Influence of winter temperature and spring ice melt on the reproductive performance of Mute Swans *Cygnus olor* nesting on offshore islands at the northern edge of its breeding range

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Abstract

The influence of winter temperature and spring ice melt on Mute Swan *Cygnus olor* abundance and productivity in a northern part of its breeding range was studied using data from 831 nests on the Kurgalsky Peninsula, in the Russian part of the Gulf of Finland, during 2006–2021. There was marked annual variation in the numbers of breeding pairs, which ranged from 17–95 per year over the 16-year study, with greatest numbers observed in years with early ice melt in the gulf. Birds nested either territorially or in colonies. Nest sites were categorised as being occupied for either short-term or long-term periods, with the latter considered likely to include cases of the same pairs nesting at the same sites over several years. Clutch sizes and hatching success were greater for territorial pairs and for those on long-term sites compared to pairs on short-term and colonial nests. Overall hatching success decreased in years with later ice melt.

Key words: climate change, colonial breeding, nest site occupancy, reproductive success, territorial breeding.

Climate warming has been linked to significant changes in the abundance and spatial distribution of many bird species observed during the 21st century (Walther *et al.* 2005; Cuervo & Møller 2013). This increases the importance of studying the dynamics of these populations at the edge of their range, as they contribute to evolutionary change (Mayr 1982; Lesica & Allendorf 1995). One species which has shown both population growth and large-scale expansion of its range in recent decades is the Mute Swan *Cygnus olor* (Cramp & Simmons 1977; Krivenko *et al.* 1990;

Wieloch 1991; Wood & Włodarczyk 2020). It first appeared as a breeding species in the Russian part of the eastern Gulf of Finland in 1987, when a nest was found on its southern coast near the Kurgalsky Peninsula (Buzun & Khrabry 1990). Within 7–10 years numbers here increased rapidly and the Mute Swan became one of the most numerous species of Anseriformes breeding in the area. Breeding strategies vary, with some pairs being territorial whilst others nest in colonies. Large differences in the reproductive parameters (clutch size, incubation success) of territorial and colonial nesting birds are also typical. Some sites are occupied every year for prolonged periods of time, while others (with apparently similar conditions) are occupied only sporadically (Kouzov 2016), a pattern also found for Mute Swans breeding more widely (*e.g.* Włodarczyk & Minias 2016) and for other swan species (*e.g.* Whooper Swans *Cygnus cygnus*; Einarsson & Rees 2002).

There has been no further significant dispersal of Mute Swans breeding to the east and northeast of the Gulf of Finland over the last 30 years. There are, however, significant annual fluctuations in the number of pairs nesting on the peninsula, which can vary by 2- to 5-fold (Kouzov 2016; Kouzov & Loseva 2016; Wood & Włodarczyk 2020), which suggests that environmental factors have a strong influence on whether pairs attempt to breed each year. Determining the weather variables associated with nest occupancy and productivity would contribute to our knowledge of factors affecting the population dynamics of the species in the region and would also bring us closer to understanding those that may be limiting further northward expansion of the Mute Swans' breeding range.

The Mute Swan is an early breeding species with a very long nestling growth period and is also a short-distance migrant which winters on the Baltic Sea (Ptushenko 1952; Cramp & Simmons 1977; Johnsgard 1978). It therefore seems likely that factors determining its annual breeding dynamics will include the timing of ice melt in the breeding areas and winter temperatures on its wintering grounds along the southwest Baltic coast. Consequently, this study aimed: (1) to investigate the effect of winter temperatures and the timing of spring ice melt on the abundance and breeding strategies of nesting Mute Swans (*i.e.* for colonial *vs.* territorial birds, and for birds at short-term *vs.* long-term occupied sites); and (2) to determine whether winter temperatures and the timing of ice melt in spring affect clutch size and incubation success, as well as the potential for different responses to these parameters by swans adopting different nesting strategies. We also hypothesised that there are two groups of birds in the population of Mute Swans nesting on the Kurgalsky Peninsula: (1) a highly productive core group of long-term breeding birds with higher average clutch size and higher reproductive success; and (2) a low-productive group of birds occupying nest areas for 1–2 years which lay smaller clutches and having lower incubation success, as similarly found for Mute Swan populations further south and for other waterbird species which form long-term pair bonds and undertake prolonged parental care (*e.g.* Ens *et al.* 1996; Rees *et al.* 1996).

Methods

Study area

Kurgalsky Peninsula is located on the southern coast of the Gulf of Finland between the mouths of the Narva and Luga rivers (Fig. 1). The area is characterised by a moraine landscape, the shoreline is highly indented, and there are many small islands along the coast. Most of the coastal water area is dominated by sandy and stony shallows 2–5 m deep, with an abundance of filamentous algae and vascular submerged aquatic plants, which create good feeding opportunities for the herbivorous Mute Swan. Coastal habitats are represented by narrow strips of grassland, turning into ribbon thickets of the Common Reed *Phragmites australis*. Large reedbeds and dense stands of Softstem Bulrush *Schoenoplectus tabernaemontani* occur in the peninsula's sheltered bays (Kouzov *et al.* 2021).

Bird surveys

Surveys were carried out on the offshore islands and coast of the Kurgalsky Peninsula during 2005–2024, as part of a general study of the ecology of waterbirds in the Gulf of Finland. Three surveys were conducted each year: the first (in the last 10 days of April–early May) searched for early clutches, the second (in the last 10 days of May–early June) searched for late clutches and revisited clutches found during the previous survey, and the third (in the second half of June) revisited late clutches. Each survey was

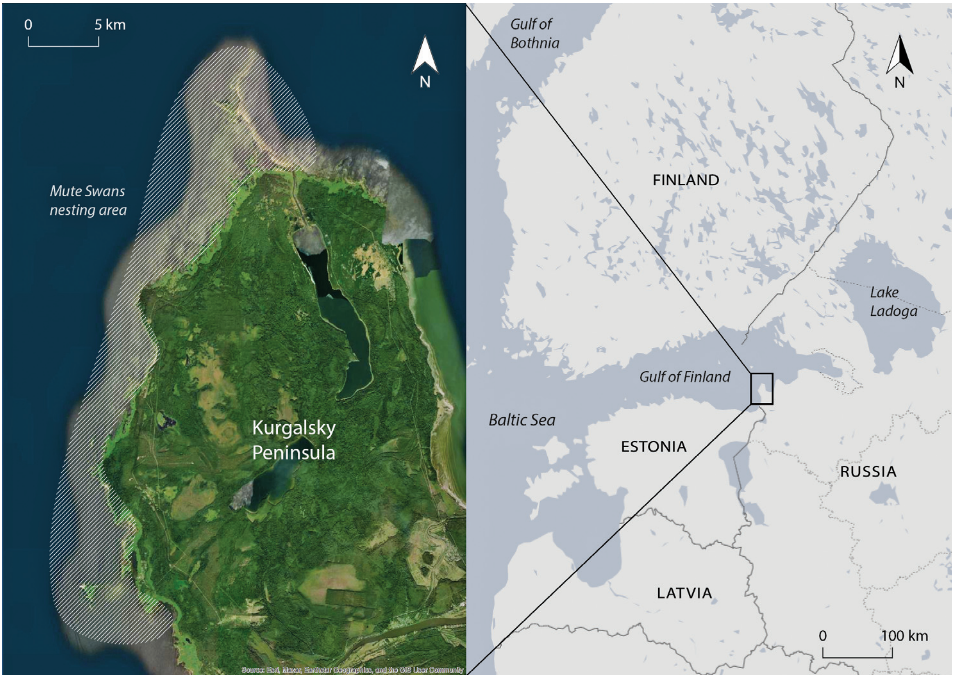


Figure 1. Location of the study area in the Russian part of the Gulf of Finland.

conducted for 4–6 days. On the islands, a total count of nests was carried out over the entire area by observers moving in a dense zigzag pattern to locate the nests. For the coastal reed beds, we first searched for swan nests in April by boat, by looking into the reedbeds from their periphery before the vegetation had started to grow. Once the location of nesting birds or territorial pairs had been determined, more detailed inspections were made, including establishing the outcome of each nesting attempt. Nest coordinates were recorded using a GPS navigator, nesting habitat was described, nests were measured, and clutch size recorded. The timing of egg laying was assessed by the water test (*i.e.* by placing the egg in water, with incubation stage determined from the buoyancy and angle of the egg in the water; Brua & Machin 1999; Mednis 2002) or was estimated from hatching dates (if small pulli were found in or near the nest). Incubation success was determined by repeat visits to the nests, with a clutch considered successful if at least one nestling hatched. Hatching success was determined by the presence of embryonic membranes in the nests, eggs with dead embryos, or traces of predation.

Mute Swans on the Kurgalsky Peninsula nest either on territories, defended by the pair, or in colonies. Depending on the nature and proximity of the nests to each other, we therefore classified most nests as being either a colonial or a territorial nest. Although an intermediate type of nesting – where a pair nested in association with a territorial site – was also described (Kouzov 2016).

Single territorial pairs usually defended an area from other pairs within 200–500 m around the nest. Such birds nested both on islands or in reeds along the coast; in the latter case, the protected areas were larger. The territory was usually strictly guarded by the male against the incursion of other swans. After taking to the water, the brood generally remained within this area until at least *c.* 60 days old.

Colonies consisted of 2–35 nests, which were built 2–15 m from each other (distances being measured from the edge of the nest). There were no areas protected by individuals within the colonies; incubating females guarded only the nest itself from intrusion. When going to feed or when alarmed, the birds often stayed in a tight group. By the time of hatching, there was often an increase in aggression by one of the males (if the colony was small), or by two males from different sides of a large colony, which resulted in the other broods being displaced from the colony itself and from adjacent waters. The other broods, however, remained in the vicinity of the colony, at distances of 20–50 m, for the first two weeks after moving to water.

Associations with territorial sites were noted only on the islands. Males from such pairs guarded a small area of water, 50–100 m wide along the water's edge and extending towards the open bay. Nests could be located at distances of *c.* 20–50 m from others, and very often the males kept apart, using different sides of an island or a large cape on the island. Broods remained in the male-protected areas for the first two weeks after entering the water, and then, as a result of conflicts, some families were driven away and the individual plots of the remaining pairs were enlarged. Preliminary analysis of data up to 2006–2015 suggested that reproductive parameters (*e.g.* clutch size and incubation success) for birds in this category were intermediate to those recorded for territorial and colonial birds (Kouzov 2016). In this study, however, we categorised such nests as territorial, because they were also in areas protected by the male during the nesting period.

Our long-term studies have shown that many of the individual stretches of water defended by territorial swans in our study area remain unchanged from year to year. Moreover, there is also little change in the location of the nests, which are usually found within *c.* 10 m of the old nest or, more rarely, on the same spot. Similar annual occupation of the nest sites occurred in the colonies, although here they within a radius 1–2 m from the old nests. In many cases the size, nest materials and location (*e.g.* whether under a bush or tree, near a boulder, or on a little spit) of the nests were identical to measures made of the old nest mounds, suggesting that they may have been occupied by the same birds in successive years. In a small number of cases it was possible to confirm this by identifying individual swans, with long-term nesting monitored for two birds marked with Latvian leg rings, two more birds (both females) with traumatic distortions of the tarsometatarsus, and for one male bird with a head injury. A high degree of philopatry to nesting territories has been reported for long-breeding Mute Swans in other parts of the breeding area (Włodarczyk *et al.* 2013), and reuse of the old nest by Mute Swans pairs returning to their territories over several years is also well-known (Cramp & Simmons 1977; Johnsgard 2016). Nonetheless, given that very few of our swans were identifiable, because of the difficulty in catching and colouring-marking them in the reedbeds and shallow coastal waters of the Kurgalsky Peninsula, it was not possible to confirm whether most nests were occupied by the same pair over several years. We therefore grouped the nests into long- and short-term nesting sites, with an underlying assumption that it was likely that the same pairs were nesting at particular sites for at least some if not all years of the study. Short-term sites were defined as those in which nests were recorded for 1–2 consecutive years, which concurred with studies of colour-marked birds in Poland where pairs breeding for 1–2 years were considered to be short-term breeders (Włodarczyk & Minias 2020), while sites occupied for ≥ 3 years were classed as long-term sites.

In addition to short-term and long-term breeding, we found that in some years there was an interruption in breeding activity at long-term occupied sites, when a pair of birds was present but did not start nesting. Studies of individually tagged Mute Swan have shown that a pair can skip breeding for 1–2 years (Minton 1968; Włodarczyk & Minias 2020), and our direct observations found that once a pair of swans occupies a new site it usually takes about two years before the first nest appears. We therefore provisionally attributed cases of 1-year interruptions to nesting activity but where a pair was present at the site to an established breeding pair skipping a breeding season at a long-term site. Cases of 2- or 3-year breaks, when birds were absent for at least in one of these years, we interpreted as cessation of nesting and settlement of new birds at the site.

Data analysis

To assess the influence of winter temperature and the timing of the spring ice melt on Mute Swan reproductive performance we grouped all nests according to the swans' nesting strategy – *i.e.* into colonial and territorial, and also into long- and short-term occupied nest sites. Although these categories overlap substantially (see Results), territorial and colonial nests were each represented in notable numbers among both short- and long-term occupied sites (Table 1).

We used average January temperatures for areas where swans are expected to winter (*i.e.* on the southwest Baltic Sea, so using data from Copenhagen Airport weather station, Denmark), as well as the timing of

Table 1. Annual variation in the nesting strategies for Mute Swans breeding on the Kurgalsky Peninsula. Overall, there were 161 long-term and 47 short-term nests on territories, and 256 long-term and 367 short-term nests in the colonies.

Year	Short-term nesting sites	Long-term nesting sites	Colonial nests	Territorial nests	Total
2006	10	16	20	6	26
2007	11	18	25	4	29
2008	48	27	64	11	75
2009	22	25	37	10	47
2010	2	24	16	10	26
2011	7	18	16	9	25
2012	16	19	21	14	35
2013	5	12	14	3	17
2014	13	29	27	15	42
2015	13	33	25	21	46
2016	38	35	58	15	73
2017	58	36	80	14	94
2018	9	25	24	10	34
2019	57	38	70	25	95
2020	49	32	62	19	81
2021	56	30	64	22	86
Total	414	417	623	208	831

ice melt in the breeding area, as factors likely to affect the number and reproductive output of birds. The January temperature data for Copenhagen Airport for each year of our 2006–2021 study period were taken from the rp5.ru website (Raspisanie pogody 2024). Dates of ice melt, expressed as days from 1 February, were determined by analysing ice charts from the Swedish Meteorological and Hydrological Institute website (https://www.smhi.se/). A more detailed description of methods used to calculate the timing of ice melt is presented in Kouzov *et al.* (2024).

The relationship between the number of nests recorded each year during 2006–2021 and the annual weather variables (temperatures in the wintering area and timing of ice melt in the breeding area; see Table 2) was tested using generalized additive models (GAM), package "mgcv" in R 4.2.2, because of nonlinearity in the data (R Core Team 2022; Wood 2011). A negative binomial distribution and log-link

Table 2. Description of the explanatory and response variables included in the generalized additive models (GAMs) of factors affecting Mute Swan nesting activity on the Kurgalsky Peninsula presented in Table 3.

Variable name	Description
NO	Overall number of nests
SK	Proportion of nesting skips at long-term occupied sites
CO	Mean clutch size for all groups
CC	Mean clutch size in colonies
CT	Mean clutch size of territorial pairs
CL	Mean clutch size at long-term sites
CS	Mean clutch size at short-term sites
HO	Hatching success of all nests
HC	Hatching success in colonies
HT	Hatching success of territorial pairs
HL	Hatching success at long-term sites
HS	Hatching success at short-term sites
YEAR	Year of observations
WT	Mean January temperatures on the wintering grounds (Copenhagen, Denmark)
ICE	Timing of ice clearance (number of days since 1 February when the waters around the islands become ice-free)

were used because of overdispersion in the count data (Zuur *et al.* 2009). Predictors were checked for multicollinearity. The pairwise Pearson correlation coefficient was $r = -0.53$ ($P = 0.033$) for ICE and WT; although this is not particularly large value it was significant, so we decided to run separate regressions for these two variables in the GAMs.

Hatching success (*i.e.* the proportion of hatched eggs in relation to the total number of eggs) and average clutch size values were taken as reproductive indicators. Hatching success was calculated as the total number of successfully hatched eggs divided by the total number of all eggs, for the whole of the breeding population and also for each group.

The relationship between clutch size (total and split by groups) and the climate variables was analysed using a GAM with gaussian distribution and identity link. Residuals were tested for normality using the Shapiro-Wilk criterion, and all fitted a normal distribution except for the relationship between the clutches of short-term breeders and winter temperatures. We attempted other transformations and model variants but could not bring the residuals to a normal distribution, so we used untransformed data in this case. To analyse hatching success (total and by group), we used a quasibinomial GAM with a logit link function. The explanatory variables were the same as in the clutch size models. Annual estimates of nest abundance, mean clutch size and hatching success (from 2006–2021 inclusive, $n = 16$) were used in all models.

We also analysed the proportion of long-term nesting sites where the birds "skipped nesting" (SK) each year, in relation to the weather variables recorded for that year. For this we used a quasibinomial GAM (with logit link), which was required because overdispersion was present in almost all of our data (Zuur *et al.* 2009).

A Mann-Whitney test was used to compare mean clutch size and hatching success in groups of birds with different nesting strategies.

Results

From 2006–2021, we recorded 17–95 Mute Swan nests each year on the islands and coastal marshes of the Kurgalsky Peninsula. Most (75.0%) were located in colonies, with a smaller proportion (25.0%) on territories. About half of the pairs (50.2%) occupied long-term nesting sites, and the rest (49.8%) nested short-term (Table 1).

In addition to the breeding swans, from 2005–2021 between 12–145 non-breeding birds were recorded during May–early June in different years, and 46–250 non-breeding birds were counted during the moult in July–August. The proportion of breeding swans ranged from 42.0%–75.4% of the total numbers in May–early June and from 25.4%–61.0% of the total numbers in July–August, illustrating the presence of a reserve of potential breeding birds in the region.

Numbers of nesting pairs increased significantly over the years ($\chi^2_{1.45} = 9.78$, $P = 0.016$; Fig. 2). The total number of nests decreased significantly in years with later ice melt ($\chi^2_{1.8} = 16.43$, $P < 0.001$; Fig. 3A) and was independent of average January temperatures ($\chi^2_{1.2} = 1.61$, $P = 0.211$, n.s.) on the wintering grounds (Table 3). The timing of ice melt also influenced the number of nests recorded for swans with different nesting strategies.

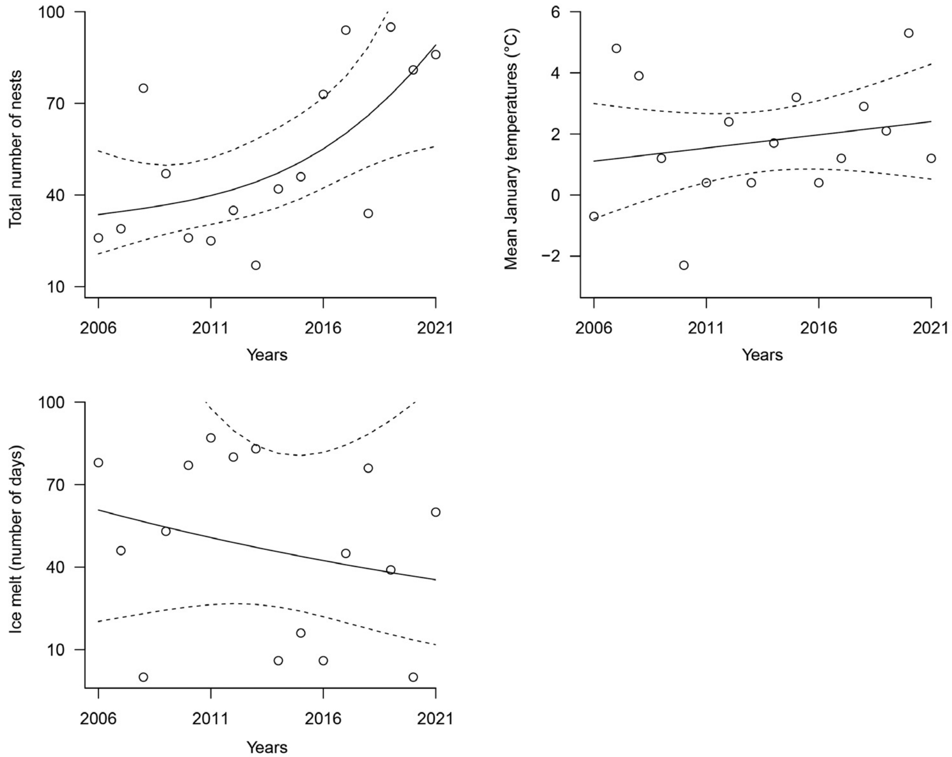


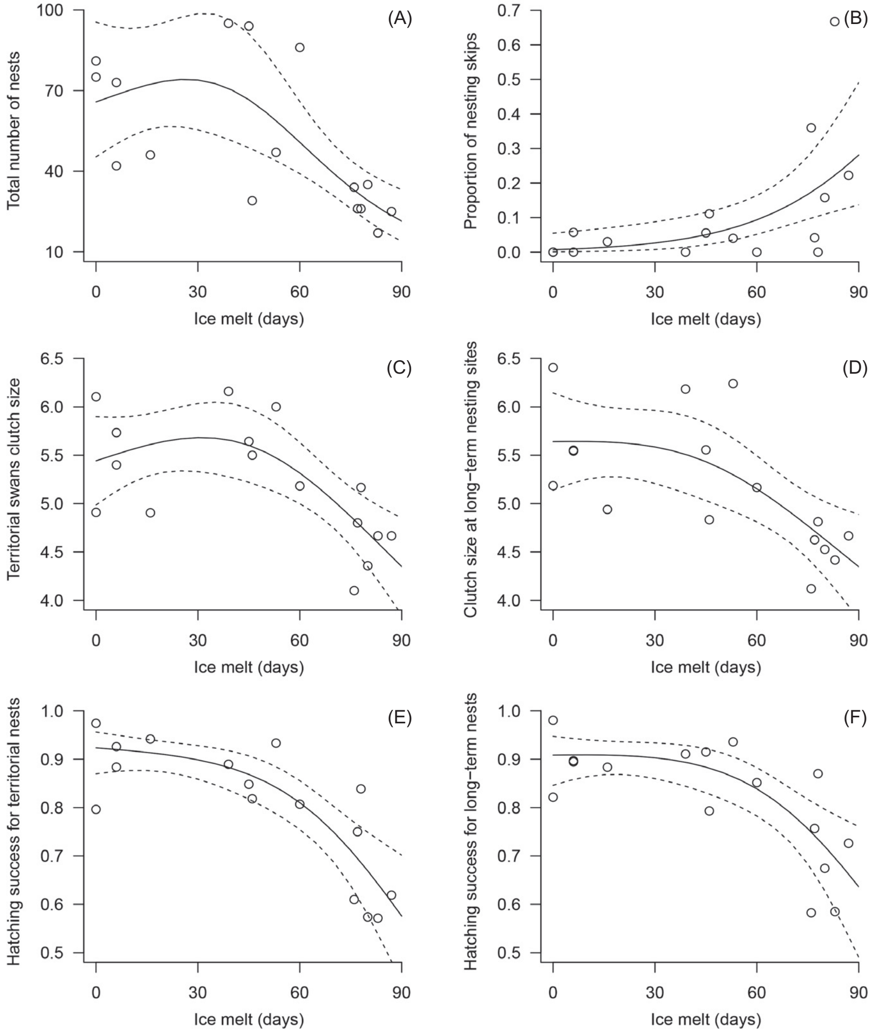
Figure 2. Time series of the total number of the Mute Swans nests, mean winter temperatures and timing of ice melt recorded for each year of the study. Continuous lines show estimated trends from the generalized additive model; dashed lines show 95% confidence intervals. The relationship between the number of nests and time is significant ($\chi^2_{1.45}$ = 9.78, P = 0.016). Mean January temperatures = temperatures recorded on the wintering grounds (Copenhagen, Denmark). Ice melt = the number of days since 1 February on which waters around the islands become ice-free.

On classifying each year as an early or a late spring (based on whether the ice cleared < 50 days of > 100 days after the start of the year; years with intermediate ice melt not included), the number of colonial nests were on average 3.2 times higher than in early than in late springs whereas the change in territorial nesting (although also higher) was less marked, and nesting at short-term occupied plots were 4.8 times higher in these years (Fig. 4).

On analysing the proportion of nesting "skips" recorded for each year at long-term occupied sites (SK), we found a positive relationship with the timing of ice melt (*i.e.* the longer the ice remains, the more long-term nesting sites were unoccupied in that year, F_1 = 8.59, P = 0.011; Table 3).

Clutch size

Clutch size was on average higher for territorial-nesting birds (5.3 ± 0.12, n = 208)



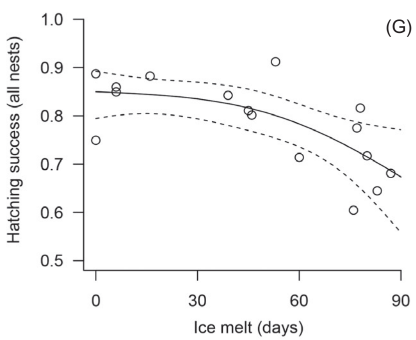


Figure 3. Estimated smoothing curves for different measures of nesting activity and breeding success recorded for Mute Swans on the Kurgalsky Peninsula, in relation to weather variables. The dotted lines are 95% confidence bands. Note that graphs are provided only for those models where $P < 0.05$ (*i.e.* for ice melt only).

Table 3. Results of generalized additive models (GAM) describing the relationship between the nesting activity of Mute Swans on the Kurgalsky Peninsula and weather variables. The variables are described in Table. 1. The notation s(YEAR) *etc.* means that smoothing was applied to the explanatory variable. *** = $P < 0.001$, ** = $P < 0.01$, * = $P < 0.05$. EDF = effective degrees of freedom.

Response variable	Explanatory variable	EDF	χ^2/F value	P value	Deviance explained (%)
NO	s(YEAR)	1.447	9.776	0.016 *	40.1
WT	s(YEAR)	1	0.625	0.442	4.3
ICE	s(YEAR)	1	0.319	0.572	1.8
NO	s(ICE)	1.841	16.430	0.0002 ***	57.4
NO	s(WT)	1.155	1.605	0.211	12.2
SK	s(ICE)	1	8.590	0.011 *	44.9
SK	s(WT)	1	0.134	0.720	1.0
HO	s(ICE)	1.591	4.462	0.025 *	43.6
HO	s(WT)	1	0.551	0.470	3.7
HC	s(ICE)	1.011	2.531	0.131	15.8
HC	s(WT)	1	0.132	0.722	0.9
HT	s(ICE)	1.710	13.950	0.004 **	70.5
HT	s(WT)	1	1.795	0.202	11.0
HL	s(ICE)	1.743	8.306	0.003 **	57.2
HL	s(WT)	1	0.683	0.423	4.4
HS	s(ICE)	1	0.993	0.336	6.6
HS	s(WT)	1	1.048	0.323	6.9
CO	s(ICE)	1	0.054	0.819	0.4
CO	s(WT)	1	0.111	0.744	0.8
CC	s(ICE)	1	0.186	0.673	1.3
CC	s(WT)	1	0.075	0.788	0.5
CT	s(ICE)	1.848	6.403	0.009 **	53.5
CT	s(WT)	1	0.467	0.505	3.2
CL	s(ICE)	1.679	5.626	0.013 *	50.6
CL	s(WT)	1	0.985	0.338	6.6
CS	s(ICE)	1.416	1.777	0.142	25.6
CS	s(WT)	1.458	0.298	0.665	9.3

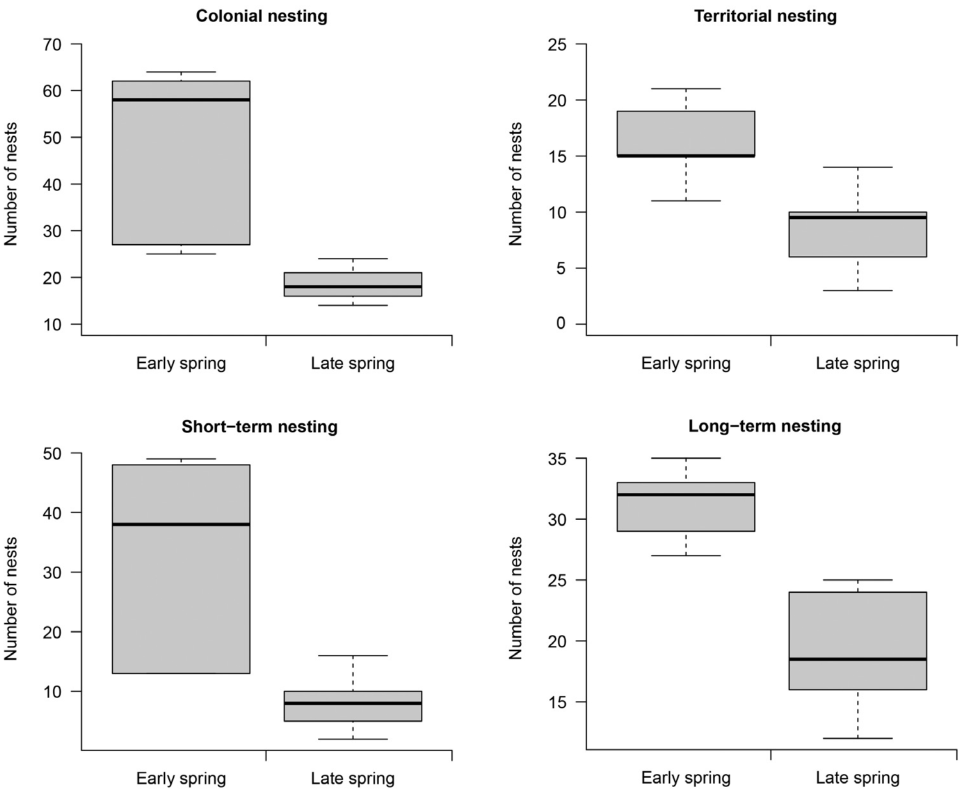


Figure 4. Number of nests in early- and late-spring years considering different nesting strategies. We classified early spring as years in which ice cleared < 50 days after the start of the year (2008, 2014, 2015, 2016, 2020), and late spring as ice clearing after > 100 days (2006, 2010, 2011, 2012, 2013, 2018). Horizontal line denotes the median value, whiskers represent minimum and maximum values (without counting outliers), and the box is drawn from the first to third quartile.

than for those breeding in colonies (4.1 ± 0.08, *n* = 623) and the difference was statistically significant ($W = 84887$, $P < 0.001$; Fig. 5). Swans at long-term occupied sites (thought to consist mainly of established breeding pairs) also had larger clutches than short-term breeders (5.3 ± 0.08, *n* = 417 and 3.6 ± 0.10, *n* = 414, respectively) ($W = 46941$, $P < 0.001$). It should, however, be noted that the nesting strategy categories (colonial/short-term and territorial/long-term) are largely overlapping (Pearson's Chi-squared test: $\chi^2_1 = 80.80$, $P < 0.001$), reflecting the tendency for most pairs to nest in colonies in our study area. Of the 831 nests visited over the years (Table 2), 61% (256) of those at the long-term sites were located in colonies, and 11% (47) of those at short-term sites were on territories. A higher proportion of swans breeding at long-term occupied sites (39% *vs.* 11%) therefore were on territories. The maximum

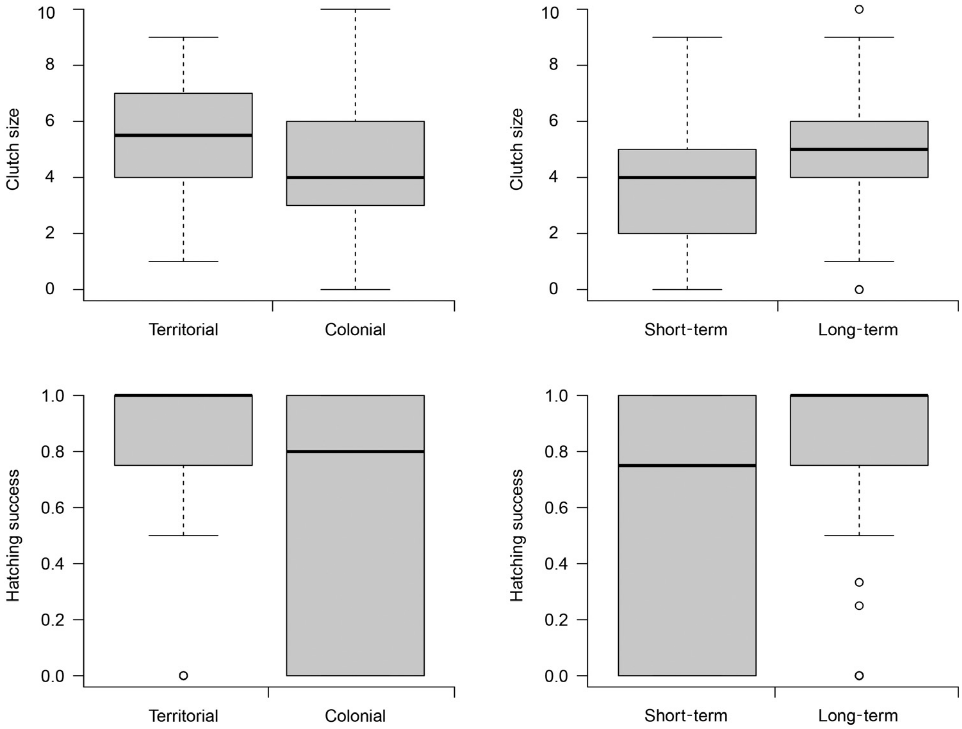


Figure 5. Clutch size and hatching success (proportion of eggs hatched) for different Mute Swan nesting strategies. Horizontal line denotes the median value, whiskers represent minimum and maximum values (without counting outliers), and the box is drawn from the first to third quartile.

clutch size observed in all years was of 10 eggs, in a nest found in the Mute Swan colony on Kiryensari Island in 2008.

The mean clutch size recorded for the whole of our study population was independent of the timing of ice melt or wintering temperatures (Table 3). On considering the relationship between clutch size for the different breeding categories and weather variables, clutches of territorial and long-nesting birds decreased significantly in years with late ice melt ($F_{1.8}$ = 6.40, P = 0.009 and $F_{1.7}$ = 5.63, P = 0.013, respectively; Table 3, Figs. 3C & 3D), but clutch sizes of colonial and short-nesting birds were not related to ice conditions. No relationships with temperature on the wintering grounds were found for any of the nesting strategy categories (Table 3).

Hatching success

Hatching success recorded for territorial swans (84.1%) was higher than for colonial-breeding birds (79.1%) (W = 75062, P < 0.001), and hatching success at the long-term nest sites (83.3%) was higher than at short-term nests (73.4%) swans (W = 61661, P < 0.001). We also note the variation in this parameter among nests of each category (Fig. 5); the interquartile range for territorial and long-nesting birds is only a quarter of that for swans in colonies and short-term nesting sites, and the median value is even close to 100%. Thus territorial and long-nesting pairs do not just successfully hatch nestlings but do so consistently from year to year, whereas those nesting in colonies and at short-term nest sites, despite also having fairly high hatching success (at 79.1% and 73.7%, respectively) are more likely to end in failure, with the interquartile range extending from 0%–100%.

On considering the relationship with weather variables, overall hatching success decreased with late ice melt (nonlinearly, starting with the dates later than March, $F_{1.6} = 4.46$, $P = 0.023$; Fig. 3G). A similar pattern was also observed for the territorial birds and long-term nest occupancy groups ($F_{1.7} = 13.95$, $P < 0.001$ and $F_{1.7} = 8.306$, $P = 0.003$, respectively), but no significant relationships of hatching success with ice melt were found for the colonial birds and short-nesting groups (Table 3). There was generally no relationship between hatching success and January temperatures on wintering grounds in any of our models (Table 3). Moreover, clutch size did not appear to have a significant effect on the swans' hatching success overall (GAM: $F_1 = 2.996$, $P = 0.105$, n.s.).

Discussion

Our studies showed significant differences in clutch size and incubation success between the groups of Mute Swans monitored on the Kurgalsky Peninsula over a 16-year period. This supports our hypothesis that the local swan population contains a highly productive core of long-term breeding birds with high reproductive potential, as well as short-breeding low-productive outsiders. Whilst we were mostly unable to identify the swans as individuals, the results concur with earlier publications. Higher annual productivity by swans breeding over several years, in comparison with shorter-term breeders, has been reported for individually marked birds in Poland (Włodarczyk & Minias 2020), and reproductive success has been found to improve with pair duration in several swan species, with the influence of this breeding experience more pronounced in some years than in others (Rees *et al.* 1996).

In our swan population, long-term nesting predominated at the territorial sites (recorded for 77.4% of 208 territorial nests), whereas short-term nesting (58.9% of 623 colonial nests) predominated among the colonial pairs. This seems to be partly responsible for the higher reproductive rates of the territorial birds compared to the colonial ones, as higher reproductive success is observed in long-term nesting birds compared to short-term nesting birds (Włodarczyk & Minias 2020). Smaller clutches among colonial birds than in territorial ones have also been noted in other Mute Swan populations (Rusanov & Krivonosov 1990; Andersen-Harild 1994; Bacon & Andersen-Harild 1987; Bacon & Perrins 1991; Bloch 1970; Cramp & Simmons 1977; Mägi *et al.* 1993; Perrins *et al.* 1994; Wieloch 1991). Perhaps these differences are partly related to the different ages of birds in these groups, as the smaller clutch size of young birds compared to old pairs has been repeatedly noted by other authors (Ptushenko 1952; Cramp & Simmons

1977; Włodarczyk & Minias 2020). Additionally, in Great Britain and in Denmark, it has been shown that the smaller clutches of colonial birds may be related to their genetic differences from territorial birds as well as to age (Bacon & Andersen-Harild 1987; Bacon & Perrins 1991), and this may be a feature of Mute Swan productivity elsewhere.

The Kurgalsky Peninsula is in the northern reaches of the Mute Swan's breeding range in Europe, and this is reflected in ice conditions having a major influence on the timing and numbers of the species attempting to breed each year. Early ice melt saw an increase in the number nesting on the Kurgalsky Peninsula, but at the same time January temperatures on the wintering grounds had no significant effect on the abundance of breeding birds or their productivity. In our opinion, this suggests that the breeding dynamics of Mute Swans in the eastern Gulf of Finland is determined primarily by the number of birds which had time to accumulate the energy resources required for reproduction on arrival in the breeding areas, rather than by variation in food availability in winter, a view supported by the long duration of the pre-breeding period. In other parts of the range, the time from the arrival of the Mute Swans to the onset of egg laying usually takes at least a month (Ptushenko 1952; Berglund *et al.* 1963; Krivonosov *et al.* 1976; Zusman *et al.* 1976; Cramp & Simmons 1977; Hästbacka & Ulfvens 1987; Rusanov 2011), with Tucakov (2005) also finding that seasonal arrival of Mute Swans in the eastern part of their range in Europe occurred immediately after ice melt. Earlier appearance of food resources on the breeding grounds, and the swans' ability to utilise them, should have an influence on the number of birds reaching optimal body condition for the start of the breeding season. As such, any future changes in the timing of the thaw together with the overall duration of the breeding season (from the accumulation of energy reserves through to cygnets fledging) may determine the Mute Swans' ability to extend their breeding range to more northerly latitudes.

Birds with more energy reserves obtained during the pre-breeding period may increase their contribution to clutch size and incubation success. According to our data, mean clutch sizes and total incubation success were not affected by winter temperatures. A significant negative dependence on the timing of ice melt was found only for overall hatching success; average clutch size for all nests did not show this dependence. However, in groups of highly productive birds (territorial pairs and pairs on long-term occupied sites), average clutch size and incubation success increased in years with early ice melt. The lack of correlation of average clutch size and incubation success with the timing of ice melt for the less productive groups (colonial birds and those on short-term occupied sites) may be due to other factors associated with individuals or pairs within these groups (*e.g.* age, duration of the pair bond and breeding experience; Rees *et al.* 1996), rather than to an absence of individual response to improved foraging conditions in years with early ice melt.

As seen above, our results support: (1) heterogeneity in the breeding structure of Mute Swans in the eastern Gulf of Finland,

and (2) different responses of reproductive parameters in birds following different nesting strategies to changes in weather conditions. An important premise for this heterogeneity is the variability in the age of first breeding which has been recorded for Mute Swans and the presence of a large pool of non-breeding birds in the population. Previous studies have shown that the age of first breeding ranges from 2–6 years for Mute Swans in Oxford (Perrins & Reynolds 1967) and south Staffordshire (Minton 1968) to 4–8 years in Denmark (Andersen-Harild 1981) and 3–10 full years for swans nesting colonially at Abbotsbury in southern England (Perrins & Ogilvie 1981). More recent data from Abbotsbury show that 27% of females started breeding at age 3 years, 31% at age 4 years and 42% at 5–8 years (Charmantier *et al.* 2006). In recent decades in Poland, the first breeding attempts of Mute Swans were recorded at an average age of 5.9 ± 0.4 years (Włodarczyk & Minias 2020). The pool of non-breeding birds also varies, ranging from 55.2% reported by Leach (1988) to 85.9% by Rutschke (1982), but most studies noted that 62.8–78.4% of the population does not breed each year (Bloch 1971; Brown 1997; Eltingham 1963; Lundin & Hansson 1956; Meek 1993; Minton 1968, 1971; Spray 1991; Trump *et al.* 1994; Wieloch 1991). This implies that the Mute Swans' physiological condition may be heterogeneous between areas, with the result that different individuals are recruited into the breeding population in different years, depending on the favourability of seasonal conditions. Within our study area, in years with early ice melt, the number of colonial nests and of swans breeding in short-term occupied plots increased the most (Fig. 4). We suggest that this may be a result of them being occupied by a higher proportion of young birds or less fit individuals (*e.g.* those lower in the dominance hierarchy, less able to gain access to a limited food supply), likely to benefit from a longer duration of the pre-breeding period, during which they could accumulate the energy resources and body condition required for breeding.

Birds breeding at the edge of their range may be particularly sensitive to fluctuations in weather conditions because they are limited by climatic factors that restrict their further distribution (Curnutt *et al.* 1996; Williams *et al.* 2003; Cuervo & Møller 2013). In more central parts of their range, however, these factors may not have such an influence on the birds' breeding season. Thus, for example, in central Poland the numbers of nesting Mute Swans are stable with low annual variability (Włodarczyk *et al.* 2013; Włodarczyk & Minias 2020), whereas in our study area nesting attempts can vary more than 4-fold between years. In this respect, extralimital nesting may be analogous to breeding at high latitudes. Many arctic-breeding geese and swans have significantly higher annual variation in the numbers and proportions of breeding birds in their populations, as well as increased clutch sizes and incubation success, in years with an early spring when it is easier to accumulate the necessary reserves for breeding (Anderson *et al.* 2014; Dickey *et al.* 2008; Mineev & Mineev 2014; Nolet *et al.* 2019; Boom *et al.* 2023; Perrins 1970). Populations of some of these species do not show such patterns when nesting further south in more temperate regions (Boom *et al.* 2023), as described above for the Mute Swans in Poland.

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Photograph: Colonial-nesting Mute Swans with gulls on the Kurgalsky Peninsula (Gulf of Finland), in April 2012, by Sergey Kouzov.

