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Breeding population increase and range expansion of the Whooper Swan *Cygnus cygnus* in Oslo and Akershus counties, southeastern Norway, during 1999–2015

Svein Dale

Department of Ecology and Natural Resource Management, Norwegian University of Life Sciences, P.O.Box 5003, NO–1432 Ås, Norway; e-mail: svein.dale@nmbu.no.

Abstract. The Whooper Swan *Cygnus cygnus* has shown a remarkable breeding population increase and range expansion in Northern Europe during recent decades. Here, I summarize the temporal and spatial pattern of the expansion in Oslo and Akershus counties in southeastern Norway, and assess current and potential future competition with Mute Swans *Cygnus olor*. The first breeding was reported in 1999, and in 2003 breeding was reported at a second site. From 2006 the number of breeding sites increased rapidly, and the species has now been reported breeding from a total of 20 sites. However, at least seven sites have been abandoned after one or a few years of breeding, leading to temporary decreases in population size in some years. Abandoned sites had lower breeding success than sites that are still occupied. Current population size is 11–14 pairs. TRIM-analyses indicated a rate of increase of 7% per year. In about two thirds of the occupied sites, breeding was preceded by one or more years with presence of pairs that did not breed. Non-breeding Whooper Swans have been observed during summer (16 May–July) at a further 24 sites, suggesting that population size is likely to continue to increase. Oslo and Akershus also has an increasing population of Mute Swans, currently estimated at ca. 50 pairs, but Mute Swans have been recorded breeding at only three of the sites (15%) where Whooper Swans have bred, and at one of these sites there has been no temporal overlap. Thus, the two swan species have had limited interaction at breeding sites so far. However, among the 24 sites that have had non-breeding Whooper Swans during summer, Mute Swans have bred at 10 sites (42%, still present at most sites). This suggests that further expansion of Whooper Swans may soon lead to increased competition with Mute Swans, but there are also numerous other potential breeding sites without Mute Swans present.

Key words: *Cygnus cygnus*; *Cygnus olor*; population changes; breeding success

INTRODUCTION

The Whooper Swan *Cygnus cygnus* has shown a remarkable population increase and range expansion in Northern Europe during recent decades. In Sweden, hunting had reduced the population to about 20 pairs in the far north of the country in 1920 (Svensson et al. 1999). Legal protection has caused an increase to a current population size of 5400 pairs spread over the whole country (Green & Lindström 2014, Nilsson 2014). There have been particularly large increases after around 1985 (Axbrink 1999, Green & Lindström 2014, Nilsson 2014) which may be due to changes in agricultural practices that have favoured the Whooper Swan (Nilsson 2014). Similar increases have been observed in Finland (Valkama et al. 2011), Estonia (Luigujoe et al. 2002, Boiko et al. 2014) and Latvia and Lithuania (Butkauskas et al. 2012, Boiko et al. 2014).

In Norway, the Whooper Swan was also restricted to the far north (especially Pasvik in Finnmark) until a gradual expansion southwards (Gjershaug et al. 1994). Gjershaug et al. (1994) estimated a population size of 100–400 pairs during the period 1970–90. The population has continued to increase and is currently estimated at 350–600 pairs (Shimmings & Øien 2015). The range expansion has recently included southeastern Norway (Shimmings & Øien 2015), and the first breeding in Akershus county was in 1999 (Dale et al. 2001) and in Oslo in 2010 (Shimmings & Øien 2015). In this paper I summarize data on the temporal and spatial pattern of breeding population increase and range expansion in Oslo and Akershus counties in southeastern Norway during 1999–2015.

The Mute Swan *Cygnus olor* has also increased in many parts of the distribution range, including Norway and Sweden (Green & Lindström 2014, Shimmings & Øien 2015). In Oslo and Akershus counties, the Mute Swan became established in 1972, and the population size was estimated at 7–10 pairs in 1982 and 20–30 pairs in 2001 (Dale et al. 2001). It has continued to increase and current population size is around 50 pairs (C. Lome and M. Helberg in prep.). An important question is whether interactions between the two swan species may cause either a limitation of the population expansion of Whooper Swans in Oslo and Akershus, or a replacement of Mute Swans by Whooper Swans. In both Sweden (Svensson et al. 1999) and Latvia and Lithuania (Butkauskas et al. 2012) Whooper Swans

have replaced Mute Swans in some areas. Although Whooper Swans rarely breed in saltwater where Mute Swans are common, and Whooper Swans do not have competition from Mute Swans at small lakes in forested areas, there is habitat overlap in particular at rich freshwater lakes (Gjershaug et al. 1994, Svensson et al. 1999). Thus, there is potential for competition in some habitats. I assess to what degree the two swan species have interacted so far, and I use data on non-breeding summering sites of Whooper Swans (which may become future breeding sites) to assess the potential for future interactions.

METHODS

Data collection

Data on breeding sites of Whooper Swans were obtained through own field observations and by searching bird reporting websites. The author has conducted mapping of bird communities at nearly 2000 sites throughout Oslo and Akershus counties during 1995–2015 (see e.g Haavik & Dale 2012, Dale et al. 2015, Dale & Hardeng 2016) of which more than 700 have wetland. This represents almost all wetlands in Oslo and Akershus counties. All wetland sites with bird community information have been visited at least once during the study period 1999–2015. I retrieved all records of observations of Whooper Swans during the breeding season (May–July) for the period 1999–2015. The starting year of 1999 was chosen because this was the year of the first known breeding of Whooper Swans in Oslo and Akershus counties (Dale et al. 2001). For all sites where breeding had been recorded (also based on breeding records found during searches of websites), all negative records during the breeding season were also noted. Thus, the number of visits during the breeding season to the 20 sites that have had breeding Whooper Swans was 1–35 (median 3).

Own observations were combined with observations reported on the websites of the Norwegian Ornithological Society, Oslo and Akershus branch (www.nofoa.no) and the Norwegian Biodiversity Information Centre (www.artsobservasjoner.no). Searches were done to identify all observations of Whooper Swans during May–July for the period 1999–2015. As done for own data, I also searched for all visits with no Whooper Swans observed for the 20 breeding sites. Absence of Whooper Swans was noted when other species had been recorded from a site, but not Whooper Swans. From these two websites the additional number of visits to the 20 breeding sites varied from zero to ca. 100 (median 5). For the most visited sites, the exact number of visits is difficult to determine, in particular regarding what constituted a visit with negative result (reports with only a few species seen at a site were generally disregarded). In total, the 20 breeding sites had been visited between two and more than 100 times (median 12.5). Summary of the data is presented in Appendix 1.

To assess overlap between Whooper Swans and Mute Swans, I collected information on presence and breeding of Mute Swans from the same sources as used above. In addition, a detailed overview of known breeding sites of Mute Swans during 2009–2014 was provided by C. Lome and M. Helberg (in prep.).

Site occupation and breeding

A site was defined as occupied if a pair of Whooper Swans had been present for at least part of the breeding season (16 May–July). Observations before 16 May were included if they indicated breeding (e.g. incubation), otherwise they were regarded as late observations of migrating individuals. A pair was regarded as breeding if a nest had been built. Nests were not inspected to assess whether eggs had hatched, but a successful breeding attempt was defined as young seen later in the breeding season. Failed breeding attempts were hence those pairs that had built a nest or started incubating, but no hatched young were seen. A skipped breeding season was defined as a pair being present in one year without any breeding activities observed (no nest building, incubation etc. observed), but I also required that this was in a year after breeding had already taken place at a site (as opposed to observations of pairs present before breeding had taken place). Breeding success was classified according to 1) whether the breeding attempt was successful or not, or 2) the largest number of young observed (i.e. as close to the number of young hatched as field observations permitted; note that this represents the minimum number of young because young may have died before the first visit after hatching).

Analyses of population trends and population size

Population trend during 1999–2015 was analysed with TRIM (version 3.53, Pannekoek & van Strien 2005), which uses log-linear models with a Poisson error distribution. Time effects model with correction for overdispersion and serial correlation was used, and trend based on imputed slope and index based on imputed values are reported.

RESULTS

Population increase

The cumulative number of occupied sites increased from two in 1999 to 20 in 2015 (Figure 1). However,

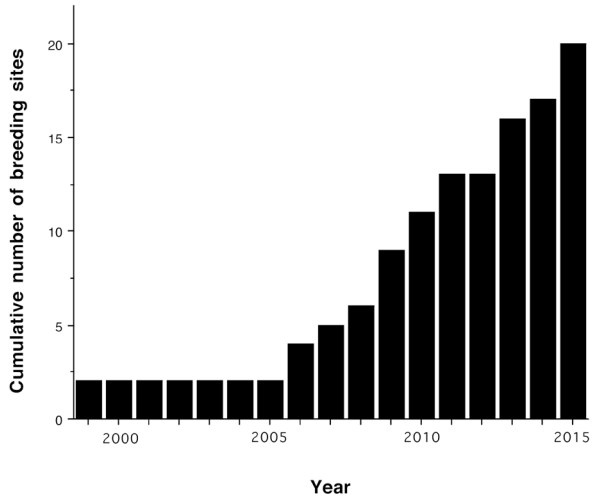

Figure 1. Cumulative number of breeding sites occupied by Whooper Swans in Oslo and Akershus counties, southeastern Norway, during 1999–2015. Numbers are based on first recorded field evidence of site occupation. Due to incomplete surveys of sites, the true distribution of cumulative numbers may be shifted somewhat to the left compared to the data shown in the figure.

at least seven sites have been abandoned after one or more years with breeding (Figure 2, Table 1). Thus, the yearly number of occupied sites estimated from TRIM did not increase continuously, but had temporary decreases from one year to another at several time

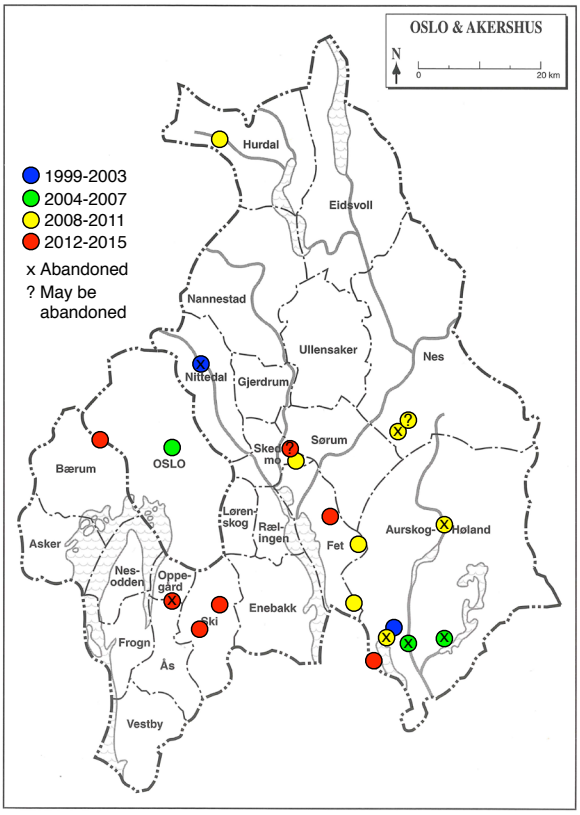

Figure 2. Spatial and temporal pattern of range expansion of Whooper Swans in Oslo and Akershus counties, southeastern Norway, during 1999–2015. The map shows the timing of first evidence of occupation of each site (n = 20).

Table 1. Overview of known breeding sites of Whooper Swans in Oslo and Akershus counties, southeastern Norway, during 1999–2015. See also Appendix 1.

Site	Municipality	First occupied	Breeding	No. of successesful breeding events	Abandoned
Skrukkelisjøen	Hurdal	2011	2014–15	1	No
Tjernsmotjernet	Nes	2010	2010	1	Yes
Vaskesjøen	Nes	2010	2010	0	?
Holmbru, Mjermen	Aurskog-Høland	2006	2007	0–1	Yes
Hellesjøvannet	Aurskog-Høland	1998	1999–2009, 2011–15	17	No
Bergsjø	Aurskog-Høland	2006	2006	0–1	Yes
Kjelle	Aurskog-Høland	2011	2013	1	Yes
Bråtevannet	Aurskog-Høland	2008	2009	0–1	Yes
Kløvstjenn	Aurskog-Høland	2014	2014–15	2	No
Sloretjern	Aurskog-Høland, Fet	2009	2009	?	No
Midtskog	Fet	2009	2009–15	1+	No
Breimosen	Fet	2015	2015	0-1	No
Kongsrudtjernet	Skedsmo	2009	2009–15	6	No
Tretjernet	Skedsmo, Sørum	2013	2013	0–1	?
Sagdammen	Nittedal	1999	2003–04	2	Yes
Maridalsvannet	Oslo	2007	2010–15	4	No
Triungsvanna	Bærum, Oslo	2013	2014–15	2	No
Slorene	Oppegård, Ås	2013	2013	0	Yes
Rullestadtjernet	Ski	2015	2015	1	No
Pungen	Ski	2015	2015	1	No

periods (Figure 3). TRIM-analysis indicated a rate of increase of 6.8% per year during the period 1999–2015. TRIM classified this as a moderate increase ($p < 0.05$). In 2015, 11 sites were known to be occupied (based on field observations), six were known to be unoccupied whereas the latter three sites were not visited in 2015. Thus, the number of pairs was 11–14. The imputed number of occupied sites in 2015 was 13 according to the TRIM-analysis.

Range expansion

Apart from the two sites that were occupied during the first years of the study period (1999–2005), the first known new establishments were in 2006 close to the Hellesjøvannet site (which had successful breeding in all these years; Figure 2, Table 1). The Sagdammen site had successful breeding in only two years (2003–2004), but a pair was seen in the ‚neighbouring' site Maridalsvannet (12–14 km away) in 2007 where breeding started in 2010 (Figure 2, Table 1). The largest number of known new establishments occurred from 2009 and onwards (Figure 1, Table 1), first mainly between the two initial sites, and then in the last period a marked expansion towards the southwest (Figure 2).

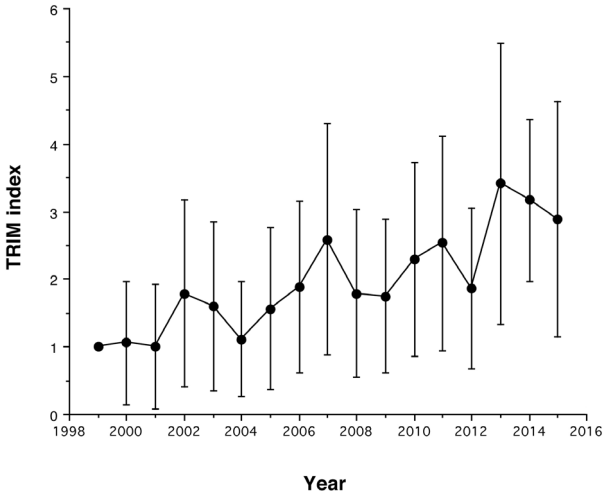

Figure 3. Population size of Whooper Swans in Oslo and Akershus counties, southeastern Norway, during 1999–2015. The figure shows results from a TRIM-analysis. The index (± SE) is based on imputed values, and the first year (1999) is set to 1.

Table 2. Overview of summering sites used by non-breeding Whooper Swans in Oslo and Akershus counties, southeastern Norway, during 1999–2015. Summering sites were defined as observations of Whooper Swans during 16 May–July in sites with suitable breeding habitat (i.e. excluding observations of birds feeding on farmland).

Site	Municipality	Year(s) of observation(s)
Skomakartjennet	Eidsvoll	2011
Hersjøen	Ullensaker	1999
Mangen	Aurskog-Høland	2007
Store Garsjøen	Aurskog-Høland	2015
Gåsvika, Setten	Aurskog-Høland	2007
Katisavika, Mjermen	Aurskog-Høland	2013
Eidsdammen	Aurskog-Høland	2013
Northern part of Bjørkelangen	Aurskog-Høland	2011
Kragtorpvika	Aurskog-Høland	2009
Kollerudvika	Aurskog-Høland	2011
Northern part of Hemnessjøen	Aurskog-Høland	2011
Vindlandstjernet	Fet	2011
Hagendammen, Tunnerud	Fet	2012
Nordre Øyeren	Rælingen, Fet	2001–11, 2013–15
Stilla	Skedsmo	2006–07
Ringstilla	Skedsmo	2015
Bergstjernet	Nittedal	2003
Østensjøvannet	Oslo	2013
Stovivannet	Bærum	2002
Spiradammen	Asker	2009
Pollevannet	Ås	2006
Østensjøvannet	Ås	2010
Midtsjøvannet	Ski	2015
Nærevannet	Ski	2013

Behaviour during establishment

There were nine sites that had been checked by observers in the years before the year of the first breeding. In six of the sites, breeding was preceded by one or more years with presence of pairs that did not breed. In the other three cases, breeding appeared to take place in the first year the site was occupied. Two other cases may also represent non-breeding in years before the onset of breeding. At Kjelle a pair was present in 2011, but probably not in 2012, whereas breeding took place in 2013. Similarly, in Maridalsvannet a pair was present in 2007, but probably not in 2008–09, whereas breeding started in 2010.

Non-breeding Whooper Swans at other sites

Non-breeding Whooper Swans have been observed during summer (16 May–July) at a further 24 sites with potential for breeding (Figure 4, Table 2). The number of summering sites used has increased with time (r_s = 0.50, n = 17 years, p = 0.046; Table 2).

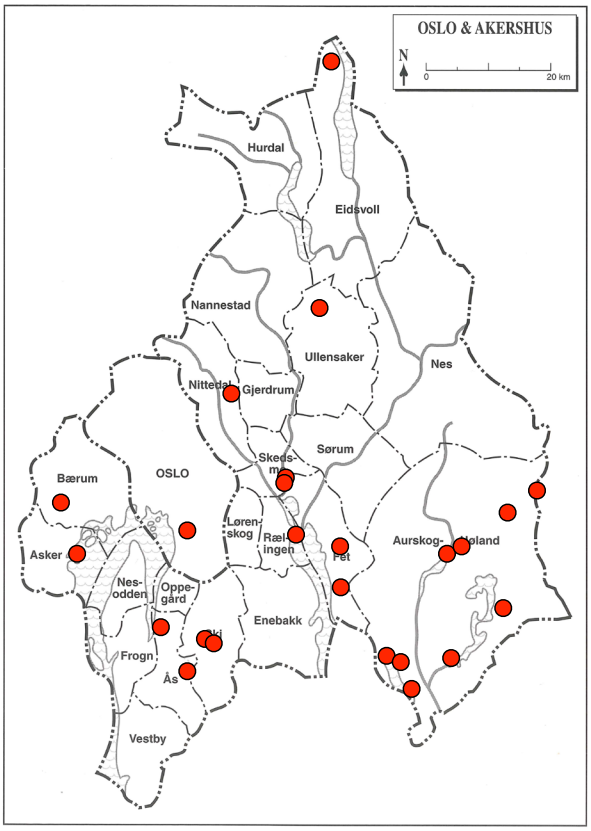

Figure 4. Location of sites where non-breeding Whooper Swans have been observed during the summer (16 May–July) in Oslo and Akershus counties, southeastern Norway, during 1999–2015 (n = 24).

Breeding success

Twelve of the 20 occupied sites have had no or only one successful breeding (Table 1), although four of these sites had their first known breeding in 2015, and breeding may continue in succeeding years. However, the oldest site (Hellesjøvannet) has been very productive, and accounts for 17 out of 40 (43%) documented successful breedings (i.e. young hatched; Table 1). Two additional sites (Kongsrudtjern and Maridalsvannet) have another 25% of documented successful breedings (Table 1). Thus, productivity has been highly variable.

Sites that have become abandoned had a higher proportion of failed breeding attempts or skipped breeding seasons than sites that are still occupied (abandoned sites: 4 successful, 6 failed/skipped; still occupied sites: 35 successful, 5 failed/skipped; Fisher exact test, P = 0.004). Furthermore, among successful breeding attempts, abandoned sites tended to have a lower mean number of young (abandoned: mean = 3.50, n = 4; still occupied: mean = 4.69, n = 35; t-test: t = 1.41, df = 37, p = 0.17). Overall, breeding success was therefore lower in abandoned sites than in sites that are still occupied (abandoned: mean = 1.40 young/year, n = 10; still occupied: mean = 4.10, n = 40; t-test: t = 3.57, df = 48, p = 0.0008).

The difference regarding successful breeding attempts was not statistically significant when using sites as sampling unit (abandoned sites [n = 4] had a median success rate of 0.67, still used sites [n = 9] had a median success rate of 1.00; Mann-Whitney U-test: z = 0.84, p = 0.40). The difference regarding mean number of young for successful breeding attempts was also not significant (abandoned sites: mean = 3.33, n = 3; still occupied: mean = 3.66, n = 9; t-test: t = 0.36, df = 10, p = 0.73). Overall, breeding success tended to be lower in abandoned sites than in sites that are still occupied (abandoned: mean = 1.83 young/year, n = 4; still occupied: mean = 3.23, n = 9; t-test: t = 1.56, df = 11, p = 0.15). However, despite the lack of significance (partly due to low power of the tests using sites as sampling unit) it should be noted that still occupied sites had a breeding success that was 77% higher than abandoned sites.

Relationship to Mute Swan

Mute Swans were recorded at only eight of the 20 sites (40%) where Whooper Swans have bred. Mute Swans have bred at only three of the 20 sites (15%), and there has been no temporal overlap in breeding of the two species at one of these breeding sites (Tjernsmotjernet). At one of the two breeding sites with temporal overlap (Hellesjøvannet), the Mute Swan disappeared after the Whooper Swan became established. At the other site (Slorene), Mute Swans have been breeding for many years, although they were temporarily absent during 2010–2013 (but were breeding at a site ca. 1 km away at least in 2011–2012). Whooper Swans made a failed breeding attempt at Slorene in 2013, and in 2014, when Mute Swans were back and bred successfully, the Whooper Swans did not attempt breeding. In 2015, Whooper Swans were not seen during the breeding season, but the Mute Swan bred successfully again.

Among the 24 sites that have had non-breeding Whooper Swans during summer, Mute Swans have been recorded at 13 sites (54%), and have bred at 10 sites (42%; last known breeding years 2011–2015). Thus, potential new breeding sites for Whooper Swans tended to have a higher frequency of breeding Mute Swans (10 out of 24) than breeding sites for Whooper Swans recorded so far (3 out of 20; $\chi^2 = 3.73$, df = 1, p = 0.053).

DISCUSSION

Pattern of population increase and range expansion

The results indicated that the population size of the Whooper Swan started to increase rapidly from around

2006, but despite the general increase there were variable fates at individual sites. Of the 20 sites that have been used at least once during 1999–2015, at least seven have become abandoned. Abandonment caused an irregular population increase so that current population size was only 11–14 pairs. The population size estimate should be considered as a minimum. Unknown breeding sites may exist because some potential breeding sites had only a few visits during the study period and visits may have been in the first part of the study before the strongest increase had started. One could also speculate that some sites have been discovered, but kept secret by observers. However, nearly half of the breeding sites were discovered by the author, and the author has also visited many of the other breeding sites regularly independently of the presence of Whooper Swans. Furthermore, suitable breeding sites have probably also been visited more often than wetlands in general. Thus, I consider it likely that a large proportion of the breeding sites have been found.

Abandoned sites appeared to be of low quality because they tended to have a higher rate of failed breeding attempts or skipped breeding seasons, and lower production of young. Although the causes of lower quality is difficult to judge, one site probably had suitable breeding conditions only in some years (Kjelle, Aurskog-Høland; the site is a wet meadow which dries out in some years) and another site had lowered water level in some years due to dam maintenance (Sagdammen, Nittedal). The Whooper Swan has been regarded as a shy bird sensitive to human disturbance (Gjershaug et al. 1994), and this could potentially have been a cause of abandonment of sites. However, I am unaware of evidence of this from the study area. Furthermore, few of the sites used in Oslo and Akershus are in wilderness areas, most are fairly close to human habitation, agricultural areas, public roads or forestry roads. Thus, the Whooper Swan does not appear to be as sensitive to disturbance as reported earlier.

The distribution range has also expanded rapidly after 2006, during 2008–11 especially in the central parts of Oslo and Akershus (yellow symbols in Figure 2), and during 2012–15 markedly towards the soutwest (red symbols in Figure 2). Non-breeding sites are likely to become future breeding sites because about two thirds of the breeding sites had non-breeding pairs in one or more years preceding breeding. Non-breeding sites were located predominantly in the southern parts of the study area (Figure 4). However, also northern parts of Akershus have many sites with suitable breeding habitat, and expansion in these areas may also be expected in the future. My subjective assessment is that there may be at least 100 sites in Oslo and Akershus that may be suitable for Whooper Swans.

The exact timing of colonization of new sites and expansion of the distribution range has some degree of uncertainty, especially during the first years of the study period, due to missing information for some sites in some years (see Appendix 1). Thus, the colonization of new sites as indicated in Figure 1 is conservative, and the true distribution of colonizations may be shifted somewhat to the left (earlier colonization). However, the pattern indicated by the TRIM-analysis in Figure 3 may on the other hand overestimate the number of occupied sites in the first part of the study period. TRIM estimated five occupied sites already in 1999 even though this was the year of the first known breeding. This was because, in addition to the two sites known to be occupied in 1999, there were four sites that had not been checked before the first year Whooper Swans were recorded as present (Appendix 1). However, Whooper Swans were discovered at these four sites as late as 2009, 2010, 2014 and 2015, respectively. I consider it unlikely that three of these four sites were occupied already in 1999 as suggested by TRIM. If these four sites were coded as not occupied in 1999, TRIM adjusted the population estimate to three occupied sites in 1999, and the imputed slope to 8.3% increase per year. Imputed number of occupied sites in 2015 remained unchanged at 13.

Relationship to Mute Swan

So far, direct interactions between Whooper Swans and Mute Swans have only taken place at two sites. Hellesjøvannet (Aurskog-Høland) had breeding Mute Swans until 1999, the same year that Whooper Swans started breeding there. Thus, establishment of the Whooper Swan may have caused disappearance of the Mute Swan at this site, as suggested by observations from other countries (Svensson et al. 1999, Butkauskas et al. 2012). Slorene (Oppegård, Ås) has had Mute Swans breeding for many years, although they were temporarily absent during 2010–2013. Whooper Swans made a failed breeding attempt there in 2013, and in 2014, when Mute Swans were back and bred successfully, the Whooper Swans did not attempt breeding, and in 2015 Whooper Swans were not seen during the breeding season. This may suggest that at this site Mute Swans were dominant over Whooper Swans.

Potential future breeding sites of Whooper Swans (used as non-breeding summering sites so far) had Mute Swans breeding more frequently than the 20 sites already used by Whooper Swans for breeding. This suggests that interactions between the two swan species may become more frequent in the future, although there are also numerous potential future breeding sites for Whooper Swans where Mute Swans are not present (in particular in boreal forest areas in eastern and northern parts of Akershus). Based on the general evidence that Whooper Swans replace Mute Swans (Sweden: Svensson et al. 1999; Latvia and Lithuania: Butkauskas

et al. 2012), one may predict that the Whooper Swan may increase at the expense of Mute Swans. However, of the total population of approximately 50 pairs of Mute Swans (C. Lome and M. Helberg in prep.), 14–18 pairs breed at saltwater sites along the coast (Andersen & Bergan 2013, C. Lome and M. Helberg in prep.). This is a habitat rarely used by the Whooper Swan (e.g. Svensson et al. 1999). Thus, the Mute Swan is not likely to be completely replaced by Whooper Swans. It is also worth noting that at one site (Slorene), the Mute Swan may have been dominant and was not replaced by Whooper Swans, suggesting that the outcome of competition between the two swan species is not always given.

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Appendix 1. Overview of documented use of each breeding site for Whooper Swans in Oslo and Akershus counties, southeastern Norway, during 1999–2015. 0 = no Whooper Swans recorded (i.e. negative result), P = pair, N = nest, Y = young. Nest does not necessarily mean that breeding failed, but may also indicate lack of data on what happened later in the breeding season. See Table 1 in main text for municipality for each site.

Site	1999	2000	2001	2002	2003	2004	2005	2006	2007	2008	2009	2010	2011	2012	2013	2014	2015
Skrukkelisjøen	0		0			0		0		0		0	P	P	P	N[1]	Y
Tjernsmotjernet	0								0		0	Y				0	
Vaskesjøen												N[2]					
Holmbru					0			P	N		0			0	0	0	0
Hellesjøvannet[3]	Y	Y	Y	Y	Y	Y	Y	Y	Y[4]	Y	Y	P	Y	Y	Y	Y	Y
Bergsjø	0		0					N						0			0
Kjelle	0		0				0	0	0	0	0	0	P	0	Y	0	0
Bråtevannet	0									P	N	0	0	0			0
Kløvstjenn																Y	Y
Sloretjern								0			N			P			P
Midtskog[5]						0					P	P	P	P	P	Y	P
Breimosen	0						0			0		0					N
Kongsrudtjernet											Y	Y	Y	Y	Y	Y	N[2]
Tretjernet														0	N		
Sagdammen	P			P	Y	Y	P	P	0	P	0	P	0	0	0		0
Maridalsvannet	0	0				0		0	P	0	0	Y	Y	Y	N[2]	P	Y
Triungsvanna	0			0	0	0	0	0	0	0	0	0	0	0	P	Y	Y
Slorene	0	0	0	0	0	0	0	0	0	0	0	0	0	0	N[2]	P	0
Rullestadtjernet	0								0	0	0	0		0	0		Y
Pungen																	Y

[1] Probably failed breeding
[2] Failed breeding
[3] A pair was present in 1998 (Dale et al. 2001)
[4] Two pairs bred successfully
[5] Based partly on local information that a pair has been present (recorded as 'P' although successful breeding may have occurred)