Seeking explanations for recent changes in abundance of wintering Eurasian Wigeon (*Anas penelope*) in northwest Europe

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We analysed annual changes in abundance of Eurasian Wigeon (*Anas penelope*) derived from mid-winter International Waterbird Census data throughout its northwest European flyway since 1988 using log-linear Poisson regression modelling. Increases in abundance in the north and east of the wintering range (Norway, Sweden, Denmark, Germany, Switzerland), stable numbers in the central range (Belgium, Netherlands, UK and France) and declining abundance in the west and south of the wintering range (Spain and Ireland) suggest a shift in wintering distribution consistent with milder winters throughout the range. However, because over 75% of the population of over 1 million individuals winters in Belgium, the Netherlands, UK and France, there was no evidence for a major movement in the centre of gravity of the wintering distribution. Between-winter changes in overall flyway abundance were highly significantly positively correlated ($P = 0.003$) with reproductive success measured by age ratios in Danish hunter wing surveys and less strongly and inversely correlated ($P = 0.05$) with mean January temperatures in the centre of the wintering range, suggesting that winter severity may also contribute to influence survival. However, adding winter severity to a model predicting population size based on annual reproductive success alone did not contribute to more effectively modelling the observed changes in population size. Patterns in annual reproductive success seem therefore to largely explain the recent dynamics in population size of northwest European Wigeon. Summer NAO significantly and positively explained 27% of variance in annual breeding success. Other local factors such as eutrophication of breeding sites and changes in predation pressure undoubtedly contribute to changes in the annual production of young and differences in hunting pressure as well as winter severity affect annual survival rates. However, it seems likely that the observed flyway population trend since 1988 has been mostly influenced by climate effects on the breeding grounds affecting reproductive success and marginally on the winter quarters affecting survival. We urge improved demographic monitoring of the population to better assess annual survival and reproductive success. We also recommend development of an adaptive management framework to remove uncertainties in our knowledge of Wigeon population dynamics as information is forthcoming to better inform management, especially to attempt to harmonise the harvest with annual changes in demography to ensure sustainable exploitation of this important quarry species now and in the future.

1. Introduction

Since the end of the Second World War, many of the huntable duck species of northwestern Europe have shown sustained increases in abundance (e.g. Eltringham & Atkinson-Willes 1961, Owen *et al.* 1986, Nagy *et al.* 2014). This has presumably been at least partially the result of more restrictive hunting legislation that has reduced uncontrolled harvest of such populations (Berry 1939, Owen *et al.* 1986). In addition, the results of site protection have presumably also reduced the rate of habitat loss and degradation for these duck species, initially in the form of local and national nature reserves and international protection, such as desig-

nation as Ramsar wetland sites of international importance, but latterly as cohesive networks of Natura 2000 sites established along their flyways. As viewed from the perspective of the late 1990s therefore, the favourable conservation status of most huntable dabbling duck species represented a major conservation success story in northwest Europe, balancing increasingly abundant populations with a harvestable offtake that was acknowledged to represent genuinely "sustainable use" within a time frame of decades.

Unfortunately, there are increasingly signs of contemporary change in this situation, as the production of young amongst Eurasian Wigeon (*Anas penelope*, hereafter Wigeon), Northern Pintail

(*Anas acuta*) and Northern Shoveler (*Anas clypeata*) in this flyway has fallen consistently over the last 30 years (as sampled by hunters, Christensen & Fox 2014) and their major EU breeding aggregations within Finland are showing recent declines in abundance (Pöysä *et al.* 2013). Between-year changes in abundance of several species listed on Annex II of the EU Birds Directive (i.e. those which may be hunted) are now showing signs of stabilisation and decline at the flyway level (Nagy *et al.* 2014, Ramão 2015). Although there is no doubt that the population abundance of these species continues to be well above those of the 1950s, the contemporary declines present a challenge to their effective management and sustainable harvest. At the very least, a greater understanding of these declines is required if we are to be in a position to be able to implement management actions to inhibit and reverse them. For this reason, it is helpful to investigate the nature of recent changes in overall abundance of these species and to look for support for various hypotheses that we could put forward for their declines.

In this analysis, we look in detail at the abundance of wintering Wigeon in northwest Europe to assess the degree of its recent decline and attempt to account for its downturn. We do this by examining data from the mid-January International Waterbird Census (IWC) gathered by national organisations throughout the Western Palearctic and centrally collated by Wetlands International (WI). We consider that the northwest European Wigeon population is relatively closed in winter because long term ringing recovery data has established that birds do not continue into north and western Africa in winter (e.g. Donker 1959, Owen & Mitchell 1988, Saurola *et al.* 2013). For this reason, we assume that the contemporary count network in northwest Europe is effective at covering the entire population and that changes in the estimated year-on-year abundance can only arise from differences in count coverage, reproductive success and survival. Recent analysis has shown that several diving duck species have extended their northwest European wintering range north and east with ameliorating winter temperatures (Lehikoinen *et al.* 2013, Pavón-Jordan *et al.* 2015). If this is the case for the Wigeon, there could potentially be large numbers of this species occurring in wetlands in Finland and Russia, avoiding detection by occurring in areas not currently subject to mid-winter IWC coverage (because they were formerly frozen in winter). The omission of such birds from the count network through winter full- or partial short-stopping (i.e. birds overwintering in areas closer to breeding areas as a result of milder winters, in this case to the north and east of their former wintering range, see Elmberg *et al.* 2014 for precise definitions) could contribute to the perception that there have been declines in overall annual abundance in recent years. For this reason, we use IWC data to look for signs of changes in the wintering distribution of Wigeon to test this hypothesis.

It is known from detailed studies at a single major Wigeon breeding resort (Mývatn in Iceland) that the size of the breeding Wigeon population in year t is highly correlated to the production of young at the same site in year $t - 1$ (Gardarsson & Einarsson 1994). Hence, it might be expected that, if the recruitment of first winter birds to the subsequent breeding class makes such a difference to overall breeding numbers, the variations in reproductive success at the flyway level may contribute to overall abundance in winter. We therefore test to see if this is the case using a combination of wing samples submitted by Danish hunters to measure annual reproductive success and IWC data on annual changes in overall population size. Given the earlier finding that Wigeon breeding success is influenced by summer temperature (Mitchell *et al.* 2008), we also look for correlations between summer North Atlantic Oscillation (NAO) indices and reproductive output to account for recent declines in productivity in this flyway (Christensen & Fox 2014).

We also check for signs of density dependence in reproductive output to see if the increase in Wigeon population size has also contributed to the decline. Finally, because recoveries of Wigeon are greater during spells of hard winter weather (Ridgill & Fox 1990), we test to find support for the hypothesis that cold winters in northwest Europe could contribute to explaining declines in the overall population size in the following years using IWC data by regressing annual change in population size against mean January temperature in the centre of the wintering range.
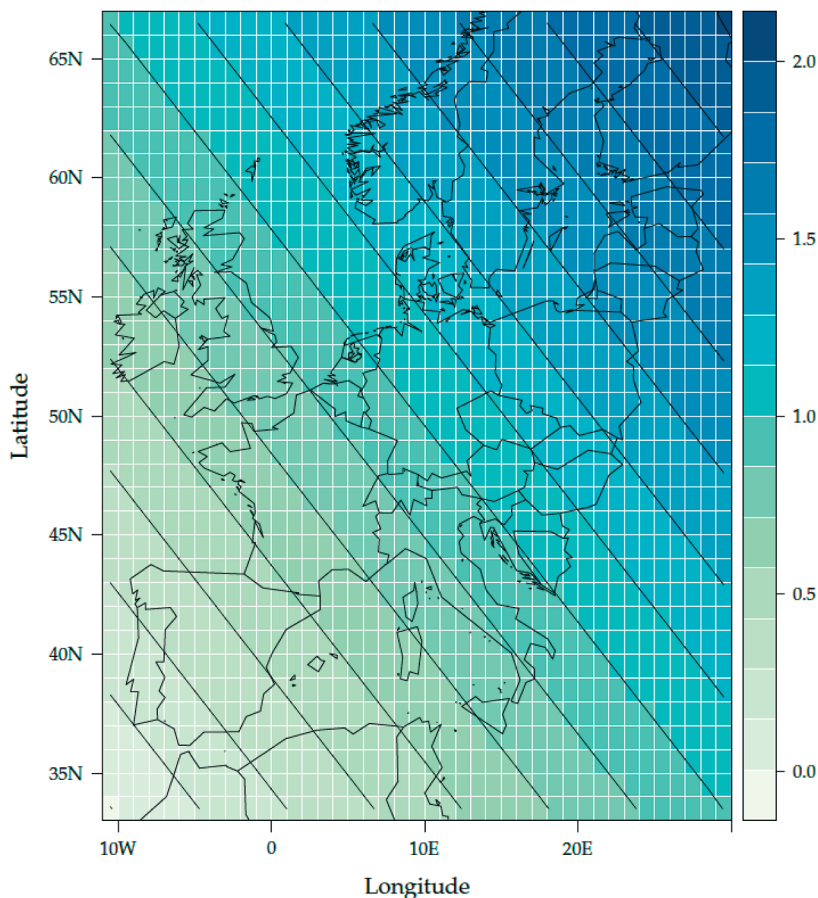
Fig. 1. Map showing the gradient of values established from SW to NE used as predictor to test the hypothesis that trends in numbers among European dabbling ducks tend to increase towards the NE.

2. Methods

2.1. Short-stopping

We used mid-January count data for Wigeon from the IWC (Gilissen *et al.* 2002, Nagy *et al.* 2014) between 1990 and 2009 from countries within the north-west European flyway (*sensu* Atkinson-Willes 1976). In all countries, only sites counted at least twice entered the analysis. We fitted trends for each country using the software TRIM version 3.54 (Van Strien *et al.* 2004, Pannekoek & van Strien 2005) imputing missing counts and estimating trends by log-linear Poisson regression. To standardise comparisons of trends and the relative magnitude of trends, we indexed the counts to a value of unity starting in 1990 for all national analyses.

To estimate site trends we calculated Kendall's Tau on log-transformed counts using the data set generated in TRIM (actual counts or in the case of missing values, imputed counts). Spatial coverage in IWC is biased towards certain countries with very dense counting schemes (e.g. United Kingdom and the Netherlands) and to compensate for the uneven distribution of sites we aggregated the site based values to a 1° by 1° grid taking the mean Tau value for all sites falling within a grid cell using the "raster" package (Hijmans 2013) in R 3.0.1 (R Core Team 2013). This resulted in a mean of 9.38 sites per grid square (range 1–77) based on 2,888 sites with Wigeon count data throughout the region.

To test if there was a tendency for grid cells located further to the northeast (closer to the breeding grounds) to show increasing numbers (i.e. positive Tau values), we fitted a generalised additive model (GAM) using the "mgcv" package (Wood 2006) with the Tau values as response variable and a gradient from southwest to northeast as

explanatory variable. We defined the SW–NE gradient as the latitude and longitude of the study region scaled from zero to one and summed, giving a vector from zero (SW) to two (NE, see Fig. 1 and Dalby 2013).

To assess whether changes in the distribution of Wigeon during 1990–2009 had resulted in systematic movement in the annual centres of gravity of abundance in wintering distributions towards the north and east during the time series, we estimated the annual and decadal centres of abundance as the weighted mean longitude and weighted mean latitude using the counts estimated from TRIM as weights.

Finally, we plotted national TRIM indices for mid-winter counts from countries along the entire flyway to test the prediction under the short stopping hypothesis that Wigeon wintering in the northeast part of the winter distribution should show greatest increases and in countries progressively south and west along the flyway would show deceasing trends as birds relocated nearer to the breeding areas in mid-winter.

2.2. Flyway trends

A TRIM model was also fitted to the entire dataset from all countries to generate a flyway index of total estimated individuals for the period 1988 to 2012 using the methods described and estimates generated by Nagy *et al.* (2014).

2.3. Effects of annual reproductive success on between year changes in abundance

Age ratios from the Danish hunter wing survey (Christensen & Fox 2014) were used as a measure of annual production of young in this population for the same period, since these are thought to provide a reasonable measure of annual production of young in the northwest European population (Fox *et al.* 2015, Fox *et al.* 2016). The ratio of first winter birds to adult females in the wing samples were used as a measure of relative annual breeding output to investigate the hypothesis that the population in a given winter was heavily influenced by the reproductive success in the previous summer.

2.4. Effects of winter weather on between year changes in abundance

To test for support for the hypothesis that severe weather on the winter quarters affects survival, we also tested for a correlation between the proportional change in winter population between year t and $t + 1$ and the mean January temperature at Schiphol Airport (52.3°N 4.76°E) in the Netherlands where most (40–45%) of the population overwinters (data from http://www.tutiempo.net/clima/Amsterdam_Airport_Schiphol/62400.htm). This meteorological station also lies within 150–200 km of the decadal centre of gravities of the wintering population (see Fig. 4).

2.5. Predicting between year changes in abundance based on reproductive success and winter weather

In the course of this analysis, we showed a strong linear relationship between the proportional change in flyway population abundance in year t (P_t) compared to year $t - 1$ (P_{t-1}) and the ratio of young to adults in the wing surveys (w_{t-1}) provided by hunters in Denmark (Fig. 7). To test how well variation in breeding success contributed to changes in year-to-year abundance, we generated an independent time series of annual estimates of the Wigeon flyway population size (P) in year t using the regression modelled proportional change in population size predicted by reproductive success in the previous year thus:

$$P_t = P_{t-1} (aw_{t-1} - b) \tag{1}$$

where P_t is the northwest European population size in the January of year t, w_{t-1} is the age ratio in the hunter wing surveys based on birds hatched in summer $t - 1$ and a and b are constants (see the actual formula in Fig. 7). The time series presented in Fig. 8 was generated starting with the known P_{t-1} in 1988 (777,343 individuals from Nagy *et al.* 2014) to generate P_t for 1989 and each subsequent P_t estimated in the same way.

We also took the same relationship from the Schiphol airport mean January model and incorporated this into a multiple regression model to generate another time series combining the modelled effects of breeding success and January win-
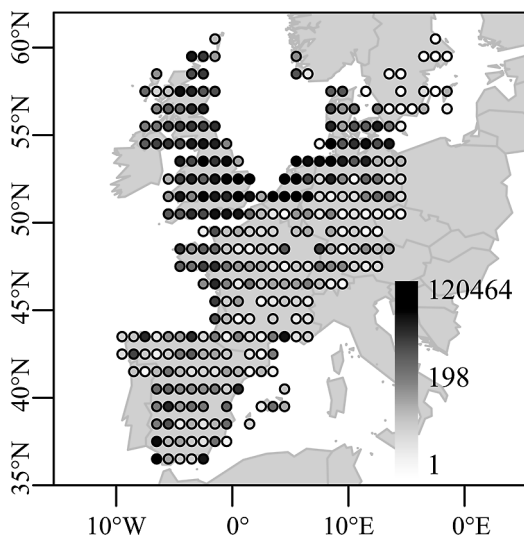
Fig. 2. Mean annual number of Wigeon counted from 1990 to 2009 aggregated into 1° by 1° grid squares by adding counts from all sites falling within each grid cell. Counts originate from the International Waterbird Census from all European countries plotted here. Missing counts were imputed using TRIM version 3.54 (Pannekoek & van Strien 2005) before calculating mean grid cell values. Note data are not shown for Ireland or Portugal because full data for 1990–2009 were not available from these schemes so gridded means would not be comparable with the rest of Europe.
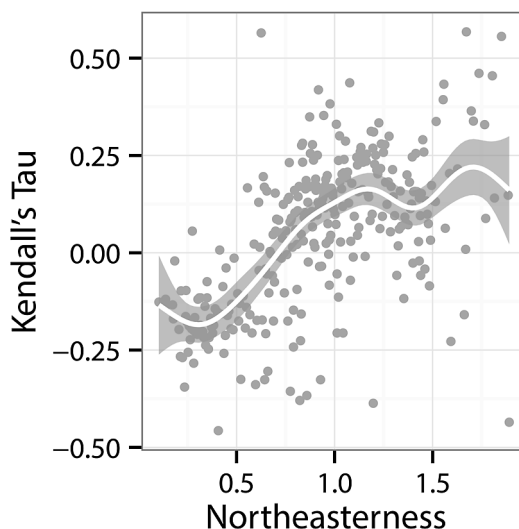
Fig. 3. Generalised additive model (GAM) of Kendall's Tau on log-transformed Wigeon counts from the International Waterbird Census from across Europe between 1990 and 2009 against a gradient from the southwestern corner (0) to the northeastern most corner (2) of the Northwest European flyway (*sensu* Atkinson-Willes 1976 and see Dalby 2013). Site based Kendall's Tau values were aggregated to 1° by 1° grid squares by taking the mean of all site Kendall's Tau values before running the analysis. Estimates are shown in white with 95% confidence intervals (shaded grey area).

ter severity. We tested goodness of fit of predicted population size generated from the two models by fitting general linear models to the annual predicted population size and those generated from count data, with the expectation that the best model would have the slope closest to unity and we compared slopes using procedure of Zar (1999). We also tested for signs of density dependence in the time series by seeking an inverse relationship between breeding success in year t and ln transformed population size in January of $t − 1$.

Finally, to test whether breeding success was linked with climatic conditions on the breeding grounds (as also confirmed for Wigeon in the Iceland population, Gardarsson & Einarsson 1997) we used the combined May–July North Atlantic Oscillation index (National Oceanic and Atmospheric Administration 2015) to test for a correlation between this summer NAO index and breeding success as measured in the Danish hunter wing surveys. The phenology and reproductive

success of several bird species has been shown to be influenced by NAO (e.g. Forchhammer *et al.* 1998, 2002, Hüppop & Hüppop 2003). Since positive NAO indices characterise the more northerly tracking of the jet-stream and storm tracks in the North Atlantic, such conditions bring warmer, drier, cloudless conditions to central Eurasia where Wigeon breed (Folland *et al.* 2009), likely enhancing breeding success in such years; in contrast negative indices reflect colder, wetter conditions on the breeding areas and would thus be expected to be associated with poor Wigeon breeding success.

3. Results

3.1. Short-stopping

Wigeon are highly concentrated in mid-winter in northwest Europe, with 40–45% of the wintering birds in this flyway occurring in the Netherlands,
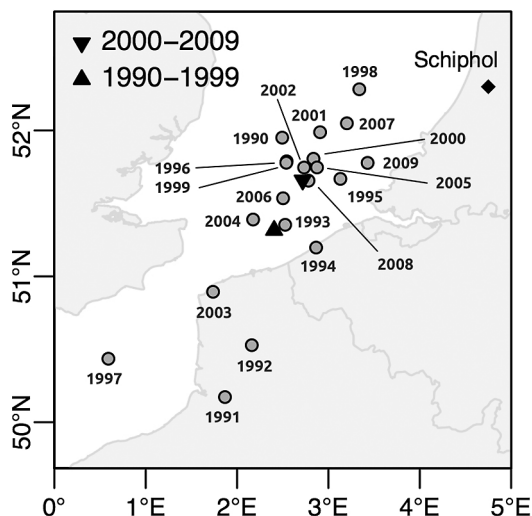
Fig. 4. Count weighted mean centroids of Wigeon counts from the International Waterbird Census across Europe for each year between 1990 and 2009. Black triangles are showing the decadal weighted mean centroid. Missing counts were imputed using TRIM version 3.54 (Pannekoek & van Strien 2005) before calculating the weighted centroids. The solid diamond indicates the location of the meteorological station at Schiphol Airport used to provide mean January temperatures used in this study.

35% in the United Kingdom and just under 10% in Germany, 6% in north France and 4% in Belgium (Fig. 2). This distribution has changed little since Monval & Pirot (1989) and Ridgill & Fox (1990), although the GAM analysis clearly showed that there were segments of the Wigeon flyway where trends increased more on the north and east of the winter range than the south and west where declines were more evident (deviance explained = 42.8%, $F_{7213,\,308} = 26.82$, $P < 0.0001$, Fig. 3). The weighted mean centroids varied between years (Fig. 4), but there was no convincing temporal trend through the years plotted here, the decadal centre of gravity for the 2000s being 43.9 km to the NE of that in the 1990s. Increasing numbers wintering in the northeast of the wintering range (significant increases from fitted TRIM models in Sweden, Norway, Denmark, Germany and Switzerland, see Fig. 5) contrasted stable trends in the centre of the range (Belgium, Netherlands, the United Kingdom and France, where the vast majority of the individuals in this flyway winter, although these countries all show some signs of re-

cent declines (Fig. 5) and declines at the western end of the flyway (significant decreases in Ireland and Spain).

3.2. Flyway trend

Following increases in abundance during the late 1980s and 1990s, Wigeon numbers have stabilised in the northwest Europe flyway and declined since the mid-2000s (Fig. 6a). Annual reproductive success as measured by the ratio of juveniles to adult females sampled from shot birds in Denmark have fluctuated since 1988, but were generally below average during 8 of the 11 years during 2002–2012 (Fig. 6b).

3.3. Effects of annual reproductive success on between year changes in abundance

The proportional change in successive winter population estimates was positively and significantly correlated with the annual ratio of young to adults in the Danish hunter wing survey in the previous year during 1988–2012 ($r^2 = 0.34$, $F_{1,\,22} = 11.4$, $P = 0.003$, Fig. 7). The annual ratio of young to adult Wigeon in the Danish hunter wing survey showed a significant positive correlation with the May–July NAO index for the preceding summer, supporting the hypothesis that climate affects the reproductive success of this population ($y = 5.640 + 0.510x$, $r^2 = 0.27$, $F_{1,\,22} = 9.97$, $P = 0.01$). Breeding success in a given summer was significantly negatively correlated with ln transformed population size in the previous January ($y = 104.6 - 7.124x$, $r^2 = 0.32$, $F_{1,\,22} = 34.9$, $P = 0.004$).

3.4. Effects of winter weather on between year changes in abundance

The proportional change in winter population estimates also showed a marginally significant positive relationship with the mean January temperature at Schiphol ($r^2 = 0.17$, $F_{1,\,22} = 4.4$, $P = 0.05$).

3.5. Predicting between year changes in abundance based on reproductive success and winter weather

Modelling the year-on-year change in flyway abundance based on the output from the model in
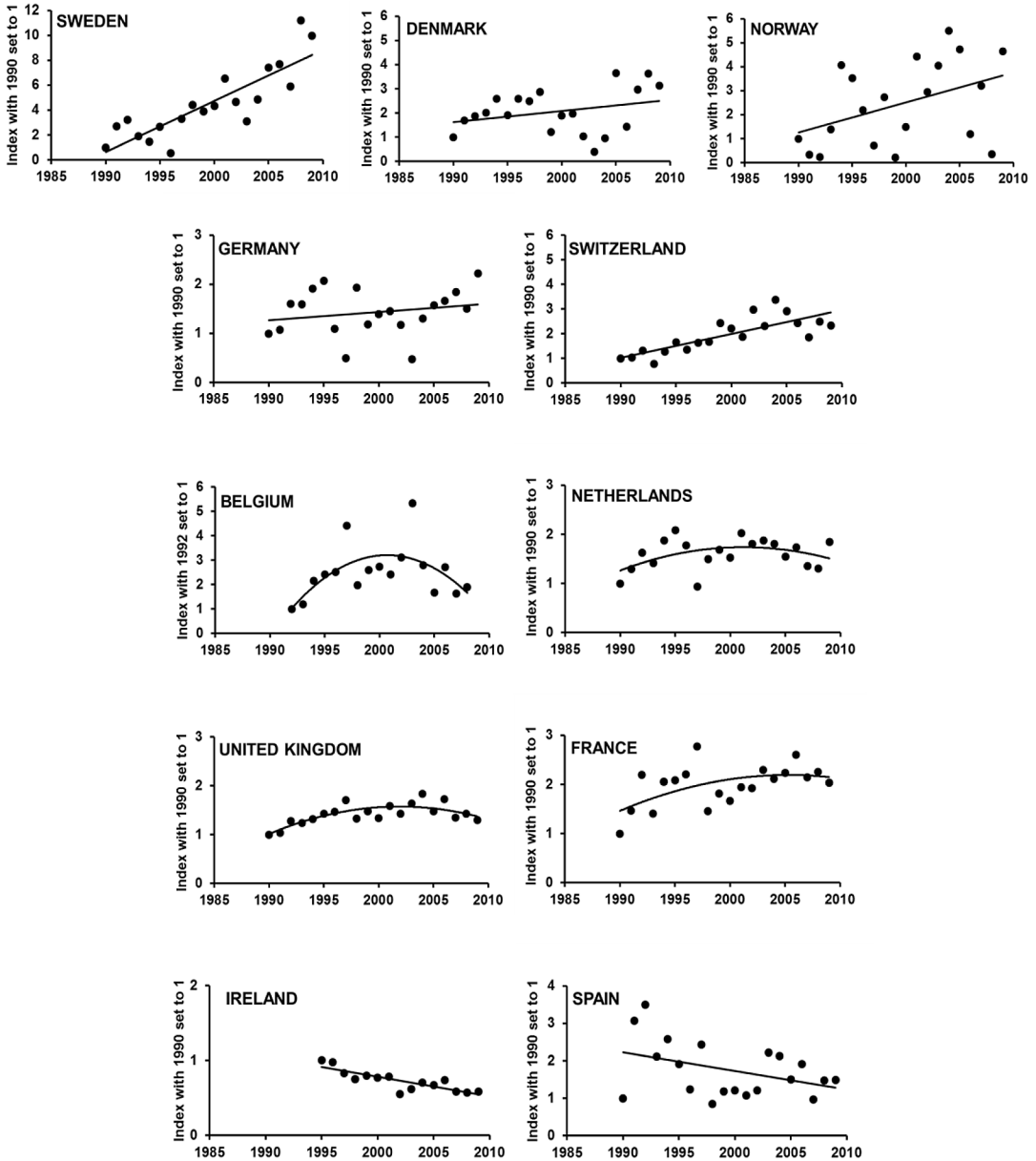
Fig. 5. National TRIM indices for Wigeon based on the International Waterbird Census data from selected European countries from 1990 to 2009, with indices set to 1 in 1990. Note different scales in the indices axes between countries.

Fig. 7 showed an extremely good fit to the time series although the combined modelled effects of this and incorporation of the relationship with Schiphol January temperatures worsened the fit (Fig. 8). The model using reproductive success to generate population size showed a significant correlation with the observed populations size with an estimated a slope of 1.013 (general linear model r^2 = 0.433, $F_{1, 22}$ = 16.89, P = 0.0005). The model incorporating both reproductive success and Schiphol January temperature gave a significant model with a slope of 0.909 (r^2 = 0.434, $F_{1, 22}$ = 16.90, P = 0.0005). The two slope estimates differed significantly (t_{44} = 5.6, P < 0.001).

a
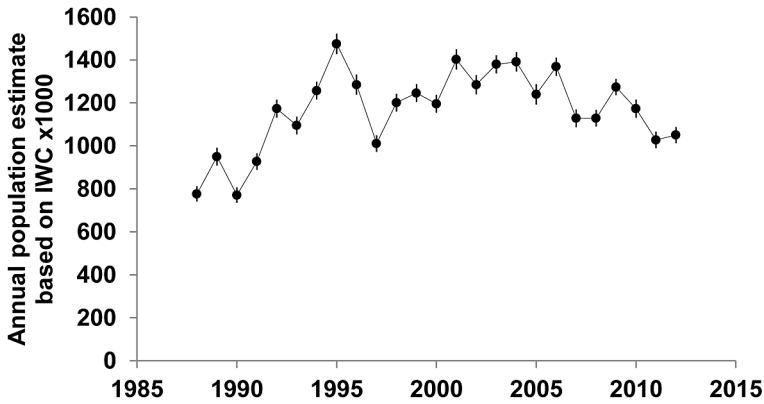
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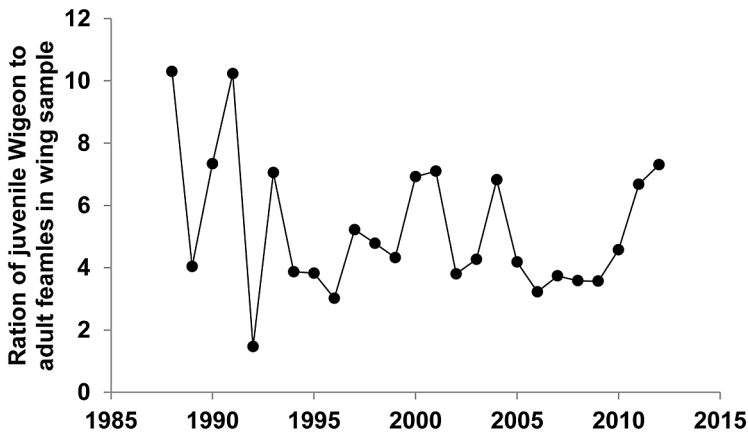
Fig. 6. (a) Combined annual TRIM indices with generated standard error estimates (see van Roomen *et al.* 2011 for methods) for Wigeon for the years 1988–2012 based on the International Waterbird Census data from the northwest Europe flyway population. (b) Annual ratio of juvenile Wigeon to adult females in wing samples voluntarily submitted by hunters in Denmark, 1982–2014 for comparison.

4. Discussion

During 1990–2009 there was good evidence for Wigeon showing patterns of short stopping in their winter distribution in northwest Europe, with the establishment and expansion of a new wintering population in Sweden and increases in Norway, Denmark, Germany and Switzerland, stable trends in Belgium, Netherlands, the United Kingdom and France (where the vast majority winter) and declines in Ireland and Spain. Interestingly, wintering numbers have tended to increase along the Baltic coast of Germany, in contrast to declines in the German Wadden Sea in very recent years (JW unpubl. data). However, overall, the increasing numbers in the northeast (c. 200,000) and decreasing numbers in the south and west (c. 85,000) of the range are relatively modest compared to the more than one million wintering individuals in the central part of the range, where relative abundance has changed little, explaining the general lack of response in the position of the annual and decadal centres of gravity of this wintering population. The count data show that there is now an established wintering population in southwest Sweden that was not present before the 1990s. IWC data also show that Wigeon remain almost completely absent as wintering birds in the Baltic States (A. Stīpniece unpubl. data) and Finland (A. Lehikoinen unpubl. data). Given the severity of winters there, we consider this is also likely to be the case throughout European Russia. For this reason, we
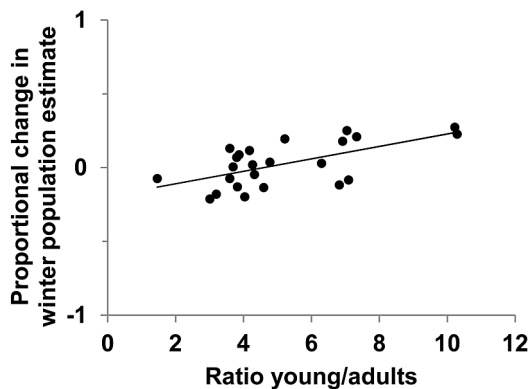
Fig. 7. Graph of the proportional change in year to year winter population estimates for the years 1988–2012 shown in Fig. 6a plotted against the ratio of young to adults in the Danish hunter wing surveys in the first of the paired years. The fitted regression model has the formula $y = 0.0384x - 0.1754$, $r^2 = 0.34$, $F_{1, 22} = 11.4$, $P = 0.003$.

conclude that, although short-stopping is clearly occurring in this species, it has not resulted in wintering Wigeon occurring in Finland and Russia where they would not be counted within the IWC network. Hence, we have confidence that the current count network is effective at sampling changes in local abundance throughout the Wigeon winter range and that the collated trend estimates are reflective of the overall abundance in this flyway population.

Based on the same reasoning, we can also take some confidence in the fact that after an increase in Wigeon abundance during the late 1980s and through the 1990s, the numbers have stabilised in recent years and fallen since the mid-2000s (Fig. 6a). The correlation between change in winter population estimates from one year to the next and the breeding output measured by proportions of first winter birds harvested in Denmark enabled the retrospective reconstruction of the current trend in overall population size based on observed abundance in 1988 and annual age ratios since. This confirmed the results of studies on the breeding grounds in Iceland, namely that the year-on-year changes in the size of the Wigeon population are related to annual reproductive success (Gardarsson & Einarsson 1994, 1997). The summers of 2002–2010 (excluding 2004) were years of relatively low reproductive success in amongst

Wigeon harvested in Denmark (Fig. 6b and Christensen & Fox 2014) and the patterns of annual variation in the proportions of young birds correlated positively with the summer NAO, so the recent decline in reproductive success may be partly explained by climate at large spatial scales. Declines in abundance of breeding Wigeon in Finland have been also been related to eutrophication of breeding lake waters, changes in predator abundance (Pöysä *et al.* 2013) and the effects of local land use, especially agriculture (Arzel *et al.* 2015). However, these effects are likely to be relatively restricted geographically compared to the extensive breeding range in the Russia taiga where changes in land use are likely to have had less impact. The results of the analyses here also suggest that some evidence for weak density dependence in breeding success. Hence, there are likely to be other local or regional factors affecting annual reproductive success as well as the dominant influence of climate. The negative relationship between winter temperature and annual changes in flyway abundance also suggests winter severity may contribute very slightly to annual survival, although this contribution was marginal over the major contribution from differences in reproductive success alone. Hence, on the basis of parsimony, the fact that the model based on reproductive success produced the best predictions against observed population size and the reduced strength of the model incorporating both parameters to predict observed population size, we conclude that reproductive success in a given year makes the greatest contribution to year on year changes in Wigeon flyway abundance.

The great weakness with this type of analysis, however, continues to be our ignorance of the inter-annual differences in annual survival of the species. The absence of ringing recovery or capture-mark-recapture as an independent means to estimate annual survival remains a major impediment in our ability to track and interpret changes in the demography of the commoner dabbling duck species, such as Wigeon, that are very important quarry species across the European continent. Our capacity to model the relative and actual effects of climate and environmental change also remains limited as long as we lack bag statistics and more geographically dispersed methods of gauging annual reproductive success (Elmberg *et al.* 2006).
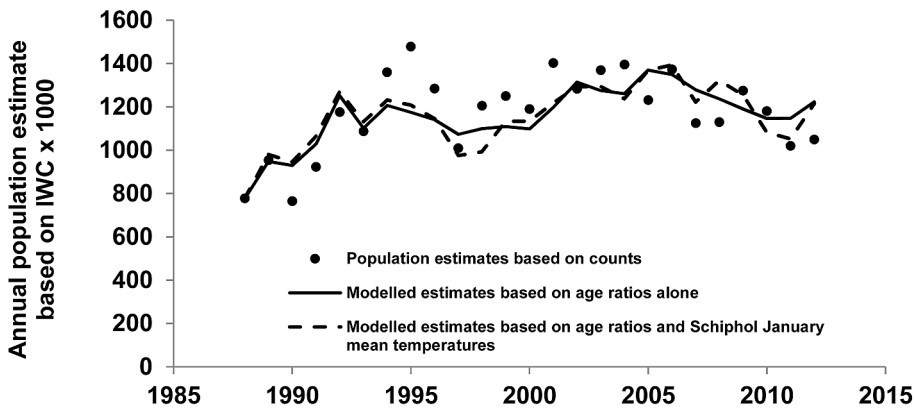
Fig. 8. Combined TRIM indices for Wigeon based on the International Waterbird Census data from the northwest Europe flyway population, showing the result of the modelled annual population size generated only from the annual wing ratios shown in Fig. 6 (solid line). Also shown are the of modelled annual population size generated by combined effects of wing ratio data and mean January temperatures at Schiphol, Netherlands (multiple regression model has the formula $y = -0.2558 + 0.0386w + 0.0199t$, where w = wing ratio and t = Schiphol temperature, $r^2 = 0.46$, $F_{2, 21} = 9.0$, $P = 0.002$).

Nevertheless, in the specific case of the Wigeon, this analysis does suggest that the unusual "boom and bust" reproductive output in this species since 1988 (and particularly the low reproductive success and absence of "booms" in the 2000s) has contributed much to the patterns of overall abundance in the flyway. This pattern in annual reproductive output amongst Wigeon has correlated with past fluctuations in reproductive success in the Dark-bellied Brent Goose (*Branta bernicla bernicla*) that have been shown to be linked to cycles in lemmings and their predators on their Arctic breeding areas (Nolet *et al.* 2013). However, it is difficult to conceive of an obvious causal link between such patterns in a high-arctic nesting goose species and a boreal nesting duck species. Whatever the cause of annual variation in Wigeon reproductive output, it would seem prudent in view of the recent sustained decline in overall abundance of this important game species to build upon this tentative analysis and create an adaptive management plan for the species. Such a framework would identify the specific need for demographical monitoring of this population and would remove uncertainties in the system as information was forthcoming to better inform management (e.g. Madsen *et al.* 2015). This would greatly enhance our understanding of the demographic drivers of the population and specifically enable the future balance of the harvest with changes in overall abundance. The development of such an adaptive management framework to attempt to harmonise the harvest with annual demographic changes are essential to ensure the sustainable exploitation of this important quarry species now and in the future.

Mitkä tekijät vaikuttavat talvehtivan haapanakannan runsauden vaihteluun Länsi-Euroopassa?

Selvitimme haapanan (*Anas penelope*) vuosittaisia runsausvaihteluita Länsi-Euroopan talvehtimisalueilla vuodesta 1988 lähtien hyödyntämällä kansainvälisiä keskitalven vesilintulaskentatietoja (International Waterbird Census) ja niihin sovitettuja log-lineaarisia Poisson regressiomalleja. Talvikanta kasvoi alueen pohjois- ja itäosissa (Norja, Ruotsi, Tanska, Saksa ja Sveitsi), pysyi vakaana keskiosissa (Belgia, Hollanti, Iso-Britannia ja Ranska) sekä taantui alueen etelä- ja länsireunalla (Espanja ja Irlanti). Tämä viittaa siihen, lajin talvirunsaus on siirtymässä kohti koillista osuen yhteen leudontuneiden talvien kanssa. Valtaosa kannasta (75 %, yli miljoona yksilöä) talvehtii kuitenkin edelleen vakaan kannan alueella Belgiassa, Hollannissa, Iso-Britanniassa ja Ranskassa, minkä takia lajin talvehtimisalueen painopisteessä ei havaittu muutosta.

Vuosittaiset koko alueen talvikannan vaihtelut olivat merkitsevästi positiivisesti yhteydessä edeltävän kesän poikastuottoon, joka mitattiin nuorten ja vanhojen lintujen suhteena tanskalaisessa metsästysaineistossa. Lisäksi vuosittaisella kannanmuutoksella oli suuntaa-antava positiivinen yhteys lajin keskeiseltä talvialueelta mitatun tammi-

kuun keskilämpötilan kanssa, mikä viittaa siihen, että kylmät talvet voivat vaikuttaa negatiivisesti lajin kannan kokoon. Näistä kahdesta muuttujasta poikastuotto selitti kuitenkin voimakkaammin talvikannan vuosittaista vaihtelua. Kesäinen laaja-alainen NAO-ilmastoindeksi selitti merkitsevästi positiivisesti 27 % vuosittaisesta poikastuoton vaihtelusta. Poikastuottoon voi vaikuttaa myös paikalliset olosuhteet kuten rehevöityminen ja saalistuspaine pesimäalueilla. Metsästyspaineen sekä talvi-ilmaston ankaruuden vaihtelulla on puolestaan todennäköisesti vaikutusta vuosittaiseen selviytyvyyteen.

Vaikuttaa kuitenkin siltä, että vuodesta 1988 lähtien talvikannan vaihteluun on vaikuttanut etenkin pesimämenestys ja vähemmässä määrin talviaikainen selviytyvyys. Haapanakannan demografiselle seurannalle on tuloksiemme perusteella suurta tarvetta ja suosittelemme kehittämään adaptiivista kannanhoitoa, jossa myös seurantatietojen epävarmuustekijät otetaan huomioon. Näillä toimenpiteillä pystymme tulevaisuudessa paremmin turvaamaan kestävän kannanverotuksen suhteessa kannanmuutokseen tällä tärkeällä riistalajilla.

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