Effects of timing of ice melt on spring stopover patterns of migrating Whooper Swans *Cygnus cygnus* and Bewick's Swans *Cygnus columbianus bewickii* in the Russian part of the eastern Gulf of Finland

SERGEI A. KOUZOV*, ANNA V. KRAVCHUK,
ELMIRA M. ZAYNAGUTDINOVA & EVGENY V. ABAKUMOV

Department of Applied Ecology, Faculty of Biology, St. Petersburg State University, Universitetskaya nab. 7/9, St. Petersburg, 199034, Russia.
*Correspondence author. E-mail: s.kouzov@spbu.ru

Abstract

Seasonal climate dynamics have a substantial impact on the timing of optimal feeding conditions for migratory birds at their stopover sites in the temperate and boreal zones. Delayed spring events (such as the timing of ice melt, and thus availability of open water) at stopover sites may result in migratory flocks forming at later dates. On these occasions, birds may be faced with the choice of maintaining their usual stopover duration, to make full use of the food resources needed to complete migration and clutch formation, or of increasing the overall speed of migration by shortening or skipping some of the stopovers, in order to arrive at their breeding sites on time. Additionally, it may be possible that the birds use alternative, non-traditional stops in such years. The purpose of this study was to determine the effect of the timing of ice melt at a major spring staging site on the migration patterns of swans. Long-term (2005–2021) censuses were conducted in an area supporting the largest concentrations of migratory waterfowl in the eastern part of the Gulf of Finland (Kurgalsky Peninsula: 59.725°N, 28.118°E). Late ice melt resulted in a reduction in the migration duration and peak abundance of both Bewick's Swans *Cygnus columbianus bewickii* and Whooper Swans *C. cygnus*. The date on which the staging period ended however varied little from year to year. Use of alternative stopover sites on agricultural land by the swans was recorded only in the most recent years, when spring was early.

Key words: Baltic Sea, climate, ice, migration stopovers, migration turnover, population dynamics, Tundra Swan, Whooper Swan.

Migratory waterbird species are threatened worldwide by climate change, over-exploitation and habitat degradation (Amano *et al.* 2020; Delany *et al.* 2007; Krivenko 1991; Maclean *et al.* 2007; Nuijten & Nolet 2020). Recent climate change has resulted in substantial changes to the timing of the spring ice melt and the development of optimal conditions for birds at migratory stopover sites and nesting areas in both arctic and boreal regions (Lameris *et al.* 2021; Nuijten & Nolet 2020; Nuijten *et al.* 2020; Rees 2006; Stillman *et al.* 2021). In this context, we need a better understanding of how the timing of avian migration changes in response to climate dynamics (Krivenko 1991), especially for those most threatened of species. The Bewick's Swan *Cygnus columbianus bewickii* is among the more threatened of arctic and boreal Anseriformes, showing apparent long-term declines in abundance in northwest Europe (Beekman *et al.* 2019; Wood *et al.* 2016). One of the key spring migration stopover areas for swans in the Western Palearctic is the eastern Gulf of Finland (Kouzov 1993, 2010; Kouzov & Kravchuk 2010; Kouzov *et al.* 2021; Malchevsky & Pukinsky 1983; Nuijten *et al.* 2020; Rees 2006; Rymkevich *et al.* 2012; Zaynagutdinova *et al.* 2019). Here, the most variable climatic factor, which strongly influences the suitability of migration sites in this area, is the timing of ice melt (Kouzov 2010; Kouzov & Kravchuk 2010; Kouzov *et al.* 2019; Zaynagutdinova *et al.* 2019). This in turn determines the timing of availability of open water, and thus of food resources (primarily aquatic vegetation) for birds at these sites.

Spring migration strategies of waterfowl are the result of resolving conflicts between two opposing needs. The first is the need to arrive at nesting sites as early as phenological conditions of the season allow, to catch optimal foraging conditions for the future young (Ankney *et al.* 1991; Stafford *et al.* 2014; Stillman *et al.* 2021). For swans, early nesting ensures that parents have enough time to raise their relatively slow-growing offspring to fledging before the end of the short summer season, when warm weather sees a rush of vegetation growth in the northern taiga and tundra water bodies. The second factor is that the birds need to accumulate maximum energy resources during the weeks prior to breeding, not only to complete their migration, but also so that the female can develop the reserves required for laying a clutch and for body maintenance during incubation. Swans and geese are heavily constrained in spring because, at the time of arrival in the breeding range, the vernal thaw at nesting sites has yet to provide optimal foraging conditions, as illustrated by studies of migratory geese (Black *et al.* 2007; Ebbinge & Spaans 1995; Prop *et al.* 2003; Stillman *et al.* 2021). The influence of this factor should be to incline birds to make fullest use of intermediate stops on migration, remaining there until they have acquired the necessary energy stores to proceed.

The aim of our study was to identify how the timing of ice melt at a northern migratory site affected key parameters that characterise use of the site by Bewick's Swans and also the migratory Whooper Swans *Cygnus cygnus*, specifically: the timing of commencement and end of stopovers,

their duration, the maximum abundance of birds, and the dates of peak abundance. We hypothesised three possible patterns of such changes influenced by the dynamics of ice melting dates (Fig. 1): (A) shifting phenology; (B) declining abundance and reduced stopover time; and (C) increasing abundance and reduced stopover time.

Hypothesis A implies the same degree of food resource exploitation at the stopover by the birds while shifting the timing of its use. Within the whole migration route,
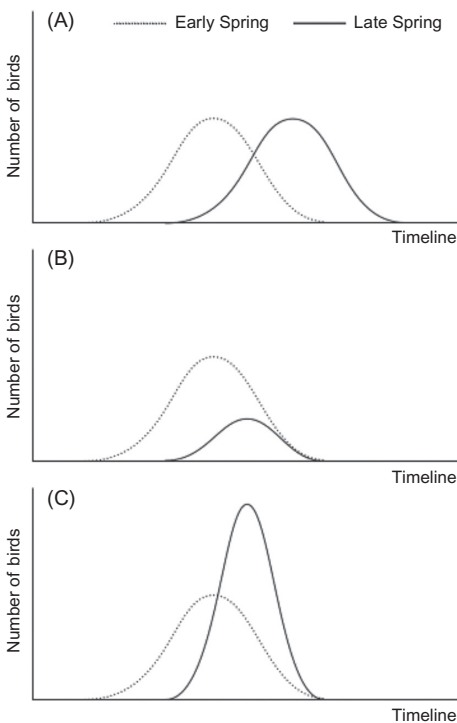

Figure 1. Possible patterns in the dynamics of migratory swan aggregations for different timing of the ice melt. (A) = shift in migration phenology; (B) = decline in abundance and reduced stopover time; (C) = increased abundance and reduced stopover time.

this strategy leads to the maintenance of similar reproductive conditions of birds in seasons with different phenology, but with a delay in their arrival to the breeding grounds (Fig. 1A).

Hypothesis B assumes that with late ice melt, birds delay migration from previous stopovers and later make a long flight to more distant stopover sites, by overflying the study area in transit or remaining there for a shorter duration. This strategy leads to a late but more rapid flight with an overall reduction in the number of stops and their duration. That is, in years with a delayed spring, birds arrive to breeding grounds at optimal dates, but their physiological condition may be worse than in seasons with an early spring. It is also possible that, if spring is delayed, birds may use alternative stopover sites (*e.g.* agricultural land) nearby. In this case, changes in the graphs of abundance dynamics at the main staging site may look similar, but with a reduction in both the duration and the abundance of the aggregation (Fig. 1B).

Hypothesis C is a kind of compromise. This proposes that in years with late ice melt, the start of the build-up in numbers (the aggregation) shifts to a later date, and there is also a sharp increase in the abundance of swans at the site because all birds are concentrated there at the same time. The birds' departure occurs at around the same dates as those for years with an early ice melt (Fig. 1C). This allows the birds to appear at their nesting sites at optimal times. However, this model implies a strong increase in competition for the limited food resource and shorter time for "refuelling".

It should be noted that the above models are for observations made of swans using one particular site, and that different patterns of site use may occur at other staging areas along the migration route, particularly where ice cover is less of a constraining factor.

Additionally, it is worth noting that the observations reported here were recorded during our larger-scale surveys, made from automobiles of waterfowl stopover sites along the southern coast of the Gulf of Finland, ranging from St. Petersburg to the Kurgalsky Peninsula. From these surveys we can state that, except for the Kurgalsky Peninsula, the Neva Bay area and the Lebyazhiy Nature Reserve (Fig. 2), there were no other large aggregations of swans found on this part of the Gulf of Finland (Zaynagutdinova *et al.* 2019).

Methods

Study area

In the eastern part of the Gulf of Finland there is a transition from the freshwater delta of the River Neva to a typical saline marine coastal area (Kouzov *et al.* 2021). The Kurgalsky Peninsula is located near the western border of the eastern part of the Gulf of Finland, at the point of its transition into the open sea (Fig. 2; Kouzov *et al.* 2021). Its coastal zone is characterised by an abundance of moraine boulder bars and islands, as well as sand and pebble spits and islets formed by sea currents. The coastline is highly indented, with many small islands, bays and capes. Water salinity is about 5.1–7.1‰. The species composition of the freshwater vegetation is highly impoverished. In areas sheltered from storms, Common Reed *Phragmites australis,* Grey Club-rush *Schoenoplectus tabernaemontani* and Sea Club-rush *Bolboschoenus maritimus* are abundant (Glazkova 2001). The dominant submerged vegetation consists of species tolerant of low salinity – Horned Pondweed *Zannichellia palustris*, Sago Pondweed *Potamogeton pectinatus* and Perfoliate Pondweed *Potamogeton perfoliatus* – with occasional clumps of slightly more saline-tolerant aquatic vascular plants such as Brackish Water-crowfoot *Batrachium marinum*, Beaked Tasselweed *Ruppia maritima* and Holly-leaved Naiad *Najas marina* (Glazkova 2001).

The earliest area to thaw in the Russian part of the Gulf of Finland is around the Kurgalsky Peninsula. During the abnormally warm winters of 2008 and 2020, there was no ice here at all. In 2014–2016, the ice had melted by mid-February. Latest ice melt (in late April) occurred in 2010–2013 and 2018.

Data collection

Here we present the results of Bewick's and Whooper Swan counts, which were conducted at six key points around the Kurgalsky Peninsula (59.725°N, 28.118°E; Fig. 2), on a fixed route along the entire coast of the peninsula from the River Vybya to Gakkovskaya Bay (*i.e.* heading east to west), where large numbers of swans are observed annually during migration. Observations were made with binoculars, and all flocks of migratory swans were also photographed, to confirm species identification and verify the counts. Observers moved between observation points by car during daylight hours, when there was little flight activity, which reduced the chance of double-counting. Since ice conditions at all sites

Figure 2. Map of the Gulf of Finland showing the detail of the study area (inset) and the six swan observation points on the Kurgalsky Peninsula: (1) = Vybya River mouth to Luoto Cape (59.692°N, 28.218°E); (2) = Lipovo village (59.741°N, 28.202°E); (3) = Kurgalsky Reef (59.787°N, 28.108°E); (4) = Kaibolovsky Cape (59.752°N, 28.041°E); (5) = Tiskolovo village (59.722°N, 28.029°E); and (6) = Gakkovo village (59.659°N, 28.025°E).

were similar, data for all points visited on each survey day were summed for analysis, thus treating waters around the Kurgalsky Peninsula as one large stopover site.

Observations were carried out once every five days in 2005–2017 and every seven days in 2018–2021, starting from 15 February and ending on 31 May each year. To ensure the comparability of the data series, we converted the weekly counts to 5-day data, with the 5-day and 7-day periods being numbered from 1 February onwards. On

converting data from 7-day to 5-day periods, we relied on the date of the particular observation. Gaps were filled as the average of species abundance recorded on the two closest observation dates. There were 22 survey days per season when the swans were counted at 5-day intervals, and 16 surveys made each year under the once-a-week scheme. Thus, when interpolating 7-day counts into 5-day counts, it was necessary to estimate data for six days each year. However, since birds were absent during part of the observation period (*e.g.* in the second half of May, or in February and most of March during late ice melt), in reality it was only necessary to estimate data for 3–5 days for Whooper Swans and 2–3 days for Bewick's Swans annually.

In addition to surveys on the Kurgalsky Peninsula, we also talked to hunters and bird-watchers about whether they encountered any swans feeding in fields at or near goose staging sites. We examined some of these sites from the car on travelling from St. Petersburg to the Kurgalsky Peninsula, usually 1–2 times a season during the peak swan migration period.

In some years, when ice was absent in winter or melted very early in January, a few over-wintering pairs or families of Whooper Swans were present in the study area. In such years we considered that the staging period commenced when the number of birds at the site first increased significantly (*i.e.* when new groups of 3–7 birds appeared), and analysed counts made at 5-day intervals from that date. In other years, the first day of the swans' arrival was taken as the beginning of stopover. We considered the last 5-day period in which swans were counted, after which no birds were recorded for at least two consecutive 5-day periods, to be the end of the swans' stopover in our study area for that season.

The dates of ice melt, expressed as 5-day intervals from 1 February, were determined by analysing ice charts from the Swedish Meteorological and Hydrological Institute website (https://www.smhi.se/). We reviewed daily distribution maps of different ice types (from the colour-coded ice chart) in the Baltic Sea in order to determine the date of ice melt in the study area. The transition from solid ice (termed "Fast ice" on maps) to open water occurs through several different states reflected on these charts; *i.e.* ranging from "Consolidated ice", through "Very close or compact ice", "Close ice", "Open ice" and "Very open ice", to "Open Water". During our surveys, we wondered what kind of change in the ice cover can influence swans' migratory stopovers and took the first change from Close ice to Open ice as such a key change. We assume that small floating ice blocks have little or no negative effect on site use by the swans, whereas denser ice clusters would have almost the same negative effect on the birds as solid ice. Thus, we considered the date when Open ice first appeared in the area of the Kurgalsky Peninsula as the date of ice melt.

We used these data to determine the relationship between the timing of the ice melt and swan migration parameters, measured as the start, end and duration of migratory stopovers, the dates of peak abundance, and the number of swans recorded during the peak count (Table 1).

Table 1. Variables included in the analysis of how the migratory patterns of Bewick's and Whooper Swans staging on the Kurgalsky Peninsula, Russia, vary with the timing of the spring ice melt.

Variable name	Description	Type
START	Time of arrival (in 5-day periods, starting from the beginning of February), when the first swans were recorded at migration sites	Continuous response variable
END	Stopover end date (in 5-day periods, starting from the beginning of February)	Continuous response variable
DURATION	Duration of staging (in 5-day periods)	Continuous response variable
PEAK_DATE	Number of the 5-day period in which peak swan abundance was recorded	Continuous response variable
PEAK_NUM	Number of birds recorded during the peak count	Continuous response variable
ICE	Timing of ice melt (number of the 5-day interval since 1 February when the waters around the islands first become open, with no closed/consolidated ice)	Continuous explanatory variable

Statistical analysis

Since scatter plots of the response variables (listed in Table 1) in relation to the timing of ice melt mostly indicated nonlinearity, generalized additive models were used to analyse the data (GAMs; Zuur *et al.* 2009). These also provided a better fit to the data than generalized linear models (GLMs), which assume linearity of parameters within the model. We used the "mgcv" package (Wood 2011) in R 4.2.2 (R Core Team 2022), with the start time (START), end time (END), duration (DURATION), maximum abundance (PEAK_NUM) and the date on which the maximum number was recorded each year (PEAK_DATE) as response variables, and the timing of ice melt (ICE) as the explanatory variable (Table 1). Data recorded for the two swan species were analysed separately. Variables representing the timing of events (START, END, DURATION, PEAK_DATE) were analysed using a GAM with Gaussian distribution and identity link. Count variables, such as PEAK_NUM, were analysed using a negative binomial GAM with log link function (due to overdispersion in the dataset). We set an upper limit for the smoothing value of the GAM at $k = 3$ to avoid model overfitting and to obtain realistic trends. This approach was applied to all migration characteristics. Homogeneity,
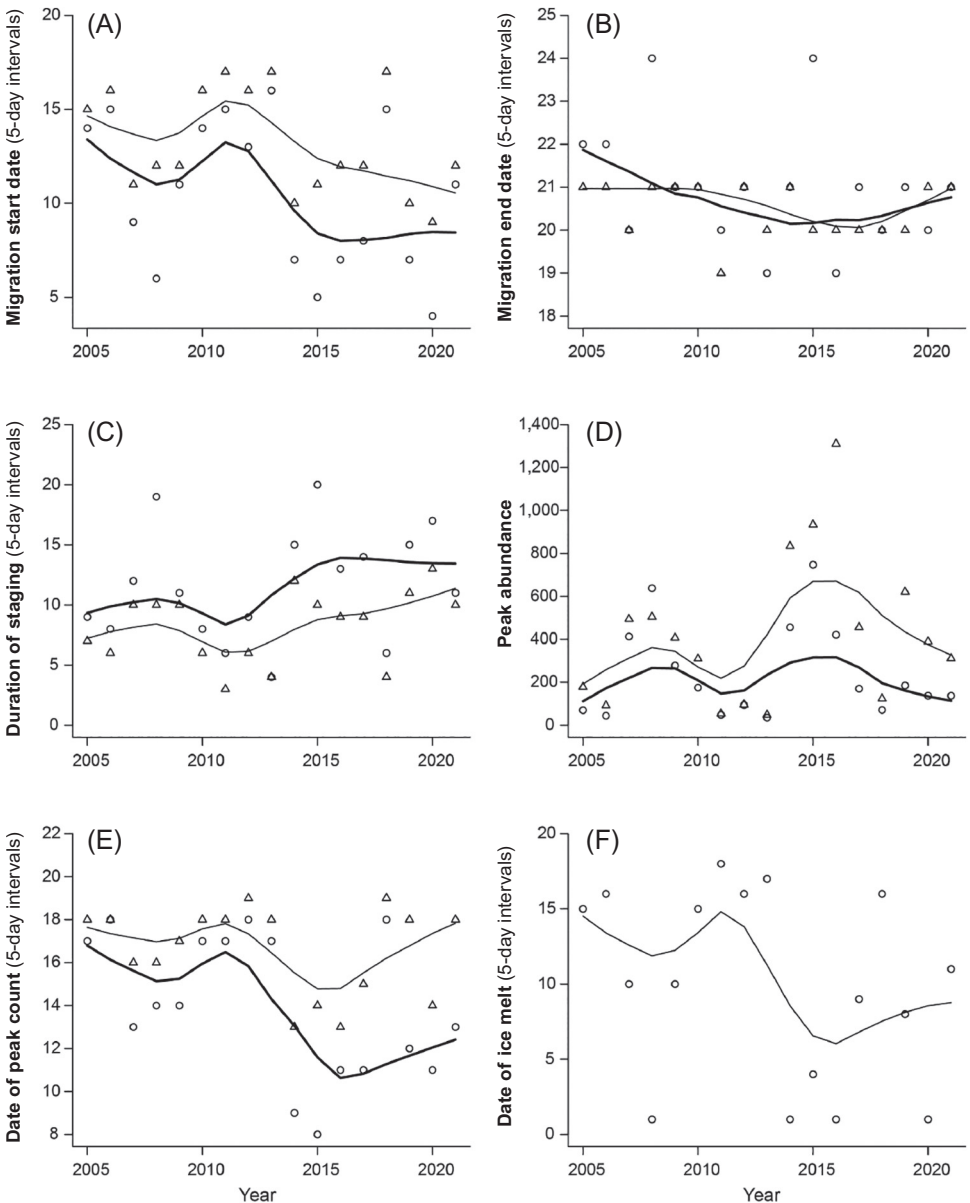
Figure 3. Time series of (A) migration start date, (B) migration end date, (C) duration of staging, (D) peak abundance, (E) date of peak count and (F) date of ice melt for the two swan species, with dates shown as 5-day intervals starting on 1 February. A LOWESS smoother with a span width of 0.5 was added to aid visual interpretation. The circles and bold line indicate Whooper Swan data; triangles and a thin line indicate Bewick's Swan data.

normality (using the Kolmogorov–Smirnov test), and absence of patterns were assessed for the residuals of all models (Zuur *et al.* 2009). Validity of the model choice was determined by comparing four variants – Gaussian and Poisson GLMs and GAMs (in case of overdispersion we applied a negative binomial model) – using the Akaike Information Criterion (AIC), with the models selected (see above) showing the lowest AIC.

On plotting the time series for our variables (Fig. 3), we added LOWESS smoothing (locally weighted scatterplot smoothing, Fox & Weisberg 2019) to aid visual interpretation of the data.

Results

Dates on which the first Whooper Swans arrived ranged from mid-February to mid-April, whereas those for the Bewick's Swans ranged from mid-March to the third 10 days of April (Fig. 3A). There was much less variability in the dates of the end of the staging period, which for both species was usually between the second and third 5-day period in May (Fig. 3B). The duration of staging ranged from 4–20 5-day periods (*c.* 20–100 days) for the Whooper Swan and 3–13 5-day periods (*c.* 15–65 days) for the Bewick's Swan (Fig. 3C). The date of the peak Whooper Swan count each year ranged from 8 March to 28 April, and that for the Bewick's Swans from 3 April to 3 May. The maximum number of swans counted during peak 5-day period each spring varied greatly between years: for Whooper Swan from 35–747 birds, and for Bewick's Swan from 48–1,310 birds (Fig. 3D).

We examined the dependence of the start, end and duration of migration stopovers, as well as the dates and abundance of birds on peak days as a function of the timing of ice melt, using additive modelling (Table 2). Significant nonlinear patterns were found (Fig. 4, Fig. 5) demonstrating a positive dependence of arrival time (for both species) upon the timing of the ice melt ($F_{1.85} = 81.61$, $P < 0.001$ for Whooper Swans; $F_{1.96} = 67.63$, $P < 0.001$ for Bewick's Swans; Table 2). No significant relationships were found between the timing of the ice melt and the end of the staging period ($F_{1.00} = 0.959$, n.s. for Whooper Swans; $F_{1.00} = 0.519$, n.s. for Bewick's Swans). The duration of stopovers clearly decreased with later ice melt dates, but for the Bewick's Swan this dependence was clearly detectable only for the dates starting from mid-March and later (Fig. 5C). Thus, it does not seem to matter much to these birds whether the water was frozen in January and February, but it is important that it becomes ice-free by March, whereas for Whooper Swans (which arrive earlier than the Bewick's Swans) the relationship between stopover duration and ice melt dates is almost linear (Fig. 4C).

Dates of maximum bird abundance occurred later when spring was late ($F_{1.82} = 27.54$, $P < 0.001$ for Whooper Swans; $F_{1.00} = 47.5$, $P < 0.001$ for Bewick's Swans), while peak abundance decreased ($\chi^2_{1.78} = 41.94$, $P < 0.001$ and $\chi^2_{1.92} = 88.04$, $P < 0.001$, respectively; Table 2). The averaged swan abundance curves in years with early (2008, 2014–2016 and 2020) and late (2005–2006, 2010–2013 and 2018) ice melt, show that the duration of spring

Table 2. Results of generalized additive models (GAMs) describing the relationship between features of migration stopovers and the timing of ice melt. Note: s(ICE) means that smoothing is applied to ICE; *denotes a χ^2 value for a negative binomial model (*i.e.* for the PEAK_NUM variable); **indicates $P < 0.001$.

Response variable	Explanatory variable	Edf	*F* value	*P* value	Deviance explained
Whooper Swan					
START	s(ICE)	1.849	81.61	< 2e-16**	92.3%
END	s(ICE)	1.000	0.96	0.343	6.0%
DURATION	s(ICE)	1.719	33.87	7.66e-06**	83.3%
PEAK_NUM	s(ICE)	1.780	41.94*	< 2e-16**	73.3%
PEAK_DATE	s(ICE)	1.823	27.54	1.5e-05**	80.6%
Bewick's Swan					
START	s(ICE)	1.959	67.63	< 2e-16**	90.8%
END	s(ICE)	1.000	0.52	0.482	3.35%
DURATION	s(ICE)	1.942	48.69	9.81e-07**	87.8%
PEAK_NUM	s(ICE)	1.920	88.04*	< 2e-16**	84.1%
PEAK_DATE	s(ICE)	1.000	47.50	5.39e-06**	76.0%

stopover periods recorded for Whooper Swans and Bewick's Swans is reduced by more than half when ice melt is delayed (Fig. 6). Maximum abundance of Whooper Swans and Bewick's Swans in such years decreased on average by > 6 times compared to values in years when the ice melted early. It can be assumed that when ice melt is delayed, most birds either stay at previous stopovers, then do not stop in our study area but transit to stopover sites further along the route, or they may stop at fields in the vicinity.

Some evidence for the swans using fields became apparent in 2020–2021, when we received information about Bewick's Swans staging on agricultural land near Koporie village (up to 350 birds) and near Gatchina (up to 200 birds) (S.G. Lobanov, unpubl. data; Kouzov *et al.*, unpubl. data); at both sites, these aggregations were observed in the second half of April. These areas were also regularly visited by bird-watchers and hunters in previous years, but swans were not recorded. It can be assumed with a high degree of certainty that this movement onto farmland is a new event, mainly in response to a revival of agriculture (planting of root crops and grain crops) in the region. Most likely, some birds move here from sites on the seacoast, in particular from the
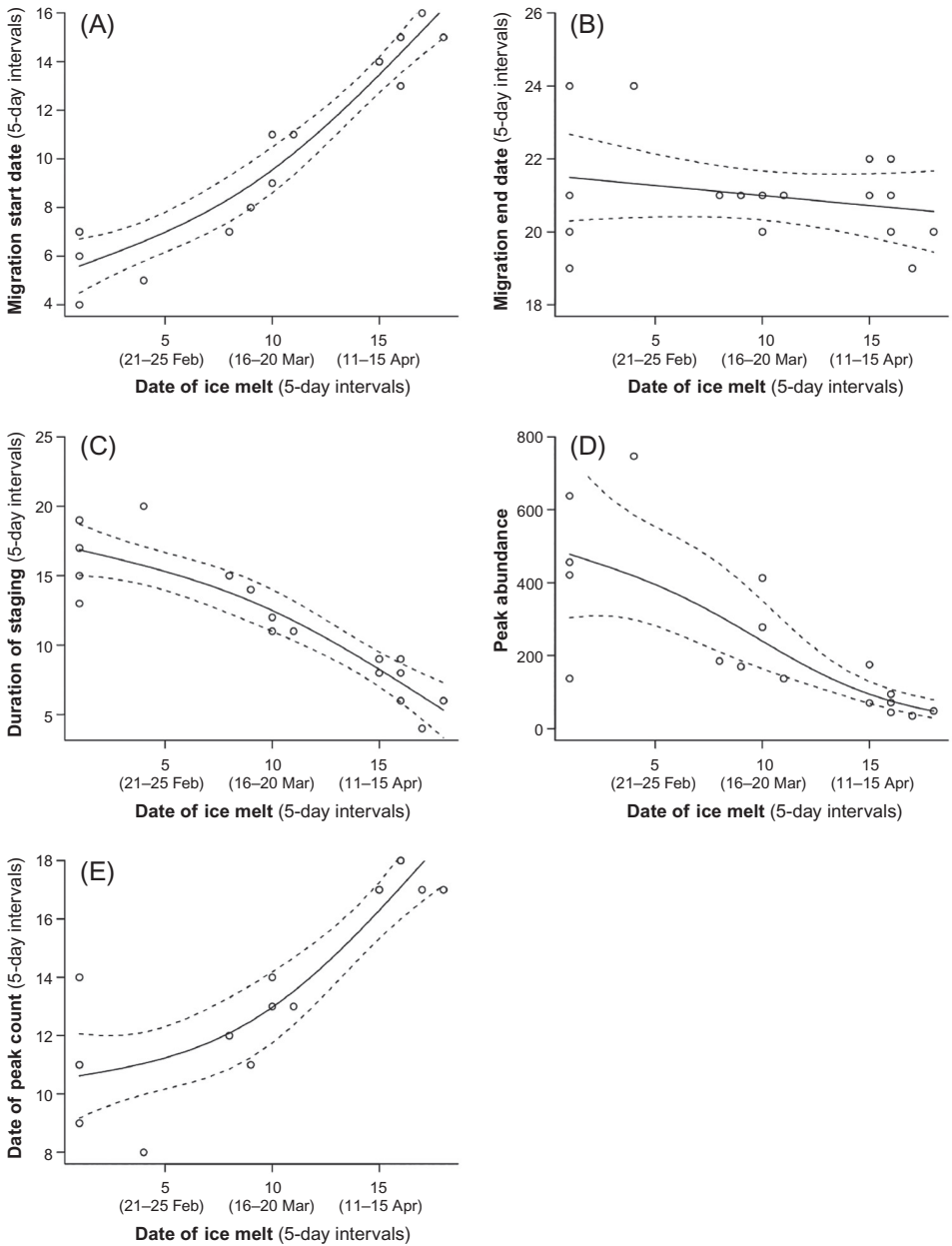
Figure 4. The relationship between the date of ice melt and Whooper Swan spring migration parameters: (A) migration start date, (B) migration end date, (C) duration of staging, (D) peak abundance and (E) date of peak count, at the Kurgalsky Peninsula spring staging on the eastern Gulf of Finland (generalized additive model; estimated smoothed curves with 95% confidence intervals).
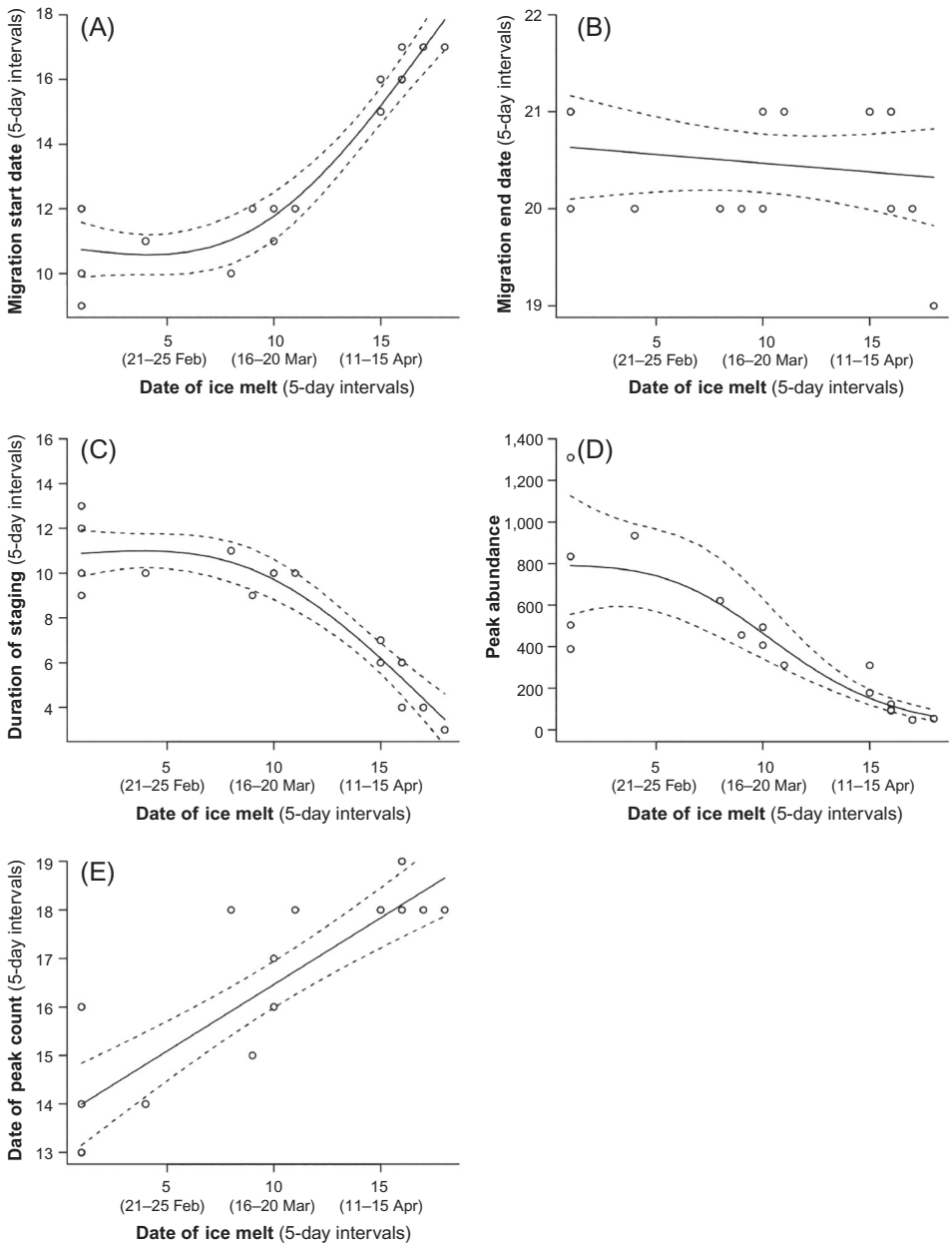
Figure 5. The relationship between the date of ice melt and Bewick's Swan spring migration parameters: (A) migration start date, (B) migration end date, (C) duration of staging, (D) peak abundance and (E) date of peak count, at the Kurgalsky Peninsula spring staging on the eastern Gulf of Finland (generalized additive model; estimated smoothed curves with 95% confidence intervals).
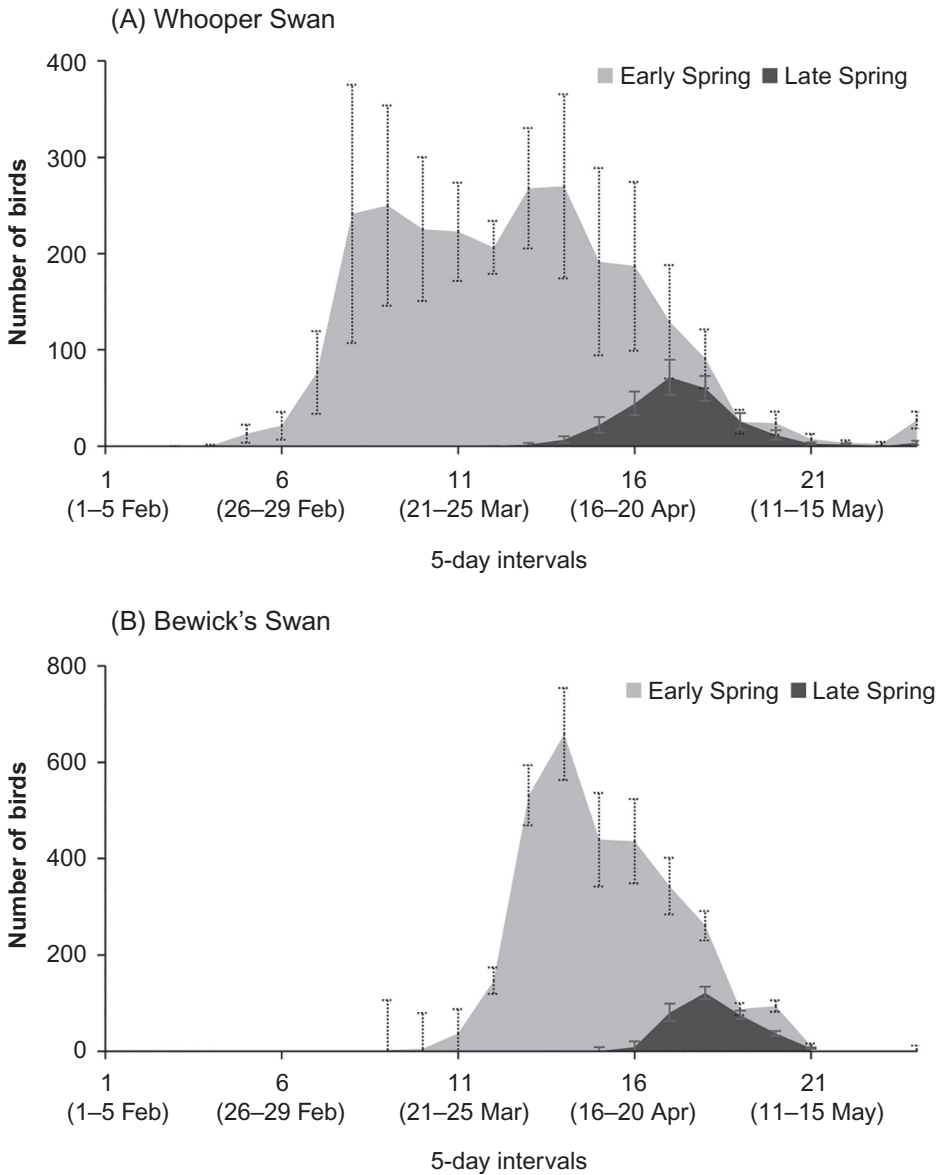
Figure 6. Average timing of the stopover period for (A) Whooper Swans and (B) Bewick's Swans in years with early (2008, 2014–2016, 2020) and late springs (2005–2006, 2010–2013, 2018). Years with an early spring were considered to be those in which the water was ice-free in February or earlier; years with a late spring were those in which the ice did not melt until April. Whiskers on the graph represent standard errors of the mean number of birds counted at intervals during spring, over the 2005–2021 study period.

Kurgalsky Peninsula, which may explain why, despite the early spring in 2020, swan abundance on the Kurgalsky Peninsula was noticeably lower than in 2014–2017, whereas the arrival dates were early and the duration of staging was long (Fig. 3). The counts from these "agricultural" stopover sites do not contradict our assumption that birds skip migratory sites when ice melt is delayed, because they were observed at these new sites in years with an early (2020) and normal spring (2021), and there was no apparent shift by the swans to these fields in years with late ice melt (2010–2013 and 2018).

Discussion

Analysis of the parameters of long-term dynamics of migratory aggregations and their dependence on the timing of the ice melt indicated that migration strategies used by Whooper Swans and Bewick's Swans supported the second hypothesis, which proposed "declining abundance and reduced stopover time" in colder springs (Fig. 1B). This is illustrated in all of the patterns found: (1) a shift in the timing of the birds' arrival and in the date of maximum abundance for later springs, (2) a reduction in the duration of staging, (3) a decrease in the peak abundance of birds, and (4) no significant influence of the onset of spring on the end dates of the staging period, and their low variability in general.

The extremely low variability in the end dates recorded for swan stopover periods in the southeastern Gulf of Finland is noteworthy. Similar observations have been made at swan staging sites in other parts of the White Sea–Baltic migration route, *e.g.* in Sweden (Månsson & Hämäläinen 2012) and

in the delta of the Northern Dvina River in northwestern Russia (Nolet *et al.* 2001). Daylength has been shown to determine the overall timing of the spring migration period from a wintering site, although weather conditions (mainly wind direction) then influence departure patterns on a daily basis (Rees 1982). It therefore can be assumed that the dates to which swans remain at spring staging sites on the Gulf of Finland are influenced primarily by photoperiod (which is consistent each year), rather than by the phenology of the season (which varies annually) (Månsson & Hämäläinen 2012). Our data, and those of Månsson & Hämäläinen (2012), both show that the timing of bird arrival at spring staging sites is determined primarily by ambient climatic factors: the timing of open water (our data) or average daily temperatures (Månsson & Hämäläinen 2012); hence the high variability in stopover start dates. Factors shaping the dates on which the last birds depart from stopover sites, however, seem more likely related to the endogenous circannual cycle (Månsson & Hämäläinen 2012), and the lack of variability in the end dates recorded for swan stopover periods in our study supports this hypothesis.

In our opinion, the decrease in the maximum number of swans on the Kurgalsky Peninsula in years with a late spring cannot be related to the redistribution of birds to other nearby staging areas. Waters around or near the Kurgalsky Peninsula open earlier than other coastal areas of the eastern Gulf of Finland and even earlier than inland water bodies. The use of fields by birds for foraging, as mentioned above, has been noted only in

the most recent years with early or normal springs, and this may be associated with the revival of agriculture in the region. Root crops and cereals have recently been grown in fields which previously were not cultivated in any way and their forage value for swans was significantly lower. The tendency for the swans to utilise the fields, however, is to some extent deterred by active spring hunting of geese in these areas, which scares the birds from terrestrial sites. A situation exacerbated for Bewick's Swans in cold springs when their arrival (which occurs later than for Whooper Swans) is delayed and coincides with the opening of the spring hunting season (usually on 15 April) in the region.

We assume that, in years with a late ice melt, most of the birds migrate at a later date and pass over traditional stopovers in our study area, to stage at the next sites along the migration route, where, by this time, the ice should already have begun to clear. This is supported by our numerous observations of transiting swan flocks near the Kurgalsky Peninsula in mid-April during 2011–2013. Such stopover sites can be found in Neva Bay on the Gulf of Finland (Afanasyeva *et al.* 2001; Kouzov 1993; Kouzov & Kravchuk 2010; Zaynagutdinova *et al.* 2019) and along the southwest coast of Lake Ladoga, where coastal shallows become ice-free in late April and early May, and swan accumulations occur at these times (Noskov *et al.* 2006; Rymkevich & Chuyko 2006).

Of course, birds cannot receive information in advance about weather conditions at the next stopover sites on the migration route. Therefore, the question of

how they make decisions on delayed and late passage movements, during which some traditional stopover sites may be skipped, becomes relevant. It is known that in short-distance migrants, including swans, photoperiodic control gives a rather wide time frame of the migration period, within which migration dates are adjusted by weather conditions and physiological conditions of birds (readiness for migration) (Rees 1982; Dawson 2008; Dawson *et al.* 2001; Dolnik 1975; Jonzen *et al.* 2006). In addition, migration rates are known to increase towards the end of the migration period (Dolnik 1975), and accordingly, migration rates are higher during late spring development (Alerstam 1990; Sparks 1999; Sparks & Braslavska 2001; Sparks & Menzel 2002). This suggests changes in the hormonal background to the birds' physiology as the time for breeding approaches.

When spring is delayed at a traditional stopover site (in our case, the Kurgalsky Peninsula), the delayed departure of birds from the previous staging area (*e.g.* western Estonia) can be explained by the fact that changes in spring temperatures in different locations in northern Europe correlate quite well with each other (Isachenko *et al.* 1965; Filatov *et al.* 2012). The dates of ice melt at sites along the migration route also correlate well with temperatures and each other (Vodogretsky 1972; Filatov *et al.* 2012). Changes in temperatures at the previous site therefore may signal to birds the probability of optimal conditions for feeding (*e.g.* probability of ice melt, or vegetation growth) at sites further along the migration route, although some species may be better able to do so than others depending on

whether a long overseas crossing (and thus ability to use spring conditions at one site as an indicator of the conditions they might encounter at the next) is involved (*e.g.* Tombre *et al.* 2008). It is assumed that for the Whooper Swan such a signal is the threshold of daily temperatures of 3–5°C (Mathiasson 1991), while for the Bewick's Swan, migrating later, this threshold should be somewhat higher. On the other hand, a long stay at the previous stopover site allows swans to accumulate more energy reserves, which reduces the need for them to stop at the Kurgalsky Peninsula when the time required to move to nesting sites has been drastically reduced. It is probably also these circumstances that stimulate the birds to increase the rate of migration and skip part of their traditional staging pattern.

The strategy of reducing the number and duration of stopovers in years with a late spring may lead to a deterioration in the birds' reproductive condition. The benefit to the birds is that they have the opportunity to reach the breeding grounds, occupy territories and lay a clutch at an optimal time, so that the greatest biomass and energy value of food is available for brood rearing (Clausen & Clausen 2013; Nolet *et al.* 2019). However, due to the deterioration in the physiological conditions of breeders in years with late springs, the overall productivity of the population may decrease, as indicated by annual variation in the brood counts recorded for Bewick's Swans (Wood *et al.* 2016) and arctic geese (Alisauskas 2002; Nolet *et al.* 2019).

On the other hand, skipping one or more stops in the middle parts of the migration route may increase the duration of staging both in the very initial sections of the journey further southwest in the Baltic Sea, and to the northeast just before the last flight to the nesting sites. For Bewick's Swans, the latter such sites may be found in the delta of the Northern Dvina River or in Czech Bay on the Barents Sea (Nuijten & Nolet 2020). It is likely that this is where the main accumulation of energy resources for reproduction occurs in years with a late spring. In other words, the overall energy balance of birds on migration in years with different weather scenarios may be similar.

Moreover, the foraging strategies of swans are quite malleable, and deficits in food or stop duration can be compensated by the intensity of feeding or by increasing the proportion of this activity in the birds' time budget, as occurs during wintering (Wood *et al.* 2021a,b). Thus, the nature of the effect of birds skipping certain sites, or reducing the time spent on them, on their reproductive condition is not completely clear and requires additional research.

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Photograph: Whooper Swans landing on the Gulf of Finland, by Sergey Kouzov.