Bewick's swans in a changing world

Species responses and the need for dynamic nature conservation

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Chapter 7

Changes in winter site and habitat use by Bewick's swans: an ecological network analysis

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Abstract

The Bewick's swan (*Cygnus columbianus bewickii*) is an obligate migratory species breeding in Artic Russia and wintering in northwestern Europe, which is included as a target species in the Natura 2000 legislation. Since the second half of the 20^{th} century, large changes in water quality management, agricultural practice and policy have taken place that most likely affected habitat quality for herbivorous birds like Bewick´s swans, and their habitat and site use has likely shifted as a result. This may have consequences for their use of the Natura 2000 network of protected areas and efforts for their conservation in general. Here we present a network analysis of key wintering sites, and changes therein, of Bewick's swans in western Europe, covering the last thirty years. Based on 43 identified network "nodes", we found that the importance of the nodes changed over time, in interaction with habitat and longitude. Network nodes in the eastern parts of the winter range gained importance, and network nodes with grassland lost importance over time. Furthermore, we found that the movements between agricultural nodes increased in recent years. Evaluating the network nodes for their protected status revealed that 6 increasingly used sites are not protected by the Natura 2000 network. This raises the question whether the static Natura 2000 legislation is fit for protecting species that dynamically respond to environmental changes such as the Bewick's swan. We envisage that a reflection on the assignment criteria for Natura 2000 sites is expedient and a more dynamic form of nature conservation is needed to protect Europe's biodiversity in this time of global environmental change.

Submitted manuscript

Introduction

Migratory species rely on a multitude of sites to complete their annual cycle and are therefore particularly vulnerable to environmental changes along their migratory routes. At the same time, conservation of these species on the proper spatial scale is challenging. Within the European Union, Natura 2000 is one of the most important tools for large-scale conservation of biodiversity. Consisting of a network of protected areas, Natura 2000 focuses on particular habitats and species in order to safeguard Europe's resident and migratory species, with the Birds Directive (European Commission, 2009, 1979) and Habitats Directive (European Commission, 1992) as core legislative documents (European Commission, 2020). Under these Directives EU member states must assign protected areas to keep or regain a favourable conservation status (FCS) for specific target habitats and species, listed in the annexes of the Directives. Conservation objectives are formulated per targeted habitat/species for each area to evaluate the effectiveness of their management and provide incentives for management decisions. The concept of a network of nature areas fits well within the framework of migratory species (Klaassen et al., 2008; Martin et al., 2007; Runge et al., 2015), however considerations regarding species' responses to a changing environment are not included when assigning and evaluating Natura 2000 areas (Iwamura et al., 2014).

One example of an obligate migratory species which is included as a target species in the Natura 2000 framework is the Bewick's swan *Cygnus columbianus bewickii*, breeding in Arctic Russia and wintering in temperate regions of Europe and Asia (Rees, 2006). The westernmost part of the breeding population traditionally winters in western Europe, with a core wintering range covering SE-England, the Netherlands and NW-Germany. Birds arrive there in Oct-Nov via stopover sites in the Baltic region and leave in Feb-Mar. Despite having a protected status across its entire flyway, Bewick's swans are faced with various human activities impacting their population dynamics. These impacts were summarized in an AEWA Single Species Action Plan (Nagy et al., 2012). Illegal or accidental shooting and suboptimal feeding conditions at stop-over and wintering sites are described as the major threats to the population (Nagy et al., 2012). At stop-over sites during migration, the swans rely mainly on aquatic resources for fuelling (B.A. Nolet et al., 2001b; Rees and Bowler, 1991; Zaynagutdinova et al., 2019). Limited information is available on the feeding conditions at these stop-over sites, especially in the northern part of the migration range, but there are indications that foraging habitat might be under pressure due to human developments and oil and gas explorations in the north (Nuijten & Nolet *unpublished* data).

On their wintering grounds, Bewick's swans use a variety of habitat types. Since the second half of the 20th century, Bewick's swans have increasingly been using agricultural fields in their western European wintering range (Merne, 1972; Mullié and Poorter, 1977). Dirksen, Beekman, & Slagboom, (1991) describe how Bewick's swans prefer aquatic habitats upon arriving the Netherlands, where they feed on pondweed tubers, then first switch to arable land in late autumn and finally to grassland in the second half of winter to gain reserves for their spring migration. While multiple factors influence the moment of switching between habitats (Nolet et al., 2002), this pattern of switching habitats is now commonly assumed to describe the Bewick's swan winter movements. However, the landscape is highly modified by human activities since. Over the last 30 years, large changes in water quality management, agricultural practice and policy have taken place that most likely affected habitat quality for herbivorous birds, and their habitat and site use may have shifted as a result (e.g. Clausen, Madsen, Nolet, & Haugaard, 2018; Noordhuis, Van der Molen, & Van den Berg, 2002). At the same time climate has changed rapidly (IPCC, 2014). Based on data from a long-term (> 50 years) monitoring scheme, a recent study indeed found a considerable shift in both space (eastward) and time (shorter stay) in the wintering range of this population of Bewick's swans, potentially in response to climate warming (Nuijten et al. *in press*). These changes may have a profound impact on the population's habitat use and within-winter movement patterns, as well as their use of Natura 2000 sites.

Their relatively small population size, the impact of agricultural developments and the recently observed changes in this population of Bewick's swans have sparked conservation concerns. Currently the Bewick's swan is listed as "Endangered" on the European Red List for Birds (Birdlife International, 2015) and categorized in Annex I of the Birds Directive of the European Commission (European Commission, 2009). In practice this means that EU member states need to designate Special Protection Areas (SPA) for their survival, and manage these areas in a way that the species maintains or regains a favourable conservation status (FCS). Particularly in the light of recent shifts in wintering range (Nuijten et al. *in press*), the conservation efforts require an update and deepening of our knowledge of the species' winter ecology.

Bewick's swans typically spend the winter in flocks at a limited number of key sites (Rees et al., 1997). Regular movements of individual swans between these sites thus create a network of interconnected sites within the wintering range. This provides an opportunity to apply tools from network theory to identify movement patterns of Bewick's swans and identify properties of the network of sites used by this population. Network-based tools are increasingly being applied to disentangle complex movement patterns and quantify ecological connectivity (Jacoby and Freeman, 2016; Kölzsch et al., 2018).

Here we build on databases compiled through citizen science to perform a network analysis of key sites, and changes therein, of Bewick's swans wintering in western Europe, covering the last thirty years. We identify core areas ("nodes") in the network based on observations of Bewick's swan flocks, and quantify the "edges" in the network (i.e. movements between nodes) based on ring resighting data. We aim to answer three main research questions: 1) How well-connected are sites used by Bewick's swans within the wintering range? 2) Did the network structure change over time? 3) Are key sites protected by the Natura 2000 network? Based on the results we elaborate on the question whether the Natura 2000 network is fit for protecting dynamic species like the Bewick's swan.

We first identify whether the winter movements form a network of sites, and subsequently test whether the network represents a single or multiple well-connected subnetworks. We hypothesize a segregation in winter range use between subgroups of Bewick's swans, one using the north of the Netherlands as a springboard to the UK, and one staying in mainland Europe visiting Germany and the south of the Netherlands (Rees and Bacon, 1996; Tijsen and Koffijberg, 2015). Next, we identify which nodes are most important in the network and whether this changes over time. We expect, in line with the general eastward shift that was found in this population (Nuijten et al. *in press*), that the important nodes of the recent years will be situated more to the east than the important nodes in early years. In addition we will assess whether there is a sequential use of these nodes during winter, and whether this is related to habitat switches as described by Dirksen et al. (1991).

Methods

We first identified the important staging sites of wintering Bewick's swans in the core wintering range in western Europe, which were used as the start and end points of the within-winter movements and thus form the nodes of the network. We used flock observations (≥10 individuals) of Bewick's swans from the databases *waarneming.nl* (Dutch observations between 1989 and 2015; spatial accuracy < 250 m) and *ornitho.de* (German observations between 2011 and 2019), including only one observation (the one with the maximum number of birds reported) per location (longitude and latitude rounded to 0.1°) per day. In total 21,477 observation were included, which we clustered by performing a hierarchical clustering in R (R Core Team, 2019) with a clustering threshold of 2.0 km. We further selected the resulting clusters based on the criteria of having ≥15 days of observations with ≥170 individuals present (all observations of a single day within a cluster summed) in at least four out of the 30 years. A threshold of 170 individuals represents the lowest Ramsar 1% threshold in our study period (Wetlands International, 2020). We created spatial polygons based on the minimal convex polygon around all observations assigned to a cluster to create the network nodes, which were used in further analyses. For the network analysis we added three extra nodes to the final set, representing the UK, Denmark and Poland. These nodes do not represent specific sites, but by adding them we were able to establish links to these important parts of the Bewick's swan wintering area as well. The same nodes were used throughout the entire study period.

To collate all movements of individual swans between node pairs, we used ring resighting data between October 1990 and March 2020 (30 winter seasons) from two ringing schemes (legrings WWT, and neckbands TH/NIOO; see Nuijten et al. *in press*). In total 72,379 resightings from 4504 individuals were included. The movements between nodes are directional, and will be referred to as the 'edges' in the remainder of this study. An edge between two nodes was identified when an individual was resighted in two nodes consecutively within a winter. We analysed the data in six five-year periods (referred to as p1 – p6) to study changes over time and still maintain sufficiently high sample sizes for the edges.

Habitat data were downloaded from the Copernicus Corine Land Cover dataset (Feranec et al., 2016). We used the maps CLC1990 (p1 and p2), CLC2000 (p3), CLC2006 (p4), CLC2012 (p5) and CLC2018 (p6) for each of the six five-year periods. For convenience we grouped the Corine Land Cover categories into four types relevant for the swans: agriculture, grassland, water, other (see S1 for the Corine categories assigned to these groups). We overlaid the polygons of the nodes with the habitat data to extract the proportions of the different habitat types within each node for each period. For each node we determined the dominant habitat type. Nodes 41-43 had no dominant habitat assigned.

After identifying all nodes and edges, we calculated network properties on the network, node and edge level. On the network level we were interested in connectedness of nodes with (dis)similar habitat types and subnetworks. Therefore we calculated network edge density, network assortativity and the maximum number of components that were strongly (i.e. two-way) connected within a period (p1 – p6). The edge density represents the ratio of the number of (realized) edges to the number of possible edges in a network with N nodes. Assortativity is defined as the extent to which nodes are connected (through edges) with similar versus dissimilar other nodes. In this study we defined similarity based on the dominant habitat type of a node. The maximum number of components that is bidirectionally connected within the network is a measure of connectedness. If the number of components is close to the total number of nodes N, the network is well-connected. If the number of components is low, the network is poorly connected. This measure could also show two sets of strongly connected nodes in the network, which would be interpreted as an indication of the presence of subnetworks.

To identify which nodes were most important in the network, we calculated the weighted node betweenness centrality (hereafter shortened as btwn). Btwn measures the number of times a node lies on the shortest path between other nodes and is a measure of node importance. We weighed the calculation of btwn by the combined edge degree of the node (see next paragraph). In addition, we compared the map with the nodes (package sp in R, Pebesma and Bivand, 2005), with the Natura 2000 areas to see whether the nodes were situated in- or outside this network of protected sites.

Furthermore, we calculated edge degree: the number of directional movements along a certain edge in that period. In order to quantify the habitat switches that the edges represented, we categorized the edges according to the habitat types they connected.

Per five-year period we did all analyses for the full winter, as well as for all winter months (Oct-Mar) separately to assess the overall network structure over the years, and changes therein within the season.

To assess the effect of habitat type and longitude on changes in important nodes over the course of the study period, we conducted a linear mixed-effects model with node btwn as a response variable, and the interactions of habitat and longitude with time (period) as explanatory variables. We included the node ID as a random effect.

For the comparison of the network nodes with Natura 2000 protected sites we downloaded a shapefile of the Natura 2000 network (version End2018) from the website of the European Environment Agency.

Results

Based on clustering the flock observations of the swans, we identified 40 network nodes, 25 in the Netherlands and 15 in Germany (Fig. 7.1; S2). The three extra nodes (UK, Denmark, Poland) were consequently numbered 41, 42 and 43, respectively. A total of 40,922 resightings were done within these nodes (~57% of all resightings in the study period), of which 13,847 in UK, Denmark and Poland combined. See Fig. S7.5 for number of resightings per season and Table S7.5 for the number of resightings and edges per period per month.

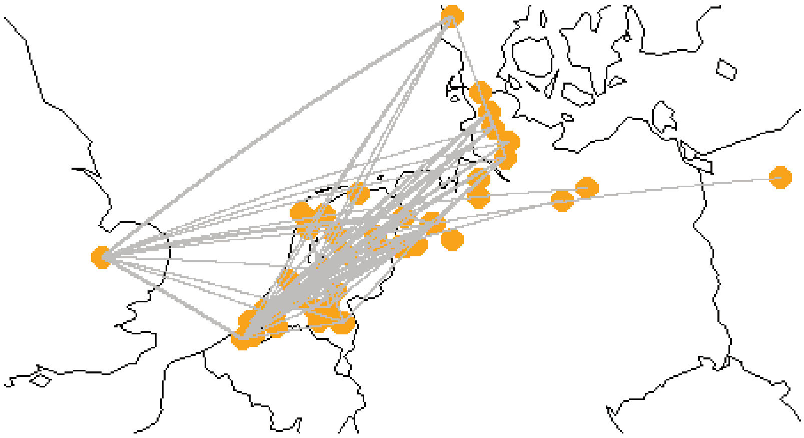

Figure 7.1: *Example network with the 43 nodes and connecting edges (for more details see S2).*

The network density increased over time, but was low in general (Fig. 7.2A). The number of components showed, for every period, a single well-connected subnetwork with, especially in the more recent years, almost all nodes involved (Fig. 7.2B).

Network assortativity also increased over time, starting with negative numbers (Fig. 7.2C). Negative assortativity indicates that nodes with dissimilar properties are linked. The magnitude of the assortativity however suggests that this effect, if at all present, is very minor. Looking at assortativity over the course of the winter season, it seems to follow a negative parabolic curve with lower values in mid-winter in all the periods (Fig. 7.2D).

Of all 40 nodes, only three had water as their dominant habitat type, of which one (node 17) did not have any ring resightings at all. Only one (node 24) had 'other' as the dominant habitat type. The other two main habitat groups (agricultural crops, or agricultural in short, and grass) were identified in 19 and 17 nodes, respectively.

For each period, we mapped the five nodes with the highest btwn (Fig. 7.3). The differences in node importance over time could be explained by dominant habitat type and longitude. Longitude significantly explained variation in node importance, with nodes in the west overall showing higher btwn, but with a significant increase in node importance for eastern nodes (Table 7.1). Although visually the nodes clearly shifted eastward with time (especially in p6; Fig. 7.3), the interaction between longitude and period was only marginally significant (Table 7.1). The interaction of period with habitat type was significant. Further analysis revealed that this was mainly due to a decreased importance of nodes with grassland as their dominant habitat type (Table S7.4). No significant change in agricultural nodes was detected (see also Fig. 7.4A), but agricultural nodes did occur more often in the top five most important nodes over time (Fig. S7.3).

Connecting all four different habitat types, we categorized the edges into 16 categories. Mapping the proportional edge degree of all edges in a certain category over time (per period per month) showed that the edges connecting two agricultural nodes were increasingly used over the study period (Fig. S7.7). We also noticed a decrease in movements from UK, Denmark, Poland (category X in Fig. S7.7) to grassland nodes (G), both within seasons (Oct-Mar) and over the study period (Fig. S7.7).

Upon combining the current Natura 2000 protected areas with the nodes identified in this study, we found that 85% of the nodes (34 nodes; excluding UK, Denmark and Poland) are within the Natura 2000 network. Nine of these sites are designated as Special Protection Areas (SPA) under the Birds Directive (5 in NL, 4 in Germany), 21 as Site of Community Interest under the Habitat Directive (11 in NL, 10 in Germany) and four sites have both statuses (all in NL: Oosterschelde (2 sites), Haringvliet, Deurnsche Peel & Mariapeel). See Table S7.3 for an overview of all Natura 2000 sites that cover (part of) the network of the Bewick's swans. 15% Of the nodes (N = 6) was not included in a Natura 2000 site (Fig. 7.5).

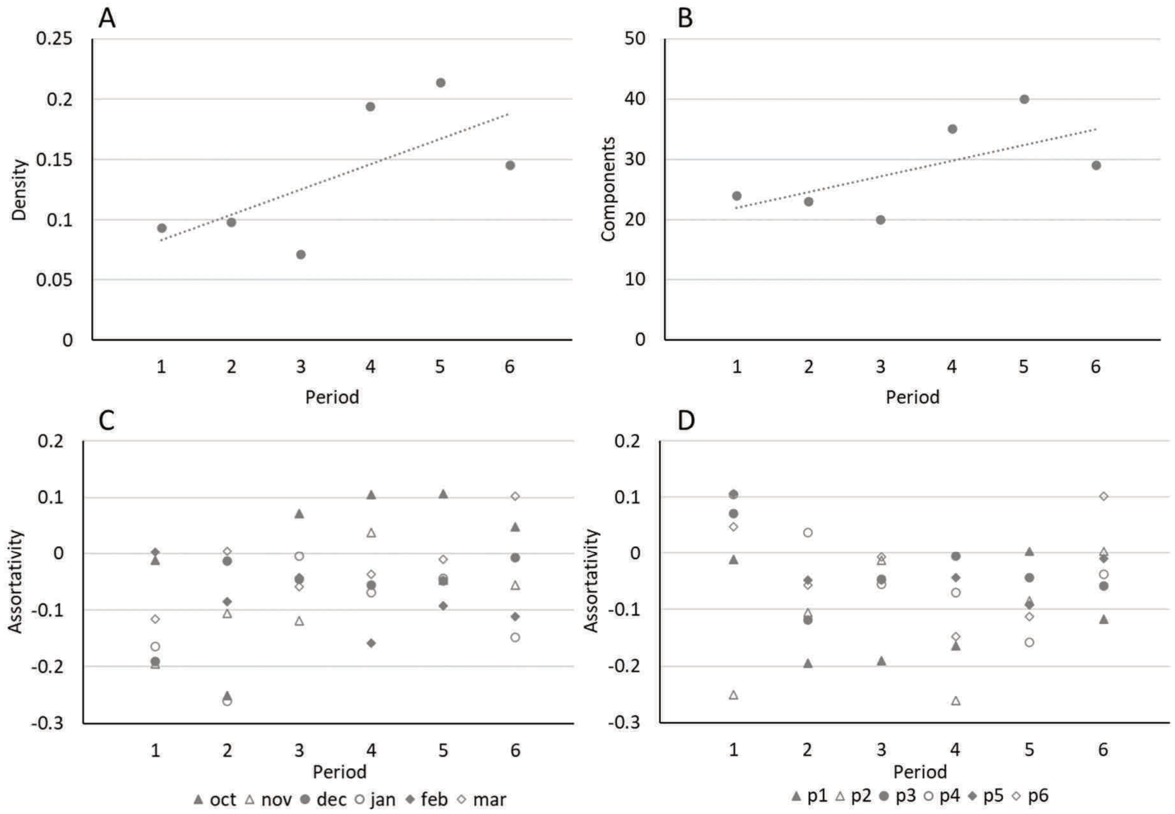

Figure 7.2: *Network properties edge density (A), components (B) and assortativity (C, D). C Visualizes assortativity per period (1-6) per month (see legend), D visualizes assortativity per month (1= oct, 6 = mar) per 5-year period (see legend).*

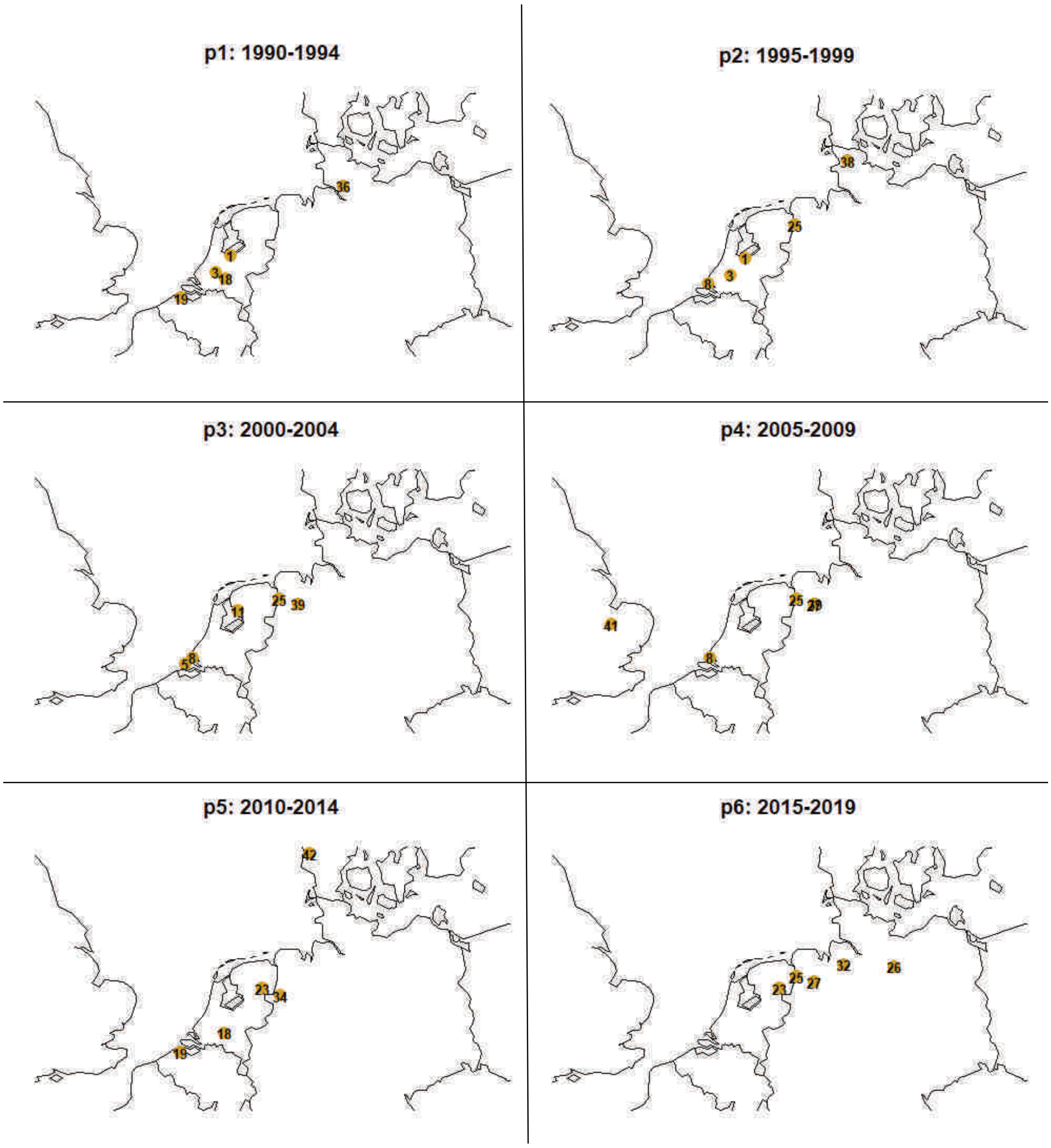

Figure 7.3: *Location and ID of the five most important nodes, based on their weighted betweenness centrality, per period.*

Table 7.1*: Model output of betweenness with response variables period, type and longitude including their interaction. Node ID was included as random factor. Type 1 = Agriculture, type 2 = Grassland. See S4 for the output from the model with the actual proportions of the habitat types within a node (W, G, A) instead of the dominant habitat types as the explanatory variables.*

Model	Parameter	Estimate	*SE*	df	t	p
Btwn	Intercept	50.51	22.19	120.1	2.28	**0.025**
	Period	-0.70	4.61	177.0	-0.15	0.879
	Type	18.12	13.41	120.1	1.35	0.179
	Longitude	**-6.49**	**2.09**	**120.1**	**-2.10**	**0.038**
	Period:Type	**-7.71**	**2.78**	**177.0**	**-2.77**	**0.006**
	Period:Lon	1.26	0.64	177.0	1.96	0.052

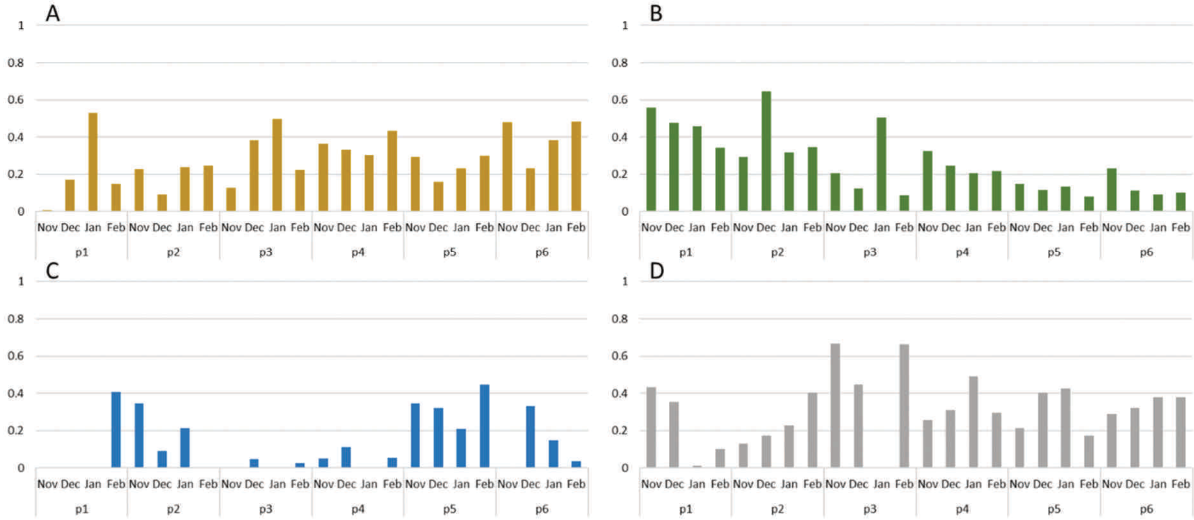

Figure 7.4: *Proportional node betweenness per period per month, categorised based on habitat type. A Agriculture, B Grassland, C Water, D UK/Denmark/Poland.*

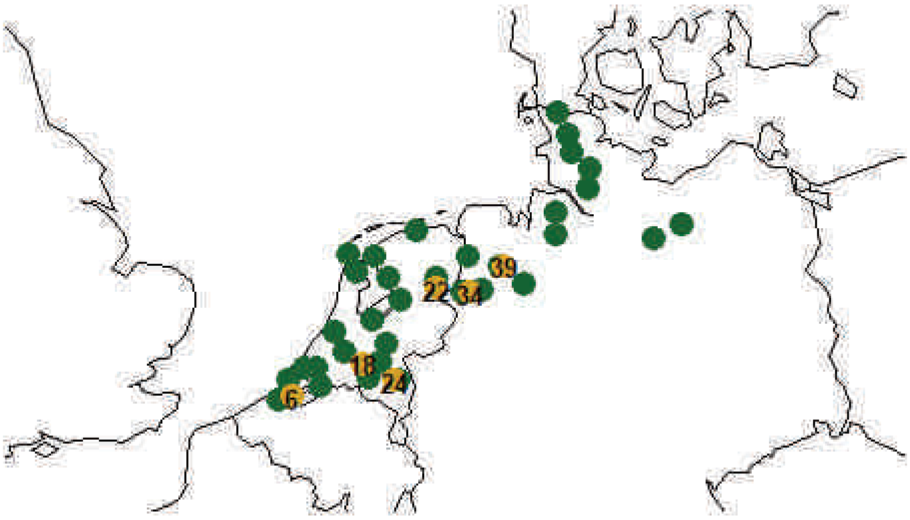

Figure 7.5: *Nodes inside (green; N = 34) and outside (yellow; N = 6) Natura 2000 protected areas.*

Discussion

Reflecting on our results, we can conclude that the Bewick's swan wintering area does appear to form a single well-connected network of interconnected sites. The maximum number of strongly connected components is close to the total number of nodes (43), indicating that there are no subnetworks present. This contradicts the notion that Bewick's swans wintering further north and south in western Europe have more or less separate within-winter migratory movements (Rees and Bacon, 1996; Tijsen and Koffijberg, 2015). For a large herbivorous migratory species such as the Bewick's swan, which needs to obtain sufficient energy reserves for maintenance in cold weather and for initiation of spring migration, relying on a network of sites allows for adaptability, for example in response to changing weather circumstances or disturbance (Jankowiak et al., 2015; Xu et al., 2020). For Bewick's swans it is known that they move further west, and even cross the North Sea, when cold spells with snow occur, making food resources unavailable (Rees, 2006). The other way around, it has recently been shown that the swans tend to stay in areas with a mean temperature of 5°C, and with the 5°C isotherm they have been gradually shifting eastwards over the last decades (Beniston, 2014, Nuijten et al. *in press*).

The edge density shows a non-significant increasing trend over time, although the absolute density appears to be low (ranging between 7 and 22 %). This could be an indication of directed movement within the network, i.e. the swans using specific paths within the network throughout the winter. Also, reaching a density of 1 (i.e. all possible edges, between all nodes of the network, are used) is unrealistic, as some nodes will always be visited more than others, for example based on the number of swans they can accommodate or on their position (either in the centre or near the edges of the winter network).

Assortativity assesses whether edges connect similar nodes (positive values) or dissimilar nodes (negative values). In our case we assessed this based on the dominant habitat type of the nodes. Assortativity seems to increase over time, but this trend was not significant. Interestingly, looking at the different months, it seems to follow a distinct pattern throughout the winter, with lower values in mid-winter compared to early and late winter (Fig. 7.2D). This can be an indication of habitat switching in the middle of the winter season as was observed before (Dirksen et al., 1991). However, looking at the different habitat switches represented by the most important edges, it becomes apparent that the lower assortativity values in mid-winter mainly concern switches involving nodes 41 – 43. For these nodes it is not possible to assign a dominant habitat, since they represent a whole country. It is however noticeable that switches to or from nodes 41 – 43 are less dominant in the early (Oct/Nov) and late (Feb/Mar) winter (Fig. S7.6). Furthermore, looking at the type of switches made over the season, it can be deduced from the panels in Fig. S7.6 that switches to grassland were more frequent in the months October and November, and switches to agricultural fields were more frequent in February and March (Fig. S7.6). The pattern that emerges over time is yet more convincing, with almost all important edges in period 6 (i.e., 2015-2019) "switching" from agricultural fields to agricultural fields (Fig S7.6). Based on our current results we could thus not verify the earlier observation by Dirksen et al. (1991) about the sequential shift in habitat types from water to agricultural fields to grassland within the winter season. This was partly due to a lack of clusters with water as their dominant habitat type, and a lack of resightings on water, but mainly because of the increased importance of agriculture nodes in late winter in recent years. This seems to be a general pattern in waterfowl, as the energetic return from foraging on especially maize stubble is relatively large (Clausen et al., 2018b).

When assessing node importance between years, the results were consistent with our hypothesis: the most important nodes were situated more to the east in recent years (Fig. 7.3). Where the swans were using sites in the SW of the Netherlands frequently in earlier years, recently sites in the NE of the Netherlands and in Germany became more important. This is in line with counts in this area (Augst et al., 2019; Wahl and Degen, 2009). The flock observation dataset used to identify the nodes in Germany did not span the whole study period (it started in 2011), this might have caused some important sites in earlier years to be not included in the current network of nodes identified in this study. However, based on the strong eastward shift found in the population (Beekman et a. 2019, Nuijten et al. *in press*), we think this effect is minor.

Observing the changes in site and habitat use by this population of Bewick's swan may raise the question of how adaptable this species is. It has been shown that the species has shifted its winter distribution and shortened its stay in the wintering range (Nuijten et al. *in press*). Both of these processes could relax the annual cycle of the Bewick's swan by significantly shortening the migration distance, but at the same time, as we show here, individuals will need to explore new, unprotected areas and potentially new food sources to fuel their migration. It is yet unclear how changes in migration strategies and winter distributions will impact the Bewick's swan. Concerns for this and other species have mainly focused on the breeding area and migratory flyway, but changes in winter condition indirectly affect the migratory and breeding performance of these species as well (Hoye et al., 2012). It therefore remains urgent to closely monitor the wintering population, increase our knowledge of within-winter movements and assess the impact of changes in their distribution and habitat use on other stages of the annual cycle and ultimately on fitness.

In addition, the changes in site importance may have important consequences for the management and conservation of the species. This is especially relevant for the Bewick's swan, as it is categorized in Annex I of the Birds Directive (European Commission, 2009). All EU member states within the species' range are therefore obliged to "maintain this species in a favourable conservation status" by conserving sites and habitats that are important for its survival. Every site that is assigned for this goal is included in the Natura 2000 network. Today, the Natura 2000 network contains > 27.000 sites spread over Europe's terrestrial and marine territory (including the UK; European Environment Agency, 2019). The conservation objectives of these protected sites are based on values at the moment of assignment. For example, if the Bewick's swan is present with ~100 individuals at the moment a certain site is assigned, the conservation objective for this site for this species could be to maintain or improve this level to obtain a favourable conservation status. A deterioration of the FCS is legally prohibited (European Commission, 2000). However, if a target species is not present in the area at the moment of assignment, no conservation objective for the species is admitted, and management decisions are not guided by, nor restricted by, the maintenance of suitable conditions for this species at the site. Although it is mandatory to add a Natura 2000 target species and formulate conservation objectives if an assessment determines its presence, this procedure of assigning and maintaining nature within the Natura 2000 sites makes it by definition difficult to warrant the protection of species that respond dynamically to environmental drivers (Bastmeijer, 2017). As a guideline, sites need to be reassessed every six years, to check their initial values with the current situation. And although EU member states must designate Special Protection Areas (SPAs) for the survival of all species listed in Annex I of the Birds Directive, this is also done on the basis of presence data at the moment of assignment, not on projected changes.

The network of Natura 2000 sites in the wintering area of the Bewick's swan is extensive, covering 14.8% and 15.4% of the Netherlands and Germany, respectively. 85% of the nodes identified in this study fall within this network. Even so, Foppen et al., (2016) concluded in a comprehensive assessment that the conservation objectives for the Bewick's swan in the majority of Natura 2000 sites in the Netherlands, are not met. While only six network nodes in our study fall outside the Natura 2000 protected area network (Fig. 7.5), these nodes, except for node 22, all occur in the top five most important nodes for Bewick's swans per period (Fig. S7.4). Some (i.e. nodes 34 and 39) even occur frequently in this top five, especially in more recent years (p4 – p6), indicating that these sites outside the Natura 2000 network have gained importance for the Bewick's swans over the years (Fig. S7.4).

We show that by means of a network analysis, we are able to better understand the space use of an individual species, revealing emergent patterns that can help inform conservation actions. Specifically, the network approach presented here makes a natural link to the already existing network of protected sites in Europe, the Natura 2000 network. With regard to the current legislation for nature conservation, we envisage that a reflection on the assignment criteria for Natura 2000 sites is expedient and a more dynamic form of nature conservation is needed to protect Europe's biodiversity in this time of global environmental change.

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Supplementary Material

1
Corine habitat categories

Legend

111	Continuous urban	311	Broad leaved forest
112	Discontinuous urban	312	Coniferous forest
121	Industrial	313	Mixed forest
122	Road and rail	321	Natural grassland
123	Port areas	322	Moors and heathland
124	Airport	324	Transitional woodland-shrub
131	Mineral extraction	331	Beaches/dunes/sands
132	Dump sites	333	Sparsely vegetated areas
133	Construction site	411	Inland marshes
141	Green urban area	412	Peat bogs
142	Sport and leisure	421	Salt marshes
211	Non-irrigated arable land	423	Intertidal flats
222	Fruit and berry tree plantations	511	Water courses
231	Pastures	512	Water bodies
242	Complex cultivation	522	Estuaries
243	Agriculture with natural vegetation	523	Sea and ocean

Used in this study:	Agriculture:	211 + 243
	Grassland:	231 + 321
	Water:	411 + 423 + 511 + 512 + 522 + 523

2
Clusters and nodes

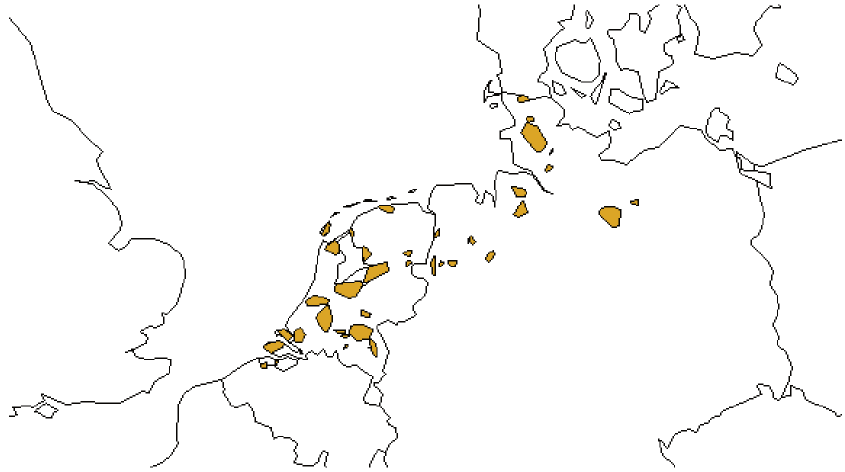

Figure S7.1: Polygons of the clusters identified based on group sightings of Bewick's swans in the Netherlands and Germany.

Figure S7.2: Numbered nodes identified based on flock observations (1-40) 41-43 represent the UK, Denmark and Poland, respectively.

Table S7.1: Number of flock observations per cluster/node (column 2) and per winter season (column 4). The year in column 3 represents the December of the winter season.

Node ID	N (flock observations)	Winter season	N (flock observations)
1	1867	1988	55
2	585	1989	62
3	1665	1990	102
4	2103	1991	108
5	594	1992	92
6	97	1993	78
7	907	1994	121
8	764	1995	151
9	1183	1996	126
10	279	1997	124
11	152	1998	127
12	805	1999	198
13	807	2000	169
14	193	2001	185
15	961	2002	250
16	1201	2003	283
17	145	2004	440
18	115	2005	688
19	292	2006	933
20	252	2007	1106
21	521	2008	166
22	251	2009	134
23	124	2010	1434
24	120	2011	1599
25	125	2012	1981
26	191	2013	1567
27	663	2014	2013
28	192	2015	1807
29	165	2016	1759
30	204	2017	1530
31	87	2018	631
32	780		
33	129		
34	253		
35	565		
36	96		
37	323		
38	143		
39	67		
40	53		

Table S7.2: Habitat type and betweenness per node.

Node ID	av. Longitude	av. Latitude	Dominant habitat type	btwn_p1	btwn_p2	btwn_p3	btwn_p4	btwn_p5	btwn_p6
1	5.353	52.273	Grass	223.592	144.646	51.333	83.837	51.037	43.377
2	5.636	51.968	Grass	28.117	25.113	9.733	27.953	7.652	0.167
3	4.787	51.883	Grass	75.033	61.775	10.083	4.688	22.277	9.527
4	5.503	51.741	Grass	6.333	9.479	0.917	16.531	91.557	0
5	3.647	51.530	Agriculture	6.500	41.333	84.150	76.050	51.765	0
6	3.738	51.321	Agriculture	0	0	0	3.033	12.432	0
7	5.025	52.852	Agriculture	15.150	5.983	43.917	14.669	8.920	0
8	3.957	51.679	Agriculture	40.217	132.277	67.833	116.423	77.699	0
9	4.562	52.126	Grass	0	0	0	0	0	0
10	4.221	51.663	Agriculture	5.667	18.900	0	0.627	0.725	3.500
11	5.671	52.771	Agriculture	0	0	98.250	38.665	76.343	2.733
12	6.219	53.362	Agriculture	3.733	5.000	0	6.000	13.442	1.693
13	5.257	51.675	Grass	0	0	4.667	28.557	5.299	0
14	5.381	53.052	Water	0	0	0	6.500	1.583	0
15	4.840	53.084	Grass	0	0	0	6.812	10.587	62.626
16	5.915	52.511	Grass	0	0	0	2.202	54.696	1.900
17	4.271	51.449	Water	0	0	0	0	0	0
18	5.154	51.725	Grass	102.669	42.467	2.333	38.406	166.669	22.587
19	3.457	51.279	Agriculture	89.471	24.430	35.917	80.363	129.466	82.107
20	5.266	51.541	Grass	0	0	0	35.619	87.130	51.349
21	5.866	51.519	Grass	0	2.451	0	77.859	57.443	31.819
22	6.635	52.647	Agriculture	0	0	0	13.821	39.079	26.751
23	6.623	52.770	Agriculture	28.683	9.400	56.483	70.387	201.588	182.845
24	5.767	51.521	None	0	0	0	12.978	48.027	53.469
25	7.280	53.044	Agriculture	4.810	52.669	67.417	130.832	85.890	146.664
26	11.024	53.279	Agriculture	0	0	0	114.384	43.701	95.687
27	7.936	52.925	Water	39.583	14.327	13.250	127.834	91.555	114.423
28	9.074	53.583	Grass	0	0	0	0	39.874	30.584
29	8.404	52.707	Agriculture	0	0	0	0	1.036	43.596
30	7.583	52.627	Agriculture	0	0	0	0	24.517	28.525
31	9.389	54.317	Grass	0	0	0	37.637	7.200	36.849
32	9.072	53.330	Agriculture	0	0	0	0	0	147.182
33	7.163	52.608	Agriculture	0	0	0	33.619	26.126	44.094
34	7.318	52.604	Agriculture	63.150	8.217	47.483	49.010	138.110	43.754
35	9.117	54.826	Agriculture	0	0	0	0	3.150	0
36	9.690	53.891	Grass	64.017	15.933	2.583	21.596	28.340	0
37	11.619	53.442	Grass	1.533	0	0	0	3.066	0
38	9.290	54.543	Grass	26.033	87.183	59.450	10.779	45.823	0
39	8.008	52.936	Agriculture	33.050	16.168	117.800	142.642	25.101	0
40	9.765	54.117	Grass	0	19.183	0	8.348	85.093	0
41	0.162	52.452	None	50.679	44.367	48.500	166.674	129.379	19.071
42	8.428	55.914	None	33.845	14.667	32.083	62.105	146.502	77.420
43	16.182	53.592	None	0	1.542	0	65.588	58.301	35.323

3
Top 5 nodes

(a)

p1	oct	nov	dec	jan	feb	mar
#1	3	1	4	8	1	1
#2	8	4	1	34	8	41
#3	41	3	8	1	27	19
#4	1	42	41	4	34	8
#5	38	38	3	3	18	31

p2	oct	nov	dec	jan	feb	mar
#1	41	1	1	1	1	42
#2	7	39	38	38	8	41
#3	39	4	4	19	3	27
#4	1	8	36	5	5	21
#5	8	27	3	8	41	8

p3	oct	nov	dec	jan	feb	mar
#1	42	1	5	1	19	25
#2	7	41	8	34	41	1
#3		5	42	5	1	8
#4		38	1		25	23
#5		34	38		8	

p4	oct	nov	dec	jan	feb	mar
#1	8	34	8	38	25	25
#2	4	38	2	41	1	7
#3	42	39	41	34	23	26
#4	1	1	34	8	41	41
#5	34	42	1	1	19	42

p5	oct	nov	dec	jan	feb	mar
#1	42	19	23	8	25	25
#2	6	8	27	41	27	42
#3	34	20	34	34	23	19
#4	38	33	20	18	34	21
#5		27	24	27	8	27

p6	oct	nov	dec	jan	feb	mar
#1	26	19	27	34	25	25
#2		25	26	26	23	26
#3		1	34	32	34	30
#4		8	25	24	5	43
#5		21	43	5	42	32

(b)

oct	p1	p2	p3	p4	p5	p6
#1	3	41	42	8	42	26
#2	8	7	7	4	6	
#3	41	39		42	34	
#4	1	1		1	38	
#5	38	8		34		

nov	p1	p2	p3	p4	p5	p6
#1	1	1	1	34	19	19
#2	4	39	41	38	8	25
#3	3	4	5	39	20	1
#4	42	8	38	1	33	8
#5	38	27	34	42	27	21

dec	p1	p2	p3	p4	p5	p6
#1	4	1	5	8	23	27
#2	1	38	8	2	27	26
#3	8	4	42	41	34	34
#4	41	36	1	34	20	25
#5	3	3	38	1	24	43

jan	p1	p2	p3	p4	p5	p6
#1	8	1	1	38	8	34
#2	34	38	34	41	41	26
#3	1	19	5	34	34	32
#4	4	5		8	18	24
#5	3	8		1	27	5

feb	p1	p2	p3	p4	p5	p6
#1	1	1	19	25	25	25
#2	8	8	41	1	27	23
#3	27	3	1	23	23	34
#4	34	5	25	41	34	5
#5	18	41	8	19	8	42

mar	p1	p2	p3	p4	p5	p6
#1	1	42	25	25	25	25
#2	41	41	1	7	42	26
#3	19	27	8	26	19	30
#4	8	21	23	41	21	43
#5	31	8		42	27	32

Figure S7.3: Five most important nodes, visualized per period per month (a) and per month per period (b). Colours indicate the habitat type of the node. Blue = Water, brown/orange = Agriculture, Green = Grassland, Grey = None. Empty cells means a betweenness of 0 for all other nodes.

p1	oct	nov	dec	jan	feb	mar
#1	3	1	4	8	1	1
#2	8	4	1	34	8	41
#3	41	3	8	1	27	19
#4	1	42	41	4	34	8
#5	38	38	3	3	18	31

p2	oct	nov	dec	jan	feb	mar
#1	41	1	1	1	1	42
#2	7	39	38	38	8	41
#3	39	4	4	19	3	27
#4	1	8	36	5	5	21
#5	8	27	3	8	41	8

p3	oct	nov	dec	jan	feb	mar
#1	42	1	5	1	19	25
#2	7	41	8	34	41	1
#3		5	42	5	1	8
#4		38	1		25	23
#5		34	38		8	

p4	oct	nov	dec	jan	feb	mar
#1	8	34	8	38	25	25
#2	4	38	2	41	1	7
#3	42	39	41	34	23	26
#4	1	1	34	8	41	41
#5	34	42	1	1	19	42

p5	oct	nov	dec	jan	feb	mar
#1	42	19	23	8	25	25
#2	6	8	27	41	27	42
#3	34	20	34	34	23	19
#4	38	33	20	18	34	21
#5		27	24	27	8	27

p6	oct	nov	dec	jan	feb	mar
#1	26	19	27	34	25	25
#2		25	26	26	23	26
#3		1	34	32	34	30
#4		8	25	24	5	43
#5		21	43	5	42	32

Figure S7.4: Same as C.1 (a) but here nodes currently not protected by the Natura 2000 network are indicated in yellow.

Table S7.3: Network nodes (Fig. S7.2) and the Natura 2000 sites they overlap with, including its sitecode, sitename, country and sitetype (SCI = Site of Community Importance; SPA = Special Protection Area). If a node fell outside the protected area network, NA was stated.

Node ID	Sitecode	Sitename	Country	Sittype
1	NL2003036	Oostelijke Vechtplassen	NL	SCI
2	NL9801023	Veluwe	NL	SCI
3	NL9802066	Donkse Laagten	NL	SPA
4	NL2014038	Rijntakken	NL	SPA
5	NL3009016	Oosterschelde	NL	SPA & SCI
6	NA	NA	NA	NA
7	NL1000001	Waddenzee	NL	SCI
8	NL3009016	Oosterschelde	NL	SPA & SCI
9	NL3000036	Nieuwkoopse Plassen & de Haeck	NL	SCI
10	NL1000015	Haringvliet	NL	SPA & SCI
11	NL9803028	IJsselmeer	NL	SPA
12	NL9802012	Lauwersmeer	NL	SPA
13	NL9801049	Vlijmens Ven, Moerputten & Bossche Broek	NL	SCI
14	NL1000002	IJsselmeer	NL	SCI
15	NL1000001	Waddenzee	NL	SCI
16	NL1000005	Uiterwaarden Zwarte Water en Vecht	NL	SCI
17	NL3009003	Brabantse Wal	NL	SPA
18	NA	NA	NA	NA

19	NL2003019	Groote Gat	NL	SCI
20	NL3000401	Kampina & Oisterwijkse Vennen	NL	SCI
21	NL1000026	Deurnsche Peel & Mariapeel	NL	SPA & SCI
22	NA	NA	NA	NA
23	NL2003032	Mantingerzand	NL	SCI
24	NA	NA	NA	NA
25	DE2909401	Emstal von Lathen bis Papenburg	DE	SPA
26	DE2832401	Niedersächsische Mittelelbe	DE	SPA
27	DE3013301	Heiden und Moore an der Talsperre Thülsfeld	DE	SCI
28	DE2320332	Osteschleifen zwischen Kranenburg und Nieder-Ochtenhausen	DE	SCI
29	DE3216301	Goldenstedter Moor	DE	SCI
30	DE3311301	Hahnenmoor, Hahlener Moor, Suddenmoor	DE	SCI
31	DE1521391	Wälder der Ostenfelder Geest	DE	SCI
32	DE2520331	Oste mit Nebenbächen	DE	SCI
33	DE3408401	Dalum-Wietmarscher Moor und Georgsdorfer Moor	DE	SPA
34	NA	NA	NA	NA
35	DE1121304	Eichenwälder der Böxlunder Geest	DE	SCI
36	DE2024391	Mittlere Stör, Bramau und Bünzau	DE	SCI
37	DE2535402	Lewitz	DE	SPA
38	DE1521391	Wälder der Ostenfelder Geest	DE	SCI
39	NA	NA	NA	NA
40	DE2024391	Mittlere Stör, Bramau und Bünzau	DE	SCI

4
Model output betweenness

Table S7.4: Model output. Model: btwn ~ (period * lon) + (period * water) + (period * grass) + (period * agriculture) + (1 | node_ID).

Model	Parameter	Estimate	*SE*	df	t	p
Btwn	Intercept	29.61	22.22	1135.92	1.33	0.185
	Period	6.42	4.58	210.00	1.40	0.162
	Longitude	**-5.27**	**2.32**	**135.92**	**-2.27**	**0.025**
	Water	0.11	0.35	135.92	0.32	0.747
	Grass	0.41	0.28	135.92	1.41	0.159
	Agriculture	0.22	0.24	135.92	0.92	0.358
	Period:Lon	**1.13**	**0.48**	**210.00**	**2.36**	**0.019**
	Period:Water	-0.11	0.07	210.00	-1.55	0.123
	Period:Grass	**-0.21**	**0.06**	**210.00**	**-3.65**	**0.001**
	Period:Agri	-0.07	0.05	210.00	-1.40	0.163

5

Edges

Figure S7.5: Number of resightings in the nodes (all combined) per winter season (the year on the x-axes indicates the December of the winter seaseon).

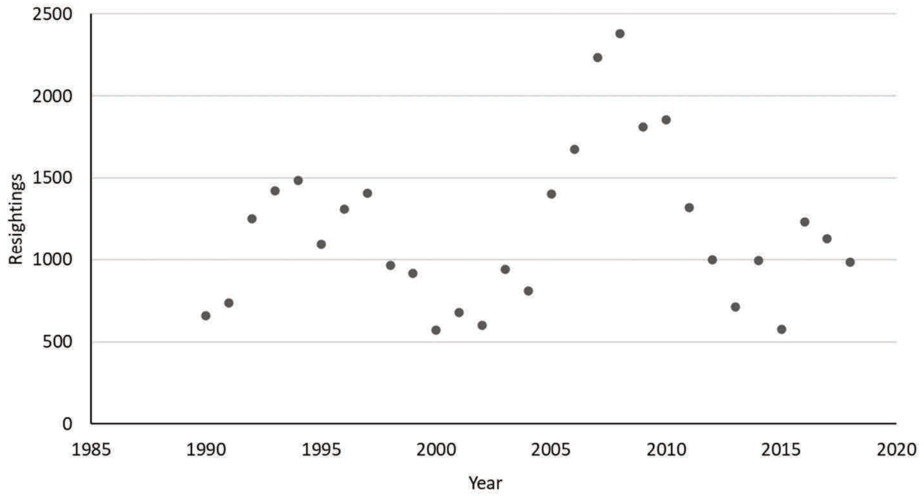

Table S7.5: Sample size resightings.

RESIGHTINGS	Oct	Nov	Dec	Jan	Feb	Mar	Total
p1	404	1938	2559	2506	2506	2434	12347
p2	628	3285	3310	3294	2947	3699	17163
p3	272	1486	1709	1808	1444	1413	8132
p4	168	1865	3372	3326	2218	1987	12936
p5	158	745	1473	2233	1586	1232	7427
p6	32	385	1066	2209	1516	764	5972

Table S7.6: Sample size edges.

EDGES	Oct	Nov	Dec	Jan	Feb	Mar	Total
p1	56	189	221	176	146	92	880
p2	35	206	184	139	182	62	808
p3	23	129	108	101	72	50	483
p4	43	329	698	641	300	163	2174
p5	48	161	323	427	310	195	1464
p6	12	59	152	343	362	171	1099

(a)

p1	Oct	nov	dec	jan	feb	mar
#1	41 - 4	41 - 4	25 - 41	19 - 41	42 - 41	1 - 21
#2	19 - 41	41 - 8	42 - 41	42 - 41	41 - 1	1 - 19
#3	31 - 3	41 - 38	1 - 8	31 - 41	1 - 8	8 - 42
#4	5 - 4	41 - 39	41 - 38	25 - 41	25 - 41	41 - 42
#5	41 - 3	41 - 7	41 - 8	39 - 23	8 - 1	31 - 19

p2	Oct	nov	dec	jan	feb	mar
#1	41 - 4	41 - 38	1 - 41	25 - 41	25 - 41	41 - 42
#2	25 - 41	41 - 7	25 - 41	1 - 41	42 - 41	41 - 21
#3	1 - 4	42 - 41	41 - 38	42 - 41	1 - 27	41 - 38
#4	41 - 38	38 - 7	19 - 41	19 - 41	19 - 41	41 - 4
#5	41 - 7	25 - 41	41 - 1	1 - 27	1 - 8	41 - 8

p3	Oct	nov	dec	jan	feb	mar
#1	41 - 4	41 - 38	25 - 41	25 - 41	25 - 41	1 - 19
#2	25 - 4	25 - 38	41 - 38	1 - 41	27 - 18	8 - 1
#3	25 - 8	25 - 41	25 - 7	19 - 41	5 - 34	41 - 1
#4	41 - 38	8 - 1	42 - 41	42 - 41	1 - 27	41 - 19
#5	41 - 7	38 - 4	25 - 39	5 - 34	25 - 1	25 - 1

p4	Oct	nov	dec	jan	feb	mar
#1	1 - 38	41 - 38	25 - 8	25 - 1	25 - 41	18 - 25
#2	41 - 4	34 - 5	25 - 38	25 - 8	25 - 1	38 - 25
#3	23 - 4	1 - 8	25 - 1	38 - 41	25 - 40	1 - 25
#4	34 - 8	1 - 38	1 - 8	38 - 1	38 - 1	38 - 42
#5	4 - 38	41 - 7	25 - 41	25 - 18	38 - 25	8 - 25

p5	Oct	nov	dec	jan	feb	mar
#1	41 - 6	41 - 6	25 - 41	42 - 41	34 - 5	23 - 25
#2	41 - 43	23 - 8	25 - 8	25 - 41	25 - 23	24 - 25
#3	41 - 38	25 - 42	25 - 24	34 - 5	24 - 8	8 - 25
#4	23 - 43	41 - 8	25 - 34	25 - 34	23 - 25	41 - 25
#5	23 - 8	34 - 14	18 - 38	25 - 8	34 - 26	34 - 43

p6	Oct	nov	dec	jan	feb	mar
#1	1 - 22	23 - 15	5 - 34	34 - 5	8 - 25	34 - 25
#2	25 - 29	25 - 41	19 - 26	25 - 34	5 - 25	25 - 32
#3	26 - 43	1 - 42	19 - 43	5 - 34	26 - 25	23 - 25
#4	39 - 11	41 - 7	26 - 19	26 - 34	34 - 25	25 - 43
#5	39 - 4	11 - 39	34 - 19	25 - 41	34 - 26	25 - 30

(b)

oct	p1	p2	p3	p4	p5	p6
#1	41 - 4	41 - 4	41 - 4	1 - 38	41 - 6	1 - 22
#2	19 - 41	25 - 41	25 - 4	41 - 4	41 - 43	25 - 29
#3	31 - 3	1 - 4	25 - 8	23 - 4	41 - 38	26 - 43
#4	5 - 4	41 - 38	41 - 38	34 - 8	23 - 43	39 - 11
#5	41 - 3	41 - 7	41 - 7	4 - 38	23 - 8	39 - 4

nov	p1	p2	p3	p4	p5	p6
#1	41 - 4	41 - 38	41 - 38	41 - 38	41 - 6	23 - 15
#2	41 - 8	41 - 7	25 - 38	34 - 5	23 - 8	25 - 41
#3	41 - 38	42 - 41	25 - 41	1 - 8	25 - 42	1 - 42
#4	41 - 39	38 - 7	8 - 1	1 - 38	41 - 8	41 - 7
#5	41 - 7	25 - 41	38 - 4	41 - 7	34 - 14	11 - 39

dec	p1	p2	p3	p4	p5	p6
#1	25 - 41	1 - 41	25 - 41	25 - 8	25 - 41	5 - 34
#2	42 - 41	25 - 41	41 - 38	25 - 38	25 - 8	19 - 26
#3	1 - 8	41 - 38	25 - 7	25 - 1	25 - 24	19 - 43
#4	41 - 38	19 - 41	42 - 41	1 - 8	25 - 34	26 - 19
#5	41 - 8	41 - 1	25 - 39	25 - 41	18 - 38	34 - 19

jan	p1	p2	p3	p4	p5	p6
#1	19 - 41	25 - 41	25 - 41	25 - 1	42 - 41	34 - 5
#2	42 - 41	1 - 41	1 - 41	25 - 8	25 - 41	25 - 34
#3	31 - 41	42 - 41	19 - 41	38 - 41	34 - 5	5 - 34
#4	25 - 41	19 - 41	42 - 41	38 - 1	25 - 34	26 - 34
#5	39 - 23	1 - 27	5 - 34	25 - 18	25 - 8	25 - 41

feb	p1	p2	p3	p4	p5	p6
#1	42 - 41	25 - 41	25 - 41	25 - 41	34 - 5	8 - 25
#2	41 - 1	42 - 41	27 - 18	25 - 1	25 - 23	5 - 25
#3	1 - 8	1 - 27	5 - 34	25 - 40	24 - 8	26 - 25
#4	25 - 41	19 - 41	1 - 27	38 - 1	23 - 25	34 - 25
#5	8 - 1	1 - 8	25 - 1	38 - 25	34 - 26	34 - 26

mar	p1	p2	p3	p4	p5	p6
#1	1 - 21	41 - 42	1 - 19	18 - 25	23 - 25	34 - 25
#2	1 - 19	41 - 21	8 - 1	38 - 25	24 - 25	25 - 32
#3	8 - 42	41 - 38	41 - 1	1 - 25	8 - 25	23 - 25
#4	41 - 42	41 - 4	41 - 19	38 - 42	41 - 25	25 - 43
#5	31 - 19	41 - 8	25 - 1	8 - 25	34 - 43	25 - 30

Figure S7.6: Five most important edges per habitat, visualized per period per month (a) and per month per period (b). Colours indicate the category of the edge (based on the habitats it connects). (blue = water-water, dark-green = grass-grass, dark-orange = agriculture-agriculture, white = none-none, light-blue = agriculture-water, light-green = agriculture-grass, blue = grass-water, light-orange = grass-agriculture). Patterns represent that either the from- (white dots) or the to-node (diagonal stripes) has no habitat type assigned to it. The background colour or the colour of the diagonal stripes represents the habitat of the other end of the edge, respectively. Movements to and from nodes with grass as their dominant habitat type were common in earlier years, whereas movements to and from agricultural fields prevailed in recent years (Fig. (a)). In addition, movements to and from UK, seemed more frequent in the months December and January (Fig. (b)).

Figure S7.7: (Below) Edges categorized per connected habitat (16 categories). Vertical categories are the habitat FROM which an edge started, horizontal categories represent the habitat TO which an edge led.