in this study. We note that its population had steeply increased during the

previous 20 years within the studied wetland. This was in contrast to the negative population trends for the majority of other breeding bird species (compare with Šálek 2013). The impact of great gulls on populations of other waterfowl has been broadly studied across the world. In many studies, great gulls have been detected as key nest predators (e.g. Götmark & Åhlund 1988, Vidal et al. 1998). On the other hand, protection from other predators has also been described (Dwernychuk & Boag 1972a). The impact of such great gulls as the Mongolian gull on the rest of the breeding bird community is certainly more complex than is seen solely in nest predation risk. It includes also competition for nest sites (Skórka et al. 2014), alterations in nesting habitat due to changes in plant composition around nests (reviewed by Vidal et al. 1998), and perhaps also higher predation pressure on hatchlings than on eggs (e.g. Dwernychuk & Boag 1972a, Chytil & Macháček 2000, Bowman et al. 2004). Therefore, Skórka et al. (2014) suggest that expansions of great gulls can have cascading and multilevel effects on populations of native species and may strongly alter the structure of the original communities. In any case, “great gulls” play an active role in shaping interspecific relationships, predation patterns, and population dynamics within wetland bird communities.

Finally, because of very intensive and long-lasting fieldwork, we cannot exclude that our results are influenced by our presence in the study plot. For example, in spite of our effort not to damage vegetation around the nests, we probably left some nests more conspicuous for predators than they had been before our visit (Dwernychuk & Boag 1972a, b). Some nests could also be betrayed to predators when incubating birds were flushed by observers (Götmark 1992). On the other hand, presence of observers in the study plot can also have a short-term positive effect, because of deterring predators directly by the observer themselves (Weidinger 2008). However, considering that our field effort covered whole study plot uniformly and intervals of visits were sparse, we believe that our influence of nest success was of minor importance and did not substantially affect the results (Götmark 1992).

In conclusion, this study reveals interspecific interactions among breeding birds within a diverse bird community inhabiting Siberian marshland is characterized by negligible anthropogenic impact and a natural structure of nest predator guilds. It demonstrates that a community consisting of a small number of actively nest-defending species together with a diverse group of passive defenders is characterized

by several complementary anti-predator tactics. In general, active nest defenders had higher chances of hatching offspring than did passive defenders. Active nest defence combined with the large body size of the Mongolian gull were two attributes resulting in the highest probability of nest survival for this species. Whereas passive defenders effectively reduced nest predation risk by nest concealment and by nesting in the proximity of active defenders, particularly the Mongolian gull, nest predation risk for birds applying active nest defence seemed to be less flexible and determined by predator incidence. As these active nest defenders built more conspicuous nests, they could increase nesting success by placing their nests farther from the forest edge and from the nests of Mongolian gulls. In any case, active nest defence itself remains the main factor positively influencing nesting success in the bird community. From a nature conservation perspective, it is particularly important to protect large colonies of active nest defenders, such as terns or smaller gulls, which may provide active

protection for nests of the most passive defenders such as ducks or waders. It is essential, moreover, to maintain proper vegetation cover which may provide safe shelter for nests of passive defenders. Finally, conservationists should consider that a sufficient area of interior wetland habitats might reduce edge effects associated with increased predation risk.

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