

Great crested grebe (*Podiceps cristatus*) synchronizes the beginning of incubation with a protecting species

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Abstract

Great crested grebes (*Podiceps cristatus*) are opportunistic breeders nesting in colonies or solitarily in different biotopes with varying nesting dates in different circumstances. On the northern coast of the Neva Bay in the eastern part of the Gulf of Finland, great crested grebes breed solitarily, in colonies situated in reed beds and in a colony on the open water in direct vicinity of a colony of black-headed gulls (*Larus ridibundus*) and black terns (*Chlidonias niger*). In the vicinity of the larid colony, grebes profit from the protecting behaviour of gulls and terns in a similar way as they do in their mixed colonies with larids. Despite the fact that small larids have a shorter incubation period than great crested grebes, the latter synchronize their beginning of incubation with the gulls and terns. The incubation of all three species in two adjoining open-water colonies started on the same dates. The incubation of grebes nesting in the reed beds began significantly later. The average clutch sizes did not differ significantly between the colonies situated on the open water near larids and those in the reeds. The average lowest distances between the nests of great crested grebes in the open water colony were larger than in the reed bed colonies. The ability to synchronize the beginning of incubation with a small protecting species helps great crested grebes to occupy otherwise unsafe habitats.

Keywords: waterfowl, protective nesting associations, reed, clutch size, distance between nests, nesting dates, black-headed gull, black tern.

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Introduction

Some species of birds protect against predators not only their nest, but a fairly large area around it. Other birds can reduce nest predation risk by exploiting the nest defence behaviour of these species. Such interactions are described for many orders of birds. Quinn and Ueta (2008) reviewed 62 studies that looked at protective nesting associations. According to their review, protective associates come from the Charadriiformes, the Falconiformes, and the Strigiformes. Protected associates are found in nine orders. The most common protected species belong to the Anseriformes, the Charadriiformes, the Passeriformes, and the Podicipediformes. Nesting of different grebe species under the protection of other species has already been reported (Ulfvens, 1988; Burger, 1995; Klimov, Melnicov, and Zemlyanukhin, 2000; Chukhareva and Kharitonov, 2009; Golovina, 2012), including for great crested grebes (*Podiceps cristatus*).

Great crested grebes are opportunistic breeders (Simmons, 1974; Ulfvens, 1989). They may breed solitarily and in colonies (Simmons, 1974; Fjeldså, 2004; Konter, 2005). The birds can build floating nests, bottom nests, stone top nests, and shore nests (Ulfvens, 1989). They may hide their nests in reeds or bulrushes. In the absence of protective vegetation, grebes often nest in association with larids (Burger, 1984; Goc, 1986; Ulfvens, 1989; Tolchin, 2011). In these cases, they

generally build mixed colonies with larids, as have been described previously. However, in the Neva Bay of the Gulf of Finland, some of the great crested grebes present did not build their platforms inside the larid colony, but formed a colony of their own on the open water directly adjacent to a colony of black-headed gulls (*Larus ridibundus*) and black terns (*Chlidonias niger*). This case poses several questions. Can grebes exploit the protecting behaviour of small gulls and terns if they are only close neighbours? Do the parameters of grebes' nesting change in a colony situated in the vicinity of these larids? What are these changes?

In mixed colonies with larids, grebes start egg laying at an earlier date than solitary breeders inside reeds (Goc, 1986). However, inside gull colonies in offshore areas, great crested grebes breed later than in a traditional habitat (Ulfvens, 1989). The timing of nesting may be earlier near the protecting species, as birds try primarily to inhabit the most secure sites; this was shown for black-necked grebes (*Podiceps nigricollis*) (Chukhareva and Kharitonov, 2009). Goc (1986) assumed that great crested grebes synchronize nesting with the gulls, but he did not prove this assumption.

In most cases, the protective associate is larger in size and has a substantially longer breeding season than the protected species; the latter then probably has little need to adjust its timing of breeding (Wheelwright, Lawler, and Weinstein, 1997; Quinn, Prop, Kokorev, and Black, 2003; Kharitonov et al., 2008; Quinn and Ueta, 2008). In some cases, the duration of nesting is similar for both associates. Then, the timing of nesting can be critical for the protected associate because their nests could become exposed and prone to predation if the protective species were suddenly to finish breeding and leave (Ueta, 1998; Richardson and Bolen, 1999; Quinn and Ueta, 2008). The incubation periods of the black tern (18–22 days) and the black-headed gull (22–26 days) are shorter than the incubation period of the great crested grebe (22–29 days). This could create difficult conditions for the grebes nesting in their direct vicinity in the Gulf of Finland. How do the grebes cope with possible problems resulting from their longer incubation?

In an attempt to answer this question, we mapped the platforms of the colonies and solitary nests of great crested grebes in the open water and in the reed beds and determined the distances between nests, the dates of the beginning of incubation, and the clutch sizes. We then compared the results for the different nesting types of the grebes. Such comparisons are important for our understanding of the abilities of birds to adapt to a changing environment. In areas lacking protecting species, grebes nest inside reed or bulrush beds only (Tolchin, 2011). The possibility to nest under protection allows great crested grebes to settle in new types of habitats (Goc, 1986; Ulfvens, 1989; Golovina, 2012).

Study area

The study was conducted in the Russian part of the Gulf of Finland near the Northern Coast of the Neva Bay Nature Reserve. The reserve is situated in the Primorsky district of St. Petersburg between the villages Olgino and Lisy Nos (Fig. 1). It includes the coast and the island Verperluda. The vegetation of the reserve consists of forest communities with a predominance of spruce, pine, birch, and black alder. There are also residual areas of deciduous oak forest. The total area of the reserve is 330 hectares (Hramtsov, Kovaleva, and Natsvaladze, 2013).

The majority of the shallow waters is covered by dense reed beds (*Phragmites australis*). The beds alternate with large areas of open water. Another dominant type of above-water vegetation is bulrush (*Scirpus lacustris*). Small patches of *Typha spp.* are also found. The above-water vegetation does not grow farther than 500 m from the coast.

The narrow belt of shallow waters along the borders of the reserve is one of the few places near the city of Saint Petersburg where waterbirds can breed and have a stop on their migration route. The most numerous species here are great crested grebe (*Podiceps cristatus*), tufted duck (*Aythya fuligula*), mallard (*Anas platyrhynchos*), wigeon (*Anas penelope*), teal (*Anas crecca*), goldeneye (*Bucephala clangula*), and coot (*Fulica atra*). The conservation of this habitat is one of the most important tasks on the Northern Coast of the Neva Bay Nature Reserve (Noskov and Botch, 1999).

Materials and Methods

Total nest counts of great crested grebe, black-headed gull (*Larus ridibundus*), and black tern (*Chlidonias niger*) were carried out in the period from 2 June to 10 June and from 24 to 27 July 2013 in the shallow water zone at a distance of 500 m from the coast, in the reed beds and on the open water. The surveys were conducted on the same territory twice in order to identify both early and late nests, as the nesting period of many waterfowl species in the area is very long, and new nests may appear from late May to July (Malchevsky and Pukinsky, 1983; Menshikova, 2005).

The surveys covered a total area of 2.5 km² with a maximum water depth of 1.2 m. The coordinates of each nest were determined with a GPS navigator. Habitat type (reeds or open water) and clutch size were estimated for each nest. Grebes start incubation before clutch completion and there is much individual variation in this. To calculate the average clutch size we only considered nests where incubation had already lasted for more than 10 days, thus excluding incomplete clutches from the calculations. The incubation stage was determined

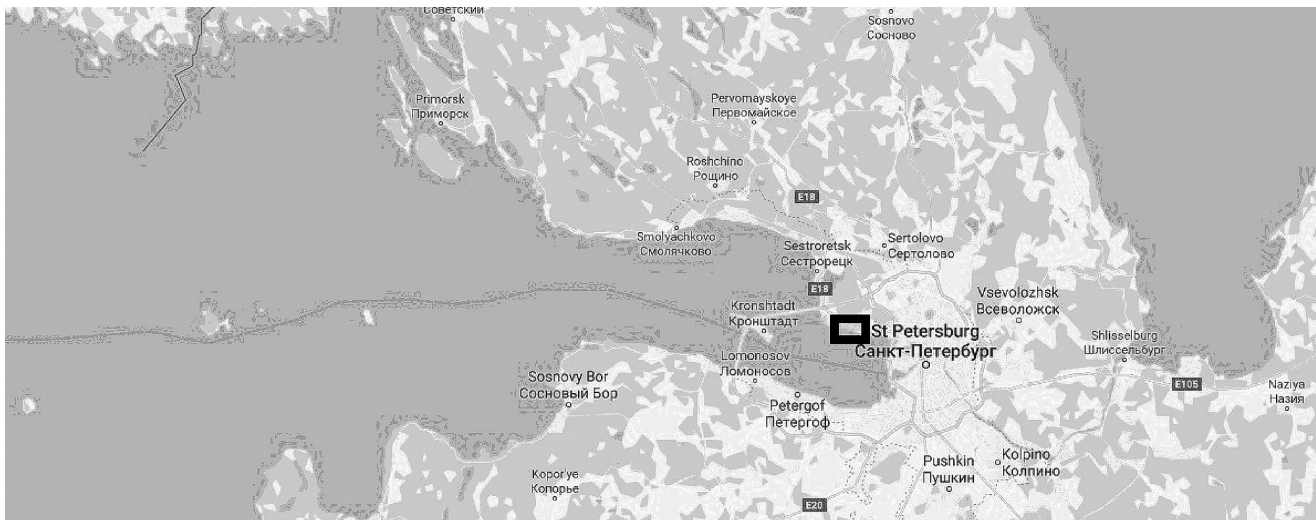


Fig. 1. Location of the study area.

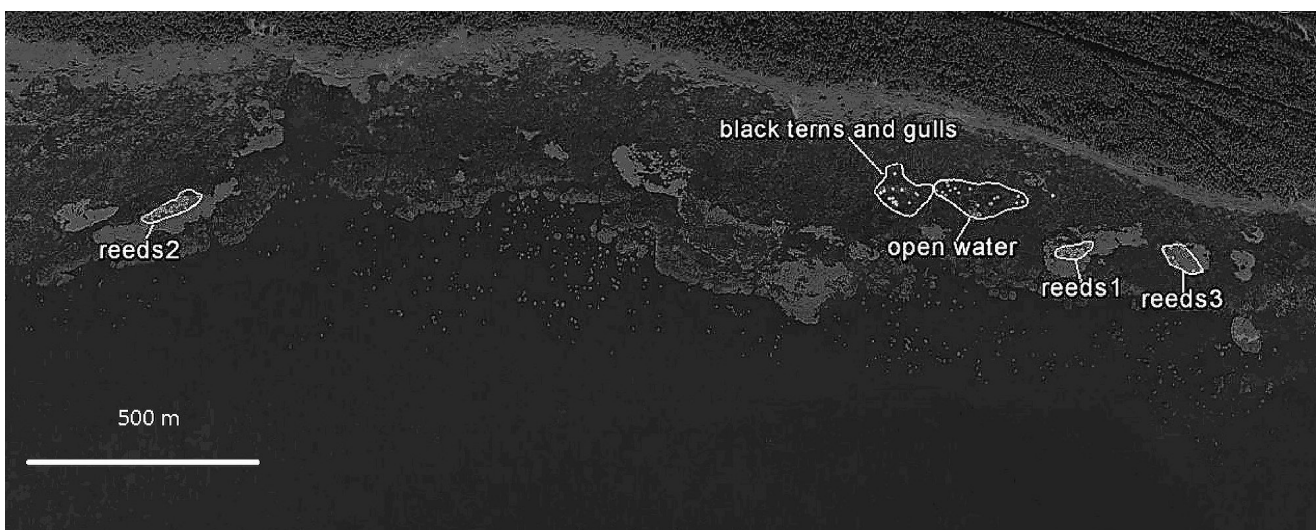


Fig. 2. Distribution of the colonies of great crested grebes, black terns, and black-headed gulls. Black terns and gulls — the colony of black terns and black-headed gulls. Open water — the colony of great crested grebes on the open water near the colony of black terns and black-headed gulls. Reeds 1, reeds 2, and reeds 3 — the colonies of great crested grebes in the reeds.

by the water test (Hays and LeCroy, 1971; Ar and Rahn, 1980; Reiter and Andersen, 2008).

Four colonies of great crested grebes and one mixed colony of black-headed gulls and black terns were found in the area under investigation (Fig. 2). The colony of black-headed gulls and black terns was situated on the open water 220 m from the coast. It was separated from the coast by reeds. We recorded 42 nests of black terns and 12 nests of black-headed gulls. The incubation stage was measured for 20 nests of black terns and 4 nests of black-headed gulls.

Three colonies of great crested grebe were located in the reed beds and one colony was found on the open water near the colony of black-headed gulls and black

terns. The colony of grebes near the colony of black-headed gulls and black terns consisted of 21 nests. In the colonies in reed beds, 32, 43, and 12 grebe nests were found. Four solitary nests of the great crested grebe were recorded there as well.

The Kruskal-Wallis test was used to compare the dates of incubation initiation in the colonies of the great crested grebes, the number of eggs in the clutches and the closest distances between the nests. In the analysis of the dates of the beginning of incubation, the earliest date (22 May) was equal to 1 while the latest date (2 June) was equal to 12.

The Mann-Whitney test was used to compare the dates for the beginning of incubation and for the hatching of black terns and great crested grebes.

Results

Incubation by colonial grebes started in the period from 22 May to 2 June. In the colony located on the open water and associated with larids, this period extended from 22 to 31 May. At the colonies located in the reeds, the birds started incubation between 25 May and 2 June. Thus, the incubation in the colony near the larids started significantly earlier than in the reed colonies (Kruskal-Wallis test: $H(3, N = 102) = 19.44, p < 0.05$) (Fig. 3).

The incubation of eggs in the nests of black terns started in the period from 26 May to 7 June. The difference between the dates of the beginning of incubation of black terns and great crested grebes was not significant (Mann-Whitney U Test: $U = 219.00, Z = 0.03, p > 0.05, N_1 = 20, N_2 = 22$). The median date of the beginning of incubation was 27 May for both species (Fig. 4).

As the incubation period of the great crested grebes (22–29 days) is longer than for the black terns (18–22 days), hatching in the nests of the grebes associated with larids was significantly later than in the nests of the terns (Mann-Whitney U Test: $U = 69.00, Z = 3.80, p < 0.05, N_1 = 20, N_2 = 22$). The median hatching date for black terns was 16 June; for great crested grebes, it was 21 June (Fig. 5).

In four nests of black-headed gulls, incubation started on 27 and 28 May, which coincides with the median date of incubation initiation by black terns and great crested grebes.

The average closest distance between nests in the colony of grebes situated near the colony of larids was 21 m. Between nests in the reed colonies, the distances were 7, 8, and 16 m (Fig. 6) and these distances were significantly lower (Kruskal-Wallis test: $H(3, N = 102) = 20.30, p < 0.05$).

The number of eggs in the clutches of the great crested grebe in the four colonies varied from one to five. The mean clutch size in the colony situated near the larids was 3.4 eggs. In the reed colonies, the averages were 3.7, 3.9, and 3.6 eggs. No significant differences in clutch size were found in the grebe colonies (Kruskal-Wallis test: $H(3, N = 70) = 1.75, p > 0.05$) (Fig. 7).

In the study area, only four solitary nests were detected. This low number does not allow including this type of nesting in the statistical analysis. However, incubation in the solitary nests began much later than in any of the colonies. In two nests, the incubation started on May 29 and June 2. These clutches consisted of five and four eggs. In the other two nests, in-

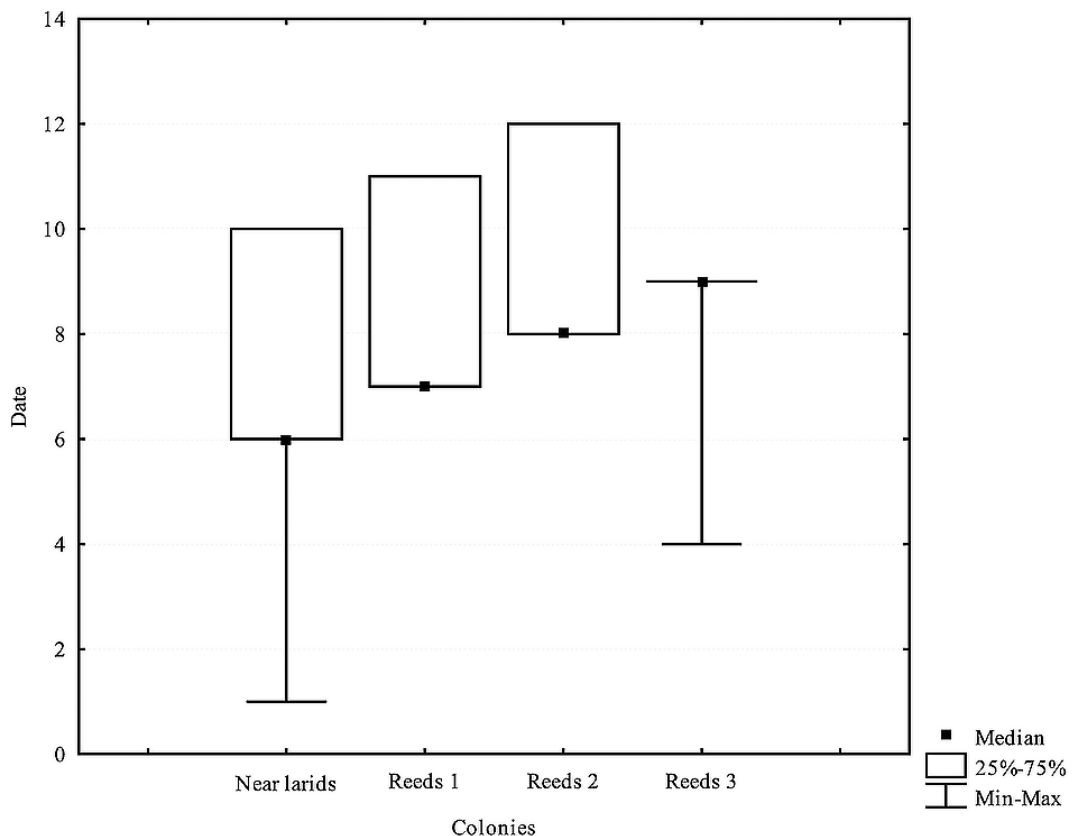


Fig. 3. The dates of the beginning of incubation of great crested grebes in the colony near the colony of larids (Near larids) and in the three reed colonies (Reeds 1, Reeds 2, and Reeds 3). The earliest date of the beginning of incubation (22 May) is equal to 1; the latest date of the beginning of incubation (2 June) is equal to 12.

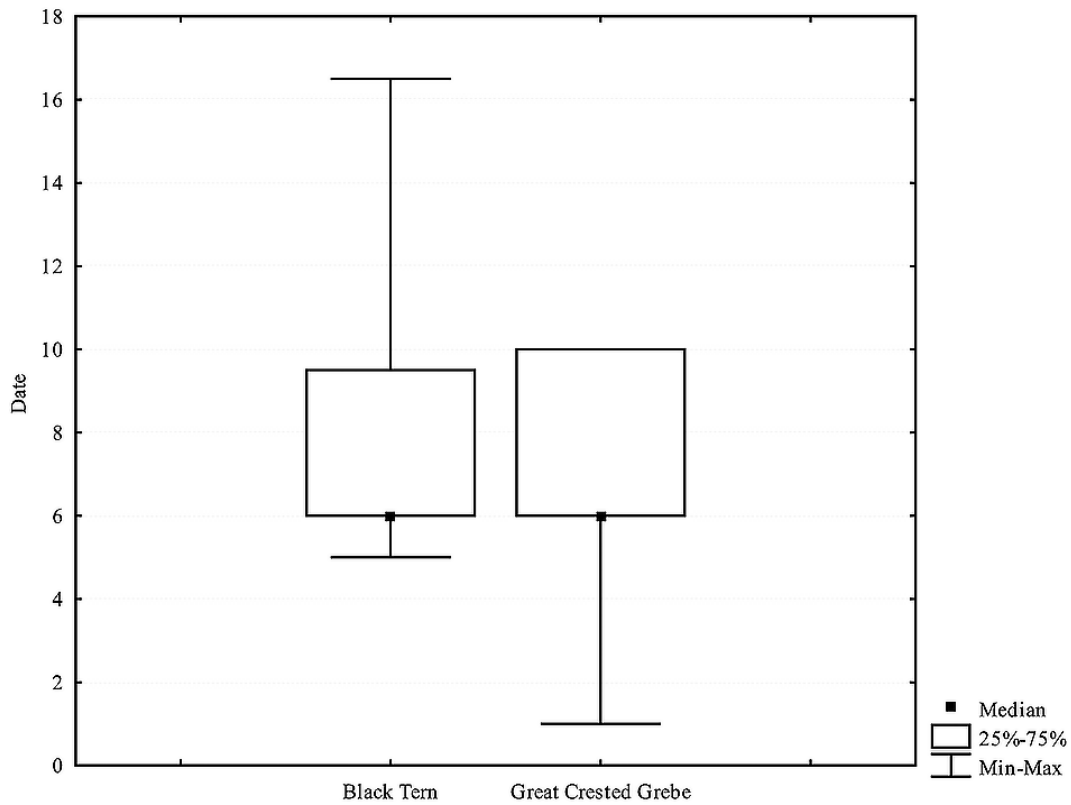


Fig. 4. The dates of the beginning of incubation in the nests of the great crested grebe in the colony situated near the colony of larids and in the nests of the black tern. The earliest date of the beginning of incubation (22 May) is equal to 1; the latest date of the beginning of incubation (7 June) is equal to 17.

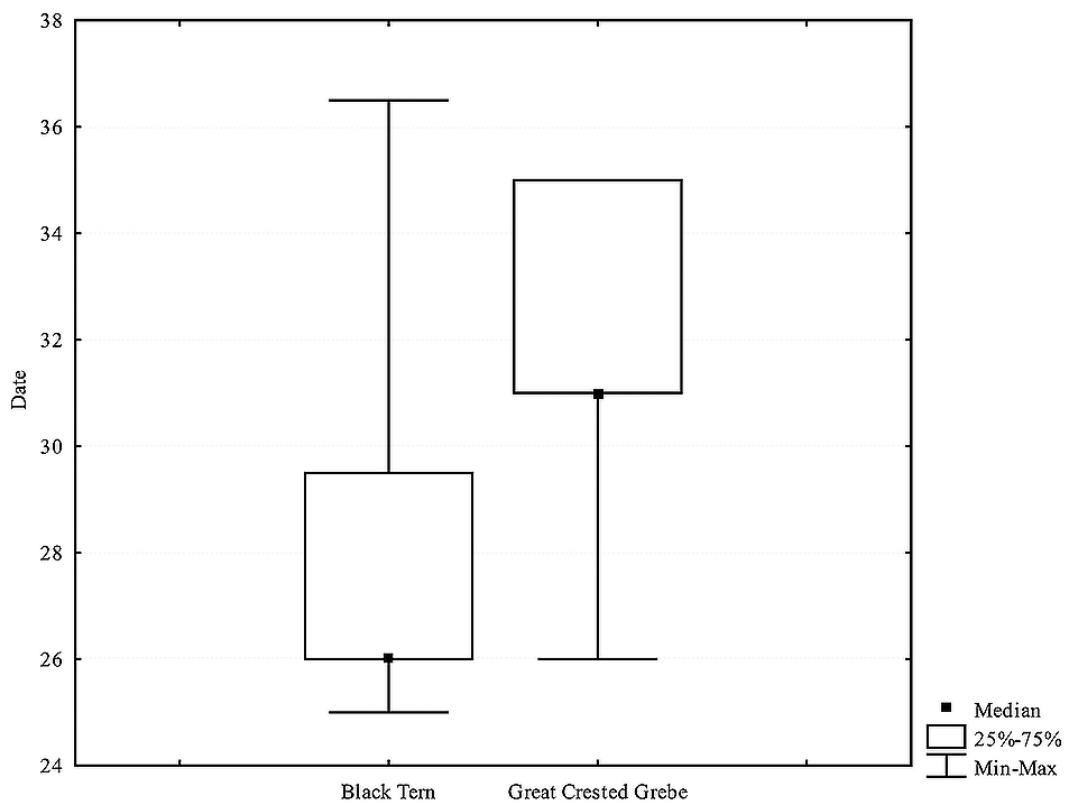


Fig. 5. The dates of the hatching in the nests of the great crested grebe in the colony situated near the colony of larids and in the nests of the black tern. The earliest date of the beginning of incubation (22 May) is equal to 1; 27 June is equal to 37.

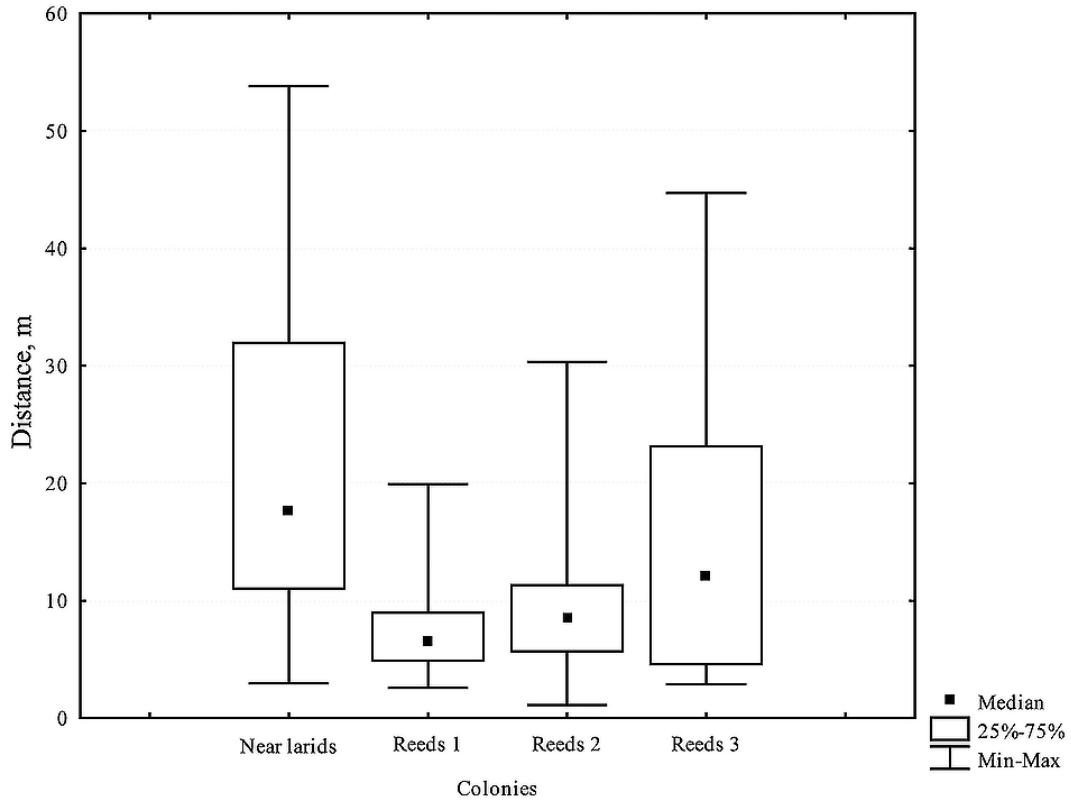


Fig. 6. The closest distances between nests in the colonies of the great crested grebe in the colony near the colony of larids (Near larids) and in the three reed colonies (Reeds 1, Reeds 2, and Reeds 3).

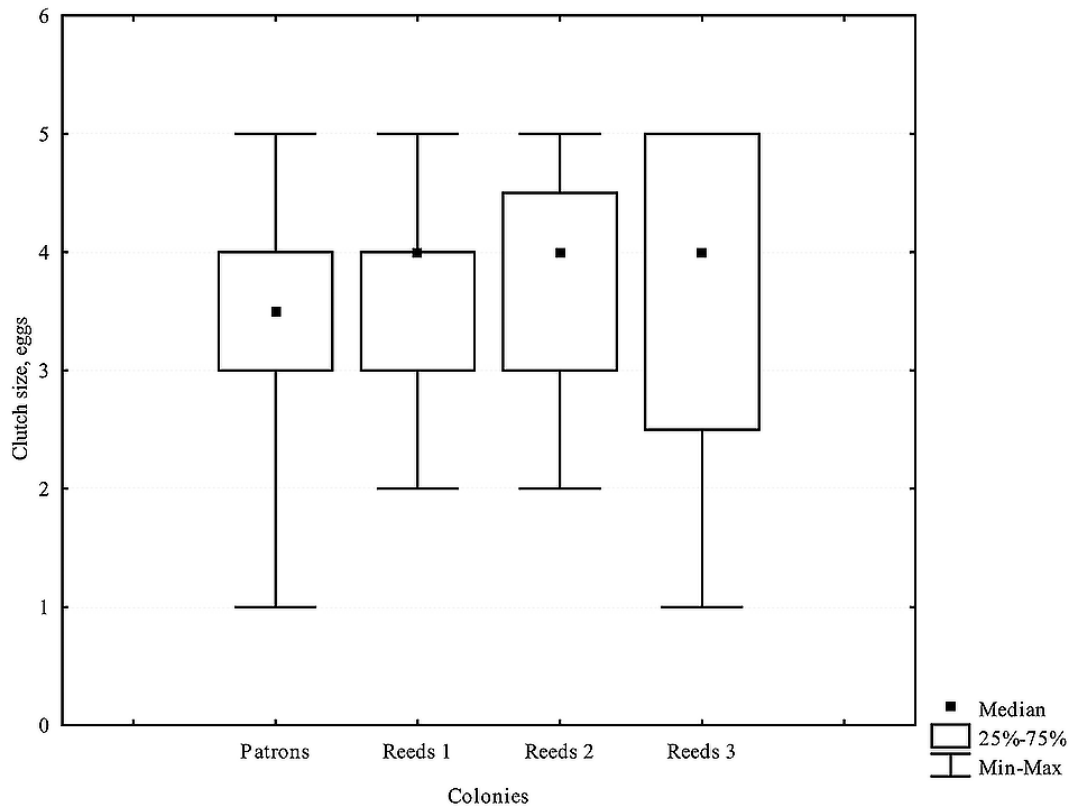


Fig. 7. The number of eggs in the nests of the great crested grebe in the colony near the colony of larids (Near larids) and in the three reed colonies (Reeds 1, Reeds 2, and Reeds 3).

cubation had not yet started by June 10. The clutches contained one and three eggs, and were probably still incomplete.

Discussion

In western (Cramp and Simmons, 1977), central (Goc, 1986), eastern (Dementiev and Gladkov, 1951) and southern Europe (Melde, 1973), most great crested grebes start nesting in May or June. In the Neva Bay of the Gulf of Finland, they follow the same nesting schedule; the incubation in the nests of grebes began in the period from 22 May to 10 June.

Incubation in the grebe colony situated near the larids started significantly earlier than in the reed colonies and in the solitary nests. Grebes nest in dense vegetation to hide their nests from predators. However, by the beginning of the nesting season, vegetation may not have developed enough to hide the nests (Stanevičius, 2001). If it is possible to nest under the cover of a protecting species, grebes can take advantage of this opportunity to nest earlier. At the same time, these could be the most secure sites, meaning that the birds will try primarily to occupy these sites (Chukhareva and Kharitonov, 2009). In the area we studied, the grebes possibly primarily tried to inhabit sites under the protection of larids, but as space there is rather limited, not all grebes would have a chance to establish their platform there. Grebes failing to gain a stronghold would have to start nesting in the reed colonies only after that.

The beginning of grebe incubation in the direct vicinity of the colony of small larids was synchronized with the protecting species: the incubation of all three species started on the same dates. The search for secure sites is linked to the laying date synchrony with protecting species because open-water habitats are not secure for grebes before the protectors start nesting. Matching their incubation dates with the protecting species allows the grebes to settle in open water habitats.

In our study, the average closest distance between the nests in the colony of grebes situated on the open water near the gulls and terns was larger than in the colonies in the reeds. Grebes' territorial behaviour could be a reason for such distribution. As birds in reeds do not directly see the adjacent nest, this could allow them to build nests closer to each other. The density of the floating vegetation could be another reason for the larger distances between the nests on the open water. If the floating vegetation is not very dense, nest building may have to be more spaced out, because the grebes have to bundle the vegetation of a greater area or because only some limited areas are suitable for nest building.

Possible nest predators for the great crested grebe are red foxes (*Vulpes vulpes*), domestic cats and dogs, rats (*Rattus spp.*), grass snakes (*Natrix natrix*), gulls (*Larus*

argentatus, *L. canus*, *L. ridibundus*), hooded crows (*Corvus cornix*), and common magpies (*Pica pica*) (Burger, 1974; Stanevičius, 2002; Vogrin, 2002). On the northern coast of the Neva Bay, where all nests are situated on the water, crows and gulls are the main predators. An analysis of 62 studies showed that half of the studies provide at least observational evidence in support of the hypothesis that protected species gain reproductive success benefits when nesting near protective associates (Quinn and Ueta, 2008). Gulls protect their colonies from predators, but they are egg predators too and occasionally steal eggs when an incubating bird leaves its nest unattended (Bourget, 1973; de Fouw et al., 2016). As a result, the clutch size near gulls' nests could be reduced. In some cases, nesting near aggressive species could protect from some predators but attract other ones. Spotted sandpipers (*Actitis macularia*) nesting near common terns (*Sterna hirundo*) are protected from minks (*Mustela vison*), but a colony of terns attracts turnstones (*Arenaria interpres*) feeding on terns' eggs and sandpipers' eggs as well (Alberico, Reed, and Oring, 1991). Terns and gulls on the open water may attract crows to their colony as well. In such a situation, nests at the edges of the gull colony could be particularly endangered. This would mean that creating a grebe colony near a gull or tern colony is a rather risky strategy. This would be different in a mixed colony where the nests of the grebes are located inside the larid colony where protection is more direct. However, if the larids protect a sufficiently big area around their colony, it could be similarly safe for the protected species to establish an immediately neighbouring colony. In our study, the number of eggs in the clutches did not differ significantly in the colonies situated near the protecting species and in the reed colonies: if egg loss to the larids occurred, it remained insignificant. Moreover, the clutch size was typical for the great crested grebe in many other regions (Ivanov, Kozlova, Portenko, and Tugarinov, 1953; Iljichev and Flint, 1982; Malchevsky and Pukinsky, 1983; Rjabitsev, 2001; Goc, 1986; Bukacińska, Bukaciński, and Jabkowski, 1993; Konter, 2005). This means that proximity to a colony of small larids can be as safe as the vegetation cover of reed beds.

The area of the mosaic of the reed beds and the open water patches is very extensive near the northern coast of the Neva Bay. A lack of open spaces, floating vegetation, or reed beds does not seem to be an obvious reason for grebes to nest near the larid colony. However, the synchronization of the beginning of incubation with the larids and the equal clutch size in the reed and open water colonies suggest that grebes exploit the protecting behaviour of the larids. The ability to synchronize their breeding terms with those of the protecting species could help great crested grebes to occupy otherwise unsafe habitats and to resist predator pressure.

The shorter incubation period by the larids is not problematic as such, as their chicks are fed on the nest and the protection of the colony thus continues beyond hatching. However, with the appearance of the chicks, the food requirements of the larid colony grow, which could present a new threat to the neighbouring grebes. It could well be that the protection for the grebes only works to their benefit with a colony of small-sized larids. To really assess the advantages of the association with the gulls and terns, an analysis of the hatching and breeding success of grebes in close proximity to a colony of larids is essential. The clutch sizes of the grebes on the hatching dates could already provide a good indication, and this could be the subject of future research.

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References

- Alberico, J. A. R., Reed, J. M., and Oring, L. W. 1991. Nesting near a Common Tern colony increases and decreases Spotted Sandpiper nest predation. *Auk* 108:904–910. <https://doi.org/10.1093/auk/108.4.904>
- Ar, A. and Rahn, H. 1980. Water in the avian egg: overall budget of incubation. *American Zoology* 20:273–384. <https://doi.org/10.1093/icb/20.2.373>
- Bourget, A. A. 1973. Relation of eiders and gulls nesting in mixed colonies in Penobscot-Bay, Maine. *Auk* 90:809–820. <https://doi.org/10.2307/4084361>
- Bukacińska, M., Bukaciński, D., and Jabkowski, P. 1993. Colonial and noncolonial great crested grebes (*Podiceps cristatus*) at Lake Luknajno: nest site characteristics, clutch size and egg biometry. *Colonial Waterbirds* 16:111–118. <https://doi.org/10.2307/1521429>
- Burger, J. 1974. Determinants of colony and nest-site selection in the Silver Grebe (*Podiceps occipitales*) and Rolland's Grebe (*Rollandia rolland*). *The Condor* 76(3):301–306. <https://doi.org/10.2307/1366343>
- Burger, J. 1984. Grebes nesting in gull colonies: protective associations and early warning. *The American Naturalist* 123(3):327–337.
- Burger, J. 1995. Nest site selection by Eared Grebes in a Franklin's Gull colony: structural stability parasites. *The Condor* 97(2):577–580. <https://doi.org/10.2307/1369044>
- Chukhareva, I. P. and Kharitonov, S. P. 2009. O prostranstvennoy strukture polivodovykh koloniy, osnovannykh chaykovymi ptitsami, na vodoyemakh yuzhnogo Zaural'ya [On the spatial structure of mixed colonies initiated by gulls on water bodies of the Southern Transurals]. *Povolzhskiy Ecological Journal* 3:238–248.
- Cramp, S. and Simmons, E. L. (eds.) 1977. Handbook of the birds of Europe, the Middle East and North Africa. Vol. 1. Oxford.
- Dementiev, G. P. and Gladkov, N. A. 1951. Ptitsy Sovetskogo Soyuza [Birds of the Soviet Union]. Vol. 1. Sovetskaya Nauka, Moscow.
- Farner, D. S. and King, J. R. 2013. Avian Biology, Vol. 2. Elsevier. Nature.
- Fjeldså, J. 2004. The Grebes. Oxford University Press.
- de Fouw, J., Bom, R. A., Klaassen, R. H. G., Müskens, G. J. D. M., de Vries, P. P., Popov, I. Y., Kokorev, Y. I., Ebginge, B. S., and Nolet, B. A. 2016. Breeding in a den of thieves: pros and cons of nesting close to egg predators. *Ecosphere* 7(6):1–12. <https://doi.org/10.1002/ecs2.1353>
- Goc, M. 1986. Colonial versus territorial breeding of the great crested grebe *Podiceps cristatus* on Lake Druzno. *Acta Ornithologica* 22(2):95–145.
- Golovina, N. M. 2012. Vliyaniye koloniy chaykovykh na raspolozheniye gnozdz vodoplavayushchikh i okolovodnykh ptits [Effect of colonies gulls and terns on the location of nests of water birds]. *The Russian Journal of Ornithology* 21(760):1197–1198.
- van der Graaf, A. J., Stahl, J., Klimkowska, A., Bakker, J. P., and Drent, R. H. 2006. Surfing on a green wave — how plant growth drives spring migration in the Barnacle Goose *Branta leucopsis*. *Ardea* 94(3):567–577.
- Hays, H. and LeCroy, M. 1971. Field criteria for determining incubation stage in eggs of the common tern. *The Wilson Bulletin* 83(4):425–429.
- Hramtsov, V. N., Kovaleva, T. V., and Natsvaladze, N. U. (eds.). 2013. Atlas osobo okhranyayemykh prirodnikh territoriy Sankt-Peterburga. [Atlas of Protected Areas of Saint-Petersburg]. Marafon. Saint-Petersburg.
- Ilijichev, V. D. and Flint, V. E. (eds.) 1982. Ptitsy SSSR. Istoriya issledovaniy Gaviiformes, Podicipediformes, Procellariiformes. [Birds of USSR. The history of study. Gaviiformes, Podicipediformes, Procellariiformes]. Moscow. Science.
- Ivanov, A. I., Kozlova, E. V., Portenko, L. A., and Tugarinov, A. Ja. 1953. Ptitsy SSSR [Birds of USSR]. Printing House of Academy of Science of USSR. Moscow, Leningrad.
- van de Kam, J., Ens, B., Piersma, T., and Zwarts, L. 2004. Shorebirds. An Illustrated Behavioural Ecology. KNNV Publishers: Utrecht, Netherlands.
- Kharitonov S. P., Volkov, A. E., Willems, F., van Kleef, H., Klaassen, R. H. G., Nowak, D. J., Nowak, A. I., and Bublichenko, A. G. 2008. Brent goose colonies near snowy owls: Internest distances in relation to abundance of lemmings and arctic foxes. *Biology Bulletin* 35(3):270–278. <https://doi.org/10.1134/S1062359008030072>
- Klimov, S. M., Melnicov, M. V., and Zemlyanukhin, A. I. 2000. Ptitsy basseyna Verkhnego Dona: Podicipediformes, Ciconiiformes, Phoenicopteriformes. [The birds of the Upper Don basin: Podicipediformes, Ciconiiformes, Phoenicopteriformes]. *The Russian Journal of Ornithology* 116:3–17.
- Konter, A. 2005. Annual building-up of great crested grebe colonies: an example from the Dutch IJsselmeer. *Waterbirds* 28:351–358.
- Konter, A. 2008. Seasonal evolution of colonial breeding in the Great crested grebe *Podiceps cristatus*: a four years' study at Lake IJssel. *Ardea* 96(1):13–24. <https://doi.org/10.5253/078.096.0103>
- Malchevsky, Yu. S. and Pukinsky, Yu. B. 1983. Ptitsy Leningradskoy oblasti i sopredel'nykh territoriy [Birds of Leningrad Region and adjacent territories]. Vol. 1. Publishing House of Leningrad University.
- Melde, M. 1973. Der Haubentaucher. [The Great crested grebe]. Wittenberg Lutherstadt.
- Menshikova, S. V. 2005. Vodoplavayushchiye i okolovodnyye ptitsy Ropshinskikh prudov (Leningradskaya oblast'). [Waterfowl and shorebirds of the Ropshinsky ponds (Leningrad region)]. *The Russian Journal of Ornithology* 14(284):291–309.
- Noskov, G. A. and Botch, M. S. (eds.). 1999. *Krasnaia kniga prirody Leningradskoi oblasti. T. 1. Osobo okhranyaemye prirodnye territorii. [Red Data Book of Nature of the Leningrad Region. Vol. 1. Protected Areas]*. St. Petersburg.
- Piersma, T. 2006. Migration in the balance: tight ecological margins and the changing fortunes of shorebird popu-

- lations; pp. 74–80. in Boere, G. C., Galbraith, C. A., and Stroud, D. A. (eds.). *Waterbirds Around the World*. The Stationary Office: Edinburgh, UK.
- Prop, J. and de Vries, J. 1993. Impact of snow and food conditions on the reproductive performance of Barnacle Geese *Branta leucopsis*. *Ornis Scandinavica (Scandinavian Journal of Ornithology)* 24(2):110–121. <https://doi.org/10.2307/3676360>
- Quinn, J. L., Prop, J., Kokorev, Y., and Black J. M. 2003. Predator protection or similar habitat selection in red-breasted goose nesting associations: extremes along a continuum. *Animal Behaviour* 65:297–307. <https://doi.org/10.1006/anbe.2003.2063>
- Quinn, J. L. and Ueta, M. 2008. Protective nesting associations in birds. *Ibis* 150 (Suppl. 1):146–167. <https://doi.org/10.1111/j.1474-919X.2008.00823.x>
- Reiter, M. E. and Andersen, D. E. 2008. Comparison of the egg flotation and egg candling techniques for estimating incubation day of Canada Goose nests. *Journal of Field Ornithology* 79(4):429–437. <https://doi.org/10.1111/j.1557-9263.2008.00181.x>
- Richardson, D. S. and Bolen, G. M. 1999. A nesting association between semi-colonial Bullock's orioles and yellow-billed magpies: evidence for the predator protection hypothesis. *Behavioral Ecology and Sociobiology* 46:373–380. <https://doi.org/10.1007/s002650050>
- Rjabitsev, V. K. Ptitsy Urala, Priural'ya i Zapadnoy Sibiri: Spravochnik-opredelitel'. [Birds of Ural, Priuralje and West Siberia: Guide]. Yekaterinburg: Printing House of Ural University.
- Simmons, K. E. L. 1974. Adaptations in the reproductive biology of the Great Crested Grebe. *British birds* 67:413–444.
- Stanevičius, V. 2001. Impact of air temperature and breeding habitat quality on the beginning of the breeding season in great crested grebe (*Podiceps cristatus*). *Acta Zoologica Lituanica* 11(2):183–193. <https://doi.org/10.1080/13921657.2001.10512371>
- Stanevičius, V. 2002. Nest-site selection by coot and great-crested grebe in relation to structure of halophytes. *Acta Zoologica Lituanica* 12(3):265–275. <https://doi.org/10.1080/13921657.2002.10512513>
- Tolchin, V. A. 2011. O gnezdovanii chomgi *Podiceps cristatus* v Vostochnoy Sibiri. [On breeding of the great crested grebe (*Podiceps cristatus*) in Eastern Siberia]. *The Russian Journal of Ornithology* 20(708):2370–2371.
- Ueta, M. 1994. Azure-winged magpies, *Cyanopica cyana*, 'parasitize' nest defence provided by Japanese lesser sparrowhawks, *Accipiter gularis*. *Animal Behaviour* 48:871–874. <https://doi.org/10.1006/anbe.1994.1311>
- Ulfvens, J. 1988. Comparative breeding ecology of the Horned Grebe (*Podiceps auritus*) and the Great crested grebe (*Podiceps cristatus*): archipelago versus lake habitat. *Acta Zoologica Fennica* 183:1–75.
- Ulfvens, J. 1989. Offshore breeding in the Great Crested Grebe *Podiceps cristatus*: two offshore areas examined in relation to an inshore in western Finland. *Ornis Fennica* 66:112–116.
- Vogrin, M. 2002. Breeding success of Great crested grebe *Podiceps cristatus* on fishponds. *Ornis Svecica* 12:203–210.
- Wheelwright, N. T., Lawler, J. J., and Weinstein, J. H. 1997. Nestsite selection in savannah sparrows: using gulls as scarecrows? *Animal Behaviour* 53:197–208. <https://doi.org/10.1006/anbe.1996.0288>
- Wilson, J. R., Nebel S., and Minton, C. D. T. 2007. Migration ecology and morphometries of two Bar-tailed Godwit populations in Australia, Emu. *Austral Ornithology* 107(4):262–274. <https://doi.org/10.1071/MU07026>