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Bewick's swans in a changing world

Species responses and the need for dynamic nature conservation

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Chapter 8

Synthesis

Biodiversity is threatened by multiple factors all around the globe, and many species are declining or threatened with extinction (IPBES, 2019). A great number of initiatives have been initiated to stop this decline, many of them directed at the species level. One of these initiatives is the updrawing of Single Species Action plans for bird species threatened in their existence. These Action Plans map the situation, hypothesize on potential causes and solutions, and guide research into the causes of decline.

Population Dynamics

Guided by the Single Species Action Plan (SAP) that was developed for the Bewick's swan in 2012 (Nagy et al., 2012), multiple in depth studies have been conducted. The research focused at the factors affecting mortality and breeding success in order to unravel the population dynamics and the cause of the observed decline of the western population of Bewick's swan between 1995 – 2010.

Illegal/accidental shooting was described as a major threat to the population (Nagy et al., 2012). Through X-ray research Newth et al. (2011) found that Bewick's swans indeed experience a substantial hunting pressure, despite national and international protection. If not lethal, embedded shotgun pellets can have severe health effects in swans (Newth et al., 2016, 2013). Misidentification might be one of the reasons that hunting pressure remains high, as the co-occurring whooper swans and mute swans have weaker legal protection (Newth et al., 2019). An extensive community conservation project in Artic Russia aims to tackle this issue in the future ('Swan champions'; Newth et al., 2019).

In addition, the SAP specified that collisions with man-made structures such as windmills and power lines, form a threat of unknown importance to the Bewick's swan population. Following this statement, research showed that food availability, despite the presence of the windmills, was the main determinant of swan presence, and that the risk of collision is low (Fijn et al., 2012; Krijgsveld et al., 2009), but longer-term effects on the population level combining both onshore and offshore windfarms need to be investigated further (Griffin et al., 2016; Rees, 2012). Collision risk with power lines has not been studied in depth for the Bewick's swan but is a considerable source of mortality in the larger mute swan (Gális et al., 2019; Kelly and Kelly, 2005), particularly in migration seasons (Gális et al., 2019). This high mortality rate is thought to arise from the size of the species, and consequently the long stretches required for takeoff and landing in a field, and low detection chance of man-made structures (Martin, 2011; Martin and Shaw, 2010). Although smaller, the Bewick's swan has these characteristics in common with the mute swan. In Estonia, an important area for Bewick's swan during both spring and autumn migration, the risk of collision with power lines by Bewick's swans is considered high (Luigujõe et al., 2013).

A more elusive threat of potentially high importance are (infectious) diseases (Nagy et al., 2012), such as avian influenza. It was found that although direct effects of an infection seem to be minor in Bewick's swans, there are indications that indirect effects can be severe, eventually leading to lower survival of infected individuals (Hoye et al., 2016).

Suboptimal feeding conditions at stopover and wintering sites were listed in the SAP as a threat of potentially high importance (Nagy et al., 2012). In the winter area observations showed that

water regimes can drastically affect the food availability for foraging swans (Nolet et al., 2016a). Less obvious, but with potentially high impact regarding the increasing population trend of mute swans, is the finding that food availability was influenced by intensive foraging by coots, ducks and mute swans in summer, leaving fewer belowground tubers to feed on for the Bewick's swans in winter (Gyimesi et al., 2011). However, drawing on a long-term dataset on Bewick's swan biometrics, no connection was found between the population decline and body condition in winter (Wood et al., 2018), potentially due to an increased use of maize fields (Clausen et al., 2018b). In addition, a local study found that food resources at a typical wintering site in the west of the UK were not limiting, despite the presence of interspecific competition with both mute and whooper swans (Wood et al., 2019).

Since the Species Action Plan was drawn, the international monitoring has continued and counts have been collated. The results of the 2015 count seem to imply a stabilization of the numbers (Beekman et al., 2019), but 2020 count results are needed to confirm this (E.C. Rees pers. comm.). Regional counts imply that numbers in UK and Ireland have been decreasing steadily (Worden et al., 2006), while in northern Germany numbers are stable or even increasing. In Germany, sites that were previously used as stopovers, are now used throughout winter (Augst et al., 2019).

Some interesting trends have been observed elsewhere as well. Chovan and Kazannik (2015) reported an increased use of the Dnieper river delta in Ukraine, and (Vangeluwe et al., 2016) presented a steep increase in overwintering Bewick's swans in the Evros Delta, Greece. However, when investigating whether the increasing trend in Greece could explain the decline in northwestern Europe, more support was found for the hypothesis that the growth of the eastern population of Bewick's swans caused them to expand to other wintering sites (Vangeluwe et al., 2018; Wood et al., 2018).

In addition to studies investigating the hypothesized factors causing the population decline, the results of the monitoring, including reproduction counts, and the resightings of the marked individuals, were analyzed to investigate the effect of survival of the different age classes and breeding success in the Arctic on the population. It was found that the proportion of juveniles in winter was negatively affected by cold summer weather and high predator abundance (Arctic fox) in the breeding range (Wood et al., 2016). Brood size in winter was associated with summer temperatures in the same direction, but was positively influenced by the mean pair bond duration of parents (Wood et al., 2016). Against expectation, no directional trend in neither of the breeding success parameters over time was detected (Wood et al., 2016). In addition, no long-term trend was found in annual survival rates of Bewick's swans, with different decadal survival rates best explaining the data (survival was highest in the 1980s and lowest in 2010s; Wood et al., 2018). None of the explanatory variables included in the study could explain this trend satisfactorily (2006Wood et al., 2018).

In this thesis, I build forth on the knowledge that was gained on the western population of Bewick's swans. In this Synthesis I will put the results of the various chapters in the perspective of the population decline, and discuss the case of this species in light of nature conservation management in Europe.

Continuing on the work of Wood and others, in **Chapter 2** of this thesis we analyzed the results of the monitoring schemes and ringing efforts again, now using an integrated modelling

framework. This allowed us to use information about survival and breeding success that is present in the counts, and vice versa, to inform the estimates of the model and by that obtain more precise output. The resulting survival rates were overall higher than what was found in the more traditional survival analysis by Wood et al., (2018), potentially due to less bias (Johnson et al., 2020). Apparent breeding success, including breeding propensity, brood size and post-fledging survival, showed a decreasing trend, with significantly higher values in years with a positive population growth rate (1970-1994) when compared to years with a negative population growth rate (1995-2015). Apparent breeding success was also the parameter with most influence on the variation in population growth rate, apart from adult survival (Chapter 2). Juvenile survival showed an interesting increasing trend over time (no trend was found for adult and yearling survival). The positive trend in juvenile survival (individuals between 0.5 and 1.5 years of age) was positively associated with the water level in Lake Peipsi, an important stopover site during autumn migration, and with temperature during summer and autumn at the breeding grounds. Although this positive interaction was counterintuitive at first, as it is assumed that with higher water levels the swans cannot reach the belowground parts of the macrophytes in the lakes (Nolet et al., 2016a, 2006) and with colder temperatures more individuals die. As our measure of juvenile survival 'starts' at the wintering grounds, it might be that in years with harsh summer/autumn conditions, only the stronger individuals are left in winter, resulting in higher subsequent survival rates for the whole juveniles age class. With regard to the water level in the lakes during autumn, it is plausible that the alternative sites that are used by the swans when the water level is too high, might be beneficial for juvenile survival due to less inter- and intra-specific competition at these alternative sites (increasing whooper swan counts was negatively associated to juvenile survival and apparent breeding success; S2.4), and to higher intake rates for juveniles on different food sources (Nolet et al., 2014). It remains a topic for future research whether juvenile survival can, to some extent, compensate for the low(er) apparent breeding success (Reed et al. 2013).

One factor that could cause the drop in apparent breeding success, as was also indicated by the SAP, is a deterioration of feeding opportunities during spring migration. Through this, individuals could reach the breeding grounds in poorer condition rendering them unable to successfully reproduce (Hoye et al., 2012; Nolet, 2006). Previous research had identified macrophytes as an important source of energy for migrating Bewick's swans, and the incorporation of a water sensor in the GPS-GSM collar allowed us to monitor whether (and where) this is still the case. Based on the methods developed in **Chapters 3 and 4**, we were able to confirm that the swans still use the same stopover sites for fuelling their migration that were identified as important stopover sites in previous research (**Chapter 5**; Beekman et al., 2002; Nuijten et al., 2014; Rees, 2006). Future tracking with similar devices could be used to monitor potential changes in these areas, especially in the northern part of the migration route (the White Sea area and the Cheskaya Bay) where developmental projects and oil and gas exploitation could threaten coastal habitats (Gautier et al., 2009; Laulajainen, 2008; Louppova, 2018).

Also in the wintering area, changing habitats might influence Bewick's swan dynamics (Nagy et al., 2012). During a period of intensifying agricultural practices in northwestern Europe (1960s – 1980s), many herbivorous waterfowl populations profited from the abundance of food that was available and as a result their population sizes increased (van Eerden et al., 2005, 1996). It was found that, when the gain of exploiting this new food source flattened, the smaller species (e.g. ducks) were either stable or declining in population numbers, but the larger

species (geese and swans) kept on increasing (van Eerden et al., 2005). For some reason, Bewick's swans were exceptional among the larger species, and their numbers declined rapidly from 1995 onwards (Rees and Beekman, 2010; van Eerden et al., 2005).

Flexibility versus Tradition

In winter, Bewick's swans are thought to be particularly traditional in their site and habitat use (Rees, 2006). However, when assessing the winter range and phenology over a ~50 year period, we found that this shifted substantially over time (**Chapter 6**). In total, the population shifted north-eastwards by 12.9 km y⁻¹ and winter duration shortened by almost 9 weeks. Surprisingly, individuals did shorten their migration distance over their lifetime (as opposed to a generational shift, e.g. Gill et al., (2019), which was confirmed to cause the shortening of winter duration; chapter 6). To explore whether the observed shifts had the potential to be microevolutionary, we calculated the selection pressure and the magnitude of change (Gienapp et al., 2008, 2007; Table 8.1). Based on this we conclude that the magnitude of the observed shifts (in both migration distance and winter duration) and the strength of selection needed are too high to be caused by microevolution alone. Cautionary note is that these calculations are based on assumptions and uncertainties, for example about the heritability of traits. Currently a heritability of 0.3 is used, which is typical for songbirds (Gienapp et al., 2007), however, further research is needed to specify the heritability for these traits in larger birds with longer generation times, such as the Bewick's swan (generation time taken to be 11 years, (Koons et al., 2014).

Table 8.1: Theoretical selection pressure (*S*) and response (*R*, in haldane) in phenotypic traits 'migration distance', 'arrival', 'departure' and 'winter duration'. For each of the traits their between individual Slope, the weighted average SD per year and the number of years (period) are presented. *R* and *S* were calculated based on eqn 1 in Gienapp et al. (2007, 2008).

	Slope	Unit	SD	Period	R	S
Migration distance	-7.37	km/y	231.17	48	-0.36	-1.17
Arrival	1.11	d/y	18.029	28	0.68	2.26
Departure	-0.36	d/y	18.606	28	-0.21	-0.71
Winter duration	-1.47	d/y	25.309	28	-0.64	-2.13

An ecological network analysis focusing on the winter movements of the Bewick's swans and how these changed over time, confirmed the eastward shift of the wintering range in recent years (**Chapter 7**). The winter area of the Bewick's swan is used as a well-connected network by the swans, but the importance of different 'nodes' of this network changed over time. The finding that some of the nodes that gained importance over time are situated outside the Natura 2000 network of protected sites, despite the Bewick's swan being a target species for de designation of these sites, raises concerns. Further down in this synthesis I will elaborate on this finding.

Changes in winter range and phenology are found in other waterfowl species as well (Fox et al., 2016; Lehikoinen et al., 2013; Pavón-Jordán et al., 2019; Podhrázký et al., 2017). What

makes this finding particularly interesting in Bewick's swans is the fact that this species has extended parental care. In their first year, including an autumn migration to the wintering area and a spring migration back to the breeding/moulting area(s), cygnets stay with their parents and supposedly learn the routes and important places to stay and forage through cultural transmission. Hence, the changes observed in winter location and especially winter duration are counterintuitive in this regard. If individuals respond to environmental circumstances, such as temperature (Chapter 6), to choose the best winter location, it could well be that juveniles follow their parents and choose similar sites in their future winters. However, if winter site and duration is 'copied' from the parents, how can it be that these traits show a generational shift over time (Gill et al., 2019; Chapter 6)? It must be that individuals, although following their parents in their first year of life, make their own choices once they are independent (as yearlings), but later on in life stick to their personal habits. We found no evidence of this shift in yearling individuals when analyzing migration distance, but this might be due to a small sample size in this age class (S6.8 this thesis). Tracking juveniles is difficult, since they occur in low numbers and suffer from relatively high mortality. We were able to track one individual for multiple years. This anecdotally showed that, as expected, the juvenile follows its mother closely in its first spring migration, but follows his/her own track in subsequent years (Fig. B.3).

Based on tracking data spanning more than 10 years (2007 – 2019), it was found that year was a significant factor in distinguishing the timing of migration (Table SB.1). This means that, the swans seem to respond to year-to-year variation in environmental circumstances, although the total variation appears to be small (Fig. B.1). Having only a limited window of opportunity to breed, the swans might also not have that much leeway in terms of responding to environmental conditions (Beekman et al., 2002). At some point in time (or space?) they will need to decide to go ahead, even if conditions seem unfavourable (Nuijten et al., 2014). This might be visible in the smaller standard deviations closer to the breeding grounds (Fig. B.1).

By using solar panels on the GPS-GSM neckbands of the swans, we were able to track individuals for multiple years. The data allowed us to examine repeatability of migration routes and timing on the individual level. Individuals were found to be highly consistent in their migration path (Fig. B.3); in 3 out of the 5 individuals for which we had 3 complete spring migration tracks, all 3 consecutive years clustered together in a similarity analysis (Fig. B.3). Also the individuals for which 2 years of spring migration tracks were available showed high similarity between years. In addition to the population phenology this too indicates high traditionality in individual migration phenology, as was suggested based on ring resightings in previous research (Rees and Bacon, 1996).

Repeatability of behaviour is an important topic of study in ecology. When considering migratory species in general, there is evidence for both flexibility and constraint (Sutherland, 1998). And although a meta-analysis by (Bell et al., 2009) found that migration in general has a low repeatability, individual studies showing repeatability have increased since (Table 8.2) and it would be interesting to redo the meta-analysis with new data that is available. In most studies it was found that individual birds were highly consistent in their migration timing (Arnaud et al., 2013; Battley, 2006; Bêty et al., 2004; Both et al., 2016; Conklin et al., 2013; Cooper et al., 2009; Gill et al., 2014; López-López et al., 2014; Lourenço et al., 2011; Sergio et al., 2014; Stanley et al., 2012; van Wijk et al., 2016; Vardanis et al., 2011), but (when assessed) flexible in routes (López-López et al., 2014; Sergio et al., 2014; Stanley et al., 2012; Vardanis et al., 2011). Only for two species, Osprey (*Pandion haliaetus*) and the great reed warbler

(*Acrocephalus arundinaceus*) flexibility, as opposed to consistency, in migration timing was found (Hasselquist et al., 2017; Vardanis et al., 2016). This can be the result of high within-individual variation (between years), but it could also be the result of low between-individual variation (i.e. all individuals have similar timings for example due to dependence on scarce food resources en route) (Conklin et al., 2013; Hasselquist et al., 2017). For the osprey a broad fronted migration (resulting in high between individual variation) and site-fidelity in use of stopover sites (resulting in low within individual variation) were hypothesized as an explanation for the deviating results (Vardanis et al., 2016).

The Bewick's swan has an interesting combination of migration characteristics in that respect: narrow-fronted migration, and site-fidelity in use of stopover sites (Beekman et al. 2002, Nuijten et al. 2014, Nuijten & Nolet *unpublished data*). This would anticipate high consistency, at least in space, and since the Arctic only provides a limited opportunity to breed, some consistency over time is to be expected as well.

Studying GPS tracking data of multiple Bewick's swans in this flyway, indeed a high level of repeatability in spring migration timing was found (Box 1). Despite indications of climate warming all along the migratory route (Stocker et al., 2013), with strong amplifications in the Arctic (ACIA, 2044), the swans seem to arrive and depart at the breeding grounds at approximately the same date every year (Nuijten et al., 2014). At the same time it was found that year is a significant factor in describing the differences in timing (not route) of migration between years (Table SB.1), indicating that variables that vary with year are driving migration timing in this species as well, although the overall variation between years is small (Fig. B.1).

Table 8.2: Examples of studies investigating repeatability / consistency in migratory birds in both time and space.

Species	Scientific name	Time	Space	Notes	Data	Source
Egyptian vulture	<i>Neophron percnopterus</i>	consistent	flexible		GPS	Lopez-Lopez et al. 2014
Marsh harrier	<i>Circus aeruginosus</i>	consistent	flexible		GPS	Vardanis et al. 2011
Osprey	<i>Pandion haliaetus</i>	flexible	consistent		GPS	Vardanis et al. 2016
Thin billed prion	<i>Pachyptila belcheri</i>	NA	flexible*	*measured as switches between moult areas	Stable carbon isotope ratio	Quilfeldt et al. 2010
Black tailed godwit	<i>Limosa limosa limosa</i>	consistent	NA		Observations	Laurenço et al. 2011
Great reed warbler	<i>Acrocephalus arundinaceus</i>	flexible*	consistent	*Low to moderate repeatabilities	Geolocator	Hasselquist et al. 2017; Tarka et al. 2015
Hoopoo	<i>Upupa epops</i>	consistent*	NA	*Only in autumn, not in spring	Geolocator	Van Wijk et al. 2016
Bar tailed godwit	<i>Limosa limosa islandica</i>	consistent	NA		Observations	Gill et al. 2014
Eastern kingbird	<i>Tyrannus tyrannus</i>	consistent*	NA	*only for females	Observations	Cooper et al. 2009
Pied flycatcher	<i>Ficedula hypoleuca</i>	consistent	NA		Observations	Both et al. 2016
Wood thrush	<i>Hylocichla mustelina</i>	consistent	flexible		Geolocator	Stanley et al. 2012
Bar tailed godwits	<i>Limosa limosa baueri</i>	consistent*	NA	*only in spring, not in autumn	Geolocator and observations	Conklin et al. 2013
Snow goose	<i>Anser caerulescens atlantica</i>	consistent*	NA	*high for migration duration and arrival, but low for departure	GPS	Béty et al. 2014
Bar tailed godwit	<i>Limosa limosa baueri</i>	consistent	NA		Observations	Battley et al. 2006
Common tern	<i>Sterna hirundo</i>	consistent	NA		Observations	Arnaud et al. 2013
Black kite	<i>Milvus migrans</i>	consistent*	flexible**	*increasing with age **measured as route length	GPS	Sergio et al. 2014

In line with the population averages, individual consistency in migration phenology was confirmed in Bewick's swans as well. This indicates a high level of traditionality and potentially even a genetic basis for this part of the annual cycle, that seems to contradict the variation in timing with year. Based on the characteristics of the two analysis, it might be that individuals are consistent in their speed, but that their timing is (more) subject to environmental influences such as temperature and ice coverage. Further research targeting these two aspects separately in repeated tracks should focus on the mechanisms and cues behind this apparent paradox in flexibility versus traditionality in the Bewick's swan.

Another aspect of interest in regard to the flexibility versus traditionality of migration phenology is the level of parental care involved in a system. Bewick's swans, like other geese and swan species and opposed to many songbird and wader species, has a system of extended parental care (Rees 2006). The cygnets follow their parents back to the breeding grounds on their first autumn migration, and spend the winter with them. They depart together on spring migration and it was recently shown (Fig. B.4) that they accompany their parents the whole route back to the breeding grounds. This was also found in white-fronted geese (*Anser anser albifrons*), where families were tracked to investigate their V-formation flight (Kölzsch et al., 2020). Such a system allows for cultural transmission that, together with the high individual consistency, can explain high values of repeatability at the population level. On the other hand, it does not explain the flexibility with environmental conditions that was also shown in Bewick's swan. Here it would be very interesting to study individuals from juvenile to adulthood, and comparing their routes and timing in their first year of independence with the phenology they 'learned' from their parents in their first year. Anecdotal results from one individual that was followed for three consecutive spring migrations, showed that while the first year the individual flew exactly the same route as his mother, in subsequent years its route deviated from this pattern (Box 1). Future tracking studies should confirm whether this is a general pattern for migratory birds that fly in family groups, as it suggests that we need to have a different perspective when studying the response of migratory species to environmental changes.

Dynamic Nature Conservation

In conclusion, answering the initial questions raised in the SAP, we can now disregard some of the hypothesis that were stated (Nagy et al., 2012). The risk of collisions with windmills appeared to be low (Fijn et al., 2012; Rees, 2012), and both food availability and interspecific competition at the wintering grounds were not limiting the Bewick's swan population (Wood et al., 2019; Wood et al. *unpublished data*).

Significant shifts in winter location and phenology (Chapter 6) raised the question whether the sharp decline observed in the population, can to some extent be explained by displacement of individuals, and thus represent a relative rather than an absolute decline. Zooming in on the Netherlands, once the core wintering area of the western population of Bewick's swans, this is very apparent. Numbers are declining drastically in the Netherlands since 1995 (Foppen et al., 2016; Hornman et al., 2020), and this decline carries on after 2015, when international counts seem to stabilize (Beekman et al., 2019). The results in this thesis show that where the international decline can, at least in part, be explained by a drop in apparent breeding success (Chapter 2), the regional declines are influenced largely by the eastward shift and shorter wintering of the swans in traditional wintering areas (Chapter 6). To keep track of the population

development, the coordinated monitoring efforts should be extended to more eastern areas that formerly only had Bewick's swans passing in migration seasons. Two questions that remain now that we know better how this species responds to environmental changes in different parts of the annual cycle is how these changes interact, and whether they have an effect on the fitness of individual swans. More specifically, future research should focus on how the transition from winter to spring migration takes shape, considering that 'winter' for the swans is now shorter and further to the east, while migration phenology was consistent in individuals. A subsequent question would then be whether the friction that could arise when different aspects of the annual cycle are disconnected (either in time or space), could lead to fitness effects such as the decreasing apparent breeding success in the Bewick's swan.

Although these questions regarding the mechanisms driving population declines are interesting and valuable in their own right, the fact that species are responding to changes in their habitat by changing their distributions and phenology, calls for a reconsideration of the way we protect biodiversity. In the current legislation for nature conservation in Europe, the Natura 2000 framework, species and habitats are listed based on their vulnerability and risk of extinction on the Annexes of the Birds and Habitats Directives (European Commission, 2009, 1992, 1979). Depending on the status on these lists, countries are obliged to designate protected areas and keep the subject in a favourable conservation status (FCS) (European Commission, 2000). In theory the resulting Natura 2000 areas are to form a connected network of protected sites that can safeguard Europe's biodiversity (European Commission, 2020). Especially in times of environmental changes, such a network should be able to facilitate species being resilient in their responses to the changes they encounter (Martin et al., 2007; Vos et al., 2008). However, the total set of sites is managed in fragments, with (apart from the approval of site designation) a lack of coordination on the national and international level (Opermanis et al., 2013). The resulting lack of focus on connectivity combined with the assignment procedure (see below) hampers the network function of the Natura 2000 sites (Verschuuren 2015).

In practice what happens is that countries assign a Natura 2000 status to areas of particular importance to one or multiple of the habitats and/or species that are listed in the Annexes of the Directives, often these overlap with already existing natural areas (Evans, 2012). For every Natura 2000 area, specific conservation objectives per target habitat/species (either quantitative or qualitative) are set and these are then regularly assessed (in principle every 6 years).

There are several issues concerning this setup, which all have to do with the fact that the protection of areas is based on the values in the area, present at the moment of assignment. Firstly, given that currently most natural areas in the EU are in an unfavourable conservation state (European Environment Agency, 2015), and that the targets per habitat and/or species are set based on values that are present in the area at the moment of assignment, this in itself is preventing improvements. Indeed, the specific target can be higher than current occurrences, but the reference is the present value.

Secondly, conservation objectives that are set based on a 'snapshot' of present values at a site, might in the long term be incompatible with each other due to a differential response of the target species to management actions that alter the habitat quality. Trade-offs between species, and prioritizing species, might become inevitable (van Teeffelen et al., 2008).

Although such trade-offs have gained little attention in the scientific literature (but see Wilson et al., 2007), they are common in many conservation-managed sites. When managing a site based on the conservation objectives set for the different target species, not only their (optimal) habitat requirements, but also their tolerance to sub-optimal management and the cost-effectiveness of different management actions need to be considered (van Teeffelen et al., 2008). When the set of species and their relative abundances present at the moment of assignment of a Natura 2000 site is such that it cannot co-exist in the long-term, conservation objectives based on this set are doomed to fail.

Thirdly, the setup seems to ignore the dynamics that are inherently present in a healthy natural system. Given the omnipresent fluctuations in climate, weather and other environmental circumstances, individuals need to adjust to new, and sometimes extreme, situations. These situations might represent the new normal, in which case microevolution might result in better adapted individuals over time (Gienapp et al., 2008, 2007), or exceptions that occur infrequently, but that they do change is a certainty.

As a result, natural dynamics are possibly counteracted by the specific goals that have been set for the protected area. This could be extra pressing in times of environmental change (Bellisario et al., 2014; Mazaris et al., 2013). When looking at the Bewick's swan situation as an example, it becomes clear why this can be a problem. The Bewick's swan used to occur in the Lauwersmeer area (53° 22' N, 06° 13'E) in substantial numbers. The area has been given a Natura 2000 status in 2010 and the Bewick's swan, being listed on Annex I of the Birds Directive, is one of the target species. The specific goal for the species is to maintain a population of on average 140 individuals at this site. However, population estimates between 2008 – 2013 showed that only 92 individuals on average visited the area annually. For the Lauwersmeer, the target was thus not met. A speculative cause for this specific site is the increase of mute swans in the area, foraging on macrophytes in summer and leaving fewer belowground parts for the Bewick's swans to forage upon arrival in autumn in the Netherlands (chapter 6). The Lauwersmeer is not an exception: in the Netherlands alone, 27 Natura 2000 areas have specific targets for the Bewick's swan, of which 14 did not reach their targets, 7 did not have either a target or a recent population estimate and 7 had population estimates above their targets (Foppen et al., 2016). In this thesis it was additionally found that Bewick's swans occur, on the other hand, in Natura 2000 areas that do not have specific targets for the species (and thus, were not designed to facilitate them), and also in areas outside the current Natura 2000 areas (Chapter 7). When considering the extent but certainly also the directionality of the changes in wintering area observed in this species (Chapter 6), the question arises whether the current system allows for protection of dynamic species such as the Bewick's swan.

Despite the concerns raised above having spurred substantial discussion, it was found that the Natura 2000 legislative framework can accommodate both ecological dynamics (Bastmeijer, 2017) and sustainable development (Kistenkas, 2013) and that the underlying Birds and Habitats Directives are "fit for [their] purpose" (European Commission, 2016). Indeed, an extensive review showed that the Birds Directive benefitted endangered bird species (Donald et al., 2007).

However, based on the formulation of the law, the assignment criteria for sites, and the topics of discussion raised above, this is not obvious. The sites and conservation objectives resulting from the legislation should therefore be seen as safeguards for an effective protection regime

(Bastmeijer, 2017). These safeguards form a legal framework within which opportunities can then be sought for nature management that focuses on resilient and dynamic natural values. Bastmeijer (2017) formulated three specific areas where the opportunities can be found in the legislation: operating an ecosystem view, incorporating resilience in the conservation objectives and regularly updating the implementation of the legislation for existing Natura 2000 sites. The first mainly states that (parts of) sites cannot be viewed in isolation, and that the 'natural characteristics' of a site are those that make it resistant to disturbance. The second is addressed in more detail by (Bijlsma et al., 2016) in a report for the Dutch ministry of Finance. They state that by categorizing the targets for a specific Natura 2000 site into 'characteristic and vulnerable', 'characteristic and robust', and 'non-characteristic' objectives, a prioritization can be given to the targets, and thus to ensuing management actions. This prevents seemingly incompatible goals, that can prevent conservation actions from being implemented. It in theory also allows for 'non-characteristic' values, to be allowed to disappear from a site (Bijlsma et al., 2016), although it needs to be stated that this is still regarded a violation of the prohibition of deterioration when it cannot be shown that the FCS of the habitat type and/or species of concern is guaranteed by other Natura 2000 sites on the regional or national level (Bastmeijer, 2017). The third way in which ecological dynamics can be better embedded in the Natura 2000 framework, is by regularly updating the conservation objectives, and even the assignment of sites. Having said that, this brings the risk of taking ad-hoc decisions, for example when the presence of the Bewick's swan in a certain area is deemed to be negligible in recent years, a flexible implementation of the legislation would allow for removing the species from the target list of that site, enabling management actions that potentially deteriorate the area for the species to be performed. In the light of the observed eastward shift of the Bewick's swan that we described in Chapter 6 of this thesis, the hypothetical site for this to happen could be the Natura 2000 site 'Polder Arkemheen' (52° 14' N, 05° 25'E) in the Netherlands, where in recent years on average only 12 of the targeted 190 individual Bewick's swans were present (Foppen et al., 2016). After removing the species-specific target from the site assignment list, regional water authorities would be able to change the water level in the area or farmers would be allowed to disturb waterfowl grazing on their fields (hypothetical examples). In the event of harsh weather conditions further east in the wintering range however, the Bewick's swans may seek refuge in this formerly known site. If this is left unsuitable for them, the FCS of the species will be at risk.

In summary, managing a site based on its present values without taking connectivity of sites into account can prevent facilitation of ecological dynamics. However, embracing some of the strategies to allow for ecological dynamics to be facilitated brings risks as well. As can be learnt from the case of the Bewick's swan presented in this thesis, the situation can be better assessed when proper information and analyses are available. Species specific knowledge on ecological needs and responses to change is needed to create species specific conservation plans (Mazaris et al., 2013), in particular for those subjects listed on the Annexes of the Habitats and Birds Directive. In addition, it would help to enable ecological dynamics to be present in Natura 2000 sites if a bandwidth of FCS would be formulated, rather than a single value, to relax the interpretation of article 6(2) from the Habitats Directive that any detectable decline in the target value represents a violation of the prohibition of deterioration (Bijlsma et al., 2016; Evans and Arvela, 2011). In the absence of the necessary knowledge to create conservation plans and FCS bandwidths, broader criteria for the requirements of habitats and species should be taken into account, to allow for resilience within the system (overarching different Natura 2000 sites), and caution should be taken in the decision to remove a species

from the target list for a certain site when conservation objectives have not been met in recent years. In some cases, habitat suitability and projection modelling could give insights to guide such decisions (Vos et al., 2008). As contrasting conservation needs for different target species could arise, a proper prioritization scheme should be in place for every Natura 2000 site (see Arponen, 2012), in consultation with other sites, to not paralyze the decision making process and enhance dynamic nature conservation.

Outlook

The presented way to deal with nature conservation legislation would require a considerable investment in research to create the necessary body of knowledge on which to base management decisions. Obtaining the vital knowledge for proper application of dynamic nature conservation in Europe is feasible for some species, for which ample data is available or can be obtained (such as the Bewick's swan), but this will not be the case for all of the habitats and species listed as targets in the current Natura 2000 legislation, let alone those that are not listed as of yet. In absence of such knowledge, in many cases 'precaution' will be the main argument for having to take certain measures. In our current human society, our focus on GDP growth will continue to increase our energy and material needs (Ward et al., 2016), creating an ever growing pressure on natural resources (Ripple et al., 2017). In this regime, it is unrealistic that the argument of 'precaution' will be valued higher by policy-makers than any economic or social argument regarding certain activities or management actions in an area. With this common practice, the current extinction rate will continue (Ceballos et al., 2010) and increase (Koh et al., 2004), with inevitable effects on our human society as well (Cardinale et al., 2012; Ripple et al., 2017).

Building on the classification of different phases of conservation science since the 1960s by Mace (2014), I believe it is now time for a new phase framing 'People as a part of nature'. Not only did we see the awareness of biodiversity declines rise, there is also a growing societal interest in sustainable living, circular economy and minimizing consumption. On all sorts of different levels, from local to global, steps are being made to reduce emissions and create a more sustainable world by taking into account the planetary boundaries (Rockstrom et al., 2009) and needs of the human population (Raworth, 2017). In this process, public awareness is creating a growing pressure on businesses and governments to take appropriate measures, but the systems remains vulnerable for 'cheaters' (Riehl and Frederickson, 2016). To ensure a sustainable future for our human society, biodiversity in general and planet Earth as we know it, long-term visions regarding sustainability and nature conservation must be reflected in governmental decisions, business practices and daily life decisions.