

Is it always beneficial to breed in the centre? Trade-offs in nest site selection within the colony of a tree-nesting waterbird

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Abstract In most of colonial avian species, central parts of the colonies offer higher safety in terms of predatory pressure. However, in heterogeneous habitats, nest sites of high physical quality are likely to offer effective protection against predators or adverse weather conditions regardless of their location within the colony. The aim of this paper was to investigate whether nest site selection in a tree-nesting waterbird, the Great Cormorant *Phalacrocorax carbo sinensis*, depends on the within-colony location of sites, their physical quality or a combination of these components. The study was conducted during 2010–2011 in a cormorant colony in central Poland. We found that early-breeding individuals preferred nest sites in the central parts of the colony and located high off the ground. The high quality of pairs nesting in these locations was confirmed with good body condition of nestlings, measured by their body masses and plasma concentrations of glucose and urea. A similar spatial pattern was found for the daily nest survival rate and reproductive success. It was found that the central nesting sites associated with high nesting densities were better protected against predators, while the physical quality of nesting sites determined the probability of nest collapse before the conclusion of breeding activities. The two-way process of assessing nest site attractiveness (nest site location vs. physical quality) suggests that, under the limitation of the most attractive nesting sites

(good-quality central sites), tree-nesting waterbirds may trade central nesting locations for the high-quality sites at the peripheries of the colony.

Keywords Coloniality · Central–periphery gradient · Great Cormorant · Nest site selection · *Phalacrocorax carbo sinensis*

Zusammenfassung

Ist ein zentraler Nistplatz immer von Vorteil? Kompromisse bei der Nistplatzwahl innerhalb einer Kolonie baumbrütender Wasservögel

Bei den meisten kolonielebenden Vogelarten bieten die Koloniezentren ein hohes Maß an Sicherheit vor Prädatoren. In heterogenen Habitaten gewähren allerdings Nistplätze mit guten physikalischen Eigenschaften unabhängig von ihrer Lage in der Kolonie effektiven Schutz vor Prädatoren oder widrigen Wetterbedingungen. Ziel dieser Studie war es, zu untersuchen, ob die Nistplatzwahl bei einem baumbrütenden Wasservogel, dem Kormoran *Phalacrocorax carbo sinensis*, von der Lage der Nistplätze innerhalb der Kolonie, der physikalischen Beschaffenheit oder einer Kombination dieser Komponenten abhängt. Die Untersuchung wurde von 2010–2011 in einer Kormorankolonie in Zentralpolen durchgeführt. Wir konnten beobachten, dass früher brütende Individuen Nistplätzen im Koloniezentrum den Vorzug gaben, die sich hoch über dem Boden befanden. Der hohe Status der Paare, welche diese Nistplätze besetzten, wurde durch die gute körperliche Verfassung der Nestlinge, bestimmt durch ihre Körpermasse sowie die Plasmawerte von Glukose und Harnstoff, bestätigt. Eine ähnliche räumliche Verteilung ergab sich bezüglich der täglichen Überlebensrate der Nester und des

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Reproduktionserfolgs. Es zeigte sich, dass zentrale Brutplätze mit hoher Nestdichte besser vor Prädatoren geschützt waren, wohingegen die physikalische Beschaffenheit der Nistplätze die Wahrscheinlichkeit eines Nestzusammenbruchs vor Abschluss der Brutaktivitäten bestimmte. Diese zwei Aspekte bei der Beurteilung der Nistplatzattraktivität (Lage des Nistplatzes kontra physikalische Qualität) legt nahe, dass wo die begehrtesten Brutplätze (zentrale Plätze von guter Qualität) limitiert sind, baumbrütende Wasservögel anstelle zentraler Nistplätze lieber solche von hoher Qualität in den Kolonierandbereichen wählen.

Introduction

Dense breeding aggregations of birds provoke intense competition for nesting sites, which often vary considerably in their attractiveness for the potential breeders (Coulson 1968). It is generally accepted that the centres of colonies offer the highest benefits in terms of fitness. As the efficiency of group defence and vigilance increases in more densely inhabited central parts of the colonies and decreases at the edges (Götmark and Andersson 1984; Yorio and Quintana 1997), pairs nesting in the centres are likely to achieve higher breeding success due to decreased predation-related losses of eggs and chicks. For this reason, individuals of higher quality, expressed by age, experience or physical condition, are likely to occupy better places in the central parts of colonies and relegate individuals of lower quality to less attractive edge sites. This, so-called central–periphery pattern of distribution is characteristic for species breeding in homogeneous habitats, where the variation in physical quality of nesting sites is low or negligible. Central–periphery distribution of pair quality has been reported for several waterbird species, mainly from the Laridae family. One of the first to confirm assumptions of central–periphery gradient in larid colonies was the study on Black-legged Kittiwakes *Rissa tridactyla*, which demonstrated higher physical condition and higher fledging success of central breeding pairs (Coulson 1968). Further research on this species revealed that its population size is limited by the availability of nesting sites in the colony centre (Porter and Coulson 1987), and that centrally nesting individuals have higher survival rates (Aebischer and Coulson 1990). Central–periphery gradients of reproductive success were also confirmed in the Black-headed Gull *Chroicocephalus ridibundus* (Patterson 1965), Ring-billed Gull *Larus delawarensis* (Dexheimer and Southern 1974) and Caspian Tern *Hydroprogne caspia* (Antolos et al. 2006). Higher chick survival in the centres of colonies has also been found in the Common Tern *Sterna hirundo* (Becker 1995) and Herring

Gull *Larus argentatus* (Savoca et al. 2011). A similar central–periphery pattern was recorded in clutch size and chick growth rates of the Whiskered Tern *Chlidonias hybrida* (Minias et al. 2011, 2012b).

Central–periphery patterns may be disrupted in heterogeneous habitats that provide considerable variation in the physical quality of nesting sites. High-quality nest sites are likely to offer effective protection against predators or adverse weather conditions and, in consequence, promote higher reproductive success of breeding birds. If there are apparent fitness consequences associated with nesting in sites of certain physical characteristics, a specific nest site selection pattern is likely to evolve (Orians and Wittenberger 1991). Under such circumstances, high-quality pairs should select nest sites of high physical quality regardless of their location within the colony. Spatial patterns of this kind (so-called random distribution) were recorded, among others, in the European Shag *Phalacrocorax aristotelis* (Velando and Freire 2001) and Brown Booby *Sula leucogaster* (Ospina-Alvarez 2008), species that breed in rocky habitats providing nest sites of varying antipredator safety.

The aim of this study was to investigate whether nesting site selection in a tree-nesting waterbird, the Great Cormorant *Phalacrocorax carbo sinensis*, depends on the within-colony location of sites, their physical quality or a combination of these components. Male Great Cormorants arrive at the colony first and establish territories that are subsequently assessed and selected by females (Schjørring et al. 1999). Since older, high-quality males are expected to more reliably judge nest site quality, relying upon their prior experience (Schjørring et al. 2000), they are likely to choose the best available sites and attract high-quality females. Preferences of high-quality pairs for central nesting site would be consistent with the central–periphery pattern of distribution, while selection according to physical quality would indicate the random model. Alternatively, assuming that both central location and physical quality of nesting site may confer similar fitness benefits, a mixed model of distribution is expected. This would indicate a certain trade-off in the nest site selection, since, under the limitation in the availability of the most attractive nest sites (good quality central sites), birds would have to choose between the net benefits of nesting in centrally located poor-quality sites and occupying the sites of high physical quality in the peripheral zones of the colony. Some empirical support for the disruptions in the central–periphery distribution of pair quality has been presented for Great Cormorant (Minias et al. 2012a). It was demonstrated with geostatistical tools of analysis that the spatial distribution of clutch size within the colony was not consistent with the central–periphery pattern. Furthermore, a positive correlation between clutch size and nest height suggested that nesting sites located high off the ground

may be preferred by high-quality breeding pairs. The correlations between nest height and clutch size have also been reported for the related tree-nesting Double-crested Cormorant *Phalacrocorax auritus* (Blomme 1979).

To assess the patterns of nest site selection, we analysed relationships of nest location characteristics (including both physical quality of nest sites and their within-colony location) with laying date and different indices of pair quality. Following other studies on tree-nesting waterbirds, we proposed nest height and tree diameter as the measures of nest site quality (Post 1990; Ranglack et al. 1991). We used nutritional state of nestlings (measured with plasma concentrations of glucose and urea) and chick body mass at the age of ca. 3 weeks as the proxies of parental quality. Such methodology could be adopted, since, in waterbirds, the nutritional state of chicks is known to depend strictly on the rearing capacities of parents, which positively correlate with such components of parental quality as age, experience and condition (Weimerskirch et al. 2000; Tveraa and Christensen 2002; Gaston and Hipfner 2006). In the second stage of the analysis, we evaluated the effects of two major extrinsic sources of brood failures (predation and nest collapses) on the reproductive success of Great Cormorants occupying nest sites of different quality and located in different parts of the colony. Finally, the relationships of nest location characteristics with nest survival and reproductive success were analysed.

Methods

The study took place in the colony of Great Cormorants at Jeziorsko reservoir (51°73'N, 18°63'E), central Poland, in 2010–2011. The colony was located in the area covered with willow shrubs dominated by white willow *Salix alba* and grey willow *S. cinerea*. For the purpose of the study, we randomly chose 50 nests in 2010 and 60 nests in 2011, which was equivalent to ca. 5–10 % of all Cormorant pairs nesting at the Jeziorsko reservoir each year. In all nests, we determined the date when the first egg was laid (henceforth laying date) with the accuracy of 1 day. All chosen nests were monitored at 3- to 5-day intervals with respect to two major sources of brood losses: predation-related egg losses and nest collapse. To estimate predation-related egg losses, we recorded all cases of eggs with clear marks of predation found inside or in the direct proximity of nests. Also, eggs lost due to unknown reasons (not assignable to such failure causes as nest collapse, dislodging from the nest or lost after clutch desertion) were considered as depredated. We recorded no cases of predation at the stage of chick rearing. Although no species of predator was unambiguously identified, both aerial (mainly corvids) and tree-dwelling (possibly beech martens *Martes foina*) predators were

likely to contribute to egg losses. During fieldwork, no acts of predation were directly witnessed, and the effect of the observer on the predation was assumed to be negligible. Brood losses due to nest collapse were assessed throughout the egg-incubation and chick-rearing stages. Where possible, we also recorded reproductive success expressed as the number of fledglings at the age of over 1 month ($n = 94$ nests).

Each year, of all monitored nests that survived until the moment of hatching, we randomly chose a subsample of 30 nests for the purpose of biochemical analysis. The chosen broods were randomly distributed within the colony, as there were no differences in the coordinates of the nests included in the study and all the other nests in the colony (Wilks: 2010: $F_{2, 121} = 0.18$, $P = 0.84$; 2011: $F_{2, 149} = 1.35$, $P = 0.26$). Blood samples for molecular sexing were collected from all nestlings ($n = 226$) within 2 days from the hatching of the last chick in each nest. Blood (ca. 10 μ l) was taken by puncturing the ulnar vein with a disposable needle. The samples were immediately suspended in 96 % ethanol and stored until the laboratory analyses. Molecular sexing was performed using the DNA extracted from the sampled blood with the Blood Mini kit (A&A Biotechnology, Gdynia, Poland) according to the kit protocol. Amplification of the region encoding chromodomain-helicase-DNA binding protein (CHD) was performed with the primer pair 2550F and 27181R (Fridolfsson and Ellegren 1999), according to the protocol described by Griffiths et al. (1998). The PCR products were stained and separated on 2 % agarose gel until the differences in the product size (ca. 200 bp) were clearly visible.

We measured body mass of all living nestlings (to the nearest 20 g) when the oldest chick in the brood reached the age of 22 ± 1 days ($n = 185$). This was the latest possible moment allowing successful collection of the data, since chicks older than 25 days may start to jump out of the nests when humans approach (Platteeuw et al. 1995; personal observation). At the same time, we collected approximately 2 ml of blood from brachial vein of each chick in order to assess the plasma concentrations of glucose and urea. Sampled blood was placed in EDTA tubes and kept in a cooler. The samples were centrifuged at 3,000 rpm for 15 min within 8 hours of collection. The plasma was separated and kept at -20°C until analysed. All plasma biochemical parameters were analysed using commercial kits and reagents with a spectrophotometer (BTS-330; BioSystems Reagents & Instruments, Barcelona, Spain).

Each year, all active nests were mapped with a handheld Global Positioning System unit (Garmin GpsMap 60Cx; Olathe, KS, USA) with the European Geostationary Navigation Overlay Service (EGNOS) ensuring accuracy of 1–1.5 m. Gathered coordinates were used to calculate

distances between all the nests in the colony. On the basis of the nest-distance matrices, the following nest location characteristics were calculated separately for each year: nearest neighbour distance (m), nest density (number of nests within the radius of 5 m), and distance to the centre of the colony (m). The centre of the colony was calculated as the mean coordinates of all the nests within the colony. Nest location characteristics were calculated for all the nests recorded in the colony throughout the entire breeding season, as reproductive activities of early- and late-breeding pairs overlapped considerably. Two indicators of nesting site quality were additionally measured: nest height and tree diameter. Nest height was taken from the ground to the bottom of the nest with a precision of 0.5 m. Nest tree diameter was measured at breast height 1.2 m above the ground to the nearest 1 mm, and was treated as an indicator of tree size (Chapman et al. 1992). Despite the presence of deep watercourses and water pools where willow shrubs could not develop, the structure of the stand and tree density was fairly homogenous across the colony and availability of high nesting trees was not limited at the peripheries of the colony even late in the season. Due to the young age of the stand (below 20 years), treetops were not fully developed and most of the trees lacked solid horizontal branches. In consequence, the number of potential nesting sites on most of the trees within the colony was highly limited and we recorded maximally two nests per tree (ca. 14 % of all nesting trees). In such cases, we have decided to randomly choose only one nest per tree for the analyses in order to avoid statistical dependence of data. From all nest site characteristics, only nest height had a distribution reasonably close to normal (skewness 0.15 ± 0.23). All other variables (nearest neighbour distance, nest density, distance to the colony centre, tree diameter) were log-transformed prior to analysis in order to improve normality.

Effects of nest location characteristics on daily nest survival rate (DNSR) were analysed with program MARK (White and Burnham 1999), according to the methodology summarized by Dinsmore et al. (2002). The analysis was performed jointly for the periods of laying, incubation and chick rearing until the oldest chick reached 22 days of age. Nests denoted as “lost” in the encounter histories included broods which failed due to predation or nest collapse. Nests lost due to inexplicable reasons or desertion were excluded from the dataset ($n = 5$). The analysis was performed on the data collected in 2010–2011 for 105 nests of known fate. We used Akaike’s information criterion corrected for small sample size (AIC_C) to select the model of best fit. In all fitted models, logit link functions were used. Significance of the relationships between particular nest location characteristics and DNSR was tested with likelihood ratio

tests by comparing the relative fit of appropriate pairs of nested models.

We used t tests to compare nest location characteristics between 2010 and 2011. To investigate relationships between particular nest location characteristics, we used Pearson’s correlation. Laying date, reproductive success, predation-related egg losses, body mass of nestlings and concentrations of plasma metabolites were fitted as dependent variables to general linear models. In each model, the effect of the year was included as a fixed factor and nest location characteristics were treated as covariates. In the analysis of nestling body mass and plasma metabolites levels, we also accounted for the effects of brood size and brood sex ratio. In order to avoid pseudoreplication, the mean value calculated for each brood was the unit of the analysis (Hurlbert 1984). To select for significant independent variables, the stepwise procedures of backward removal were used. Percent of variance in the dependent variable explained by particular independent factors was evaluated with partial eta-squared (η^2). Probability of nest collapse was analysed with the generalised linear model for binominal distribution and logit link function. For this purpose, nest collapse rate was codified binomially with ‘1’ for nests which collapsed during the period of egg incubation or chick rearing and ‘0’ for nests which did not collapse. All nest location characteristics were included in the model as covariates. We did not include the effect of year into the model due to low sample size of collapsed nests. Significance of the relationships in the generalised linear model was determined using Wald statistics. Analogously to the general linear models, the backward removal procedures were used to select for significant independent variables. All statistics followed Zar (1996).

Results

Nest site characteristics

Range and mean values of nest site characteristics are given in Table 1. There were no significant differences in the nest location characteristics between the years 2010 and 2011 (t test, all $P > 0.15$). There was a negative relationship between nest density and distance to the colony centre ($r = -0.47$, $n = 110$, $P < 0.001$). In contrast, distance to nearest neighbour increased together with the distance to the colony centre ($r = 0.29$, $n = 110$, $P = 0.002$). We also found that Cormorants nested higher at the peripheries of the colony ($r = 0.34$, $n = 110$, $P < 0.001$). As expected, nest height correlated with tree diameter ($r = 0.29$, $n = 110$, $P = 0.002$).

Table 1 Range and mean values \pm SE of nest site characteristics ($n = 110$) in the colony of Great Cormorants *Phalacrocorax carbo sinensis* at Jeziorsko reservoir in 2010–2011

Variable	Mean	SE	Min	Max
Nest density (number of nests in 5 m radius)	1.73	0.15	0	7
Nearest neighbour distance (m)	3.44	0.32	0.50	22.42
Distance to colony centre (m)	50.25	2.15	12.10	110.21
Nest height (m)	6.25	0.11	3.5	9
Tree diameter (mm)	156.77	4.89	86	323

Note that the high minimum value of the distance to the colony centre is due to the small water pool located in the very centre of the colony

Laying dates

In 2010, the laying period spanned from 15 March to 13 April (median date: 21 March), while in 2011, laying started on 18 March and finished on 21 April (median date: 1 April). After accounting for the effect of the year ($F_{1, 102} = 21.67, P < 0.001$), we found that laying date was significantly related with nest height ($F_{1, 102} = 20.18, P < 0.001$) and distance to the colony centre ($F_{1, 102} = 8.90, P = 0.004$). Early breeders nested higher off the ground ($\beta = -3.05 \pm 0.68$) and closer to the colony centre ($\beta = 0.10 \pm 0.03$), when compared with late-breeding conspecifics.

Nestling body mass

There was a positive relationship between mean body mass of chicks and nest height ($F_{1, 52} = 7.06, P = 0.010$; $\beta = 61.73 \pm 23.23$; Fig. 1). The relationship remained significant ($F_{1, 49} = 4.39, P = 0.041$; $\beta = 42.41 \pm 20.24$) after accounting for the effects of year ($F_{1, 49} = 8.62, P = 0.005$), and brood sex ratio ($F_{1, 49} = 6.24, P = 0.016$). The effect of nest height explained 11.9 % of variance in the mean chick body mass. There was no relationship between chick body mass with brood size or with other nest location characteristics (all $P > 0.10$).

Concentrations of plasma metabolites

Relationships between plasma urea concentrations of nestlings and nest location characteristics had different patterns in both years. In 2010, we found a significant relationship between mean brood urea level and nest height ($F_{1, 25} = 6.40, P = 0.018$). The relationship was negative ($\beta = -1.04 \pm 0.41$), which indicated higher body condition of chicks raised in nests located high off the ground. Nest height explained 14.0 % of variance in mean brood urea level. By contrast, in 2011, the effect of nest height

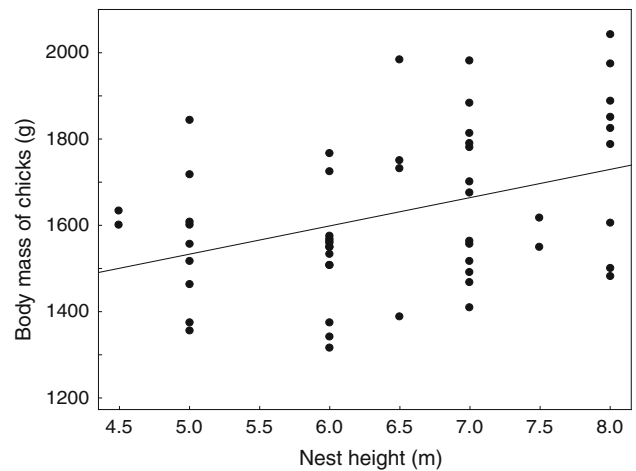


Fig. 1 Body mass of Great Cormorant *Phalacrocorax carbo sinensis* nestlings raised in nests located at different heights at Jeziorsko reservoir in 2010–2011. Each point represents the mean value of chicks from one brood ($n = 53$)

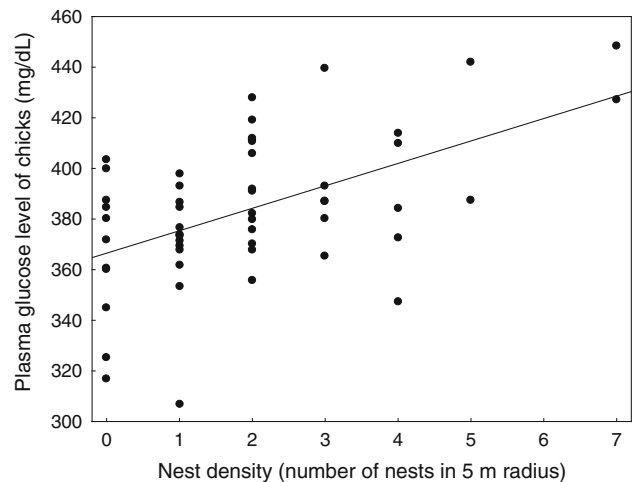


Fig. 2 Plasma glucose concentrations of Great Cormorant nestlings raised in areas of different nest densities at Jeziorsko reservoir in 2010–2011. Each point represents the mean value of chicks from one brood ($n = 53$)

was excluded from the model ($P = 0.24$), but we found a negative relationship between brood urea level and nest density ($F_{1, 26} = 5.50, P = 0.027$; $\beta = -0.63 \pm 0.27$). Nest density explained 16.7 % of variance in mean brood urea level of nestlings. We found no other relationships between mean brood urea level of nestlings and nest location characteristics in 2010 (all $P > 0.10$) and 2011 (all $P > 0.20$).

We also found that pairs nesting in high densities raised chicks with higher plasma glucose concentrations ($F_{1, 52} = 16.67, P < 0.001$; $\beta = 24.12 \pm 5.91$; Fig. 2). Nest density explained 35.4 % of variance in mean brood

glucose level of nestlings. There was no significant effect of year, brood sex ratio, or brood size on the plasma glucose concentration of nestlings (all $P > 0.45$). All other nest location characteristics were also removed from the model (all $P > 0.55$).

Daily nest survival rate and reproductive success

The constant model estimated daily nest survival rate (DNSR) at 0.991 ± 0.002 . The most parsimonious model indicated that DNSR varied with nest age (Table 2), as there was an increase in nest survival probability with increasing age of nests ($\beta = 0.06 \pm 0.02$). At the beginning of laying period, DNSR was estimated at 0.953 ± 0.019 and exceeded 0.990 around the moment of hatching (at 26th day of nest age). The most parsimonious model also indicated the effects of nest height and distance to the colony centre. Likelihood ratio tests revealed significant differences in the fit of the most parsimonious model S (age, h , d_{centre}) with the fit of S (age, d_{centre}) and S (age, h), which demonstrated that both effects explained significant part of variation in DNSR (nest height: $\chi^2 = 4.69$, $df = 1$, $P = 0.030$; distance to the colony centre: $\chi^2 = 7.98$, $df = 1$, $P = 0.005$). We found that nests located high off the ground and in the colony centre had higher DNSR ($\beta = 2.25 \pm 1.02$ and $\beta = -1.12 \pm 0.41$, respectively). The effects of nearest neighbour distance on DNSR had less support in the data ($\Delta\text{AIC} = 0.75$), but there was an indication for the negative character of the relationship between these variables

Table 2 Evaluation of daily nest survival models with associated values of Akaike's information criterion with correction for small samples sizes values (AIC_c), ΔAIC_c , AIC weights (w_i), the number of estimable parameters in each model (K) and deviance (Dev)

Model	AIC_c	ΔAIC_c	w_i	K	Dev
S (age, h , d_{centre})	200.90	0.00	0.37	4	192.88
S (age, h , $d_{\text{neighbour}}$)	201.65	0.75	0.25	4	193.63
S (age, $d_{\text{neighbour}}$)	201.75	0.85	0.24	3	195.74
S (age, d_{centre})	203.58	2.68	0.10	3	197.57
S (age)	206.53	5.63	0.02	2	202.53
S (age, h)	206.87	5.97	0.02	3	200.86
S ($d_{\text{neighbour}}$)	219.02	18.12	<0.01	2	215.02
S (d_{centre})	221.69	20.79	<0.01	2	217.69
S (h)	224.32	23.42	<0.01	2	220.31
S (.)	225.15	24.25	<0.01	1	223.15
S (density)	225.31	24.41	<0.01	2	221.31
S (td)	226.13	25.23	<0.01	2	222.13
S (y)	226.59	25.69	<0.01	2	222.59

Model subscripts: (.) constant daily survival, y year, td tree diameter, density nest density, h nest height, d_{centre} distance to the colony centre, $d_{\text{neighbour}}$ nearest neighbour distance, age nest age

($\beta = -0.13 \pm 0.05$). There was no indication for the effects of tree diameter and nest density on DNSR. There were also no between-year differences in this trait, as indicated by low fit of S (y) model (Table 2).

Mean reproductive success of Great Cormorants breeding at Jeziorsko reservoir was 2.10 ± 0.18 fledglings per pair ($n = 90$). Successful pairs raised on average 3.32 ± 0.09 fledglings ($n = 57$). There was no between-year variation in reproductive success of Great Cormorants ($F_{1, 86} = 0.31$, $P = 0.58$). Similarly to the daily nest survival rate, reproductive success was significantly related with distance to the colony centre ($F_{1, 88} = 6.92$, $P = 0.011$) and nest height ($F_{1, 88} = 4.20$, $P = 0.043$). Great Cormorants nesting far from the colony centre and low off the ground raised a lower number of fledglings ($\beta = -1.09 \pm 0.42$; $\beta = 0.37 \pm 0.18$, respectively). However, when laying date was included in the models, the effects of both nest site characteristics lost their

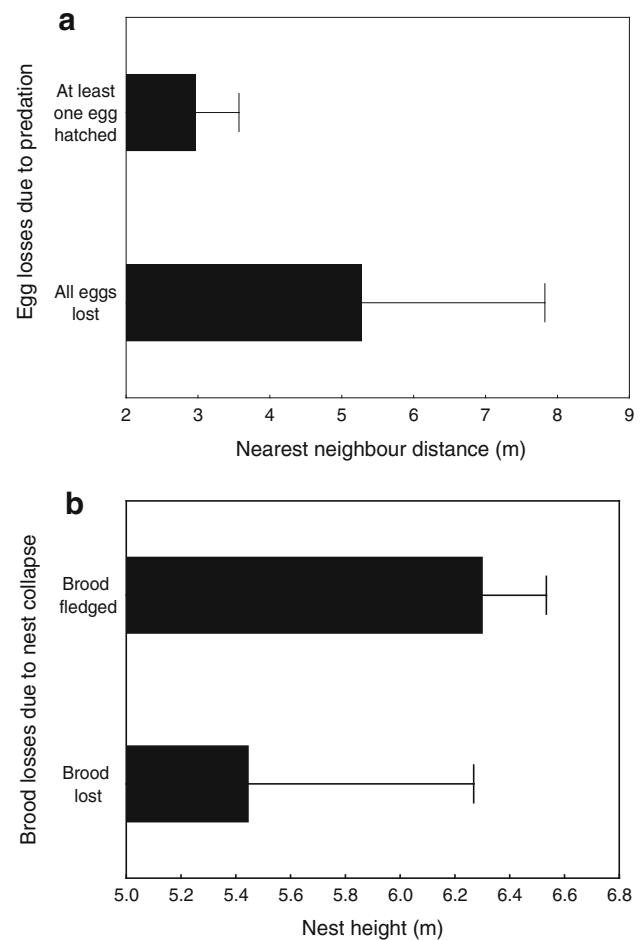


Fig. 3 Two major sources of brood losses, predation (**a**) and nest collapse (**b**), in relation to the nest site location characteristics, nearest neighbour distance (**a**) and nest height (**b**), in the colony of Great Cormorants at the Jeziorsko reservoir in 2010–2011. Horizontal bars with whiskers represent mean + $1.96 \times \text{SE}$

significance ($F_{1, 87} = 2.08$, $P = 0.15$; $F_{1, 87} = 1.44$, $P = 0.23$; respectively).

Sources of brood losses

Predation-related egg losses were recorded in 39.6 % of clutches ($n = 96$). On average, 0.84 ± 0.13 egg was lost per nest. In 23.7 % of the clutches, predation-related losses of eggs were recorded at the stage of egg laying ($n = 96$). The losses of the entire clutches during the incubation period were recorded in 11.5 % of all the nests ($n = 96$). There was no between-year variation in the rate of egg loss ($F_{1, 89} = 0.12$, $P = 0.73$). We found a positive relationship of predation-related egg losses with distance to nearest neighbour ($F_{1, 94} = 5.50$, $P = 0.21$; $\beta = 0.38 \pm 0.16$; Fig. 3a). The effects of nest density, distance to the colony centre, nest height and tree diameter were excluded from the model (all $P > 0.15$).

Nest collapse was recorded in 9.9 % of all nests ($n = 91$). There was a significant relationship between probability of nest collapse and nest height ($W = 4.29$, $P = 0.038$, Fig. 3b). Nests located at lower heights had higher probability of collapsing during the breeding season ($\beta = -0.76 \pm 0.36$). Other nest location characteristics were excluded from the model (all $P > 0.10$).

Discussion

One of the major findings of this study was that body condition of Great Cormorant nestlings varied with regard to both within-colony nest location and physical quality of nest sites. Nest height was identified as significant component of nest site quality in the studied colony. We here assume that birds of high quality choose the sites of highest quality. Pairs nesting high off the ground raised offspring of higher condition, which was confirmed by, among others, their greater body masses at the age of ca. 3 weeks. Body mass of chicks is considered a reliable proxy of parental quality in waterbirds. A number of studies reported significant effects of parental age and condition on growth rates or body masses of chicks in this avian group (Lorentsen 1996; Wendeln and Becker 1999; Tveraa and Christensen 2002; Gaston and Hipfner 2006). Better nutritional state of chicks from nests located high off the ground was also confirmed with lower plasma concentrations of urea. Plasma levels of nitrogenous excretion components, including urea, are known to reliably reflect condition of birds since they increase in response to starvation, when the tissue proteins are actively mobilized as a source of energy (Alonso-Alvarez and Ferrer 2001). We also found that the mean plasma urea concentrations of nestlings decreased with increasing nest density. The opposite relationship was

found for plasma glucose level, a parameter that has been reported to especially well correlate with body condition of Great Cormorant chicks (Minias and Kaczmarek 2013). Both relationships confirmed higher condition of nestlings in the areas of high nest aggregations, characteristic for the central parts of the colony.

The analysis of laying dates and chick body condition indicated that high-quality pairs of Great Cormorant selected for nest sites located in the central parts of the colony and high off the ground. Since phenotypic quality of nesting birds tend to correlate with the quality of occupied nest sites, the effects of both these factors on reproductive success could not be unequivocally distinguished without appropriate experimental manipulations. In fact, high parental quality in combination with safe nest location was likely to be responsible for the lower rate of egg losses in the central parts of the colony. Despite the complexity of this pattern, it seems that better protection against predators may be considered as the main advantage of choosing centrally located nest sites by Great Cormorants. In contrast, the physical quality of nest sites, expressed by the size of the nesting tree, affected nest stability and determined the probability of nest collapse during incubation of the eggs and the chick-rearing period. Nests located higher off the ground are usually built on higher and stronger trees, which are more resistant to high winds and prevent chicks or eggs from being dislodged (McNeil and Léger 1987). In contrast, the nests located low over the ground are more likely to collapse before the conclusion of reproductive activities due to insufficient strength of the bush-type vegetation to withstand the weight of the nests with growing chicks. Nesting in high positions may confer some additional benefits, such as better visibility, which may promote the successful escape of adult birds in the case of danger (Bregnballe and Gregersen 2003). Although it was not demonstrated in our study, nests located high off the ground could also provide a better anti-predator protection, as they may be less accessible for ground- or tree-dwelling predators. In the White Ibis *Eudocimus albus*, higher brood survival in the nests located high off the ground was proved to reflect differences in the ease of access for predators (Post 1990). A positive relationship between the number of raised offspring and nest height has been reported also for Great Cormorants breeding in Kenya (Childress and Bennun 2000).

The two-way process of assessing nest site attractiveness (nest site location vs. physical quality) suggests that, under the limitation of the most attractive sites in the colony, tree-nesting waterbirds may experience a trade-off in nest site selection in response to predation pressure and nest stability. When all good-quality nesting trees in the centre of the colony are already occupied by high-quality pairs, late-breeding pairs may face a choice between low

nesting trees or bushes located centrally and high nesting trees in the peripheral zones of the colony. Taking into account high nesting densities in most waterbird colonies, such a situation may occur frequently, as all good-quality central sites are likely to be occupied at the beginning of the breeding season. Although predation is considered a major source of nest failure in birds (Martin 1993), we suggest that in the Great Cormorant the selective pressure to choose the site which would guarantee a low probability of nest collapse may be of comparable importance as the selective force to reduce predation risk. In the studied colony, 11.5 % of breeding pairs experienced predation-related losses of all eggs within a clutch, which was nearly equivalent to the 9.9 % rate of nest collapse. Nevertheless, nest stability may be associated with relatively stronger fitness consequences for breeding birds. Nest collapse often takes place during the advanced stages of breeding, frequently at the stage of chick rearing (personal observations). Losing the brood at an advanced stage of development is preceded by allocation of a considerable amount of parental time and energy into reproductive activities and, thus, it is likely to preclude a re-nesting attempt during the same breeding season. In consequence, unsuccessful pairs experience great reproductive costs that do not add to their lifetime reproductive success. By contrast, the detrimental effects of predation prevail at the early stages of breeding, during egg laying or at the beginning of incubation when the nests are more frequently left unattended. Predation-related loss of clutch at the beginning of the breeding season promotes laying of replacement clutches during the same breeding season, as has been found in several avian taxa, as well as in waterbirds (Hipfner et al. 1999).

To our knowledge, this study provides the first evidence for the potential trade-offs in nest site selection within the colonies of tree-nesting birds. Generally, most of the studies on nest site selection have failed to take into account more than one source of nest loss, which limits our understanding on the complexity of cues affecting algorithms of nest site choice in birds (Fisher and Wiebe 2005). As one of the exceptions, the study of Coulson (1968) demonstrated that the competition for good-quality nesting sites was substantially intensified in the centre of a Black-legged Kittiwake colony when compared with the peripheral zones. He concluded that, for this reason, both physical quality and central location of the site should yield certain benefits for breeding adults, which was confirmed in later studies on this species (Regehr et al. 1998).

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