Connectivity between flyway populations of waterbirds: assessment of rates of exchange, their causes and consequences

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Summary

1. Conservation and management of migratory waterbirds use flyway populations as the basic unit, and knowledge of the delineation, rate of exchange and gene flow between populations is fundamental. However, for the majority of global flyway populations, information is too fragmentary to address connectivity between populations and, hence, insufficient to inform management.

2. We investigated the demographic connectivity between the eastern (breeding in Svalbard and wintering in Denmark, the Netherlands and Belgium) and western (breeding in Greenland or Iceland and wintering in Britain) flyway populations of pink-footed geese *Anser brachyrhynchus* based on resightings of marked geese from both populations. Previous genetic analyses suggested a modest gene flow between the two populations.

3. Capture–recapture analysis conservatively estimated that mean annual movement probabilities were low (eastern to western population: 0·071%, 95% CI = 0·033–0·15%; western to eastern: 0·076%, 95% CI = 0·031–0·18%). Movement probability from eastern to western flyway populations increased in years with high snow cover in the southernmost winter range in Belgium. Life histories of exchanged individuals from eastern to western (32 different individuals during 1988–2010) revealed that the majority entered Britain via Belgium and the Netherlands during winter; some returned to the eastern population via Belgium and/or the Netherlands, others moved northwards in Britain during the spring and appear to have migrated directly from Britain (western population) to Norway (eastern population). None of the birds from the eastern population emigrated permanently, but some individuals turned up in Britain in consecutive years. Out of nine individuals switching from western to eastern flyway populations, three returned to Britain; the others were not subsequently resighted. An alternative winter strategy and spring flyway over Britain to Norway is suggested, used by hundreds to thousands of eastern birds, particularly following severe winters. Thus, the two populations currently appear to be demographically closed; low genetic connectivity probably reflects dispersal over longer time.

4. *Synthesis and applications.* Current initiatives to internationally manage the eastern population of pink-footed geese do not need to consider net immigration in predictive harvest models. For waterbirds in general, a targeted approach to evaluate connectivity, using classic marking studies in combination with molecular methods and focussed sampling on breeding grounds, is recommended to better underpin management decisions at population levels.

Key-words: cold weather movement, demography, E-SURGE, genetic connectivity, multistate model, pink-footed geese, population delineation

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Introduction

Throughout the world, conservation and harvest management of waterbirds rely on flyway populations as the basic management unit, for example, in the African-Eurasian Waterbird Agreement, the Ramsar Convention and the North American Waterfowl Management Plan (for an overview, see Boere, Galbarith & Stroud 2006). Hence, in cases where a species has been divided into more than one population, knowledge of delineation of populations, rate of exchange and gene flow between populations is a fundamental prerequisite for population conservation, harvest management, designation of networks of key sites and disease transmission risk assessments. With the unprecedented current rate of global climate and land-use change, many populations undergo dramatic range contractions or expansions (McCarty 2001; Bohning-Gaese & Lemoine 2004; McDonald *et al.* 2012), increasing the need for up-to-date information on population structures and distributions and understanding underlying drivers, including potential dispersal between populations. Assessments of population delineation have traditionally been based on direct methods such as recoveries of dead ringed birds, observations of marked individuals, tracking of birds marked with transmitters and, more recently, by indirect and direct genetic methods. However, with few exceptions where marking and genetic sampling have systematically covered the geographic populations of a species (e.g. Williams *et al.* 2008; Shorey *et al.* 2011; Kraus *et al.* 2013), existing information remains too patchy to make other than qualitative judgements about connectivity between flyway populations.

The pink-footed goose *Anser brachyrhynchus* (hereafter pinkfeet) is an Arctic and sub-Arctic breeding species, which is divided into two flyway populations: the Iceland/ Greenland population wintering in the British Isles (western population) (Mitchell *et al.* 1999) and the Svalbard population migrating via Norway to wintering grounds in Denmark, the Netherlands and Belgium (eastern population) (Madsen *et al.* 1999). The two populations follow different migration routes and spend the winter in Britain and continental Europe, respectively. As most western Palaearctic goose populations, the two populations of pinkfeet have increased dramatically in numbers during recent decades (Fox *et al.* 2010). Large concentrations winter relatively close to each other in Norfolk in southeast England and Flanders in Belgium (*c.* 150 km apart across the English Channel). Resightings of marked individuals have revealed that a small number of pinkfeet move from east to west at least in some years, roughly representing a few hundred individuals (Madsen *et al.* 1999). Exchange is possibly related to winter severity. Thus, in cold winters in north-western Europe, ringed individuals of eastern pinkfeet may move to France (Holgersen 1960; J. Madsen, unpublished data) and

Britain (Madsen *et al.* 1999), and heavy snow cover in Belgium can split large aggregations of geese into smaller flocks that spread over a larger area (Madsen *et al.* 1999).

Genetic analyses based on mitochondrial DNA (mtDNA) have shown a population structure, but also suggested gene flow between the two populations of pinkfeet, with a low level of female gene flow from west to east, but a relatively higher flow from east to west (Ruokonen, Aarvak & Madsen 2005). These analyses provide information about genetic connectivity, defined as the degree to which gene flow affects evolutionary processes within populations, but they do not give precise information on demographic connectivity, defined as the degree to which population growth and vital rates are affected by exchange of individuals (Lowe & Allendorf 2010). Precise estimates of demographic exchange rates in pinkfeet are needed because the Svalbard population has recently been selected as the first European case for implementing adaptive harvest management at the flyway scale, under the auspices of the African-Eurasian Waterbird Agreement (Madsen & Williams 2012). This will require fine-tuned monitoring of demographic variables and modelling of an optimal harvest strategy.

The aim of this paper is to quantify the demographic connectivity between the two populations of pinkfeet based on resightings of individually marked birds in both populations. We hypothesize that exchange from east to west increases with cold winter spells in continental north-west Europe. Furthermore, to see whether there is evidence of permanent emigration (dispersal), temporary movements or alternative migration strategies in the populations, we describe the fate of individuals that switch between populations in terms of their subsequent life histories. We compare the direct observations with the indirect evidence of genetic connectivity and discuss the results in relation to international waterbird management needs.

Materials and methods

STUDY POPULATIONS

Svalbard population

The population has increased from *c.* 10 000 in the 1950s to 80 000 individuals in 2012 (Madsen *et al.* 1999; J. Madsen, unpublished data). In autumn, geese make a stopover in central Norway from late September to early November; in Denmark, geese arrive in late September, and the majority of the population concentrates here during early October and then move on to Friesland in the Netherlands. Here, numbers peak from October–November, after which geese move onwards to the polders in Flanders, Belgium. In Belgium, numbers peak in December, but later that month, geese migrate northwards back to Denmark. In winters with heavy snowfall in Denmark, the geese migrate back to Belgium. The population is concentrated in Denmark from February–late March, and during April, geese migrate to staging sites in central Norway and subsequently to Vesterålen, north

Norway. Around mid-May, the geese migrate to the Svalbard breeding grounds.

Iceland/Greenland population

The geese breed in Iceland and along the east coast of Greenland and migrate to wintering grounds in Scotland, Lancashire, in north-west England and Norfolk in south-east England. The population has increased from *c.* 30 000 in the 1950s to more than 350 000 individuals in 2012 (Mitchell 2013). Pinkfeet arrive in Britain from the beginning of September, and in most years, it is estimated that 95% of the western population is present in Britain by mid-October (Mitchell 2002). In Lancashire and Norfolk, peak numbers are observed in January (Mitchell *et al.* 1999). From there, geese initiate northward migration within Britain from late January. Individual marking shows that birds from Lancashire and Norfolk move to staging areas in east and north-east Scotland before leaving Britain (Mitchell *et al.* 1999). Pinkfeet leave Britain by mid-April and migrate via stopover sites in the southern lowlands of Iceland to the breeding grounds.

MARKING AND RESIGHTING DATA

The analysis is based on pink-footed goose ringing data collected by Aarhus University (AU), Denmark, the Wildfowl & Wetlands Trust (WWT), UK, and the Icelandic Bird Ringing Scheme. The AU data comprise ringing data and resightings of plastic neck bands and plastic leg rings dating back to 1988 (leg rings only used in 1988 and 1989) (see program details and online reporting system at www.geese.org), while the WWT and Iceland data date back to 1987 and involve both plastic leg rings and neck bands. In the analysis, observations of metal leg rings have not been used because they rarely produce repeated resightings. Over the years, ringing of pinkfeet has not been constant (Fig. S1, see Appendix S1, Supporting information). This study is based on resightings of pink-footed geese ringed in Denmark, Svalbard, Britain and Iceland in the period 1987–2010. In total for this period, 38 001 and 305 924 resightings of neck bands and leg rings have been reported for the British/Iceland and Danish/Svalbard marking programmes, respectively. The known exchange events were often of short duration and based on few resightings in the foreign flyway; to describe possible individual migration routes and subsequent life histories, we carefully validated the whereabouts of individuals before and after the observed exchange and excluded single resightings that were unlikely. Different colours and codes were used in the marking schemes in the two flyways; hence, observers were believed to pay extra attention to foreign rings, reducing the risk of misidentification.

DATA SELECTION FOR QUANTITATIVE ESTIMATION OF EXCHANGE RATES

To further minimize the impact of resighting error on parameter estimation, an individual was regarded as encountered if it had been recorded three times (for neck-banded birds) or twice (for leg-ringed birds) during the observation season from October to April. Individuals marked during the observation season were included in the data set from marking, whereas those marked during summer in the breeding areas were included from the

first season when they fulfilled the encounter criterion. A few individuals were originally leg-ringed and later neck-banded at recapture; these were treated as losses on capture and re-entered as new individuals. The total number of individuals included in the analysis was 2237 leg-ringed and 2006 neck-banded in the western population, and 393 leg-ringed and 3294 neck-banded in the eastern population. For the very few individuals encountered in both populations during one observation season, the encounter indicating movement was retained (with the same encounter criterion applied as above).

STATISTICAL ANALYSES

Probabilities of movement between populations were estimated using multi-state capture–mark–recapture (CMR) models (Hestbeck, Nichols & Malecki 1991; Lebreton & Pradel 2002). These models allow estimation of probabilities of survival, encounter and transition among states (here, populations). One of the basic assumptions of multi-state (and single-state) CMR models is that all individuals alive and present in a study area or state have the same probability of being encountered. This assumption is obviously not met for observations of wintering geese that are spread over large parts of northern Europe; birds using well-known sites frequented by observers have a much higher probability of being encountered than those using more remote sites. We thus expected a very high level of heterogeneity in the resighting data, and this was confirmed in goodness-of-fit tests, particularly for the eastern population (see Results). A mixture model, where individuals are allowed to move between two unknown or latent states (high and low observability), provides a robust way of dealing with encounter heterogeneity (Pledger, Pollock & Norris 2003; Péron *et al.* 2010; Cubaynes *et al.* 2012). Our model thus included two groups (neck-banded and leg-ringed birds) and four states: high and low observability in the eastern and western populations. This model has a large number of parameters, including initial state probabilities and probabilities of moving between observability states. Here, we focus on the estimation of movement probabilities between the two physical states (populations). For more details on the modelling approach, see Appendix S1 (Supporting information). Goodness of fit was tested separately for each population (because observed movement was very rare) in U-CARE (Choquet *et al.* 2009), and models were fitted in E-SURGE (Choquet, Rouan & Pradel 2009). Model selection used Akaike Information Criterion, corrected for overdispersion and sample size (QAIC$_c$, Burnham & Anderson 2002), and the importance of environmental covariates was evaluated using analysis of deviance (ANODEV, Skalski, Hoffmann & Smith 1993; Grosbois *et al.* 2008).

Several studies have found negative effects of neck collars on survival of geese (Alisauskas & Lindberg 2002; Alisauskas *et al.* 2006), and it is also likely that collars are lost, thus making birds unobservable. Both processes could cause an underestimation of probabilities of movement between the two flyways. There are no studies of neck collar effects on survival in pinkfeet, but an earlier study indicated that collar loss in the western flyway was around 8% per year (Frederiksen *et al.* 2004) and around 1–3% per year in the eastern population (Madsen, Frederiksen & Ganter 2002). However, because of the very low number of observed movements, model structure had to be kept relatively simple, and we did not include models with marker-type effects on survival or movement probabilities. The estimated movement

probabilities may thus be biased low, but this bias is likely to be relatively small, particularly given that estimated survival was high (Appendix S1, Supporting information).

We hypothesized that the probability of moving from the eastern to the western population was related to snow cover in the continental north-west Europe and its impact on foraging opportunities. No long-term quantitative data on snow cover were available. Instead, we used daily weather records from Oostende in Belgium to calculate an annual snow index, as the seasonal (December–February) sum of precipitation (in mm) on days with mean temperature below 0 °C. Temperature and precipitation data were downloaded from the National Oceanic and Atmospheric Administration, USA (http://www.ncdc.noaa.gov).

Results

DISTRIBUTION OF INDIVIDUALS SWITCHING

In total, including all individuals only seen once or more in the foreign flyway, a total of 32 neck-collared individuals ringed in Denmark or in Svalbard were subsequently resighted in Britain during the winter seasons 1988/1989–2009/2010 (Fig. 1). The 32 individuals were resighted 125 times in Britain. The majority of individuals (63%) were observed during winter (December–February) for the first time. Almost all sightings fall within the known range and sites of western pinkfeet in Britain (Fig. 2). Peak numbers of exchanges were recorded in the winters of 1996/1997 and 2009/2010. During 1987/1988–2009/2010, a total of 5 birds with plastic leg rings and 4 birds with neck bands marked in Britain and Iceland were resighted in the eastern population, including one individual recovered as dead. Three out of the nine birds were registered outside the known range and sites used by eastern pinkfeet. The initial observations of the nine individuals were evenly spread from autumn to spring.
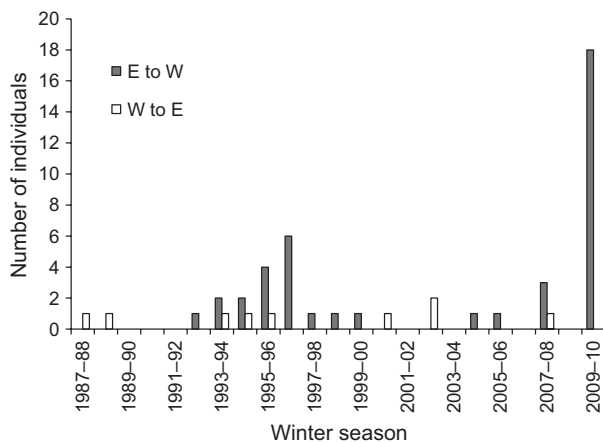

Fig. 1. Numbers of marked pinkfeet switching from eastern (E) to western (W) and from western to eastern flyways during the winter seasons 1987/1988 to 2009/2010. The data set for eastern to western shifts shows the number of moves made by 32 different birds, of which nine have been observed in more than one winter.

RATES OF EXCHANGE

As expected, goodness-of-fit tests were highly significant for both leg-ringed and neck-banded birds in both populations (Table 1). In particular, test components 3.SR (sensitive to differential survival over the first year after marking) and 2.CT (sensitive to trap dependence, i.e. differential observability of birds seen or not seen the previous year) were extremely significant. The directional tests indicated transience (lower apparent survival over the first year) in the western population, the opposite pattern ('antitransience') in the eastern population and pronounced 'trap happiness' (higher observability of birds seen the previous year) in both populations. Simultaneous significance of test components 3.SR and 2.CT is a good indication of general recapture heterogeneity, that is, variation among individuals in observability (Crespin *et al.* 2008). We therefore used a model with two observability states in each population and calculated an overdispersion factor from the remaining components of the goodness-of-fit test as the ratio of the summed chi-square statistics to the summed degrees of freedom: $\hat{c} = 347 \cdot 3/190 = 1 \cdot 83$. A multi-state goodness-of-fit test on the combined data set gave very similar results; the component testing for memory effects was significant ($\chi^2 = 10 \cdot 5$, d.f. $= 3$, $P = 0 \cdot 015$), but too few moves were observed to fit memory models, where the probability of return moves is different from outward moves in the same direction.

Initial model testing and selection led to a basic model with variation over time in survival and encounter probabilities separately for the two populations (see Appendix S1, Supporting information). Encounter probabilities were high and fairly constant for neck-collared geese in the high-observability state, but substantially lower for other classes of individuals (see Appendix S1, Supporting information). The estimated mean annual movement probabilities were low (eastern to western: 0·071%, 95% CI = 0·033–0·15%; western to eastern: 0·076%, 95% CI = 0·031–0·18%). The addition of temporal variation in movement probabilities in either direction did not improve the model (Table 2). However, a model where movement probability from the eastern to the western flyway was modelled as a function of the snow index was preferred by $QAIC_c$ (Table 2). The importance of this covariate was confirmed by ANODEV ($F_{1,20} = 9 \cdot 26$, $P = 0 \cdot 0064$, $R^2 = 32\%$), and the estimated coefficient was in the expected direction with confidence limits not overlapping zero ($\beta = 0 \cdot 1141$, 95% CI = 0·0004–0·2278). The predicted movement probability increased from 0·03% at a snow index value of 0 to about 0·5% at the highest recorded value of the snow index (Fig. 3). Observed movements from eastern to western populations were recorded in 5 years, with the highest frequency in 2009 (three recorded moves in the statistical analysis) when the snow index reached its maximum recorded value (Fig. 3). The high estimated movement probability from eastern to western in 1989 was related to the return movement of
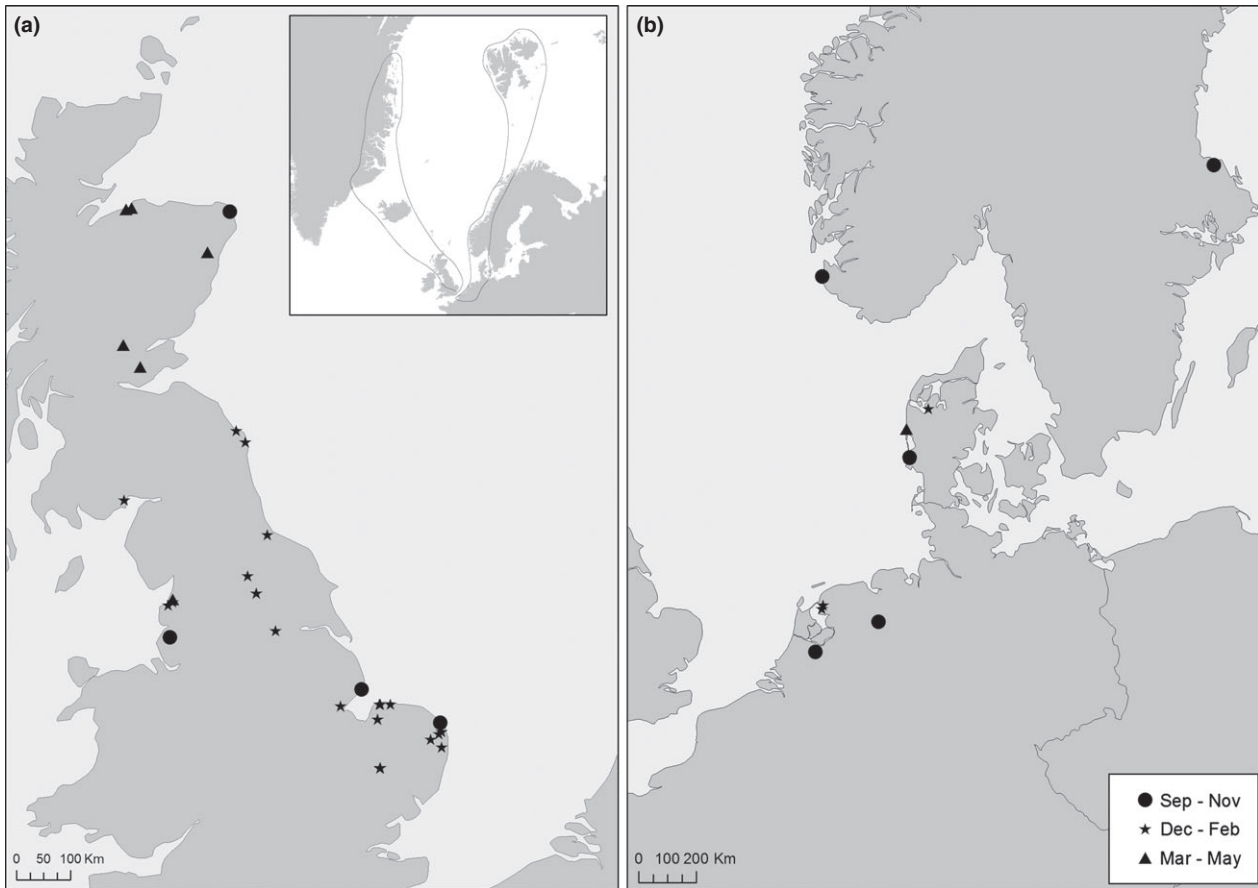
Fig. 2. Distribution of initial resightings in Britain of pinkfeet marked in Denmark and Svalbard (a) and first-time resightings in continental Europe of pinkfeet marked in Britain and Iceland (b). Initial resightings are grouped by season. Insert map shows the flyways of the two populations.

Table 1. Results of the goodness-of-fit test of the pink-footed goose data set in U-CARE, split by flyway and marker type. For the four components (3.SR, 3.SM, 2.CT and 2.CL), the *chi-square* statistic, degrees of freedom and *P*-value are shown. For the directional tests for transience and trap happiness (subsets of test components 3.SR and 2.CT, respectively), the standardized normal *z* score and *P*–value are shown

	3.SR			Transience		3.SM			2.CT			Trap happiness		2.CL		
	χ^2	d.f.	*P*	*z*	*P*	χ^2	d.f.	*P*	χ^2	d.f.	*P*	*z*	*P*	χ^2	d.f.	*P*
W leg	61·8	19	$2*10^{-6}$	6·4	$9*10^{-11}$	55·3	32	0·006	53·1	19	$4*10^{-5}$	−6·5	$1*10^{-10}$	77·6	50	0·007
W collar	40·3	15	0·0004	4·2	$1*10^{-5}$	82·4	21	$3*10^{-9}$	105·7	14	$3*10^{-16}$	−7·4	$1*10^{-13}$	22·2	21	0·38
E leg	17·4	2	0·0002	−3·5	1	4·6	3	0·2	7·9	6	0·24	−1·9	0·057	5·1	5	0·41
E collar	113·8	14	0	−8·1	1	35·2	18	0·009	3614	18	0	−56·7	0	64·9	40	0·008

one bird originally marked in the western population and recorded in spring 1989 in Denmark.

FATE OF INDIVIDUALS SWITCHING BETWEEN POPULATIONS

East to west exchanges

Among the 32 eastern pinkfeet that were observed in Britain, 21 were resighted in subsequent years; all 21 individuals were subsequently resighted in continental Europe. No

individuals are known to have permanently emigrated to the western population, but the destiny of 11 individuals was unknown.

Before 2009/2010, eastern birds (14 different individuals) appear to have crossed over to Britain via Belgium and the Netherlands; they did not appear to make a northwards movement within Britain, and the available observations (*n* = 4) suggest that they left Britain by moving back to the eastern flyway via Belgium, the Netherlands, Denmark and Norway. This is in contrast to the behaviour of the birds exchanged during winter 2009/

Table 2. Model selection for movement probabilities between the two flyways. The basic model had variation over time in survival and encounter probabilities separately for the two flyways and constant movement probabilities (for further details, see Appendix S1, Supporting information). Deviance and Akaike Information Criterion, corrected for overdispersion and sample size (QAIC$_c$), were adjusted for overdispersion according to the goodness-of-fit test ($\hat{c} = 1.83$)

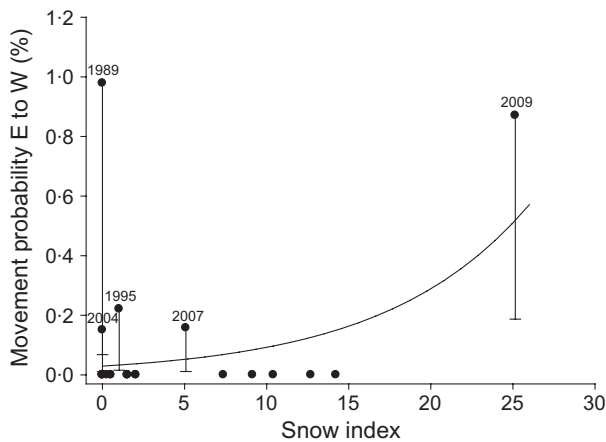| Model	Quasi-deviance	No. of parameters	ΔQAIC$_c$
Snow effect on movement from eastern to western	23055·2	104	0
Basic model	23058·6	103	1·4
Time-dependent movement from eastern to western	23047·9	124	33·1
Time-dependent movement from western to eastern	23051·7	125	38·9

Fig. 3. Estimated movement probability from eastern (E) to western (W) flyways as a function of the snow index. The line shows the modelled relationship from the covariate model. The symbols indicate annual estimates from the model with full temporal variation, with lower 95% confidence limits for the five estimates different from 0 (labelled with year). Confidence intervals are asymmetric, and upper confidence limits extend well outside the graph.

2010, when a total of 18 eastern individuals were resighted in Britain. For individuals with multiple observations within Britain within the same winter season, spring movements of eastern birds were all northwards. Figure 4 shows the suggested spring migration of four eastern pinkfeet. In total, at least seven eastern pinkfeet showed this migration pattern in spring 2010. Except for the Norwegian records, there were no resightings of the seven birds along the eastern flyway, and the northward movement within Britain strongly suggests direct flights from Britain to Norway. This is supported by the dates of the last resightings in Britain and the first resightings in Norway. Only one individual observed in south-east England during the winter 2009/2010 is known to have undertaken a stepwise return along the traditional eastern flyway. For the remaining 10 geese observed in Britain in 2009/2010,

we have insufficient resightings to unravel the likely spring migration route. In 2009/2010, eight of the 18 eastern geese observed in Britain were seen in the Oostende area in Belgium for the last time before being seen in Britain. Oostende is at the south-western limit of the wintering range of the eastern pinkfeet.

Four individuals marked in Denmark were observed during consecutive winters in Britain, but were also observed back in the eastern flyway after the first observation in Britain. Since none of these four birds were resighted in Iceland or Greenland (where resighting effort is very low), it is not possible to tell whether they followed the western population to the breeding grounds or returned to Svalbard every spring for breeding. However, two of them were resighted in Britain in successive winter seasons and subsequently observed in Norway in May in the same year, strongly suggesting Svalbard as the breeding ground. Of the four birds, three returned to Britain in early autumn, indicating that they made a direct autumn flight overseas from Svalbard/Norway to Britain. The remaining individual returned to Britain three times following the traditional flyway of the eastern population.

So far, only adult eastern pinkfeet (3 years or more) have been observed in Britain. No birds were exchanged in their second winter, even though *c.* 23% of the eastern pinkfeet were ringed as first winter birds.

West to east exchanges

Of the nine western birds observed in the eastern flyway, three were subsequently observed in the western flyway again. Three western geese were observed in the eastern flyway either during spring migration in Norway or during early autumn in Norway and Denmark, suggesting that they had spent the summer in Svalbard. Remarkably, two females ringed in Iceland in the summer of 2002 appeared in the Netherlands in February 2003. There are no further resightings of these two individuals from the breeding area, but their presence in the Netherlands at the reported time fits with the general winter strategy of the eastern population.

During the period of study, a single first winter bird, two-second winter birds and six adults crossed over from the western to the eastern population.

Discussion

The delineation of populations is an important prerequisite for the conservation and management of waterbirds. Taking the western Palaearctic swans, geese and ducks as an example, a total of 43 native species and subspecies breed and winter in the region, among which 21 occur as one defined population, while 22 species or subspecies occur in two or more (up to seven) defined populations (derived from Scott & Rose 1996; Wetlands International 2013). Our study is the first to quantitatively assess the rate of exchange between flyway populations of a western
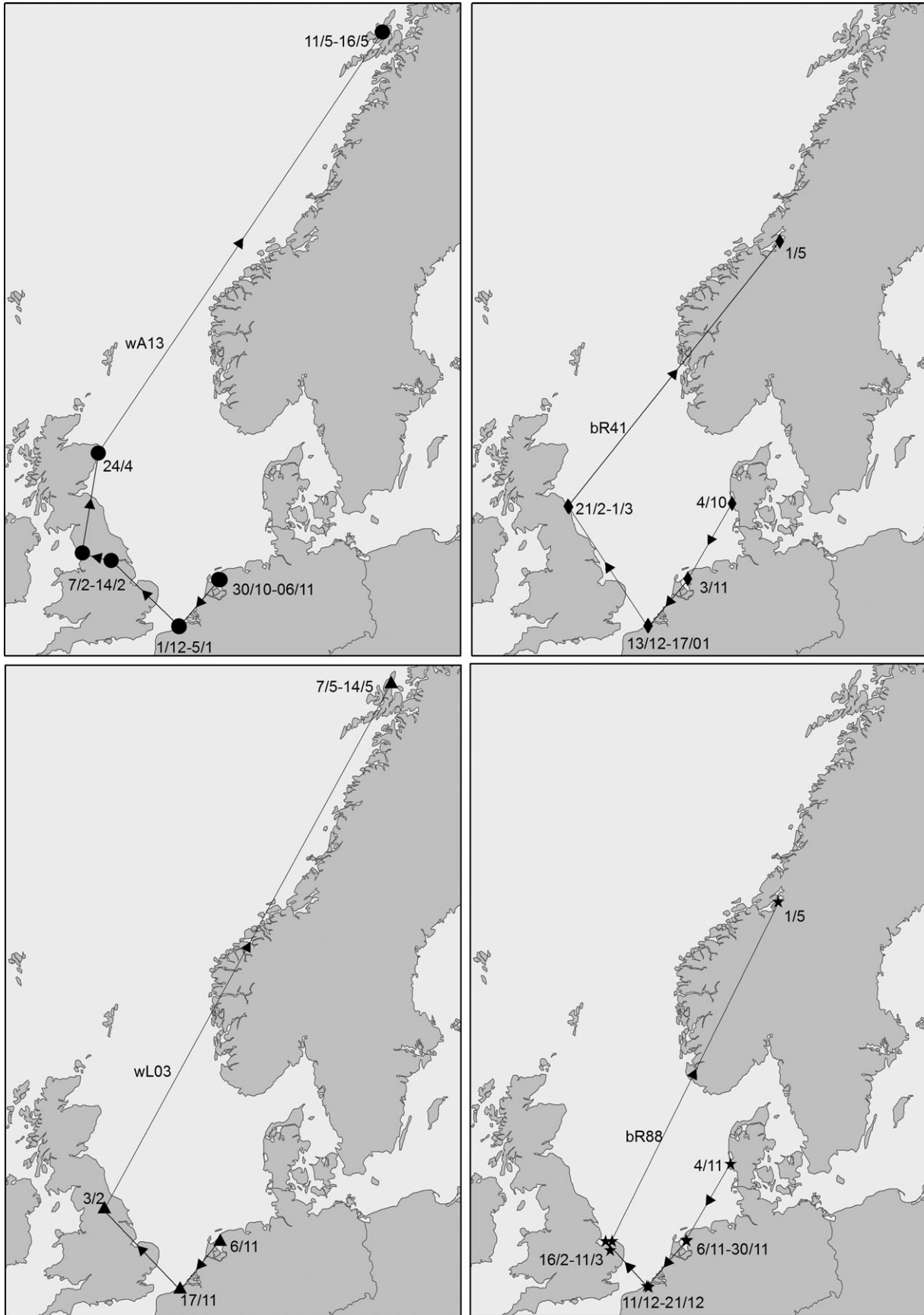
Fig. 4. Four cases of routes taken by pinkfeet marked in Denmark/Svalbard and switching to Britain in the winter of 2009/2010. Regional dates of first and last resightings are shown.

Palaearctic waterfowl species and the fate of individuals that switch. It is unique because we were able to make use of data from two recent marking and resighting schemes, coinciding in time and methodology, although not designed with a common purpose. Such parallel schemes have existed for other western Palaearctic goose populations as well (see Fox & Madsen 1999); however, except for a few long-term studies such as the barnacle goose *Branta leucopsis* (e.g. Owen & Black 1991), there is no sufficient information to perform quantitative analyses of exchange. Hence, for populations such as white-fronted geese *Anser a. albifrons* and greylag geese *Anser anser*, delineation of flyways and emigration/immigration rates remain unresolved. In the case of greylag geese, the current growth of populations and expansion of ranges, including re-established stocks in Scotland and continental Europe, blur the interpretability even further.

With regard to Palaearctic duck populations, the flyway delineations (Scott & Rose 1996) are generally based on more patchy data than for geese. For widespread species like teal *Anas crecca*, the proposed western Palaearctic flyways are regarded as doubtful (Guillemain, Sadoul & Simon 2005). At the extreme end of the spectrum, for mallards *Anas platyrhynchos*, which have a Holarctic distribution, genetic analyses based on mtDNA as well as nuclear markers have confirmed previous evaluations based on ringing (Scott & Rose 1996) that there is no clear population structure at least at the continental scale, suggesting that continental flyway populations cannot be defined (Kulikova *et al.* 2005; Kraus *et al.* 2011, 2013). Nevertheless, for practical management purposes, biogeographical 'stocks' have been defined both in the Old World (Delany & Scott 2006) and the New World (e.g. U.S. Fish & Wildlife Service 2012). In North America, adaptive harvest management operates with three stocks of mallards, justified by geographic differences in their reproduction, mortality and migrations, suggesting that there may be corresponding differences in optimal levels of sport harvest. The three stocks are defined by their non-overlapping breeding distributions, while it is recognized that there is some mixing in non-breeding areas. In contrast, in the western Palaearctic, stocks are defined on the basis of winter distributions (Scott & Rose 1996), which has no true biological justification, but is a pragmatic approach taken because this is where ducks are monitored (Delany & Scott 2006).

Throughout Europe, most dabbling duck ringing has been performed on staging, moulting and wintering grounds and not on the breeding grounds. Combined with the fact that most of the resulting data are ring recoveries of shot birds and not multiple resightings of marked individuals such as for geese, this makes it difficult to decipher flyways correctly. In order to derive a better description of migration systems, it is important that future ringing, tagging or molecular sampling focuses on the breeding grounds to which waterfowl are known to show natal and breeding-site fidelity; in ducks, notably among females (Anderson, Rhymer & Rohwer 1992).

For pinkfeet, the capture–resighting analyses showed that exchange of individuals between the two populations takes place, but is a relatively rare event. Because we restricted the quantitative statistical analyses to individuals for which we have three or more neck-band resightings in a season, and because of differences in resighting probabilities in the two flyways and at certain times of the season, the rates of exchange are minimum estimates. As hypothesized, exchange from east to west increased in winters with much snow extending to the south-western part of the winter range of the eastern flyway; however, the relationship was driven by the winter of 2009/2010, when there was a thick snow cover throughout the winter range from Denmark through to Belgium. Qualitative assessments from previous winters with extensive snow cover, for example, 1996/1997, support the results of the statistical analyses (Madsen *et al.* 1999). In the winters of 1996/1997 and 2009/2010, the geese moved all the way to the limit of the range in south-west Belgium before crossing over to Britain. Based on a rough extrapolation of exchange rates to population level and taking into account that the rates of exchange are minimum estimates, the exchange in cold winters could constitute hundreds if not thousands of individuals, perhaps >1% of the eastern population. The general winter climate in Britain is known to be more mild and wet compared to continental Europe, and eastern birds using Britain as an alternative winter ground in severe winters might not make a 'bad' choice moving westwards, which is common in waterfowl in continental Europe (Ridgill & Fox 1990).

In this study, all exchanged eastern birds with known destiny reappeared in the eastern population, suggesting no permanent emigration to the western population. Eastern birds seen in Britain either crossed back to Belgium or the Netherlands or showed northward movement within Britain with a suggested direct crossover from Britain to Norway (in 2009/2010). Hence, the movements do not appear to be erratic, and the geese appear to have knowledge of their whereabouts in Britain and can orient themselves back to their original flyway. Eastern and western pinkfeet most likely mix on the staging areas in Britain, and the departure towards Norway in a north-easterly direction probably takes place when western birds are on their way towards Iceland in a north-westerly direction. The apparent crossing of the North Sea from Scotland to Norway by several individuals suggests that this is an alternative migration route, particularly used following cold winters. The appearance of eastern birds in Scotland in autumn may be a sign of a migration route established by the same group of geese using the reverse route in spring (although this has not yet been confirmed by individually marked birds). The fact that the majority of exchanged individuals were older birds supports the suggestion that the exchanges are not erratic events (as might be expected if it were younger birds), or related to young mate-searching birds, but more likely to be an alternative winter strategy. Western geese switching to the

eastern flyway were not confirmed to emigrate on a permanent basis either.

At first glance, the capture–resighting analyses appear to support the genetic analyses, suggesting gene flow between the two populations and primarily from east to west (Ruokonen, Aarvak & Madsen 2005). However, detailed examination of the life histories of exchanged individuals raised some interesting questions about this interpretation. While the mtDNA-based genetic analysis suggested effective dispersal, that is, reproduction in the foreign population, the direct observations did not confirm this. There may be several reasons for this discrepancy:

1. The sampling of birds used for genetic analyses may accidentally have included birds from the eastern or western population that were temporarily visiting the foreign population, thus leading to a false expression of gene flow. However, in the genetic study, samples were taken in both of the two breeding and non-breeding ranges and the fact that haplotypes in Britain and Iceland (representing the non-breeding and breeding grounds of the western population) were similar contradicts this hypothesis and suggests that gene flow has occurred.

2. Dispersal takes place, but is not captured by the direct observations. Because resighting effort is very low in Iceland and on Svalbard, we cannot exclude that some foreign individuals have escaped observation and have bred in the 'wrong' flyway.

3. The genetic analyses estimate gene flow in a historic time perspective, while the mark–resightings express the current situation of exchange. Hence, in a longer time perspective, there has been effective dispersal between the two populations.

It should also be borne in mind that the statistical analyses based on the mtDNA genotype frequencies have their limitations in quantifying population structure and gene flow (e.g. Abdo, Crandall & Joyce 2004). With the recent advances in the use of molecular markers and population genomics, analytical options have now become much more powerful, and exchange can be measured directly, potentially assigning individuals to their parents (Broquet & Petit 2009). For the moment, we conclude that in terms of present demography, the two populations of pinkfeet are virtually closed, although they partially overlap in time and space, particularly following cold winters, but there is a genetic connectivity due to low levels of dispersal (earlier or present) between populations. Higher future rates of exchange will not necessarily imply a higher genetic mixing of the two populations, because individuals are likely to find their way back to their original flyway. More regular exchange may lead to the evolution of alternative migration routes, for example, birds migrating from Svalbard via staging sites in Norway across to wintering sites in Britain.

PERSPECTIVES AND IMPLICATIONS FOR MANAGEMENT

In relation to the current plans to introduce adaptive harvest management of the Svalbard population of pinkfeet (Madsen & Williams 2012), this study shows that there is no imminent need to consider emigration and immigration in demographic models that are developed to predict an optimal harvest. In the case of cold winter movements to Britain, eastern geese may be exposed to additional harvest mortality; in Britain, the inland hunting season closes on 31 January and shooting on the foreshore closes on 14 February, while pinkfeet are fully protected in Belgium and the Netherlands and have a hunting season in Denmark closing on 15 January. However, even at the current peak rates of exchange (in total up to a few thousand individuals), harvest in Britain is unlikely to have a critical impact at the population level.

In essence, existing information about the connectivity of western Palaearctic flyway populations is insufficient for population management, except for taking a very prudent conservation approach. The majority of marking schemes for waterbirds in Europe have been set up by individual researchers or teams, rarely coordinated between flyway populations and mostly without a clearly stated purpose to underpin management. Several of the marking schemes on geese, ducks and swans have been difficult to maintain in the long term and thus cannot help explain recent dramatic changes in population sizes and ranges. There is a growing wish to internationally coordinate management of waterbirds in Europe and in the African-Eurasian region, as manifested by the recent strategy of the African-Eurasian Waterbird Agreement (AEWA 2008). This is exemplified with the international management plan for the Svalbard population of pinkfeet (Madsen & Williams 2012) and plans in progress for cormorants *Phalacrocorax carbo* (Behrens, Rauschmayer & Wittmer 2008). If this approach is to be applied more widely, there is an urgent need to rethink waterbird marking schemes, to design and sustain them in order to better underpin management needs.

New population genomic tool kits give promise for making quick and cost-effective advances in understanding population structures and dispersal, such as has been shown for mallards *A. platyrhynchos* (Kraus *et al.* 2013). Future studies should take advantage of combining the classic and the molecular tools. As demonstrated for pinkfeet, the combination of methods leads to supplementary insights, which would otherwise not be possible.

Genetic analyses in pinkfeet and North American mallards show gene flow, while demographic analyses give justification for separation in stocks or demographic populations. In both cases, a demographically based population definition is needed for current management planning, while for longer-term conservation of the species, the genetic definition has more bearing. We recommend that to support management decisions at population levels, future studies of connectivity should use classic marking in combination with molecular methods and focus sampling on waterbird breeding grounds.

Acknowledgements

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Supporting Information

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

Appendix S1. Estimate rate of exchange.

Table S1. Initial model selection of survival and encounter probabilities.

Fig. S1. Overview of the ringing data used for the analysis.