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Apparent survival of an Arctic-breeding migratory bird over 44 years of fluctuating population size

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Following increases in numbers during the second half of the 20th century, several Arctic-breeding migrant bird species are now undergoing sustained population declines. These include the northwest European population of Bewick's Swan *Cygnus columbianus bewickii*, which declined from c. 29 000 birds on the wintering grounds in 1995 to 18 000 in 2010. It is unclear whether this decrease reflects reduced survival, emigration to a different area, or a combination of both. Furthermore, the environmental drivers of any demographic changes are also unknown. We therefore used an information-theoretic approach in RMark to analyse a data set of 3929 individually marked and resighted Bewick's Swans to assess temporal trends and drivers of survival between winters 1970/71 and 2014/2015, while accounting for effects of age, sex and different marker types. The temporal trend in apparent survival rates over our study period was best explained by different survival rates for each decade, with geometric mean survival rates highest in the 1980s (leg ring marked birds = 0.853, 95% confidence interval (CI) = 0.830–0.873) and lowest in the 2010s (leg ring = 0.773, CI = 0.738–0.805; neck-collar = 0.725, CI = 0.681–0.764). Mean (\pm 95% CI) resighting probabilities over the study period were higher for birds marked with neck-collars (0.91 ± 0.01) than for those marked with leg-rings (0.70 ± 0.02). Weather conditions in different areas across the flyway,

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food resources on the winter grounds, density-dependence and the growth of numbers at a relatively new wintering site (the Evros Delta in Greece) all performed poorly as explanatory variables of apparent survival. None of our 18 covariates accounted for more than 7.2% of the deviance associated with our survival models, with a mean of only 2.2% of deviance explained. Our results provide long-term demographic information needed to help conservationists understand the population dynamics of Bewick's Swans in northwest Europe.

Keywords: Animal demographic rates; Bewick's Swan *Cygnus columbianus bewickii*; global environmental change; herbivorous waterbirds; life history; mark recapture data

The world's migratory bird species, which account for 19% of all extant birds, have become increasingly threatened since the 1980s (Kirby *et al.* 2008, BirdLife International 2013). These population declines represent a growing concern for conservationists, both in their own right and also because such migratory species are potential sentinels of environmental change, as their numbers integrate information on the ecological status of multiple habitats across their migratory range (Piersma & Lindström 2004, Stillman *et al.* 2015). However, the fact that migrants integrate over a range of areas and environmental conditions can make it challenging to identify specific environmental factors associated with population change, and the demographic mechanisms that underpin these observed declines remain unclear in many cases. To inform conservation strategies that aim to halt and reverse population declines, we need to understand the patterns and drivers of temporal changes in demographic rates, such as survival, that determine population size and growth rates (Kirby *et al.* 2008, Frederiksen *et al.* 2014).

The northwest European population of Bewick's Swans *Cygnus columbianus bewickii* (Fig. 1) has undergone a sustained period of rapidly changing population size over the past 30 years; numbers increased from 16 283 in 1984 up to 29 780 individuals in 1995, before falling to 18 057 individuals in 2010 (Rees & Beekman 2010, Nagy *et al.* 2012). In Europe, Bewick's Swan has been a species of conservation concern for many years; the species is listed in Annex I of the European Union Birds Directive (2009/147/EC), and an international species action plan (the Bewick's Swan Single Species Action Plan: BSSAP) developed for the population was adopted by the African-Eurasian Waterbird Agreement (AEWA) in 2012 (Nagy *et al.* 2012). Reflecting growing concern regarding the conservation status of the population, it was also recently classified as Endangered on the European Red List of bird species (BirdLife International 2015). Data on the age- and sex-specific demographic rates of Bewick's Swans, and how such rates have changed over time, are needed in order to understand the observed changes in population size. A recent study found no long-term decline in Bewick's Swan breeding success (Wood *et al.* 2016), but survival has not yet been examined.

The BSSAP highlights multiple threats that may have impacted on both adult and juvenile survival across the flyway, including changes in environmental conditions such as weather conditions and food supplies (Nagy *et al.* 2012). Environmental conditions in different parts of the flyway have been shown to influence the survival rates of migratory birds across a wide range of species (Newton 2006, Grosbois *et al.* 2008, White 2008). For example, adverse weather conditions at breeding, wintering, or migratory stopover sites may reduce survival (Newton 2006, Sedinger & Alisauskas 2014). Low temperatures are known to increase thermoregulatory energetic costs for swans (Bech 1980), which may reduce their survival rates (White 2008). The effects of low temperatures may not affect all age classes

and sexes equally; in particular, younger birds have smaller energy reserves and are likely to show higher cold-induced mortality than older age classes (Davidson & Evans 1982).

Similarly, the need to defend feeding patches for their mate and offspring during both breeding and non-breeding periods means that paired adult males with young show reduced food intake and increased energy expenditure, and thus are typically in poorer body condition than paired females in late winter (Bowler 1994). Frozen water and ground during periods of low temperatures and snowfall may prevent swans from accessing aquatic and subterranean (e.g. plant tubers) food resources, respectively, which can increase starvation risk in all parts of the swans' range (Andersen-Harild 1981, Nilsson 2008). Periods of snowfall may also increase mortality risk during migration, as low visibility during snowfall may increase the probability of flying accidents (Newton 2007).

The intensification of agriculture in northwest Europe since the 1950s has enhanced the availability and quality of terrestrial food resources for swans on the wintering grounds (van Eerden *et al.* 2005, Davis *et al.* 2014). Historically, winter was a time of low food availability for herbivores such as swans, because of the seasonal senescence of both aquatic and terrestrial plants (Bakker *et al.* 2016). A study by van Eerden *et al.* (1996) reported that total numbers of herbivorous waterbirds showed positive correlations with overwinter availability of crops. Therefore, swans may show higher survival during periods in which greater food resources are available. However, the benefits of additional food resources will depend on the numbers of individuals using those food resources. Swan populations can deplete local food supplies (Nolet *et al.* 2006, Wood *et al.* 2012), leaving less for subdominant individuals or later arrivals. For example, Nolet and Drent (1998) reported depletion of aquatic plant tubers by Bewick's Swans, a key food resource during migration, at the White Sea stopover site. Furthermore, subdominant swans may not be able to exploit fully

available food resources at high swan densities because of interference competition from dominant individuals (Gyimesi *et al.* 2010). Thus, swan survival may show evidence of density-dependence resulting from competition for food resources on the breeding grounds, wintering areas, and stopover sites.

Winter numbers of Bewick's Swans have been rising on parts of the coasts of the Aegean and Black Seas, most notably at the Evros Delta in Greece, over the last 20 years with substantially higher numbers observed from 2010 onwards (Royal Belgian Institute of Natural Sciences and Evros Delta Management Body, unpublished data; Litvin & Vangeluwe 2016). The species was virtually unknown in Greece prior to 1996 (Handrinos & Arkriotis 1997), and small numbers have also been reported in autumn and winter on coastal wetlands in the Ukraine, Romania, Bulgaria, and Turkey in recent years (Kirwan *et al.* 2014, Chovan & Kazannik 2015). However, the origin of the birds wintering in southeastern Europe remains unclear, with only limited evidence from the resighting of marked birds to indicate movements between the two regions. Between 1997 and 2016 three individuals marked with neck-collars in northwestern Europe were resighted subsequently at the Evros Delta; these three individuals demonstrate that the switching of winter areas does occur, but are insufficient to evaluate the levels of interchange. The low numbers of individuals known to have switched wintering areas might be due to a relatively low proportion of marked birds in the northwestern European population in recent years in which the population in southeast Europe increased, limited resighting effort in southeastern Europe, or both of these factors. An alternative hypothesis would be that there is no link between the decrease in the number of Bewick's Swans in northwestern Europe and the increase in southeastern Europe. Bewick's Swans from the northwest European population have traditionally been considered to show high winter site fidelity (Rees 2006). However, if part of the northwestern European

population has redistributed from their core wintering area of northwestern Europe to the Aegean and Black Sea region of southeastern Europe, we would expect to detect a negative association between the apparent survival of the northwestern European population and the rising numbers at new sites in southeastern Europe. Previous research has found that migratory waterbirds can show relatively abrupt switches between discrete wintering areas (e.g. Keller 2000).

We used long-term mark-recapture data obtained from the wintering grounds to determine whether the northwestern European Bewick's Swans' annual survival rates between winters have varied over time, and to determine the factors affecting inter-annual variation in survival. Our survival estimates accounted for the effects of age and sex, and the effects that different marker types can have on survival; all effects have been shown previously to be important in determining swan survival (e.g. Nichols *et al.* 1992, Varner & Eichholz 2012, Meixell *et al.* 2013, Ely & Meixell 2016). We tested three predictions related to the apparent survival of Bewick's Swans. Firstly, we predicted that their apparent survival would vary over our 44-year study period in line with observed population trends (i.e. higher survival during the period of population increase between 1970 and 1995). Our second prediction was that inter-annual differences in Bewick's Swan apparent survival would also be explained, at least partly, by air temperatures and snowfall intensity across the flyway, and by the abundance of food resources on the winter grounds. Our third prediction was that annual variation in Bewick's Swan apparent survival would be explained in part by emigration to new wintering areas in southeast Europe, and specifically the growth in numbers counted at a key overwintering site in Greece.

METHODS

Study system

The northwestern European population of Bewick's Swans spends the winter predominantly in the UK and the Netherlands (Fig. 1; Rees 2006). In spring the birds subsequently migrate northeast via key stopover sites, which include coastal and freshwater habitats in Estonia and Dvina Bay in the White Sea (Rees 2006, Nuijten *et al.* 2014). The swans then nest adjacent to the many pools, lakes and channels on the open maritime tundra of European Arctic Russia, west of the Ural Mountains, with non-breeders also frequenting lakes and bays within the breeding range (Rees 2006). Finally, during the autumn migration back to the winter grounds, the birds use a number of stopover sites; in particular, freshwater habitats in the Karelia region of Russia, and freshwater and coastal habitats in Estonia (Luigujõe *et al.* 1996, Rees 2006).

Swan capture, marking and resighting

A total of 3929 Bewick's Swans (2006 females and 1923 males) were caught and marked between winters 1970/1971 and 2014/2015. Of these, 2901 were caught at sites on the wintering grounds in the UK and the Netherlands, and 89 in Germany as the birds gathered on the edge of the wintering range in preparation for their return migration. A further 939 were caught on the moulting grounds in Russia (Supporting Online Tables S1 & S2). Over the study period a mean (\pm standard deviation) of 87 ± 66 birds were caught, marked, and released annually (median = 67; range = 8–275). During the winter, birds were caught using cannon nets when on agricultural fields, or by using a baited blind-ended net trap termed a 'swan pipe' when on water (Evans 1982, O'Brien *et al.* 2016). In Russia, birds were captured

by hand-net from a boat while flightless during the mid-summer primary feather moult. Of the 3929 swans, 2365 were captured as adults (individuals in their third winter onwards), 603 as yearlings (individuals in their second winter), and 961 as cygnets (individuals in their first winter) (Table S2). Plumage characteristics, and in particular the relative proportions of grey feathers, were used to determine the age class at capture of each individual (Rees 2006). In all cases, sex was determined by cloacal examination, and from 2005 onwards for birds caught in the Netherlands, verified genetically from blood samples. Genetic sex determination agreed with cloacal examination on between 79 and 95% of occasions depending on the experience of the examiners; in all cases of disagreements we took the sex as determined via genetic analysis to be the definitive sex. Each captured individual was fitted with either a plastic leg-ring (UK 1970–2014: $n = 2386$; Russia 1992–2014: $n = 939$) or neck-collar (Netherlands 1988–2014: $n = 515$; Germany 1989–2003: $n = 89$) that featured a unique alpha-numeric code to allow subsequent identification at distances of up to 300 m and 600 m, respectively (Ogilvie 1972, Rees *et al.* 1990). In all cases, a smaller engraved metal leg-ring (issued by the relevant National Ringing Scheme) was also attached, which allowed subsequent identification of marked individuals in the event that the plastic ring or collar was lost (Rees *et al.* 1990). Recaptured individuals found to have lost their leg-ring or neck-collar were fitted with replacement markers, which was not treated as a new release in our analyses, but rather a continuation of the original release. Whilst these individuals were unavailable for resighting during the temporary period of marker loss, given the small numbers of individuals involved (e.g. 139 out of 3304 individuals marked with leg-rings) and the high resighting rates throughout our study period we do not believe that temporary marker loss had a major effect on our estimates of survival. The inclusion of the birds fitted with leg-rings in Russia with the winter-ringed individuals meant that the initial period during which birds were captured extended from the moult period through to the subsequent winter period. This

increased heterogeneity applied to the first survival period after the initial capture period only, for 939 out of the 3929 individuals (23.9%) and only in 15 of the total 44 years of study, and had the benefit of increasing our sample size. However, to check that the inclusion of these Russian-marked birds had not biased our survival estimates, we compared the estimated survival rates from the best-supported temporal model for datasets in which the Russian-marked birds were both included and excluded. Resightings of marked birds were made by a network of professional and amateur ornithologists across the winter range in northwestern Europe. For all years following the year of capture, we collated resightings of marked birds between October and March across all wintering sites in northwestern Europe between 1971/1972 and 2014/2015 (Table S3); birds that were seen at least once during a winter were determined to have been alive in that winter. Of the 3929 individuals that were captured, marked, and released, a total of 3079 (78.4%) were resighted in at least one subsequent winter.

Environmental covariates

In addition to the sex, age class and marker type of each individual, we also considered the following potential explanatory variables, related to environmental conditions within the flyway, in our analysis of Bewick's Swan survival rates: weather conditions, food resources, and density-dependence. Weather conditions were measured as North Atlantic Oscillation (NAO) index values for the wintering area, as well as the mean temperature and the number of days on which snowfall occurred at breeding, stopover, and wintering sites, covering the periods for which Bewick's Swans were present in these areas (Appendix S1). To account for any effect of changes in winter food availability on survival, we required data on the availability of two key agricultural food resources used within the wintering range; Sugar

Beet *Beta vulgaris* and winter-sown Wheat *Triticum aestivum* (Dirksen *et al.* 1991, Laubek 1995, Rees 2006). Annual estimates of both the total area sown and the absolute yield of harvested Sugar Beet and winter-sown Wheat were therefore obtained for the wintering grounds (taken as the sum of the values for the UK and the Netherlands, the countries where the majority of the population occurred in mid-winter; Rees 2006) from the Food and Agriculture Organization of the United Nations database (Food and Agriculture Organization of the United Nations 2016). The lack of equivalent data for aquatic plant below-ground tissues precluded their inclusion in our analysis. However, even where aquatic food resources are used swans are observed to switch to terrestrial agricultural foods during winter (e.g. Nolet *et al.* 2002), and so agricultural food resources were assumed to represent the major component of the total food resources available on the winter grounds.

To aid our assessment of the effects of density-dependence on apparent survival over our study period (1970/1971–2014/2015), annual estimates of the northwestern European Bewick's Swan population over our study period were derived from the International Swan Census (ISC) surveys conducted in 1958, 1972, 1976, 1978, 1983, 1986, 1990, 1995, 2000, 2005, 2010, and 2015 (Rees & Beekman 2010, Wetlands International/IUCN-SSC Swan Specialist Group unpublished data), with linear interpolation used to yield population estimates for years between surveys (Fig. S1). Peak counts of winter numbers of Bewick's Swans at the Evros Delta were available from annual surveys carried out over our study period (Royal Belgian Institute of Natural Sciences and Evros Delta Management Body, unpublished data, Litvin & Vangeluwe 2016). The annual change in the peak count (E_{Change}) was calculated as:

$$E_{Change} = E_{Count(t)} - E_{Count(t-1)},$$

where $E_{Count(t)}$ and $E_{Count(t-1)}$ represented the peak counts in years t and $t-1$, respectively.

Annual change integrated information on both the absolute number and trend in the swan counts, and so was preferable as an explanatory variable to either raw counts (which did not account for trend) or population growth rate (which did not account for absolute number).

Survival analysis

To estimate apparent survival between successive winters, and the associated resighting probabilities, we carried out a capture-mark-resight analysis in Program R version 3.3.0 (R Development Core Team 2016), using the RMark package version 2.2.0 (Laake 2013), which implemented analyses using Program MARK version 8.0 (White & Burnham 1999).

Following the notation of Lebreton *et al.* (1992), apparent survival and resighting probabilities are denoted as ϕ and p , respectively. Prior to the survival analysis, goodness of fit tests were conducted in U-CARE version 2.3.2 (Choquet *et al.* 2009), to determine the fit of the data to our global Cormack-Jolly-Seber (CJS) model with group effects ($\phi(\text{sex} * \text{age class} * \text{marker type} * \text{time})$, $p(\text{marker type} * \text{time})$). We calculated \hat{c} as the χ^2 value associated with the global goodness-of-fit tests ($\chi^2 = 2882.9$, $P < 0.001$), divided by the total degrees of freedom ($df = 1132$), which yielded a \hat{c} value of 2.5, below the maximum \hat{c} value of 3.0 recommended for reliable survival modelling (Lebreton *et al.* 1992). The directional tests (Tests 2 and 3) provided additional information on goodness-of-fit. The results of Test 2 indicated some evidence of trap-dependence ($\chi^2 = 2418.3$, $P < 0.001$). Detailed inspection of Test 2 results for each group showed evidence of significant (i.e. $P < 0.05$) negative trap-dependence (indicating trap-happiness) among 6 of our 12 groups: adult males withleg-rings, adult females withleg-rings, adult females with neck-collars, yearling males withleg-rings, cygnet males withleg-rings, female cygnets withleg-rings, and male cygnets with neck-

collars. The diversity of age classes, sexes, and marker types within this suite of trap-happy precluded an obvious biological explanation that could account for trap-dependence amongst these groups but not the others. The results of Test 3 suggested some evidence of transience ($\chi^2 = 464.6$, $P = 0.009$). However, a detailed inspection of Test 3 results for each group showed no significant transience (i.e. $P < 0.05$) associated with any group, which prevented the formulation of a biological explanation for transient effects within our study population. Overall, trap-dependence and transience accounted for 83.9% and 16.1% of the lack-of-fit associated with our model, respectively. Despite the statistical significance of the results of Test 2 and Test 3, our \hat{c} value of 2.5 associated with our global goodness-of-fit was lower than the maximum value of 3.0 recommended by Lebreton *et al.* (1992) for reliable parameter estimation in survival analysis. Thus, whilst we found some evidence of deviation from the assumptions of the CJS model associated with trap-dependence and transience, such heterogeneity was within bounds of what can be modelled as overdispersion via \hat{c} in survival models. The apparent lack of a known biological mechanism for either trap happiness or transience precluded modelling these effects directly. Furthermore, attempting to account for both trap-dependence and transience directly in all of our candidate models would have increased the number of parameters that our models were required to estimate. Instead, we accounted for lack-of-fit as overdispersion by using our \hat{c} value of 2.5 to adjust the QAIC_c values of our candidate models. Accounting for relatively minor levels of lack-of-fit has been commonly used in survival analyses, including in recent papers published on long-lived birds (e.g. Guillemain *et al.* 2015).

We carried out our survival modelling as a two stage process in order to quantify, and then explain, the temporal pattern in swan survival. First, we tested models describing different temporal trends in Bewick's Swan apparent survival: (i) time-independence (\cdot), (ii)

full time-dependence (t), (iii) linear effect of time (Y_L), (iv) quadratic effects of time (Y_Q), (v) different survival rate for each decade (Y_D), (vi) different survival rate for each half-decade (Y_H), (vii), one survival rate for the period of population increase up to 1995, and a different survival rate for the period of decrease thereafter (Y_P), and (viii) one survival rate for the period of population increase up to 1995, and different survival rates for each year thereafter (Y_R). Our three group variables (age class, sex, and marker type) were included in all candidate models, with sequential models run to test for additive and interactive effects of each group variable. Resighting probability was modelled as all combinations of marker- and time-dependence. As survival and resighting probabilities are only estimable as a product in full time-dependent models, we excluded the estimates for the final time interval (i.e. survival from winter 2013/2014 and 2014/2015) from our results for full time-dependent models.

In the second stage of the survival modelling process, we ran a suite of covariate models in order to try to explain the temporal pattern in swan survival rates. We tested all additive and two-way interactive combinations of the following time-dependent explanatory covariates: northwest European Bewick's Swan total population size (P_{Europe}), the annual change in the peak count of Bewick's Swans wintering at the Evros Delta in Greece (E_{Change}), mean temperature and days of snowfall on the breeding grounds during the breeding period (T_{Breed} and S_{Breed} , respectively), mean temperature and days of snowfall at the White Sea during spring stopover (T_{WSea} and S_{WSea} , respectively), mean temperature and days of snowfall in Estonia during spring stopover (T_{EstS} and S_{EstS} , respectively), mean temperature and days of snowfall in the Karelia region during autumn stopover (T_{Kar} and S_{Kar} , respectively), mean temperature and days of snowfall in Estonia during autumn stopover (T_{EstA} and S_{EstA} , respectively), mean winter temperature and days of snowfall in the UK (T_{UKWin} and S_{UKWin} , respectively), mean winter temperature in the Netherlands during winter (T_{NWin}), winter NAO

value (NAO), and the area and yield of key food resources on the winter grounds (F_{Area} and F_{Yield} , respectively). Again, our three group variables (age class, sex, and marker type) were included in all candidate models, with sequential models run to test for additive and interactive effects of each group variable. As we had no *a priori* expectations that our environmental covariates, or age-class or sex, had major effects on resighting probabilities, we again tested the effects of all combinations of marker- and time-dependence only on resighting probabilities. For both our models of temporal patterns in survival and our covariate models, we compared the relative support within each set of models using second-order Akaike's information criteria, adjusted for sample size and our \hat{c} value ($QAIC_c$), model weights (w_i), relative likelihood (RL) and evidence ratio (ER) (Burnham *et al.* 2011). In order to avoid selecting candidate models with uninformative parameters (*sensu* Arnold 2010), we considered models with one additional parameter competitive only if the associated $QAIC_c$ values were lower than the more parsimonious model. Furthermore, Richards (2008) cautioned that for overdispersed models only candidate models with $\Delta QAIC_c$ values < 6.0 should be considered competitive. Due to the large numbers of models tested, only the candidate models with $QAIC_c$ weights (w_i) > 0.01 were presented in our results. We used the outputs of our best-supported model to estimate annual values of apparent survival and resighting probability for all groups. As swans were only marked with neck-collars from winter 1988/1989 onwards, we limited our estimates of apparent survival and resighting probability for neck-collar marked birds from winter 1989/1990 onwards. We used Pearson's correlations to test for collinearity among our explanatory covariates, and did not permit collinear (where $r \geq 0.3$; Thomas *et al.* 2013) variables within a candidate survival model (Table S5). Furthermore, although we judged collinearity on the associated r -values, rather than P -values, the P -values were nonetheless adjusted using the Holm-Bonferroni correction for multiple comparisons (Holm 1979). Finally, to calculate the proportion of temporal

variation in apparent survival accounted for by each environmental variable we calculated the proportion of deviance (R^2_{Deviance}) explained by each as:

$$R^2_{\text{Deviance}} = (\text{Deviance}_{(\cdot)} - \text{Deviance}_{(\text{covariate model})}) / (\text{Deviance}_{(\cdot)} - \text{Deviance}_{(t)})$$

where $\text{Deviance}_{(\cdot)}$ is the deviance associated with the time-invariant model, $\text{Deviance}_{(\text{covariate model})}$ is deviance from the covariate model of interest, and $\text{Deviance}_{(t)}$ is the deviance associated with the time-dependent model (Grosbois *et al.* 2008).

RESULTS

Temporal variation in survival and resighting rates

A comparison of candidate models indicated that the temporal pattern in Bewick's Swan apparent survival was best explained by different survival rates for each decade for each group, with additive effects of sex, age class, and marker type; resighting probability was best explained by full time-dependence and an effect of marker type (Table 1). All other candidate models for which $\Delta\text{QAIC}_c \leq 3.0$ were extensions of this best-supported model (i.e. contained these and at least one or more additional parameter). Indeed, models that comprised different survival rates for each decade represented our four best-supported models (Table 1). In contrast, the best-performing time-invariant and full time-dependent models, which were those with additive group effects, had associated ΔQAIC_c values of 12.3 and 42.5 relative to our best-supported model (Table 1).

Our best-supported model indicated that, across all age classes and both sexes, geometric mean apparent survival rates increased slightly from the 1970s (leg ring = 0.845, 95% confidence interval = 0.820 – 0.867) to the 1980s (leg ring = 0.853, CI = 0.830 – 0.873), before declining marginally in the 1990s (leg ring = 0.830, CI = 0.806 – 0.852; neck-collar =

0.790, CI = 0.758 – 0.819). Estimated survival rates then rose subsequently in the 2000s (leg ring = 0.840, CI = 0.815 – 0.861; neck-collar = 0.801, CI = 0.769 – 0.830), before declining more sharply to their lowest in the 2010s (leg ring = 0.773, CI = 0.738 – 0.805; neck-collar = 0.725, CI = 0.681 – 0.764) (Fig. 2 & 3). Hence, over our study period, apparent survival rates were highest in the 1980s and lowest in the 2010s. Annual estimates of apparent survival from the full time-dependent model indicated that the major decrease in survival between the 2000s and 2010s began after the 2008/09 winter (Fig. 2 & 3). The removal of the individuals marked in Russia had little effect on survival estimates or their confidence intervals; over all five decades the mean \pm SD difference in apparent survival between estimates including and excluding Russian-marked birds was 0.010 ± 0.006 , with a range of 0.004–0.019. Furthermore, the temporal pattern in estimated survival remained the same regardless of the exclusion of these 939 individuals (Appendix S2).

For all age classes and marker types, females had higher apparent survival compared with males; however, the between-sex difference in survival rates was just 0.001 for all comparisons (Fig. 2 & 3). Furthermore, for both sexes and marker types, adults and yearlings both had apparent survival rates that were 0.046 and 0.051 higher, respectively, than cygnets (Fig. 2 & 3). Finally, across all age classes and sexes, birds marked with leg-rings were predicted to have apparent survival that was a geometric mean of 0.04 higher (i.e. 4.0% greater) than individuals marked with neck-collars (Fig. 2 & 3).

Our best-supported model indicated that resighting probabilities for leg-ringed birds ranged from 0.454 to 0.857 over years 1971–2014, with a geometric mean \pm CI of 0.700 ± 0.023 (Fig. 4). Over the period in which both types of marker were fitted to swans (i.e. over

years 1989–2014) resighting probabilities for leg-ringed birds ranged from 0.620 to 0.857, with a geometric mean \pm CI of 0.728 ± 0.021 , whilst for neck-collared birds the resighting probability ranged from 0.861 to 0.958, with a geometric mean \pm CI of 0.910 ± 0.008 (Fig. 4). Finally, the probability of resighting an individual across all subsequent winters showed only relatively small differences between the three main capture regions, consistent with the difference in annual resighting rates for leg-ring and neck-collar marked birds (Appendix S2).

Temporal variation in survival rates

We detected collinearity (i.e. where $r \geq 0.3$) in 43 of the 171 combinations of the explanatory covariates tested (Table S5). In particular, mean temperatures at the breeding grounds and at all stopover sites were positively correlated with year. Additionally, the number of days of snowfall in Karelia in autumn, and Estonia in spring, showed negative correlations with year. However, we found no evidence of correlations between year and either the mean temperature or number of days of snowfall on the winter grounds, nor with winter NAO value (Table S5). As expected, the mean temperature and number of days of snowfall at each particular site were highly significantly correlated negatively with each other (Table S5). Similarly, the mean winter temperature and mean number of winter days of snowfall in the UK showed highly significant positive and negative correlations, respectively, with the mean winter temperature in the Netherlands (Table S5). Finally, winter NAO values were positively correlated with the mean winter temperatures in the UK and the Netherlands, and negatively correlated with the mean number of winter days of snowfall in the UK (Table S5).

A comparison of all candidate models indicated limited support in the data for effects of any of the 18 covariates tested (Table 2). The covariate model with the lowest QAIC_c value was comprised of the mean temperature in Estonia during the spring migration period, the mean temperature in the White Sea region during autumn migration, and the mean number of days of snowfall in the UK during the winter period, along with the effects of marker type, sex and age class (Table 2). A model comprised of the mean temperature in the White Sea region during autumn migration and winter crop yield, together with the effects of marker type, sex and age class, had an associated Δ QAIC_c value of 1.2 (Table 2). However, we argue that because no covariate models had an associated Δ QAIC_c value of 6.0 lower than our null model, no covariate model can be considered to have received greater support than the null model. In our view this suggests limited support for an effect of any covariate on survival rates. The poor explanatory performance of our range of covariates is further evidenced by the fraction of temporal variation in survival accounted for by the environmental variables. A mean of 2.2% of model deviance was explained by our covariates, with no covariate explaining more than the 7.2% of deviance explained by the mean temperature in Estonia during the spring migration period (Table 3). Across all best performing candidate models, resighting probability was once again best explained by full time-dependence and marker type (Table 2).

DISCUSSION

We present the first estimates of survival rates for the northwestern European population of Bewick's Swans, a population that has been declining in size since 1995 and was recently classified as Endangered on the European Red List of bird species (BirdLife International 2015). We quantified the temporal pattern in survival rates over 44 years and tested a range

of variables known to influence survival in long-lived migratory waterbirds. Our findings highlight a recent, but currently unexplained, reduction in the survival of a declining population of this species.

We found some support in our data for temporal variation in Bewick's Swans' apparent survival in line with the observed population trend, our first prediction. Apparent survival was found to increase slightly from the 1970s to 1980s, concurrent with the observed rising population size. Whilst the effect size was small, the growth rate of swan populations is known to be highly sensitive to small changes in survival rates (e.g. Wood *et al.* 2013). Similarly, this sensitivity means that the small decrease in survival between the 1980s and 1990s could have been sufficient to precipitate the decline in population size observed after 1995. However, survival rates subsequently showed a small increase between the 1990s and 2000s, during which time the numbers on the winter grounds of northwest Europe were continuing to fall (Rees & Beekman 2010). Indeed, only between the 2000s and 2010s was a sharper drop in survival rates detected, which the full time-dependent model suggested was from winter 2008/2009 onwards. Hence, the most substantial temporal decrease in survival found in our study occurred much later than the onset of the decline in population size which occurred after 1995. We detected no decrease in resighting probability in the 2010s; indeed, our continued high resighting rates suggested that the decrease in survival was not an artefact of recently-marked swans remaining unseen. Our findings indicated that a reduction in survival from 2008/2009 onwards had occurred for all age classes and sexes, with little evidence of age- or sex-specific effects. Hence, the factors responsible for reduced survival are likely to be pressures that act on all parts of the swan population; however, this cannot be confirmed until the drivers of reduced survival have been identified.

The documented temporal decline in survival was not well explained by environmental conditions within the northwest European flyway; thus our findings offered little support for our second prediction. Despite evidence of rising mean air temperatures and reduced snowfall at the Bewick's Swans' breeding grounds, winter grounds, and migratory stopover sites, we found little support in our survival models for any influence of weather conditions, or directional climatic change, on the observed temporal changes in survival rates. In contrast, an earlier study by Andersen-Harild (1981) reported that survival rates in adult Mute Swans *Cygnus olor* in Denmark showed considerable annual fluctuations linked with the severity of the winter. Bewick's Swans are known to move to suitable habitat further southwest during incidences of very cold winter weather (Rees 2006), which may mean that the Bewick's Swan population is less at risk of the effects of harsh winter weather compared with the more sedentary, non-migratory Mute Swan populations of northwestern Europe. The poor explanatory power of our environmental variables could reflect our finding that survival was relatively constant within decades (i.e. our best-supported model indicated constant survival in each decade), and hence survival did not show high degrees of inter-annual variation. However, because we used fixed time intervals within a year to estimate the magnitude of our weather covariates each year, it is also possible that there was a degree of mismatch between the periods of our covariates and the periods of site use by the swans, as the latter will vary between years (Johnston *et al.* 2016). Moreover, there are many possible weather variables that could be tested as environmental covariates in survival models, which are frequently correlated with each other (Catchpole *et al.* 1999). For example, the number of days below freezing may explain overwinter survival better than averaged winter temperature for some species of waders (e.g. North & Morgan 1979). Fitting alternative covariates therefore could yield a modest improvement in model fit, but given the poor explanatory performance of our environmental covariates we consider it unlikely that any correlated

alternative variables would have resulted in anything other than a marginal difference to our findings. Whilst it is never possible to include all possible environmental covariates of interest, and future analyses may throw further light on the extent to which environmental change has influenced Bewick's Swan survival rates, we believe that our current focus on weather conditions and food resources is justified given the concerns regarding these variables expressed in the BSSAP (Nagy *et al.* 2012).

Although we found that both the area and yield of key food resources on the winter grounds had increased over time due to the intensification of agriculture in northwest Europe, such increases have not resulted in improved survival rates. Furthermore, the lack of support for the effect on survival of an interaction between either food area or yield and total population size offered no evidence of a *per capita* effect of food abundance on Bewick's Swan survival rates. The lack of an effect of winter food resources on survival rates may reflect the widespread availability of food plants of high nutritional quality within agricultural landscapes (Dirksen *et al.* 1991, van Eerden *et al.* 1996), coupled with the fact that Bewick's Swans are generalist herbivores that feed on a wide range of terrestrial and aquatic vegetation (Rees 2006). Future studies of swan foraging behaviour and energetics could be undertaken to confirm that terrestrial and aquatic food supplies at key winter and stopover sites are adequate to allow body mass and condition to be maintained at optimal levels. Previous research has reported that food supplies can be depleted by swans during stopover periods (Nolet & Drent 1998), but to date the link between food supplies and survival rates has been difficult to quantify due to a lack of long-term information on food abundance (e.g. aquatic plant below-ground tissues) and swan densities in such areas.

Our study offered little support for our third prediction of an association between the decline in the apparent survival of the northwest European population and the rise in numbers of Bewick's Swans wintering on the Aegean and Black Sea coasts. The Evros Delta in Greece is viewed as the most important of these new sites in terms of the numbers supported, which have risen from typically zero during the mid-1990s to over 8000 individuals in 2015/2016 (Royal Belgian Institute of Natural Sciences and Evros Delta Management Body, unpublished data, Litvin & Vangeluwe 2016). Given these relative changes in the numbers of Bewick's Swans, future work to determine the origin of these individuals is ongoing to improve our understanding of Bewick's Swan population dynamics across flyways. Recent increases in mark-resighting effort and individual-tracking studies across the northwest European, Caspian, and East Asian flyways will improve our understanding of the degree to which individuals move between wintering areas, and allow the levels of interchange between the three populations to be quantified. Genetic studies could help to resolve the origins of the growing numbers of wintering swans on the Aegean and Black Sea coasts (e.g. Jonker *et al.* 2013).

Our suite of 18 explanatory variables accounted for little of the observed inter-annual variation in apparent survival. Therefore, additional explanatory covariates must have influenced the temporal variation, and in particular the recent decline, in Bewick's Swan survival over our study period. The presence of embedded ammunition within 31% of Bewick's Swans x-rayed on the winter grounds in Britain between the winters of 1970/71 and 2008/09, despite full legal protection across the flyway, suggests that illegal shooting is likely to have an impact on Bewick's Swan survival (Newth *et al.* 2011). Similarly, Newth *et al.* (2013) found that 23% of Bewick's Swans found dead while wintering in Britain between 1971 and 2012 had died of lead poisoning. A recent study by Green and Pain (2016) found a

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correlation between duck population trends and relative ingestion of lead, suggesting that lead poisoning can have population-level impacts on waterbirds. Whilst we lacked the time-series data on illegal shooting and exposure to lead ammunition that would have been required to test the effects of illegal shooting and lead poisoning, we suggest that these two factors appear worthy of further study in light of the recent decline in survival rates. In particular, further research which identified the temporal pattern in the incidences of illegal shooting and lead poisoning, and their potential role in Bewick's Swan demography, might be useful in helping to understand the observed fluctuations in survival and population size.

Our models suggested that apparent survival rates were higher for birds marked with leg-rings compared with neck-collars. However, any such effect must be interpreted with caution given that marker type and winter sites were confounded in our analysis, with leg-rings used in the UK and Russia and neck-collars used in the Netherlands and Germany. Previous studies have reported lower apparent survival estimates for birds marked with neck-collars compared with leg-rings across a range of avian species (e.g. Schmutz & Morse 2000, Alisauskas & Lindberg 2002). Three key explanations have been offered by researchers to account for reduced apparent survival of birds marked with neck-collars: ice formation on neck-collars (Zicus *et al.* 1983), reduced foraging efficiency and energy gain (Schmutz & Morse 2000), and preferential selection of neck-collar marked individuals by hunters (Caswell *et al.* 2012). Inequalities in apparent survival rates between different marker types could also be artefacts of heterogeneous rates of marker loss among birds marked with different marker types, for example if the rates of marker loss were greater for neck-collars compared with leg-rings. Unfortunately, estimates of marker loss were not available for both leg-rings and neck-collars across our 44-year study period, and so it was not possible to account for marker loss within our analysis or compare rates of ring loss between marker

types. Yet long-lived birds such as swans are known to damage and lose markers; indeed, an earlier study of 1569 Bewick's Swans marked with leg-rings found that after a period of two years that rings needed to be replaced for 6.0% of females and 14.7% of males, due to damaged, broken, or lost leg-rings (Rees *et al.* 1990). As these rates include not only lost rings, but also worn or damaged rings that were removed on recapture (and which otherwise would have remained on the individual), we could not use these data to estimate the true rate at which individuals lost their markers during our study. Furthermore, no estimates of marker loss were available for Bewick's Swans marked with neck-collars. However, it is clear from the earlier leg-ring data that some loss of markers occurs in our study population. Accordingly the survival estimates presented here should be considered as minimum values that may underestimate true survival. Apparent differences in survival between individuals fitted with different markers could reflect wintering location if some winter sites are associated with higher mortality than others. Hence, more detailed assessment of the survival of individual swans using different wintering regions and habitats types is warranted in future analyses. Ultimately, whether lower survival rates of neck-collar marked Bewick's Swans reflects higher mortality of birds marked with neck-collars, higher rates of marker loss, an effect of winter site, or a combination of these, requires further detailed investigation via controlled comparisons. Compared with marker type, our other two grouping variables (age class and sex) had smaller effects on Bewick's Swan apparent survival rates.

Our study has quantified the long-term trend in Bewick's Swan survival rates over periods of both population increase and subsequent decline. The estimates of survival derived here can be used in future research to understand the causes of the decline in Bewick's Swan population size and inform conservation efforts. In particular, such temporally-explicit survival rates are a prerequisite for the construction of demographic population models and

retrospective population perturbation analyses, which retrodict the effects of changes in demographic rates on population size and structure (Caswell 2000, Cooch *et al.* 2001).

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Supporting information

Additional Supporting Information may be found in the online version of this article:

Supporting Information Table S1: The locations of the capture sites used during the Bewick's Swan marking programme between winters 1970/71 and 2014/15.

Supporting Information Table S2: A summary of the numbers of individuals of each age class caught, marked, and released in each year of our study.

Supporting Information Table S3: A summary of the total numbers of resightings made each winter in northwest Europe.

Supporting Information Appendix S1: Information on the extraction of weather condition covariates used in our analysis.

Supporting Information Figure S1: The northwest European Bewick's Swan population size, showing the linear interpolation used to derive population estimates in non-survey years.

Supporting Information S5: A summary of the results of the Pearson's Correlation tests for collinearity between our potential explanatory variables.

Supporting Information Appendix S2: A comparison of the estimated survival and resighting rates for datasets in which Russian-marked birds were included and excluded.

Tables

Table 1: The relative support associated with our best-supported models of the temporal variation in Bewick's Swan's apparent survival (ϕ) and resighting probability (p), as well as time-invariant and full time-dependent models. Only the candidate models with QAIC_c weights (w_i) > 0.01 are presented here. The best-supported model is indicated in bold. k refers to the number of fitted parameters within the candidate model, whilst RL and ER refer to the relative likelihood and evidence ratio of candidate models. Variables Y_D and Y_H refer to different survival rates for each decade and half-decade, respectively, Y_L and Y_Q refer to linear and quadratic trends over time, respectively, whilst Y_P represents one survival rate for the period of population increase up to 1995, and a different survival rate for the period of decrease thereafter.

Candidate model	k	QAIC _c	Δ QAIC _c	RL	w_i	ER	QDeviance
$\phi(\sim Y_D + \text{marker} + \text{sex} + \text{ageclass}), p(\sim \text{marker} + \text{time})$	54	14115.15	0.00	1.00	0.33	1.00	6889.74
$\phi(\sim Y_D + \text{marker} * \text{sex} + \text{ageclass}), p(\sim \text{marker} + \text{time})$	55	14116.41	1.27	0.53	0.17	1.88	6889.00
$\phi(\sim Y_D + \text{marker} * \text{ageclass} + \text{sex}), p(\sim \text{marker} + \text{time})$	56	14117.01	1.86	0.39	0.13	2.54	6887.58
$\phi(\sim Y_D + \text{marker} + \text{sex} * \text{ageclass}), p(\sim \text{marker} + \text{time})$	56	14118.37	3.22	0.20	0.07	5.01	6888.94
$\phi(\sim Y_L + \text{marker} + \text{sex} + \text{ageclass}), p(\sim \text{marker} + \text{time})$	51	14118.41	3.26	0.20	0.06	5.10	6899.04
$\phi(\sim Y_L + \text{marker} * \text{sex} + \text{ageclass}), p(\sim \text{marker} + \text{time})$	52	14119.63	4.49	0.11	0.03	9.42	6898.25
$\phi(\sim Y_L * \text{marker} + \text{sex} + \text{ageclass}), p(\sim \text{marker} + \text{time})$	52	14119.93	4.78	0.09	0.03	10.92	6898.55
$\phi(\sim (Y_L + Y_Q) + \text{marker} + \text{sex} + \text{ageclass}), p(\sim \text{marker} + \text{time})$	52	14120.04	4.89	0.09	0.03	11.54	6898.66
$\phi(\sim Y_L + \text{marker} * \text{ageclass} + \text{sex}), p(\sim \text{marker} + \text{time})$	53	14120.70	5.56	0.06	0.02	16.08	6897.31
$\phi(\sim Y_D * \text{marker} + \text{sex} + \text{ageclass}), p(\sim \text{marker} + \text{time})$	58	14121.26	6.11	0.05	0.02	21.22	6887.80
$\phi(\sim (Y_L + Y_Q) + \text{marker} * \text{sex} + \text{ageclass}), p(\sim \text{marker} + \text{time})$	53	14121.26	6.11	0.05	0.02	21.24	6897.87
$\phi(\sim Y_H + \text{marker} + \text{sex} + \text{ageclass}), p(\sim \text{marker} + \text{time})$	58	14121.46	6.31	0.04	0.01	23.46	6888.00
$\phi(\sim Y_L + \text{marker} + \text{sex} * \text{ageclass}), p(\sim \text{marker} + \text{time})$	53	14121.62	6.48	0.04	0.01	25.48	6898.23
$\phi(\sim (Y_L + Y_Q) + \text{marker} * \text{ageclass} + \text{sex}), p(\sim \text{marker} + \text{time})$	54	14122.32	7.18	0.03	0.01	36.15	6896.92
$\phi(\sim Y_D * \text{sex} + \text{ageclass} + \text{marker}), p(\sim \text{marker} + \text{time})$	58	14122.37	7.23	0.03	0.01	37.11	6888.92
$\phi(\sim Y_P + \text{marker} + \text{sex} + \text{ageclass}), p(\sim \text{marker} + \text{time})$	58	14122.37	7.23	0.03	0.01	37.11	6888.92
$\phi(\sim Y_H + \text{marker} * \text{sex} + \text{ageclass}), p(\sim \text{marker} + \text{time})$	51	14122.70	7.55	0.02	0.01	43.68	6903.33
$\phi(\sim (Y_L + Y_Q) + \text{marker} + \text{sex} * \text{ageclass}), p(\sim \text{marker} + \text{time})$	59	14122.72	7.58	0.02	0.01	44.15	6887.25
$\phi(\sim \text{marker} + \text{sex} + \text{ageclass}), p(\sim \text{marker} + \text{time})$	50	14127.48	12.33	0.00	0.00	475.92	6910.12
$\phi(\sim \text{marker} + \text{sex} + \text{ageclass} + \text{time}), p(\sim \text{marker} + \text{time})$	93	14157.64	42.49	0.00	0.00	1.68*10 ⁹	6853.56

Table 2: The relative support associated with our best-supported (QAIC_c weights $w_i > 0.01$) explanatory covariate models of Bewick’s Swan apparent survival (ϕ) and resighting probability (p). All models where QAIC_c weights $w_i < 0.01$ are not shown. The best-supported model is indicated in bold. k refers to the number of fitted parameters within the candidate model, whilst RL and ER refer to the relative likelihood and evidence ratio of candidate models. Covariates: the annual change in the peak count of Bewick’s Swans wintering at the Evros Delta in Greece (E_{Change}), days of snowfall on the breeding grounds during the breeding period (S_{Breed}), mean temperature and days of snowfall at the White Sea during spring stopover (T_{WSea} and S_{WSea}), mean temperature and days of snowfall in Estonia during spring stopover (T_{EstS} and S_{EstS} , respectively), mean winter temperature and days of snowfall in the UK (T_{UKWin} and S_{UKWin} , respectively), mean winter temperature in the Netherlands during winter (T_{NWin}), winter NAO value (NAO), and the area and yield of key food resources on the winter grounds (F_{Yield}).

Candidate model	k	QAIC _c	Δ QAIC _c	RL	w_i	ER	QDeviance
$\phi(\sim T_{EstS} + T_{WSea} + S_{UKWin} + \text{marker} + \text{sex} + \text{ageclass}), p(\sim \text{marker} + \text{time})$	53	14124.88	0.00	1.00	0.04	1.00	6901.49
$\phi(\sim T_{EstS} + T_{WSea} + \text{marker} + \text{sex} + \text{ageclass}), p(\sim \text{marker} + \text{time})$	52	14125.09	0.21	0.90	0.03	1.11	6903.71
$\phi(\sim T_{EstS} + \text{marker} + \text{sex} + \text{ageclass}), p(\sim \text{marker} + \text{time})$	51	14125.40	0.52	0.77	0.03	1.29	6906.03
$\phi(\sim T_{EstS} + T_{WSea} + T_{UKWin} + \text{marker} + \text{sex} + \text{ageclass}), p(\sim \text{marker} + \text{time})$	53	14125.98	1.10	0.58	0.02	1.74	6902.59
$\phi(\sim T_{EstS} + T_{WSea} + S_{UKWin} + \text{marker} * \text{sex} + \text{ageclass}), p(\sim \text{marker} + \text{time})$	54	14126.08	1.20	0.55	0.02	1.82	6900.67
$\phi(\sim T_{WSea} + F_{Yield} + \text{marker} + \text{sex} + \text{ageclass}), p(\sim \text{marker} + \text{time})$	52	14126.09	1.21	0.55	0.02	1.83	6904.72
$\phi(\sim T_{EstS} + T_{WSea} + NAO + \text{marker} + \text{sex} + \text{ageclass}), p(\sim \text{marker} + \text{time})$	53	14126.14	1.26	0.53	0.02	1.88	6902.75
$\phi(\sim T_{EstS} + T_{WSea} + \text{marker} * \text{sex} + \text{ageclass}), p(\sim \text{marker} + \text{time})$	53	14126.25	1.37	0.50	0.02	1.99	6902.86
$\phi(\sim T_{EstS} + \text{marker} * \text{sex} + \text{ageclass}), p(\sim \text{marker} + \text{time})$	52	14126.52	1.64	0.44	0.02	2.27	6905.14
$\phi(\sim F_{Yield} + \text{marker} + \text{sex} + \text{ageclass}), p(\sim \text{marker} + \text{time})$	51	14126.59	1.71	0.42	0.02	2.36	6907.23
$\phi(\sim T_{WSea} + \text{marker} + \text{sex} + \text{ageclass}), p(\sim \text{marker} + \text{time})$	51	14126.62	1.74	0.42	0.02	2.39	6907.25
$\phi(\sim S_{EstS} + T_{WSea} + \text{marker} + \text{sex} + \text{ageclass}), p(\sim \text{marker} + \text{time})$	52	14126.66	1.78	0.41	0.02	2.43	6905.28
$\phi(\sim NAO + F_{Yield} + \text{marker} + \text{sex} + \text{ageclass}), p(\sim \text{marker} + \text{time})$	52	14126.76	1.87	0.39	0.01	2.55	6905.38
$\phi(\sim T_{EstS} + T_{WSea} + S_{UKWin} + E_{Change} + \text{marker} + \text{sex} + \text{ageclass}), p(\sim \text{marker} + \text{time})$	54	14126.85	1.97	0.37	0.01	2.68	6901.45
$\phi(\sim S_{EstS} + \text{marker} + \text{sex} + \text{ageclass}), p(\sim \text{marker} + \text{time})$	51	14126.86	1.98	0.37	0.01	2.70	6907.50

$\phi(\sim T_{EstS}+T_{WSea}+T_{NWIn}+\text{marker}+\text{sex}+\text{ageclass}),p(\sim \text{marker}+\text{time})$	53	14127.05	2.17	0.34	0.01	2.95	6903.66
$\phi(\sim T_{EstS}+T_{WSea}+T_{UKWin}+\text{marker}*\text{sex}+\text{ageclass}),p(\sim \text{marker}+\text{time})$	54	14127.17	2.29	0.32	0.01	3.14	6901.76
$\phi(\sim T_{EstS}+T_{WSea}+S_{UKWin}+\text{marker}*\text{ageclass}+\text{sex}),p(\sim \text{marker}+\text{time})$	55	14127.17	2.29	0.32	0.01	3.15	6899.76
$\phi(\sim T_{EstS}+S_{WSea}+\text{marker}+\text{sex}+\text{ageclass}),p(\sim \text{marker}+\text{time})$	52	14127.25	2.37	0.31	0.01	3.26	6905.87
$\phi(\sim T_{UKWin}+F_{Yield}+\text{marker}+\text{sex}+\text{ageclass}),p(\sim \text{marker}+\text{time})$	52	14127.28	2.40	0.30	0.01	3.32	6905.90
$\phi(\sim T_{EstS}+T_{WSea}+NAO+\text{marker}*\text{sex}+\text{ageclass}),p(\sim \text{marker}+\text{time})$	54	14127.32	2.44	0.30	0.01	3.38	6901.91
$\phi(\sim T_{EstS}+T_{WSea}+\text{marker}*\text{ageclass}+\text{sex}),p(\sim \text{marker}+\text{time})$	54	14127.33	2.44	0.29	0.01	3.40	6901.92
$\phi(\sim S_{UKWin}+\text{marker}+\text{sex}+\text{ageclass}),p(\sim \text{marker}+\text{time})$	51	14127.36	2.48	0.29	0.01	3.46	6908.00
$\phi(\sim \text{marker}+\text{ageclass}+\text{sex}),p(\sim \text{marker}+\text{time})$	50	14127.48	2.60	0.27	0.01	3.66	6910.12
$\phi(\sim T_{EstS}+\text{marker}*\text{ageclass}+\text{sex}),p(\sim \text{marker}+\text{time})$	53	14127.48	2.60	0.27	0.01	3.66	6904.09
$\phi(\sim S_{EstS}+S_{Breed}+\text{marker}+\text{sex}+\text{ageclass}),p(\sim \text{marker}+\text{time})$	52	14127.58	2.70	0.26	0.01	3.86	6906.20

Table 3: The percentage of the temporal variation in Bewick’s Swan apparent survival accounted for by each of our explanatory covariates, based on model deviances. Covariates: northwest European Bewick’s Swan total population size (P_{Europe}), the annual change in the peak count of Bewick’s Swans wintering at the Evros Delta in Greece (E_{Change}), mean temperature and days of snowfall on the breeding grounds during the breeding period (T_{Breed} and S_{Breed} , respectively), mean temperature and days of snowfall at the White Sea during spring stopover (T_{WSea} and S_{WSea} , respectively), mean temperature and days of snowfall in Estonia during spring stopover (T_{EstS} and S_{EstS} , respectively), mean temperature and days of snowfall in the Karelia region during autumn stopover (T_{Kar} and S_{Kar} , respectively), mean temperature and days of snowfall in Estonia during autumn stopover (T_{EstA} and S_{EstA} , respectively), mean winter temperature and days of snowfall in the UK (T_{UKWin} and S_{UKWin} , respectively), mean winter temperature in the Netherlands during winter (T_{NWin}), winter NAO value (NAO), and the area and yield of key food resources on the winter grounds (F_{Area} and F_{Yield} , respectively).

Covariate	Deviance	R^2 Deviance (%)
$T_{EstoniaSpring}$	6906.03	7.2
$T_{WhiteSea}$	6907.25	5.1
F_{Yield}	6907.23	5.1
$S_{EstoniaSpring}$	6907.50	4.6
$S_{UKWinter}$	6908.00	3.8
$T_{Breeding}$	6908.34	3.1
NAO	6908.46	2.9
P_{Europe}	6908.97	2.0
$T_{UKWinter}$	6909.08	1.8
$T_{EstoniaAutumn}$	6909.46	1.2
F_{Area}	6909.43	1.2
$T_{KareliaAutumn}$	6909.88	0.4
$S_{Breeding}$	6909.96	0.3
$S_{KareliaAutumn}$	6909.93	0.3
$EVROS_{Change}$	6909.94	0.3
$S_{EstoniaAutumn}$	6910.06	0.1
$S_{WhiteSea}$	6910.12	0.0
T_{NWin}	6910.10	0.0
Time-invariant model	6910.12	-
Time-dependent model	6853.56	-

Figures

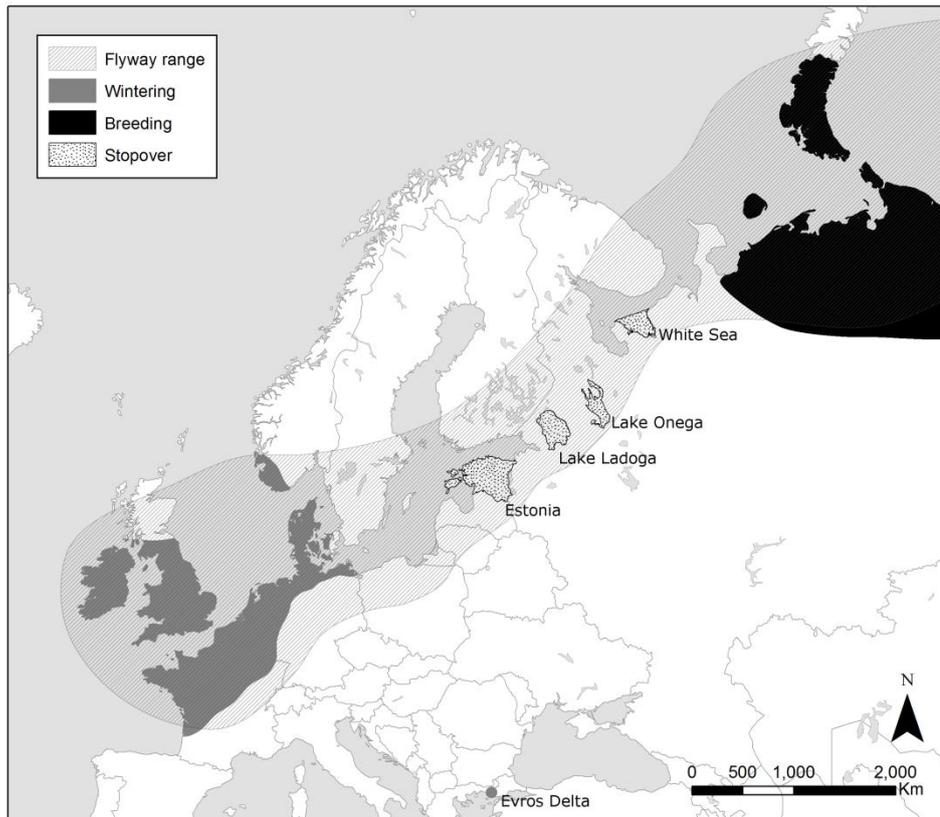


Figure 1: The flyway of the northwest European population of Bewick's Swans, showing the extent of the wintering and breeding grounds over our study period (1970/71–2014/15), as well as the key stopover sites used during migration, based on the information presented in Rees (2006). The key stopover areas are Estonia, the Karelia region (which includes Lakes Ladoga, Onega, and the surrounding area), and the Dvina Bay region of the White Sea. The location of the Evros Delta wintering area in Greece is also indicated.

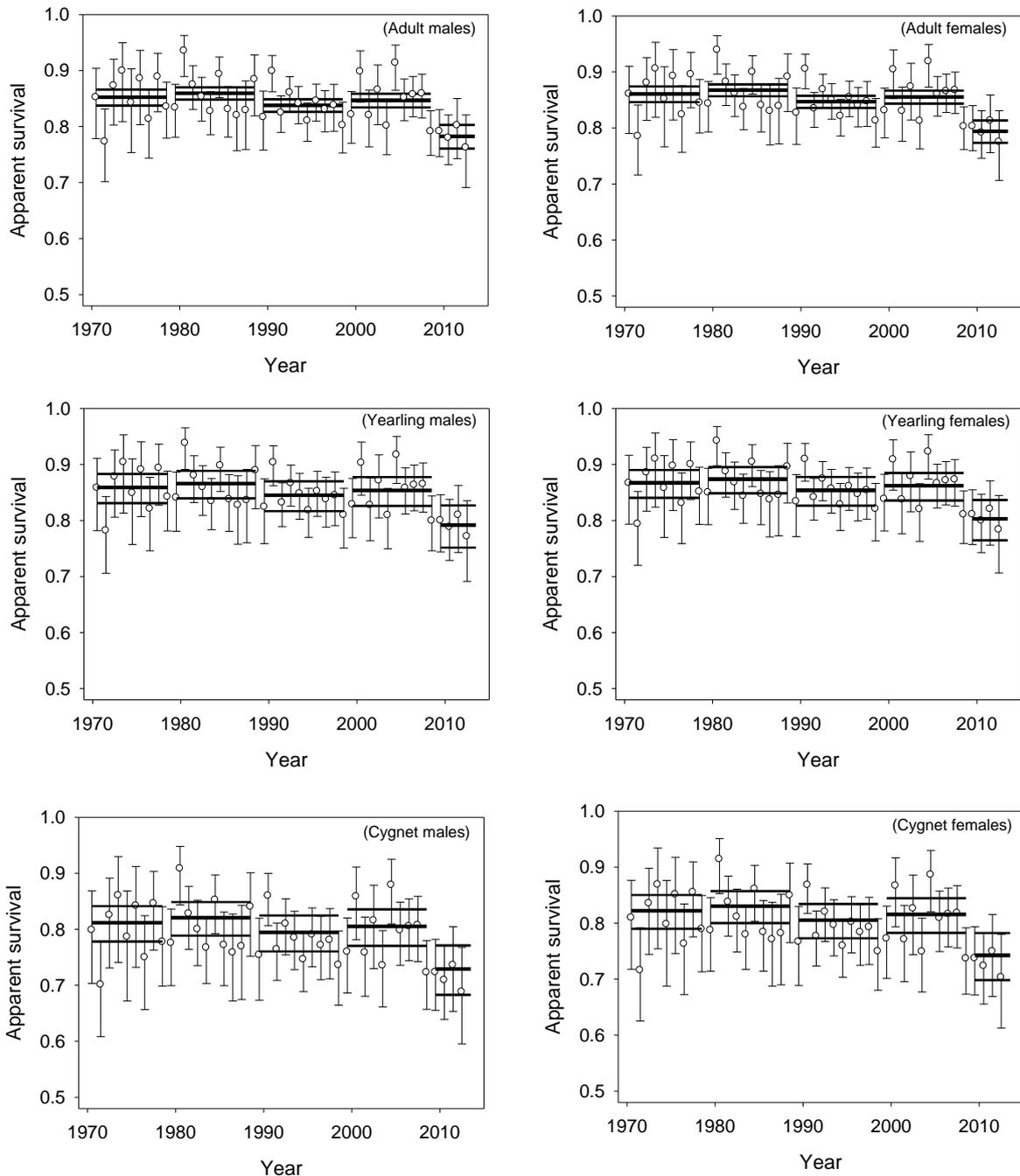


Figure 2: The mean (\pm 95% CI) annual apparent survival probabilities of Bewick's Swan males and females of each age class, for individuals marked with leg-rings, based on the estimates of our best-supported temporal model (solid lines). The mean (\pm 95% CI) estimates of the full time-dependent model (open circles), are presented for comparison (with the exception of the estimate for the final year, which is not shown as only the product of the final survival and resighting rates can be estimated for a full time-dependent model).

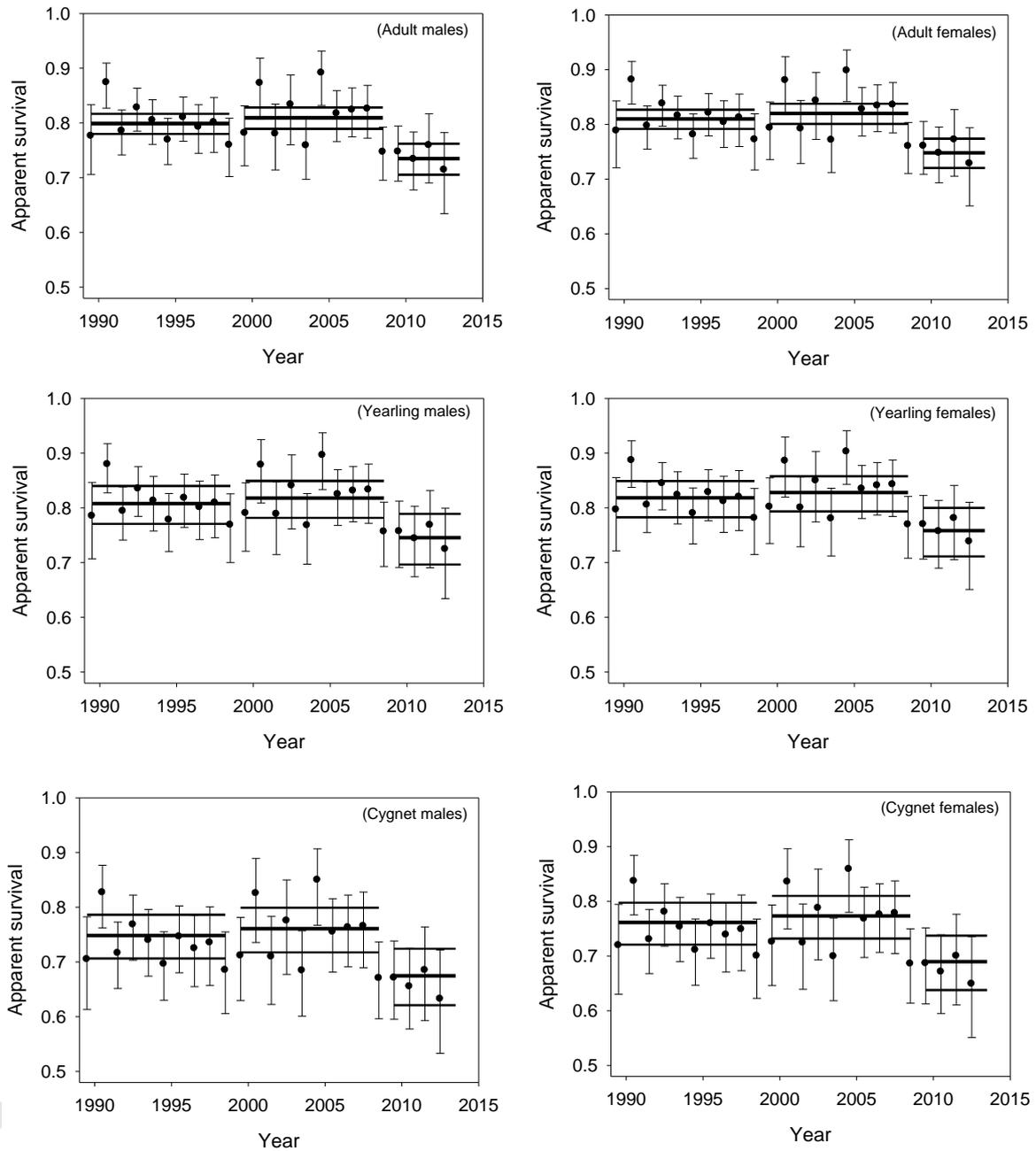


Figure 3: The mean (\pm 95% CI) annual apparent survival probabilities of Bewick's Swan males and females of each age class, for individuals marked with neck-collars, based on the estimates of our best-supported temporal model (solid lines). The mean (\pm 95% CI) estimates of the full time-dependent model (solid circles), are presented for comparison (with the exception of the estimate for the final year, which is not shown as only the product of the final survival and resighting rates can be estimated for a full time-dependent model).

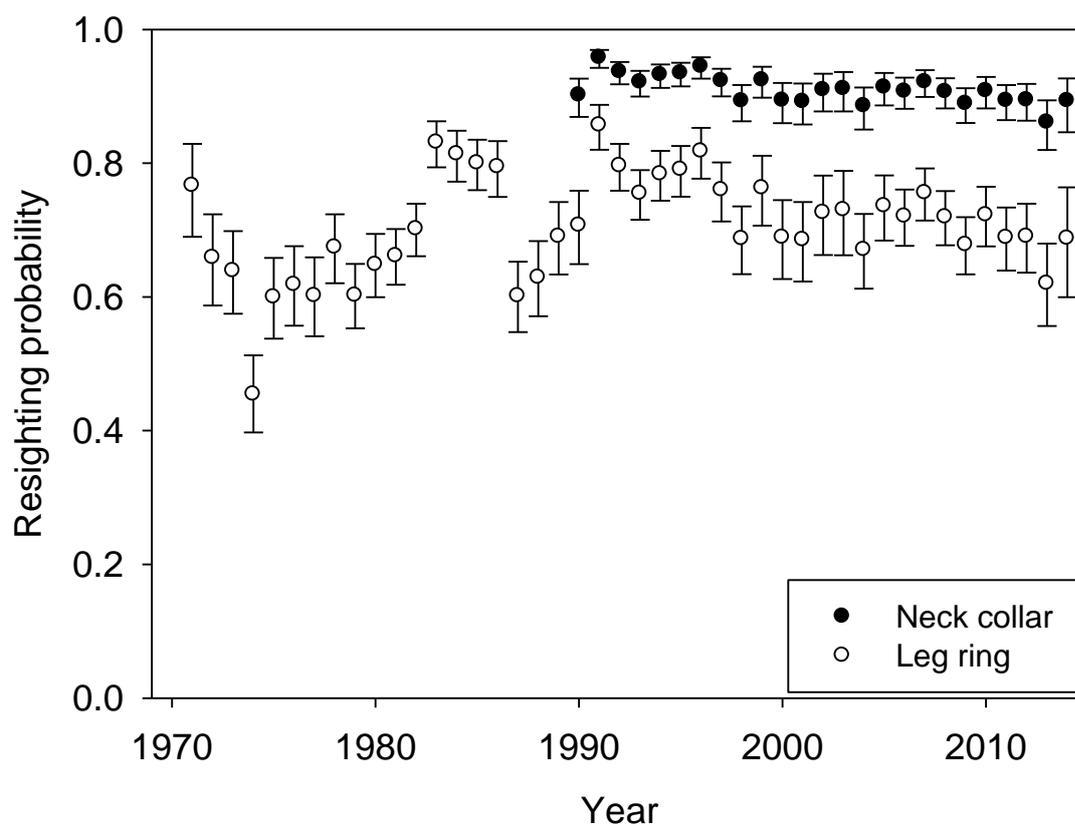


Figure 4: The mean (\pm 95% CI) annual resighting probabilities for individuals marked with neck-collars (solid circles) and leg-rings (open circles).