



## UvA-DARE (Digital Academic Repository)

### Bewick's swans in a changing world

*Species responses and the need for dynamic nature conservation*

Nuijten, R.J.M.

**Publication date**

2020

**Document Version**

Other version

**License**

Other

[Link to publication](#)

**Citation for published version (APA):**

Nuijten, R. J. M. (2020). *Bewick's swans in a changing world: Species responses and the need for dynamic nature conservation*. [Thesis, externally prepared, Universiteit van Amsterdam].

**General rights**

It is not permitted to download or to forward/distribute the text or part of it without the consent of the author(s) and/or copyright holder(s), other than for strictly personal, individual use, unless the work is under an open content license (like Creative Commons).

**Disclaimer/Complaints regulations**

If you believe that digital publication of certain material infringes any of your rights or (privacy) interests, please let the Library know, stating your reasons. In case of a legitimate complaint, the Library will make the material inaccessible and/or remove it from the website. Please Ask the Library: <https://uba.uva.nl/en/contact>, or a letter to: Library of the University of Amsterdam, Secretariat, Singel 425, 1012 WP Amsterdam, The Netherlands. You will be contacted as soon as possible.



## Chapter 5

---

# **Chains as strong as the weakest link: remote assessment of aquatic resource use on spring migration by Bewick's swans**

Rascha J.M. Nuijten, Bart A. Nolet

### **Abstract**

Large birds that use flapping flight, like Bewick's swans, need stopovers for refueling during migration. Bewick's swans largely feed on aquatic macrophytes during migration, that may disappear when nutrient levels, waves and turbidity exceed some threshold. Macrophyte collapse has been suggested as a reason for the sharp decline of the Bewick's swan population in 1995 – 2015. Where macrophyte cover is regularly recorded along the southern half of the swans' migration route, our knowledge about the northern half is poor, partly because remote sensing of macrophyte cover is difficult. We used Bewick's swans equipped with GPS/GSM neck-collars including an accelerometer and water sensor to record the occurrence of aquatic foraging. We concentrated on spring, when stopovers are longer than in autumn, and focused on four key sites identified in earlier tracking studies. Within these sites, we identified areas that are protected based on the World Database on Protected Areas (WDPA). In three years (2017 – 2019), we obtained a total of 64 complete spring tracks, mostly of adult females ( $n = 50$ ) and young males ( $n = 9$ ). The majority of swans showed aquatic foraging along the coast of Estonia and in Dvina Bay, and about half in the Gulf of Finland and Cheskaya Bay. In Estonia and in the Gulf of Finland, swans predominantly used protected zones, but in Dvina Bay swans also foraged extensively in areas that are currently not protected according to WDPA. No protected areas occur in Cheskaya Bay. Macrophyte vegetation is under pressure by on-going or planned construction works in the Gulf of Finland and Dvina Bay, while future oil and gas exploitation threaten Cheskaya Bay. Our example shows how migrants can be used as sentinels to pinpoint areas that require further attention in order to maintain a chain of suitable stopovers on their migration.

## Introduction

Migratory species are threatened worldwide through climate change, overexploitation and habitat changes due to habitat destruction and creation of barriers (Wilcove and Wikelski, 2008). What kind of habitat changes cause problems for migratory species depends largely on their type of locomotion. For running and swimming migrants the creation of fences and dams can cause serious obstacles (Hayward and Kerley, 2009; Ziv et al., 2012), while for flying migrants this is likely to be less of a problem, and availability of suitable habitat could be of more importance.

Two main modes of flight exist: flapping and soaring. Flapping flight is energetically expensive, whereas soaring flight is energetically cheap but dependent on thermal energy. Obviously, this has implications for the habitat requirements for successful migration. For soaring flyers land corridors are essential to cross large water bodies where thermals are weak or absent (Vansteelant et al., 2017), whereas flapping flyers need prime foraging habitat along the migratory route for fueling their flight (Hedenström and Ålerstam, 1997; Piersma et al., 2016). Because migration speed is mainly determined by fueling rate at stopovers (Ålerstam, 1991; Lindström et al., 2019), and large birds have low fueling rates (Hedenstrom and Ålerstam, 1998; Lindström, 2003), suitable stopover habitat is particularly important for large birds using flapping flight. Effective conservation of especially large migratory bird species with flapping flight therefore requires knowledge about where the birds stop and forage and the state of these sites.

Tracking of birds equipped with PTT- or GPS-tags, or for the smaller birds geolocators, have revealed where they stop (Bridge et al., 2011), but these devices generally do not provide information about their (foraging) behavior. Attempts have been made to derive such behavior from (high-frequency) GPS fixes (De Weerd et al., 2015), but addition of extra sensors has greatly improved the ability to record behavior remotely (Wilmers et al., 2015). A well-known example is the accelerometer that measures static and dynamic acceleration, usually in three directions (Kays et al., 2015; Yoda et al., 2001). By correctly interpreting the resulting data, the behavior of free-ranging individuals at the moment of measurement can be deduced (Andrea Kölzsch et al., 2016; Shamoun-Baranes et al., 2012). This technique has previously been used to measure foraging time and estimate fueling rates of birds (Dokter et al., 2018; van der Kolk et al., 2020). Addition of a water sensor enabled the distinction between terrestrial foraging and aquatic foraging in swans (Nuijten et al., 2020).

Swans are among the largest species using flapping-flight and their migration distance is thought to be restricted by their fueling time (Hedenstrom and Ålerstam, 1998). The European population of the Bewick's swan (*Cygnus columbianus bewickii*) breeds in the Russian tundra and winters in western Europe. Bewick's swans need several stopovers to complete their migratory journey, especially in spring (Beekman et al., 2002). Direct observations revealed that they mainly forage on aquatic macrophytes at these stopover sites (Nolet et al., 2001; Rees & Bowler, 1991; Zaynagutdinova et al., 2019). Aquatic resources are often preferred, at least by adult swans (Nolet et al., 2002; Nolet et al., 2014). The main advantage over terrestrial foraging is that the swans can feed on aquatic macrophytes day and night, whereas on agricultural fields and grasslands foraging is restricted to daytime, supposedly to reduce predation risk (Nolet et al., 2002, 2007).

Macrophytes are ecosystem engineers able to maintain aquatic environmental conditions that are beneficial for themselves as well as a suite of other species, including swans (Jeppesen et al., 1998; Scheffer, 1990). Under a wide range of circumstances, macrophytes are able to reduce nutrient levels, waves and turbidity. When environmental stressors like eutrophication, increased wave action, or turbation by for instance bottom-dwelling fish exceed a certain threshold, macrophytes may however disappear and phytoplankton takes over (Phillips et al., 2016; Sayer et al., 2010). Once a water body has changed in a phytoplankton-dominated state, return to a macrophyte-dominated state is hampered because nutrient concentrations, water movement and turbidity are no longer tempered by the presence of macrophytes (Scheffer et al., 1993).

It is known that macrophyte cover changed in some areas but not in others along the southern half of the flyway of Bewick's swans. In Lake Veluwe, The Netherlands (52.4 °N, 5.7 °E), macrophytes largely disappeared in the 1970s due to eutrophication, but recovered thanks to water purification and bio-manipulation measures (van Vierssen et al., 1994), accompanied by disappearance and re-appearance of water bird fauna (Noordhuis et al., 2002). In contrast, the macrophyte vegetation of Lake Peipsi on the border between Estonia and Russia (58.7 °N, 27.5 °E) is rather stable (Nõges & Nõges, 2006), despite fluctuations in nutrient loading (Nõges et al., 2005). Our knowledge about macrophyte cover, let alone changes therein, in the more remote northern half of the migratory route is however poor. Some attempts have been made to map macrophyte cover along the whole Bewick's swan migration route by remote sensing (Beekman et al., 1996), but this proved to be difficult especially when the macrophytes are totally submerged (Gyimesi et al., 2012b).

Between 1995 and 2015, Bewick's swans have been declining rapidly for unknown reasons. A species action plan was adopted that amongst others called for maintaining suitable aquatic macrophyte availability at a chain of key sites along the migratory route as these are vital for the swans to complete their migration (Nagy et al., 2012). We equipped Bewick's swans with GPS/GSM neck-collars including an accelerometer and water sensor, enabling us to remotely assess their use of aquatic resources during migration. Here we concentrate on spring migration when use of stopovers is longer than in autumn, because in spring swans progress with the melting ice, fueling for both migration and reproduction (Nolet, 2006; Nuijten et al., 2014). We compare the areas where aquatic foraging was recorded with those currently protected by law, and discuss overlap, discrepancies and potential threats for the sustainability of these important fueling sites for the Bewick's swan and other migratory waterfowl species.

## Methods

In December or January of three consecutive winters, 2016/17, 2017/18, and 2018/19, we caught 104 Bewick's swans in total on agricultural fields in the province of Noord-Brabant (The Netherlands) using canon nets. Birds were aged by plumage characteristics and sexed by cloacal inspection; a blood sample was taken for molecular sexing afterwards (success rate of cloacal inspection proved 94%). We aimed to equip adult females (> 2 years old) and young males (< 2 years old) with specifically designed, 3D-printed, white neck-collars. This yielded 30, 6, and 15 GPS-tagged individuals in the three winters, respectively. The collar weighed 70 g, with an inner diameter of 51 mm and a height of 80 mm, and each had a unique black alpha-numeric code to allow for individual recognition in the field. The collar contained a GPS, a tri-

axial accelerometer (ACC) and a water sensor, and sent its data remotely via the GSM network to a server on a daily basis. Previous trials in captivity showed that collared swans preened more than their partners without collars in the first four weeks, but no differences in behavior were present thereafter (Nuijten et al. 2014).

The sampling frequency of the different sensors was dependent on season and the energy level of the device (Nuijten et al., 2020). In spring, the period of interest for this study, GPS positions were taken every 15 min, ACC measurements every 2 min (with a bout duration of 2 s, and bout frequency of 20 Hz) and water detection every second (binary) in the collars applied in the first winter. For the collars applied in the second and third winter, the measurement frequency of the GPS and ACC sensor was increased to 5 min and 1 min, respectively. Settings could not be changed after deployment.

The water sensor detected water by measuring conductivity, and was triggered when both probes, placed on opposite sides of the collar were submerged (as checked in the lab). We determined whether the water sensor was associated with aquatic foraging by linking positive values to the ACC recordings, more specifically the mean angle of the vertical axis (i.e., parallel to the neck of the swan). An angle of  $+90^\circ$  or  $-90^\circ$  corresponds to the neck being straight up or straight down, respectively. For aquatic foraging one would expect the neck to be below the horizontal position (i.e.,  $< 0^\circ$ ). For 80% of all observations for which water was detected ( $N = 439,813$ ), this was indeed the case (Nuijten et al. *in press*). The remaining 20% at least partly also represents aquatic foraging, because that consists of a sequence of trampling, submerging and breathing (Brouwer & Tinbergen, 1939; Nolet et al., 2001), and water will be dripping from the collar during trampling and breathing. Another part may consist of incidences in which the swan was resting or preening on open (sea)water with high waves or during periods when heavy rain triggered the water sensor. In order to limit misidentification, we summarized the raw water sensor data to aggregates of 5 min (i.e. 300 s), and specified submergence (“aquatic foraging”) to be detected (a total of  $> 30$  s ‘1’ in raw data) or not ( $> 270$  s ‘0’ in raw data).

For each individual, we merged the water sensor dataset, i.e. the 5 min aggregates, with the GPS tracking data based on the time stamp attached to both measurements. In case of the 15 min interval GPS data (for the collars deployed in winter 2016/2017) there could be up to three aggregates of 5 min linked to the same GPS location. We used this number as a measure of aquatic foraging intensity (see Results). We selected the period between 1 Feb and 25 May (“spring migration”, including pre-migratory fueling).

We focussed specifically at the locations where aquatic foraging was detected within four main stopover sites identified by a previous tracking study (Nuijten et al. 2014). These stopovers were (with SW and NE corners): the coast of Estonia (21.5E, 57.8N – 24.0E, 59.2N), the Gulf of Finland near St Petersburg (27.9E, 59.4N – 30.5E, 60.7N), the Dvina Bay (39.6E, 64.5N – 40.8E, 65.1N) and Cheskaya Bay (44.8E, 66.5N – 48.0E, 67.8N). Within these stopover sites, we looked which areas are currently protected based on the World Database on Protected Areas (WDPA; IUCN UNEP-WCMC 2019).

We tested whether there were differences in usage for aquatic foraging among the four main sites and the three years using a logistic regression with site and year as fixed factor and individual as random factor to avoid pseudo-replication, using a likelihood ratio test. We ran

this analysis for all swans and for the adult females (with 78% by far the most common sex-age category) separately, using R package lme4 (Bates et al., 2015). The interaction between site and year was not significant and therefore left out. We checked for overdispersion by testing whether the deviation was larger than the mean.

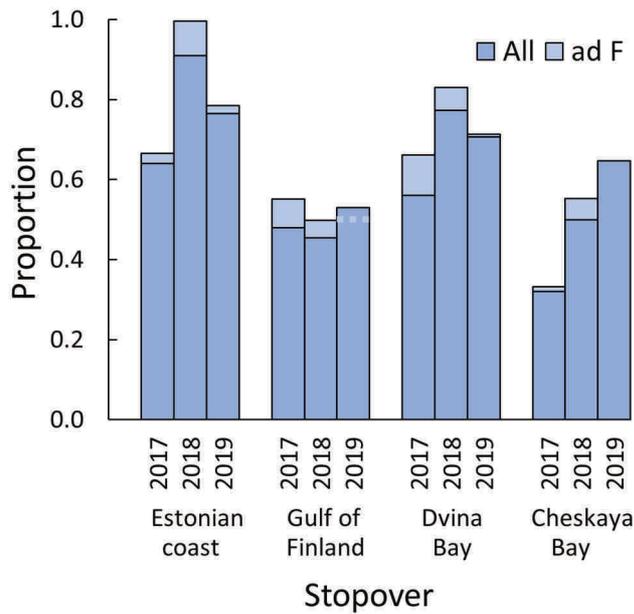
The tracking study was approved by the Centrale Commissie Dierproeven (license 2016518), and catching and handling was licensed by exemptions Flora- en Faunawet 75A obtained through Dienst Regelingen (FF/75/2016/044) and Wet natuurbescherming issued by Omgevingsdienst Brabant Noord (Z/046757).

## Results

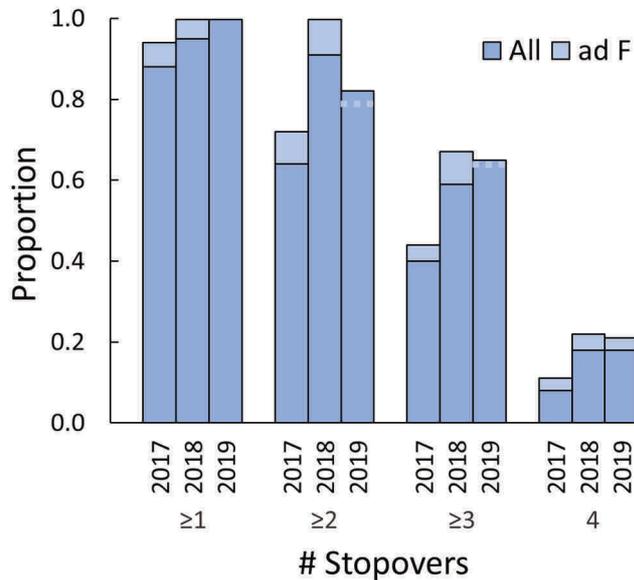
We obtained complete spring tracks of 39 Bewick's swans between wintering and summering grounds in 2017 ( $n = 25$  individuals), in 2018 ( $n = 22$ ), and in 2019 ( $n = 17$ ). None of the selected birds flew together, neither as a male-female nor parent-offspring pair. Most tracks were of adult females ( $n = 50$ ) and of young males ( $n = 9$ ). Six individuals were tracked in all three years, twelve individuals were tracked in both 2017 and 2018, and one in 2018 and 2019 (Table S5.1). All individuals basically followed the same route from the North Sea countries through the Baltic States, Leningrad Oblast, Karelia, Archangelsk Oblast to Nenets Autonomous Okrug (Fig. S5.1, S5.2 and S5.3).

Aquatic foraging was recorded in all four main stopover sites. At the west coast of Estonia, many of the swans stopped, mainly using Matsalu Bay, Haapsalu Bay and Väike Strait where they were foraging aquatically. Further to the north, in the Gulf of Finland, about half of the swans stopped to stage and refuel on aquatic resources. In Dvina Bay again, the majority of swans stopped and foraged aquatically, whereas in Cheskaya Bay approximately half did so (Fig. 5.1). These differences in aquatic resource use among sites were significant, both for all individuals ( $\chi^2_3 = 18.521$ ,  $P = 0.003$ ), and for adult females only ( $\chi^2_3 = 18.591$ ,  $P = 0.003$ ) (no overdispersion was apparent in either of these cases, with deviation / mean being lower than 1 in both cases: 0.93 and 0.99, respectively). The patterns in aquatic resource use by the swans in the different stopovers was marginally significantly different among years, both for all swans ( $\chi^2_2 = 5.985$ ,  $P = 0.050$ ) and for adult females only ( $\chi^2_2 = 4.898$ ,  $P = 0.086$ ). Nearly all swans foraged aquatically in at least one of these sites, whereas only a minority used aquatic resources in all four main sites during one spring season (Fig. 5.2).

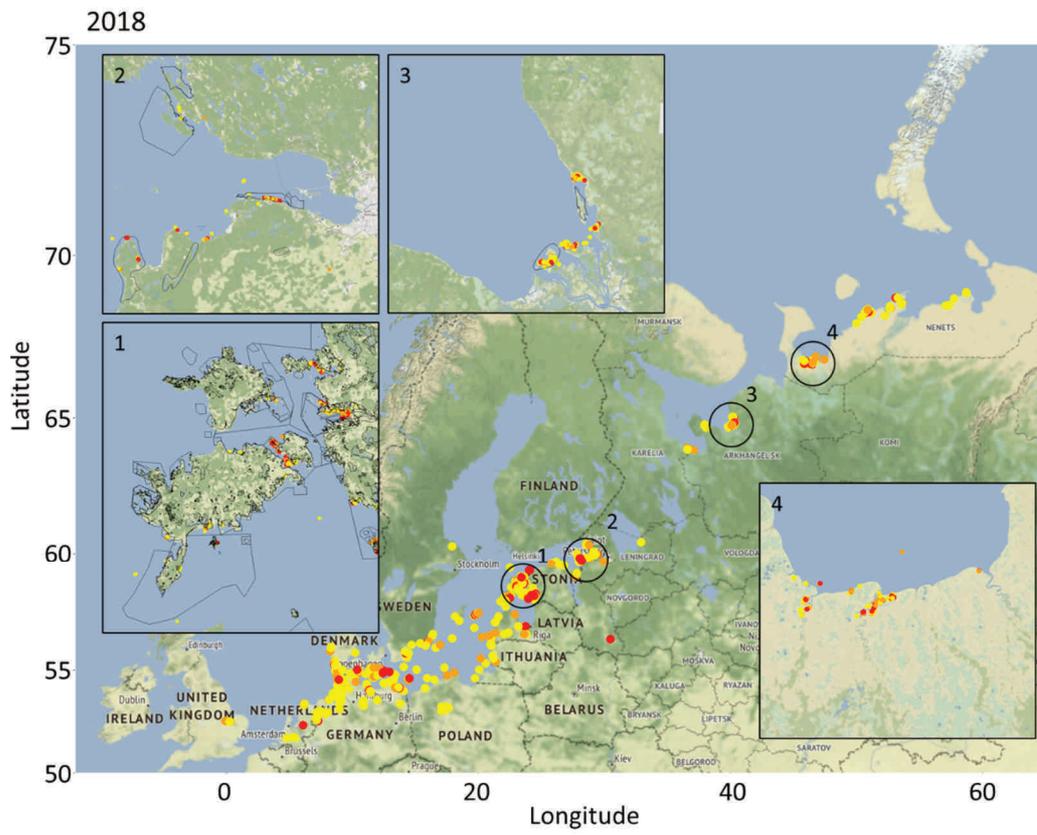
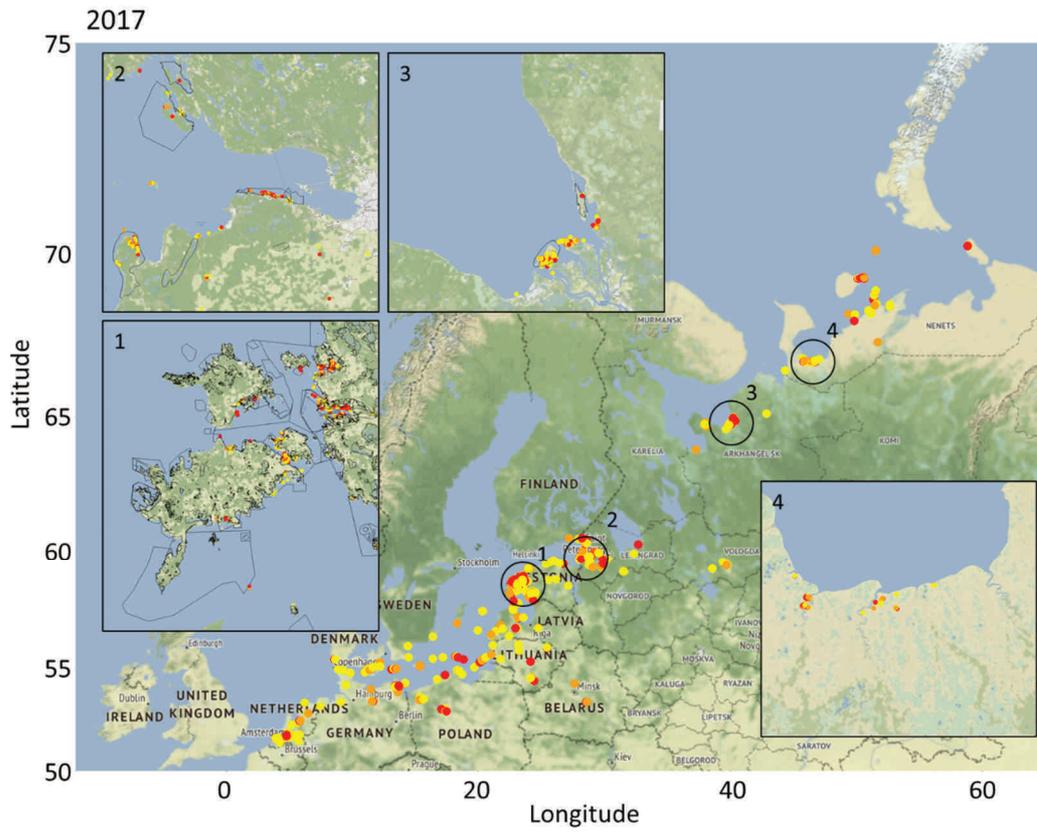
Where present, the swans heavily used protected zones. In Estonia, the swans mainly used Matsalu Bay, Haapsalu Bay and Väike Strait to fuel for migration, which all have a protected status (Fig. 5.3). In the Gulf of Finland, they also almost exclusively foraged within the boundaries of the protected areas along the south coast (Fig. 5.3). In the White Sea, where two protected areas are present in the Dvina Bay, the southern one was frequently used for aquatic foraging by the swans (Fig. 5.3). The other one is a terrestrial protected area enclosing the island of Mud'yug that is not suitable for swans. However, the swans also foraged extensively in areas that are currently not protected in the Dvina Bay, at least according to the WDPA, most noteworthy in the shallow tidal area east of Mud'yug Island (Fig. 5.3). In the Cheskaya Bay there are currently no protected areas listed in the WDPA, but aquatic foraging was recorded there in all three spring seasons (Fig. 5.3).

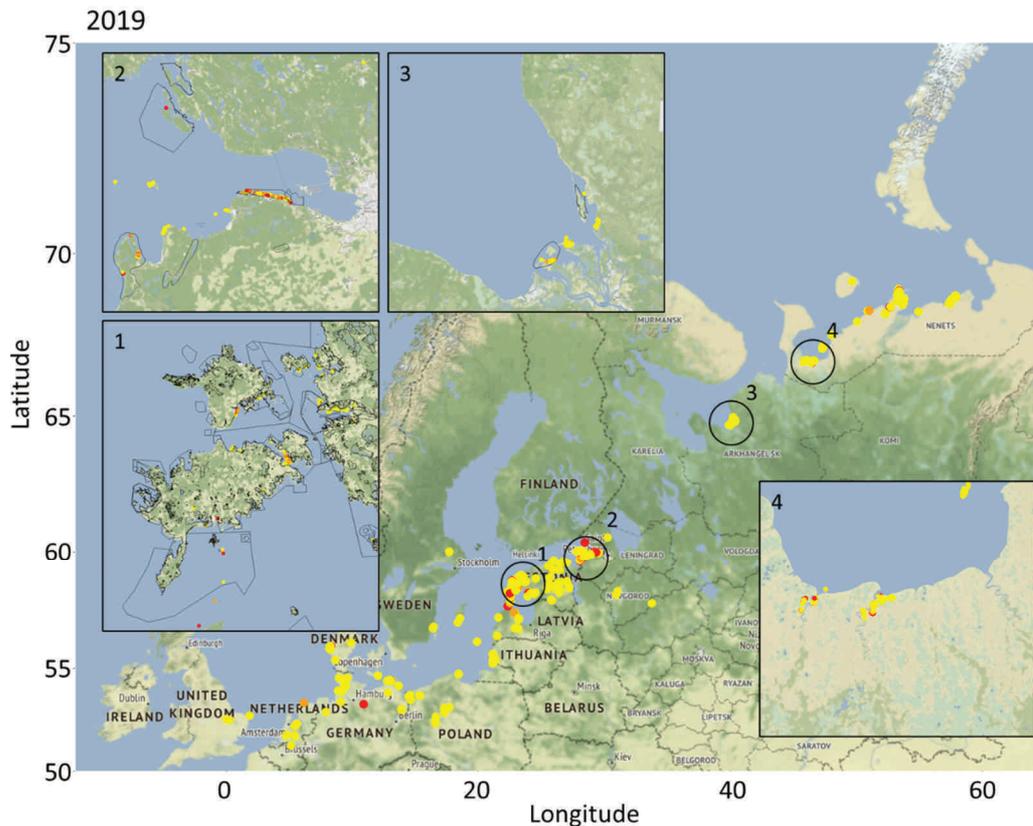


**Figure 5.1:** Proportion of tagged Bewick's swans, all and adult female only, recorded to forage aquatically in the four main stopover sites during spring migration of three consecutive years. Usage of stopover sites was significantly different, with differences among years being only marginally significant (see main text). For all sites and years a higher proportion of adult females compared to all individuals foraged aquatically at the stopovers, except for Gulf of Finland 2019 where a dotted line indicates the proportion of adult females.



**Figure 5.2:** Proportion of tagged Bewick's swans, all and adult female only, recorded to forage aquatically in at least one, two, three or in all four main stopover sites during spring migration of three consecutive years. In all cases a higher proportion of adult females was recorded, except for  $\geq 2$  and  $\geq 3$  stopovers in 2019 where a dotted line indicates the proportion of adult females.





**Figure 5.3:** Locations used for aquatic foraging by the swans during spring migration in (A) 2017, (B) 2018 and (C) 2019. Every dot indicates a GPS point during which aquatic foraging was identified based on the water sensor data. Since the interval of the GPS is 15 min for most of the tracks (the tracks in 2017, and those that continued to yield data in 2018 and 2019; see Table S5.1), and that of the water sensor is five minutes, we distinguished three different levels: yellow, orange and red for aquatic foraging detected for 5, 10 and 15 min, respectively per GPS fix. Insets show important stopover sites used by the swans being western Estonia (1), the Gulf of Finland (2), the Dvina Bay (3) and Cheskaya Bay (4). The black polygons indicate protected areas as listed in the WDPA (IUCN UNEP-WCMC, 2019).

## Discussion

By tracking swans fitted with GPS/ACC-tags with an additional water sensor we found that nearly all Bewick's still forage aquatically in at least one of the key stopover sites previously identified, with about half of the swans foraging aquatically in three of those sites. The majority of the swans foraged aquatically along the west coast of Estonia and in Dvina Bay, with lower proportions using aquatic resources in the Gulf of Finland and in Cheskaya Bay. Aquatic foraging mainly took place within protected areas, but with notable exceptions especially in the northern part of the migration route.

The areas where we recorded aquatic foraging by Bewick's swans during spring migration correspond to important stopovers as identified in earlier tracking studies covering 1993-2011 (Beekman et al., 2002; Nolet et al., 2001; Nuijten et al., 2014). The major importance of aquatic foraging sites in Estonia is also in line with previous research based on counts and ring readings of Bewick's swans (Luigujõe et al., 1996). The Gulf of Finland is another known

important stopover area from ground observations, but counts indicate that numbers are presently lower than 20 or more years ago (Zaynagutdinova et al., 2019). Aerial counts of the Dvina Bay followed by direct observations in the shallow tidal area east of Mud'yug Island revealed that this area was used for aquatic foraging by large numbers of Bewick's swans in the mid-1990s (Nolet et al., 2001). Much less is known from previous research about Cheskaya Bay in spring. The proportions of swans using  $\geq 2$  sites (Fig. 5.1 and 5.2) highlights the 'chain' function that these areas have.

The availability of a chain of suitable stopover habitat is thought to be crucial. Bewick's swans in this flyway are slowed down by the retreat of ice in spring (Nuijten et al., 2014), a process that is variable between the years. Dealing with this variation is facilitated by having multiple sites along the route available because this enhances predictability of and adjustment to conditions ahead (Bauer et al., 2020; Kölzsch et al., 2015). Based on their migration speed Bewick's swans are partly capital breeders (Nolet, 2006). This means that they collect stores on their migratory stopovers to fuel both the migration itself and part of the subsequent breeding effort. In autumn, Bewick's swans skip the Dvina Bay, but they can probably afford to do so because in that season they do not need to carry stores for reproduction (Beekman et al., 2002). Similarly, white-fronted geese migrate slower in spring than in autumn, using more stopovers, and flying less far to the next stopover for a given time spent at a stopover (A. Kölzsch et al., 2016). This again suggests that also these geese fuel in spring for both migration and reproduction, and indeed white-fronted geese are partly capital breeders (Spaans et al., 1999). Recent work in barnacle geese showed that skipping stopovers in spring enables these birds to arrive earlier in the breeding grounds, but not to commence breeding much sooner because they have to refuel first before they can start egg-laying (Lameris et al., 2018). This underlines the importance of spring fueling for successful reproduction.

With the loss of natural wetlands in the last 100 years or so many birds have been forced to look for alternatives. Bewick's swans are no exception, and in their wintering range they switched to agricultural resources in the 1970s when aquatic vegetation was disappearing due to eutrophication (Merne, 1972; Mullié and Poorter, 1977). While the aquatic vegetation has recovered in many places, nowadays swans still switch to agricultural resources when aquatic plants become depleted in the course of winter (Nolet et al., 2002). For a full appreciation of the importance of suitable aquatic stopover sites, one should realize that such alternative terrestrial resources are lacking in more northerly sites (Petrie and Wilcox, 2003).

While nearly all swans foraged aquatically in at least one of the key sites, more detailed time budgets showed that there was considerable individual variation in the time spent on this behavior (Nuijten et al., 2020). Previous research indicated that such variation in aquatic foraging during autumn migration was associated with increased body condition prior to spring migration, as well as increased subsequent breeding success (Hoye et al. 2012). Further research is needed to look into the consequences of individual variation in aquatic foraging during spring migration.

Differences in the occurrence of aquatic foraging among years seemed to be consistent among sites (the interaction was not significant), suggesting that the swans were not compensating for a lesser use of one stopover site by foraging more aquatically at another site. Differences among years were however small.

Whether the locations that the swans used for aquatic foraging during their spring migration within the main stopovers were situated inside protected areas varied among sites. In Estonia, these locations were mainly within protected areas. Two sites within the region that the swans use on their spring migration (Vilsandi and Matsalu), with a long history of protection, are nowadays protected as National Parks, the highest level of protection in Estonia.

In the Gulf of Finland the aquatic foraging locations were also mostly situated inside protected areas. Here the situation is however less secure. Close to the harbour of St. Petersburg, littoral areas have recently been lost due to construction works, but many of these waters were void of aquatic macrophytes, at least in the 1980s (Beekman et al. 1996). Construction work remains a threat, not only leading to direct loss of shallow waters, but also causing massive turbidity that may result in die-off of aquatic macrophytes (Phillips et al., 2016; Zaynagutdinova et al., 2019). This underpins the need to safeguard the areas and their quality in the Finnish Gulf currently in use by the swans, to ensure this site remains available for fueling their migration.

In Dvina Bay there was also extensive aquatic foraging taking place outside protected areas. While Mud'yug Island itself is a protected area, this for Bewick's swans still important area next to it is not, whereas here the swans could be sensitive to changes in hunting, water quality, and industrial developments. Recently, Russia and China together launched the plan to build a deep sea port near Archangelsk in order to exploit the increasing possibilities for cargo vessels to use the new Northern sea route that connects Western Russia with Eastern Asia (Buxbaum 2018; Laulajainen 2008). The new port is supposed to be built near the Mud'yug Island, just north of the shallow tidal sea, 50 km from the current port of Archangelsk (Louppova, 2018). The location of the port is close to the intensively used area by the Bewick's swans that we tracked in this study in spring 2018. Further developments in the area could threaten the suitability as a stopover site, with potential consequences for the population. Potentially a larger part of the Dvina Bay would be affected, as traffic will increase between the new and the current port of Archangelsk.

In Cheskaya Bay, the northernmost stopover site considered in this study, no protected areas were present whereas aquatic foraging was recorded there as well. Cheskaya Bay is a sparsely populated area just above the Arctic circle. Being close to the breeding grounds, this site might be an important 'springboard' for the swans, since from here they are likely to be able to predict circumstances in the breeding area and can time their arrival based on this information (Kölzsch et al., 2015). The changing climate has made Arctic Russia of increasing interest for oil and gas exploitation, Cheskaya Bay being no exception (Gautier et al. 2009; sites TPB1 and TPB2). Further exploitation of these resources might influence the suitability of this stop-over site for Bewick's swans.

Aquatic macrophytes are an important food source not only for Bewick's swans but also for other migratory waterfowl species in this flyway. Diving ducks often accompany foraging swans and benefit from *Potamogeton* tubers dug up by swans (Gyimesi et al., 2012a). In the 1990s there was a large seagrass *Zostera marina* bed in Dvina Bay that was used by dark-bellied brent geese on their way to Taimyr (Clausen, 1997; Green et al., 2002), and construction works near that area is possibly also impacting this species. Similar threats of important wetland stopovers are reported from other flyways (Piersma et al., 2016; Yang et al., 2011).

Our example shows how migrants can be used as sentinels to pinpoint areas that require further attention in order to maintain a chain of suitable stopovers on their migration. By tracking over longer time frames, the exciting possibility may arise that we can start using the tracked animals also as sentinels of environmental conditions (Kays et al., 2015; Ropert-Coudert and Wilson, 2005).

*Acknowledgments* - We are grateful to everyone that helped with the catching and tagging (Gerard Müskens, Youri van der Horst, Erik Kleyheeg, Peter de Vries, Thomas Lameris, Chiel Boom, Robert van der Meer, Anna Hermsen, Jan Vegelin, Fred Cottaar). Special thanks go to the late Theo Gerrits (madebytheo) for the design and manufacturing of the neck collars. We thank Elmira Zaynagutdinova for providing information about the protection status of sites in Russia, and Henk van der Jeugd for providing comments that helped to improve the manuscript.

## Supplementary Material

### 1

#### Sample sizes

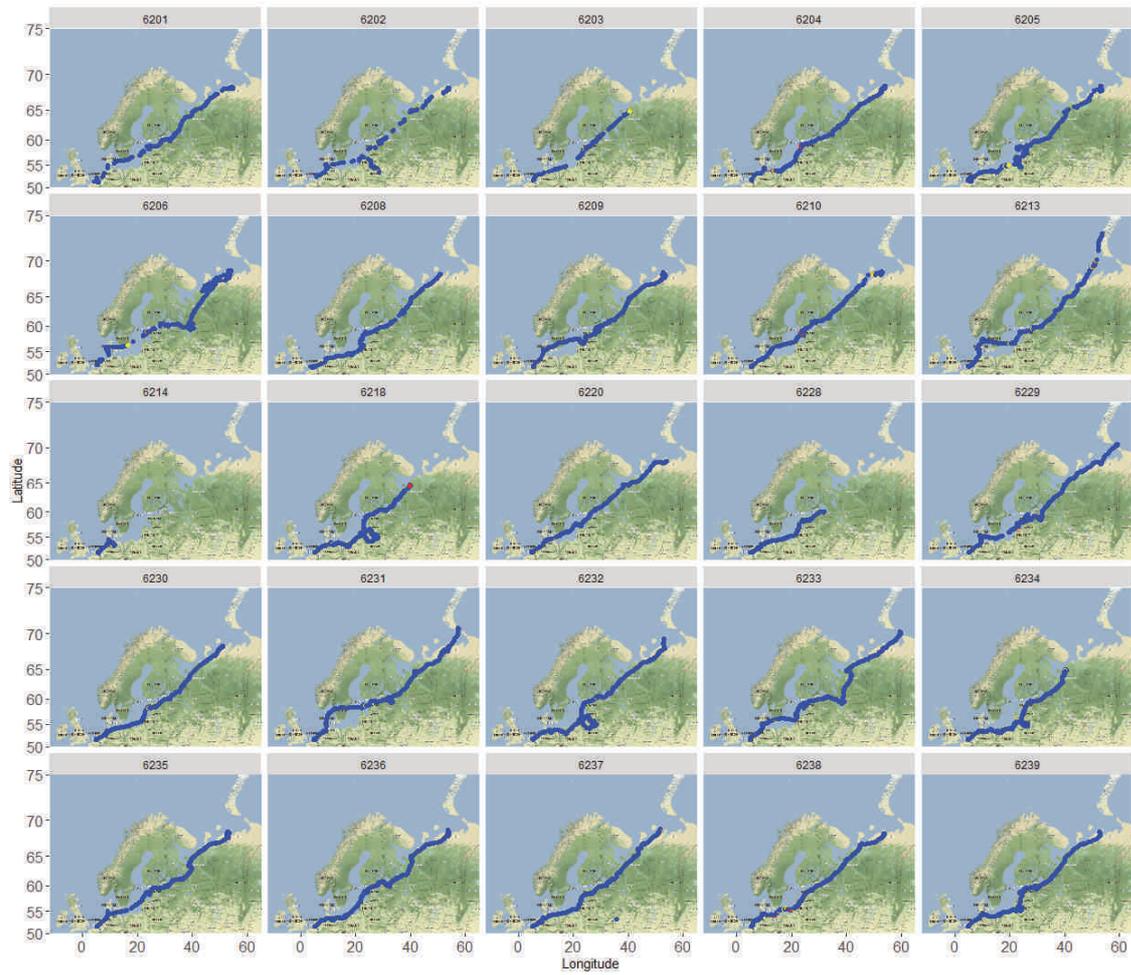
**Table S5.1:** Swans of which complete spring tracks were obtained, and whether (1) or not (0) aquatic foraging was recorded in the four key stopover sites (1 – 4) (see Fig. 5.1 in main text). Grey cells indicate no track.

Swan ID	Year of catch	Sex	Age at catch	Spring 2017				Spring 2018				Spring 2019			
				1	2	3	4	1	2	3	4	1	2	3	4
200	2018/19	M	A									1	0	1	1
201	2016/17	M	Y	1	0	1	1								
202	2016/17	F	A	0	1	1	0	1	0	1	0				
203	2016/17	F	A	0	1	1	0								
204	2016/17	M	S	1	0	0	0	1	0	0	0				
205	2016/17	F	A	1	1	1	0								
206	2016/17	F	A	1	1	0	1	1	0	1	0				
208	2016/17	F	A	1	0	0	0	1	0	1	0	0	1	1	1
209	2016/17	F	A	0	0	1	0	1	1	1	0				
210	2016/17	F	A	1	0	1	1	1	0	1	0				
213	2016/17	F	A	1	1	1	1	1	1	0	1	1	0	1	1
214	2016/17	F	J	0	0	0	0								
217	2017/18	F	A					1	1	1	0				
218	2016/17	M	J	1	1	1	0	0	1	1	0				
220	2016/17	F	A	1	1	1	1	1	0	0	1				
222	2017/18	F	A					1	0	1	1	1	1	1	0
223	2017/18	F	A					1	1	1	1				
225	2017/18	F	A					1	0	1	0				
226	2018/19	F	A									1	0	1	1
227	2018/19	F	A									1	0	0	0
228	2016/17	M	J	0	0	0	0								
229	2016/17	F	A	1	0	1	0								
230	2016/17	F	A	0	0	0	0	1	1	1	1	0	0	1	1

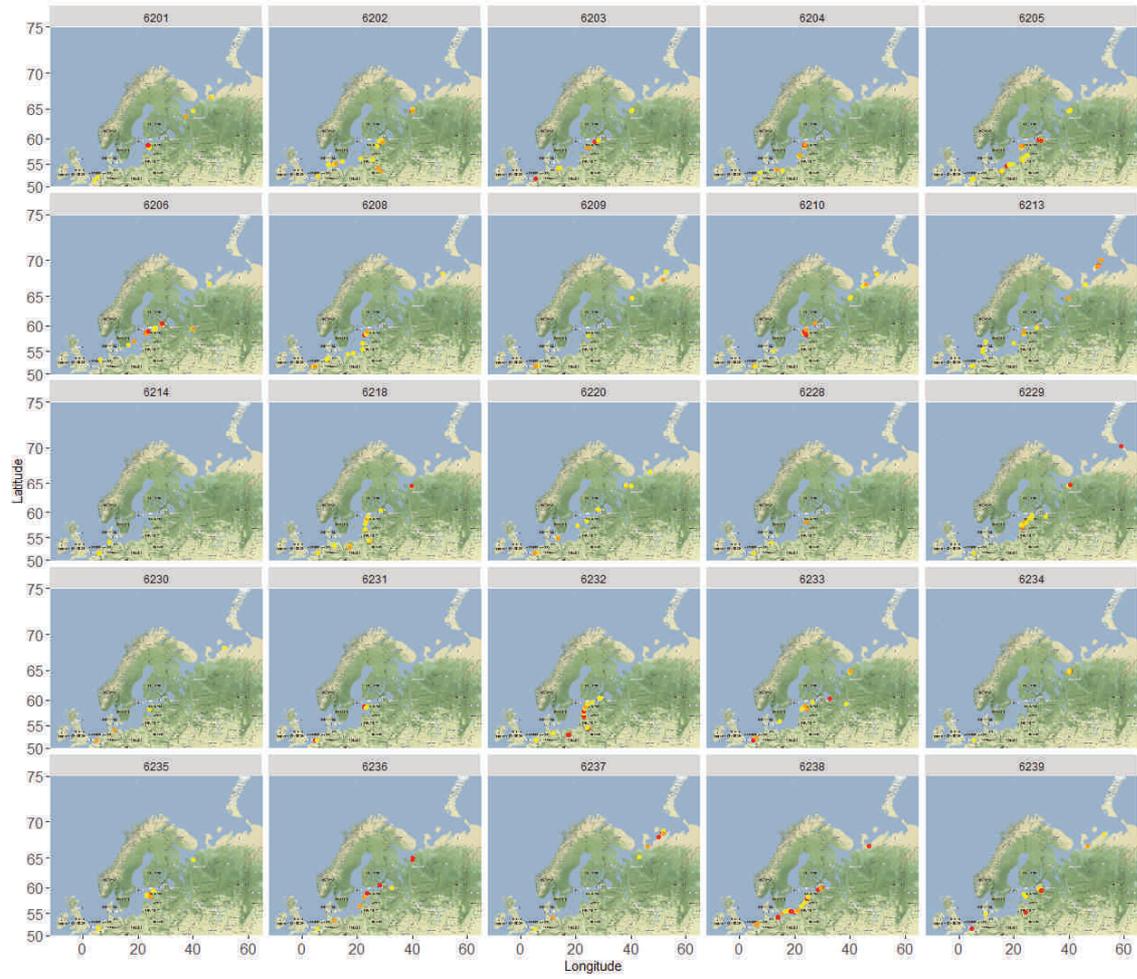
231	2016/17	F	A	1	0	0	0	1	0	1	1				
232	2016/17	M	J	1	1	0	0	0	0	0	0				
233	2016/17	F	A	1	0	1	0	1	1	1	1				
234	2016/17	F	A	0	0	1	0								
235	2016/17	F	A	1	1	1	0	1	0	1	1	1	1	1	1
236	2016/17	F	A	1	1	1	0	1	1	1	0				
237	2016/17	M	J	0	0	0	1	1	0	1	1	0	1	1	0
238	2016/17	F	A	0	1	0	1	1	1	0	1				
239	2016/17	F	A	1	1	0	1	1	1	1	1	1	1	1	0
240	2018/19	F	A									1	1	1	1
242	2018/19	F	A									1	0	0	1
243	2018/19	F	A									1	1	0	1
245	2018/19	F	A									0	0	1	0
246	2018/19	F	A									1	0	0	0
247	2018/19	F	A									1	1	1	1
249	2018/19	M	J									1	1	0	1

## 2 GPS and aquatic foraging, individual data

A

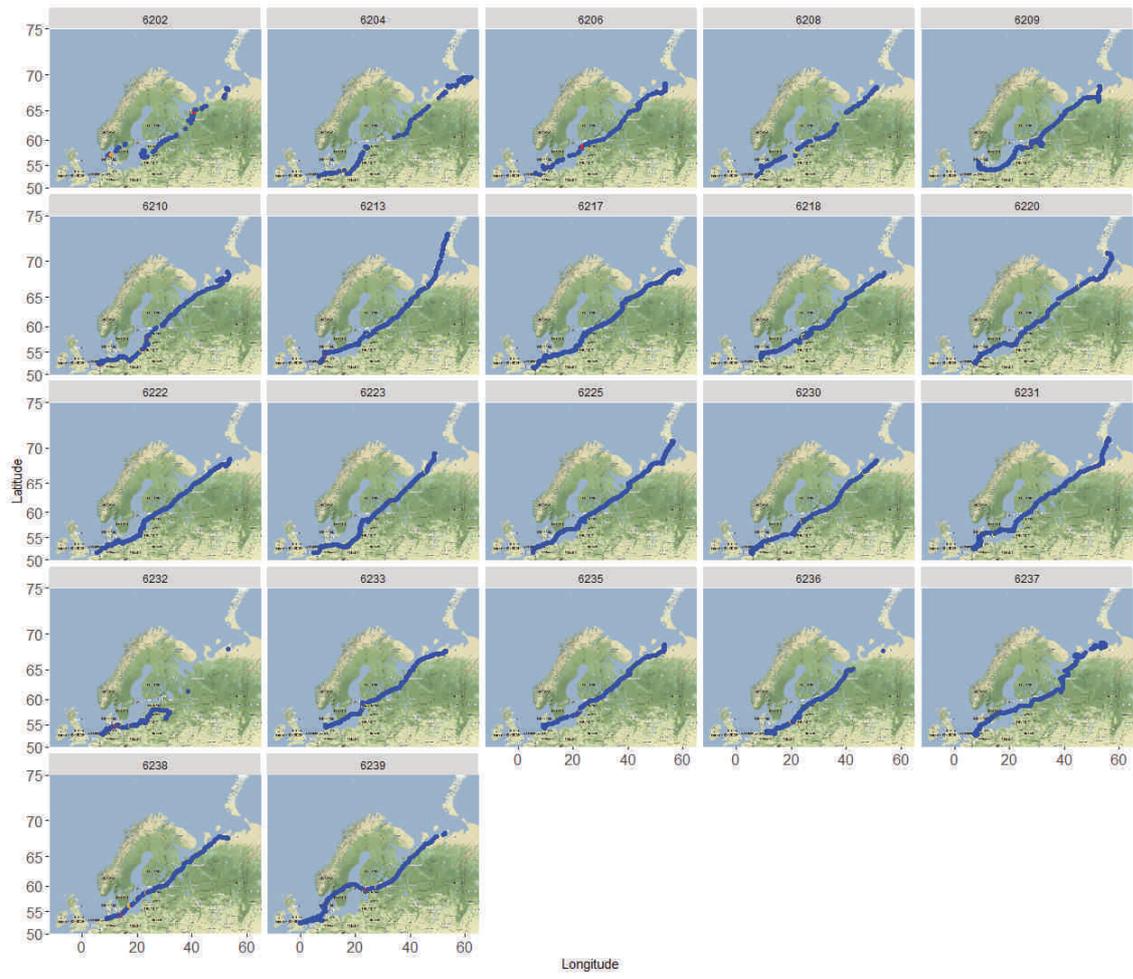


**B**

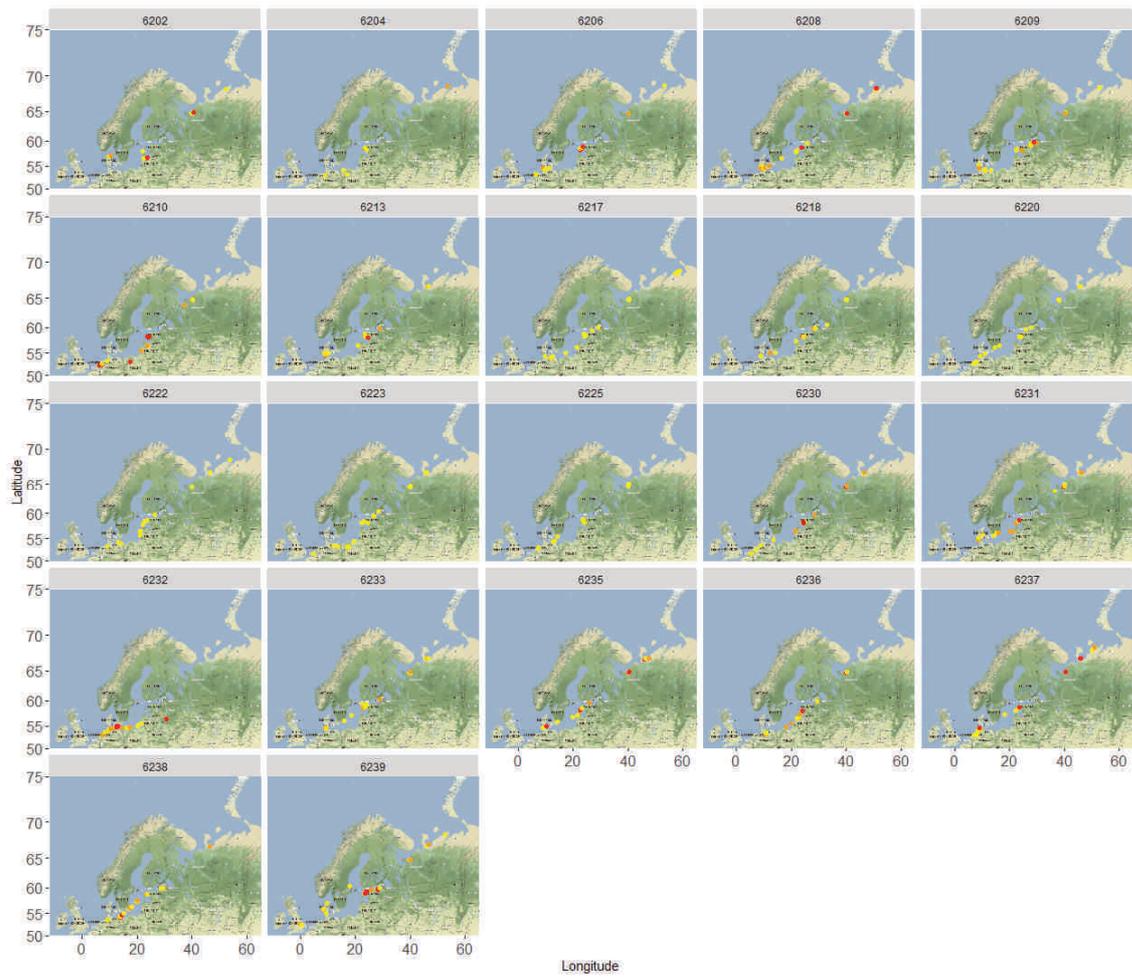


**Figure S5.1:** Spring 2017 (A) All GPS fixes and (B) GPS fixes with aquatic foraging (yellow, orange and red; see Fig. 5.1 in main text).

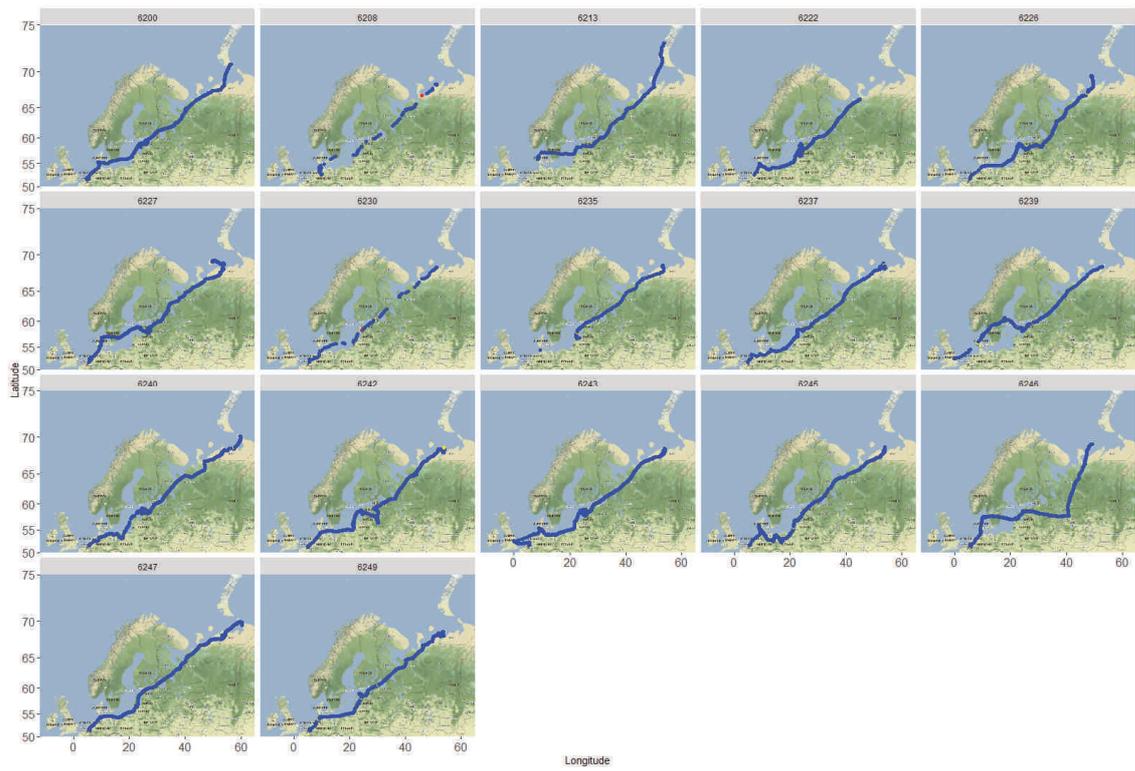
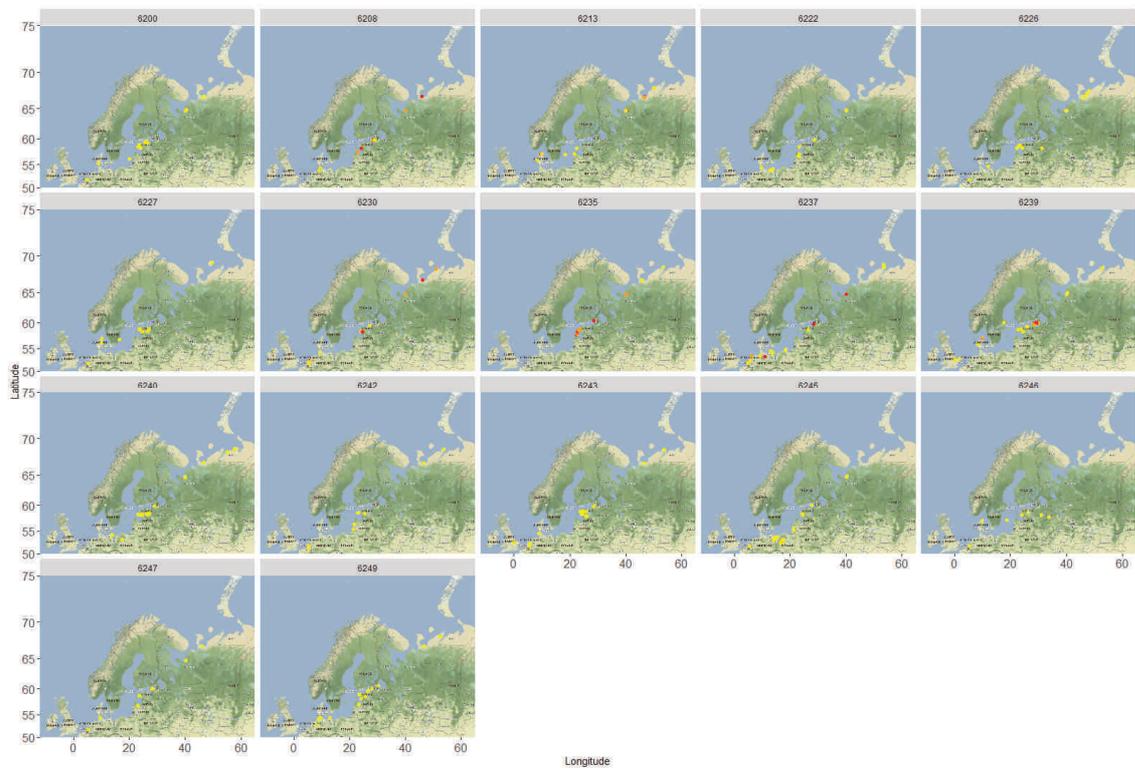
**A**



**B**



**Figure S5.2:** Spring 2018 (A) All GPS fixes and (B) GPS fixes with aquatic foraging (yellow, orange and red; see Fig. 5.1 in main text).

**A****B**

**Figure S5.3:** Spring 2019 (A) All GPS fixes and (B) GPS fixes with aquatic foraging (yellow, orange and red; see Fig. 5.1 in main text).