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Patterns of spatial distribution and migration phenology of common pochards *Aythya ferina* in the Western Palearctic: a ring-recoveries analysis

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We used ringed-recoveries to assess: 1) the connectivity (movements of individuals) between the three putative flyways (north–west Europe, central Europe, south–west Asia) of common pochards in the Western Palearctic, 2) possible spatio-temporal variations in the distribution of the species, and, 3) temporal evolution in spring and autumn migration dates. Based on winter counts of common pochards in the north–west European flyway, we distinguished three periods in the analyses (1960–1990, 1991–2000 and 2001–2016), which correspond to successive periods of population increase, peak and decline, respectively. Whatever the season (wintering or breeding) and period of ringing, large probabilities of ring-recoveries outside the flyway of origin (ringing) were recorded, suggesting a high connectivity between the three putative flyways. There was a significant trend towards an earlier departure from the wintering area, and an eastward shift of spring recoveries over periods. In contrast, neither autumn/winter recovery locations, nor departure dates from the breeding area in Latvia and Russia changed over periods. The latter results do not support the hypothesis that short-stopping (i.e. a reduction of fall migration distances/delaying of departure dates from the breeding area) could explain the observed decline of wintering common pochards in the north–west European flyway. Indirect recoveries support that large proportions of individuals wintering in western Europe may originate from the south–west Asia flyway and more particularly from a region in Siberia located in the Ob river catchment area. Considering trends in numbers for the three flyways together confirmed the "vulnerable" IUCN status of common pochard in the Western Palearctic as a whole, with a 35% decline over the last decade. The important connectivity between the northwest, central European and southwest Asian flyways call for considering such conservation problems at a much broader scale than the regional flyway.

Establishing the link between breeding and non-breeding areas is a prerequisite for delineating management units and implementing sustainable management policies (Williams and Johnson 1995, Webster et al. 2002). The conservation status of waterfowl populations is currently established at the flyway level (BirdLife International 2015), which is defined as "the entire range of a migratory bird species (or groups of related species or distinct populations of a single species) through which it moves on an annual basis from breeding areas to non-breeding areas, including intermediate resting and feeding places as well as the area within which the birds migrate" (Boere et al. 2006). The first authors having delineated flyways in the Western Palearctic stressed that they should not be considered "impermeable" from each other, implicitly raising the potential risk of using them as management units (Isakov 1967, 1976, des Clers 1976, see also Scott and Rose 1996). Moreover, population boundaries can change over time, owing to factors like climate or habitat change (Knick and Rotenberry 2002, Huntley et al. 2007), which has led some authors to stress the need of re-evaluating flyway delineations on a regular basis (Madsen et al. 2014). Re-assessing migratory connectivity in a rapidly changing world and therefore flyways delineation is important because it can result in changes in IUCN conservation statuses and associated management and conservation policies (Cao et al. 2010, Ramesh et al. 2017).

The common pochard is a partial and differential migratory (Lundberg 1988) freshwater diving duck, in which one fraction of the population is migratory and the other sedentary (Gourlay-Larour et al. 2013) and females migrate farther south than males (Carbone and Owen 1995). Its breeding range extends from western Europe through central Asia to south-central Siberia and northern China, and the bulk of the population spends the winter throughout Europe, north

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Africa, the Mediterranean, Black and Caspian Seas and Asia (Kear 2005). Three flyways have been initially recognised in the Western Palearctic (Scott and Rose 1996) based on ring recoveries, species' distribution and expert opinion (Isakov 1967, des Clers 1976, Atkinson-Willes et al. 1980): northwest Europe (hereafter NWE flyway), central Europe/Black Sea/Mediterranean (hereafter CE flyway), and southwest Asia (hereafter SWA flyway) (Fig. 1a–c).

Since the middle of the 18th century, the common pochard has experienced a significant expansion of its breeding range north- and westwards towards Scandinavia and northwestern Europe and, in the past twenty years, spread into Mediterranean countries including the Maghreb region (Fox et al. 2016). The number of wintering individuals in the NWE flyway has been gradually increasing during the second half of the 20th century as the breeding range expanded. Recently, however, a dramatic decline in the number of wintering individuals has been recorded in most countries of this flyway (Nagy et al. 2014). This decline raises concern about the status of the species as a whole, which is now considered as endangered in Europe (BirdLife International 2015), as well as questioning the drivers of population trajectory. A recent review indicates a marked decline of both the number of breeding birds and breeding success at the European scale, particularly in Scandinavia and central Europe (Fox et al. 2016). Such declines on the Scandinavian and central European breeding areas have been supposed to be among the main drivers of the observed decline in numbers of pochards wintering in the NWE flyway. However, an alternative hypothesis would be that the observed declining trend in wintering numbers could results from a northeastward shift of the wintering population in response, for example, to global warming (winter short-stopping, sensu Elmberg et al. 2014), with birds gradually evading the counts in the NWE flyway to an increasing extent over time as they remain in the other flyways. In other words, as observed in other European or North American migratory birds, climate and habitat changes over the past decades could have allowed common pochards to spend a greater share of the annual cycle in formerly inhospitable areas (Schummer et al. 2010, Guillemain et al. 2013, Lehikoinen et al. 2013, Elmberg et al. 2014, Notaro et al. 2016) of the north-eastern parts of the distribution range, through earlier spring migration, colonization of breeding areas further east or northeast, and delayed autumn migration.

The major aim of the present study was to use the most recent ring-recovery databases in order to update our knowledge about the spatial distribution and movements of common pochard *Aythya ferina* populations of the Western Palearctic and therefore assess the pertinence of flyway delineation (Madsen et al. 2014). We also assessed whether temporal changes in the spatial distribution of ring-recoveries could provide some clues about the observed decline of the wintering population of common pochards in western Europe, keeping in mind that the observed patterns could either reflect changes in the distribution of birds or changes in hunting pressure, or both. Another aim of our study was to address the question of possible changes in migration phenology seeking, for example, to assess whether 'short-stopping' during the fall phase of migration could account for the observed decline of the population of wintering in NWE flyway. To address these questions, we used ring-recoveries of individuals ringed during both the wintering and breeding season in countries of the NWE flyway (European countries and countries of the former USSR) from 1960 to 2016.

Methods

This study relies on two ring recovery databases. The largest one, which was provided by Euring (<www.euring.org/>), covers the period 1960–2016, whereas the second dataset is part of an ongoing diving duck capture–mark–recaptures/recoveries programme initiated in France in 2004 (Guillemain and Caizergues 2010). Together, these datasets provided a total of 7078 ring-recoveries at 278 sites throughout the species' distribution range. Dead-recoveries of individuals known to suffer from any illness, crippled, injured or killed during handling and those whose cause of death was unknown were removed from the analyses in order to minimize possible biases. Throughout the paper, flyway delineations are those suggested by Scott and Rose (1996).

Three ringing periods (1960–1990, 1991–2000 and 2001–2016) were distinguished based on of the results of a segmented regression analysis (R package 'stucchange', Zeileis et al. 2001) of common pochard January counts in the NWE flyway (respectively increase, population peak and decrease, Fig. 2). Strictly speaking, however, the apparent increase in numbers of common pochards counted in winter in NWE flyway during the first period (1960–1990) may reflect an increase in sampling effort (number of sites counted) rather than an increase of the size of the wintering population, at least until the mid-1980s. In contrast, both, the peak in numbers in the 1990s (second period) and the decrease since the beginning of the 21st century (third period) likely represent a "demographic" reality (Wetlands International 2017).

The probability of recovering an individual ringed in the NWE flyway in the different flyways, and, possible shifts in the average position (average longitude) of ring-recoveries during breeding and wintering were compared over these three periods. In order to minimise possible biases due to changes in hunting pressure over space and time, only months and countries in which hunting took place over the entire study period (1960–2016) were kept in the analyses. Our analyses are therefore based on a total of 5491 ring-recoveries (see Table 1 for details). Spring (April–May) and autumn–winter (September–January) hunting have remained legal over the entire study period in countries of the former USSR (Russia, Belarus, Ukraine and Kazakhstan) and countries of the European Union (Spain, France, Italia, Belgium, United Kingdom, Ireland, Germany, Denmark and Poland), respectively. Nevertheless, we cannot totality exclude that changes in hunting pressure or ring-reporting rates occurred between periods, months, or countries, and hence could somewhat bias the location of recoveries (Korner-Nievergelt et al. 2010). However, by considering only months and countries where hunting remained legal throughout the 56 years of the study, we can assume such potential biases were minimized, although the results should still be interpreted with caution concerning this aspect. Data concerning possible variations

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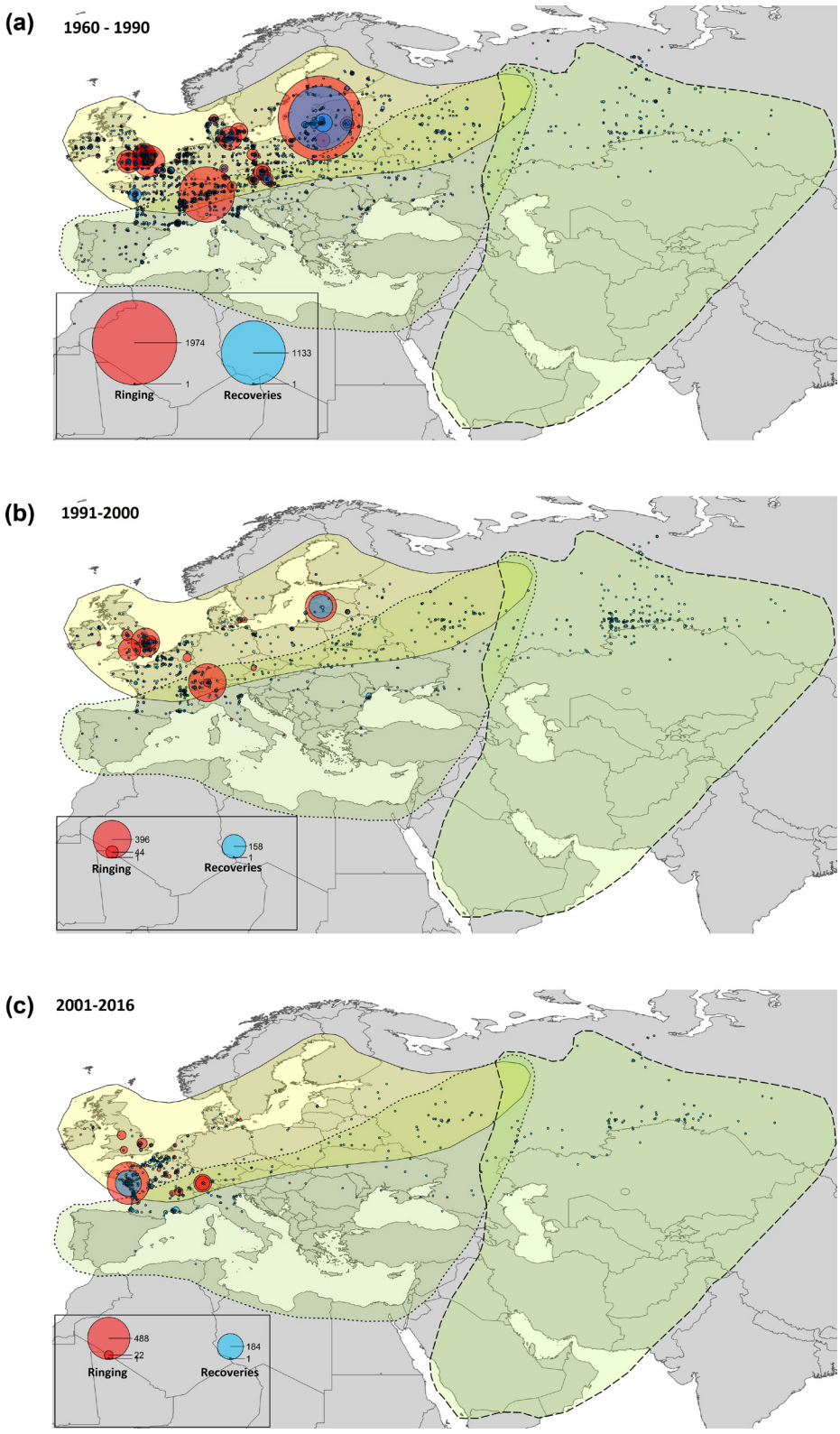


Figure 1. The three putative common pochard flyways in the Western Palearctic, delimited by Scott and Rose (1996), together with ringing (red circles, proportional to numbers of individuals ringed by site) and recovery (blue circles, proportional to numbers of recoveries for by site) locations of individuals ringed during the three studied periods: (a) 1960–1990; (b) 1991–2000; and (c) 2001–2016 in the NWE flyway. Ringing sites in the Eastern part of the range (east-central Europe, Latvia and former countries of USSR) are sites where individuals have been ringed exclusively during the breeding season. — NWE, ···· CE and ---- SWA flyway limits.

in hunting pressure (number of validated hunting licenses, hunting bags and more importantly number of ducks actually exposed to hunting) were eventually available for the most recent period (2001–2016) and for a limited number of countries and seasons only (reviewed by Guillemain et al. 2016). It was therefore not possible to properly address

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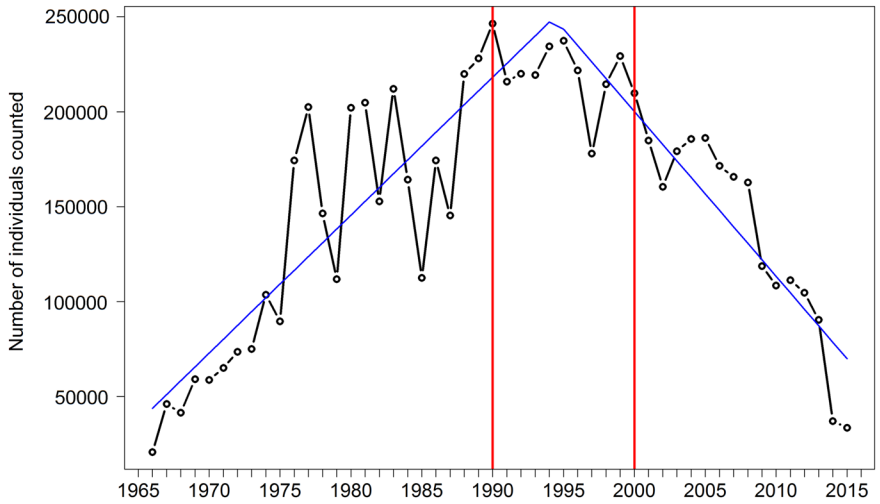


Figure 2. Changes in numbers of wintering common pochards counted in NWE flyway from 1960 to 2016 (Wetlands International 2017), along with the three periods (red lines) delimited thanks to a segmented regression analysis (blue line), considered in our analyses of ring recoveries (increase 1960–1990; peak 1991–2000; decline 2001–2016).

the issue of possible changes in hunting pressure properly. Furthermore, the bulk of the dataset included only those individuals having been recovered, and, in many instances, data concerning ringed (but not recovered) individuals were simply not computerised meaning that possible variations in recovery or reporting rates (Potvin et al. 2017) could not be assessed. Finally, despite repeated effort, we were not able to gather ringing data from Russia and Latvia, although these data were probably computerised.

Finally, because both the date and the location or ringing may affect the date and the location of ring-recoveries we assessed whether these variables changed significantly over time using linear regressions.

Migratory connectivity and its temporal dynamic

The probability that an individual ringed in the NWE flyway was latter recovered in the same flyway, or one of the other two (the CE and SWA flyways), as well as possible changes of this probability over time, were assessed by computing the number of individuals ringed in the NWE flyway (including the overlapping zone with CE flyway) and later recovered in each of the three flyways for each of the three periods considered (Fig. 1). Recoveries of individuals caught in winter and during the breeding season were considered separately in the analyses, as well as direct (i.e. recoveries made during the same ringing season) and indirect recoveries (i.e. recoveries made during the following seasons). To avoid that individuals recovered in the overlapping zone between flyways be ascribed to more than one flyway, data were processed as follow: all individuals recovered in the NWE flyway, including the overlapping areas with the CE and with the SWA flyways, were exclusively ascribed to this flyway, whereas the ascription to the CE flyway excluded individuals recovered in the overlapping zone with the NWE flyway but included the overlapping area between the CE and SWA flyways. Ascription to the SWA flyway excluded individuals in the overlapping zones with both the NWE and CE flyways.

Changes in the probabilities of recoveries (of pochards ringed at the NWE flyway) in the three different flyways over time (periods), according to the type of recovery (direct versus indirect recoveries) and the season of ringing (wintering versus breeding season) were tested simultaneously using a multinomial logistic regression in a Bayesian framework (Dey et al. 1999, R code available in Supplementary material Appendix 1). Convergence was assessed using the Gelman–Rubin convergence diagnostic (Gelman and Rubin 1992). Estimation of parameters were derived every ten MCMC samples from 1 000 000 iterations after a burn-in procedure of 100 000 iterations.

Table 1. Number of recoveries of common pochards ringed during the breeding (former USSR and Latvia) and wintering (Denmark, Germany, Switzerland, United Kingdom, Netherlands, Sweden, Italia, Czech Republic, France, Belgium and Poland) seasons in the NWE flyway, per period (1960–1990: population increase, 1991–2000: population peak, 2001–2016; population decrease).

	Season of ringing	
Period of ringing	Wintering	Breeding
1960–1990	1581	2199
1991–2000	881	206
2001–2016	616	8

Changes in recovery locations over time

Possible changes in the longitude of recoveries over time (periods) were assessed in two steps using Kolmogorov–Smirnoff tests. In a first step, we assessed temporal changes in the longitude of recoveries performed during the breeding season (April–May) in countries where hunting took place over the whole study period (Russia, Belarus, Ukraine and Kazakhstan) for individuals ringed during the wintering season (October–February) in the NWE flyway (mostly France, United Kingdom, Switzerland). Then, we assessed temporal changes in the longitude of recoveries during winter (September–January) in countries of western Europe where hunting took place over the whole study period (Spain, France, Italia, Belgium, United Kingdom, Ireland, Germany, Denmark, Poland) for individuals ringed during

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the breeding season (April–July) in Latvia and Russia. It should be noted that only the ringing sites located in the NWE flyway were considered in these analyses.

Temporal changes in migration phenology

Temporal changes in the phenology of migration were assessed by calculating the proportions of individuals "having left their wintering area" following the method in Guillemain et al. (2006) whereby an individual was considered to have left its wintering area when it was recovered more than 200 km east from its winter ringing site. The proportion of such individuals was computed for each month and each of the three periods separately. We then tested for possible changes in the migration initiation date (month) over the three periods of the study using general linear mixed modelling with a random effect on the ringing sites (R ver. 3.3.3, <www.r-project.org/>). A total of 1490, 870 and 635 recoveries for the first (1960–1990), second (1991–2000) and third (2001–2016) periods were considered, respectively. The main aim of this analysis was to assess possible advancement/delay of migration departure/return dates (months) over the study period.

Results

Dates of ringing did not display any particular trend over time (linear regression, $t=0.125$, $p=0.9$). In contrast, there were trends towards temporal decreases in both the latitude and longitude of ringing (linear regressions, $t=-6.471$, $p < 0.001$ and $t=-6.157$, $p < 0.001$, respectively). Fortunately, these changes in ringing locations were moderate (less than 250 km over the whole study period) and within the range of movements commonly observed during winter in this species (Gourlay-Larour et al. 2012). Nevertheless, possible biases due to these changes in ringing sites locations over time were minimised by including the effect of site as a random variable in the analyses.

Most recoveries were recorded within the limits of the three known flyways, although some individuals were recovered further east (Fig. 1). Whatever the period, the distribution range of common pochard, inferred from the cloud of recovery dots, tended to stretch at mid-latitude along a well-marked north-eastern–south-western axis largely encompassing the three putative flyways (Fig. 1). One can also notice that an area located at the northern border of Kazakhstan, in the region of the Ob river, yielded numerous recoveries especially during the second period of the study (1991–2000) which corresponds to the peak of abundance of the common pochard population wintering in the NWE flyway (Fig. 1b).

Migratory connectivity and its temporal dynamics

Whatever the season/area of ringing, most of direct recoveries were recorded close to the ringing site in the flyway of origin (NWE flyway) with a probabilitly always above 0.85 (range 0.855–0.959, Table 2). The probability that a direct recovery was recorded outside the flyway of ringing (the NWE flyway) was low except for individuals ringed during winter and recovered in the CE flyway (range 0.097–0.13). In contrast to direct recoveries, the probabilities for indirect recoveries to be recorded outside the NWE flyway were relatively high (Table 2), especially for those individuals ringed in winter during the second period (1991–2000), which had a 0.28 probability of being recovered in the SWA flyway (see also Fig. 1b). Overall

Table 2. Recovery probabilities of common pochards ringed in NWE flyway during the breeding (USSR and Latvia) and wintering (Denmark, Germany, Switzerland, United Kingdom, Netherlands, Slovenia, Italia, Czech Republic, France, Belgium and Poland) seasons, by flyway (NWE: north–west European, CE: central European, SWA: south–west Asian), period (1960–1990: population increase, 1991–2000: population peak, 2001–2016; population decrease) and type of recovery (direct: current season versus indirect: subsequent seasons).

Ringing season	Recoveries	Period	NWE (SD)	CE (SD)	SWA (SD)
Breeding	indirect (subsequent seasons)	1960–1990	0.894 (0.015) n=349	0.088 (0.014) n=34	0.018 (0.007) n=6
		1991–2000	0.798 (0.044) n=50	0.080 (0.026) n=6	0.122 (0.034) n=8
		2001–2016	0.771 (0.093) n=4	0.126 (0.063) n=1	0.103 (0.071) n=0
	direct (current spring)	1960–1990	0.957 (0.005) n=1726	0.041 (0.005) n=76	0.002 (0.001) n=2
		1991–2000	0.959 (0.013) n=138	0.034 (0.012) n=4	0.007 (0.006) n=0
		2001–2016	0.931 (0.044) n=3	0.037 (0.023) n=0	0.032 (0.036) n=0
Winter	indirect (subsequent seasons)	1960–1990	0.765 (0.012) n=924	0.141 (0.010) n=171	0.094 (0.008) n=112
		1991–2000	0.574 (0.019) n=393	0.146 (0.013) n=99	0.28 (0.017) n=190
		2001–2016	0.686 (0.025) n=230	0.169 (0.020) n=58	0.145 (0.019) n=49
	direct (current winter)	1960–1990	0.869 (0.017) n=311	0.129 (0.017) n=47	0.003 (0.003) n=0
		1991–2000	0.855 (0.024) n=160	0.130 (0.023) n=27	0.015 (0.008) n=2
		2001–2016	0.895 (0.018) n=246	0.097 (0.017) n=26	0.007 (0.005) n=1

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therefore, whatever the period, there was a strong probability for individuals ringed during the wintering season in the NWE flyway to be recovered in another flyway, including the farthest one (SWA flyway, Fig. 1, Table 2). If we exclude the peak of indirect recoveries in the SWA flyway in the second period (1991–2000), which matched the historic peak in numbers of common pochards wintering in the NWE flyway, no temporal trend could be detected.

Changes in recovery locations over time

There was a trend towards an eastward shift over periods concerning spring recoveries of individuals ringed during winter in western Europe (Fig. 3), but the difference in average longitudes was statistically significant between the last two periods only (1991–2000 and 2001–2016; $D = 0.18823$, $p = 0.0404$). In contrast, autumn and winter recoveries of individuals ringed during the breeding season in former USSR and Latvia did not display any particular temporal pattern ($D = 0.12192$, $p = 0.8516$) (Fig. 4). One should notice that no data was available for the last period considered (2001–2016) due to the cessation of hunting in these breeding areas.

Temporal changes in migration phenology

The GLMM analysis revealed significant effects of month (third order polynomial effect) and year of recovery (plus their interaction) on the proportion of individuals ringed in western Europe and later recovered more than 200 km eastwards to their ringing site (R^2 marginal = 0.36 and R^2 conditional = 0.46) (Fig. 5, 6, Supplementary material Appendix 2). From April to September more than 80% of individuals were recovered more than 200 km eastwards from their ringing site, indicating a non-local origin of most individuals wintering in western Europe (Fig. 5). Conversely, December and January were always the months with the lowest proportions of such individuals (range 19 to 34% depending on the month and the period).

September to November were the months when the greatest decreases in the proportion of individuals recovered more than 200 km eastwards were observed (Fig. 5), which matches the known periods of autumn migration towards south-western countries in this species. Conversely, the greatest increases in the proportion of individuals recovered more than 200 km eastwards from their ringing site were recorded from January to March, indicating an initiation of spring migration at that time of the year (Fig. 5). There was also a significant effect of Year and Month × Year, which was mainly due to greater proportions during spring and summer (increasing share of non-local birds in the dataset) and a steeper increase from January to March, suggesting an advancement in the date of spring migration (Fig. 6).

No particular trend could be detected concerning the temporal evolution in the proportions of individuals recovered eastwards during the period of autumn migration (Fig. 6). The results of the present analysis, therefore, do not support a delayed departure from the breeding area as predicted by the short-stopping hypothesis.

Discussion

Migratory connectivity and the potential large proportion of 'easterners' into the population wintering in western Europe

The notion of flyway permeability or connectivity refers to individuals changing flyway in the course of their life (Madsen et al. 2014). Numerous studies not only showed that connectivity between flyways was relatively high in many bird species including ducks, but also that the contribution of individuals breeding in the eastern parts of the Western Palearctic could be substantial (Guillemain et al. 2005, 2017, Calenge et al. 2010, Kraus et al. 2011, Shephard et al. 2013).

In the present study, the origin (breeding site or area of birth) of individuals ringed during the wintering season,

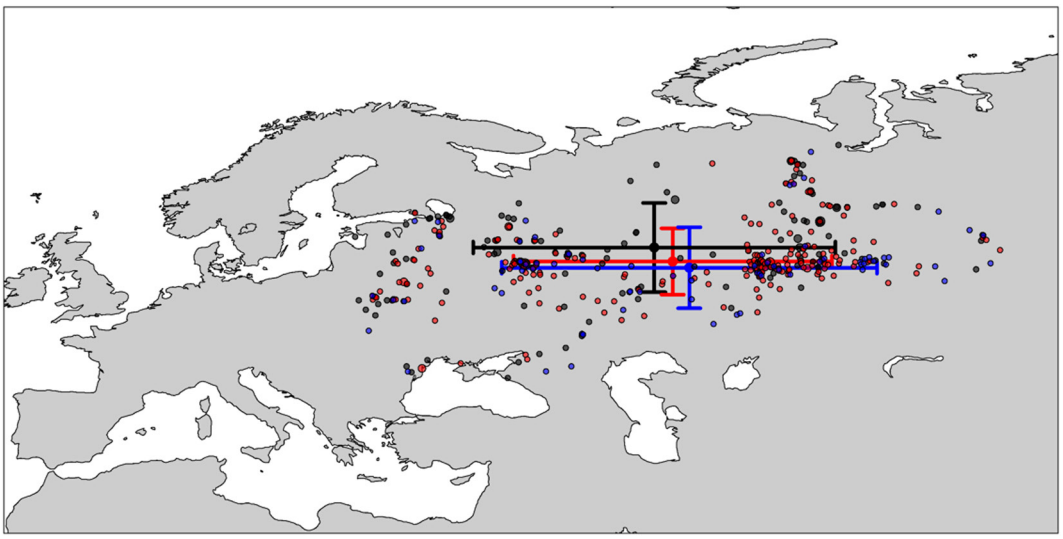


Figure 3. Average (± SE) spring recovery locations of common pochards ringed in western Europe and later recovered in countries of the former USSR where hunting was allowed over the entire study period (Russia, Belarus and Kazakhstan). Black, red and blue colours stand for recoveries in the periods 1960–1990; 1991–2000 and 2001–2016, respectively.

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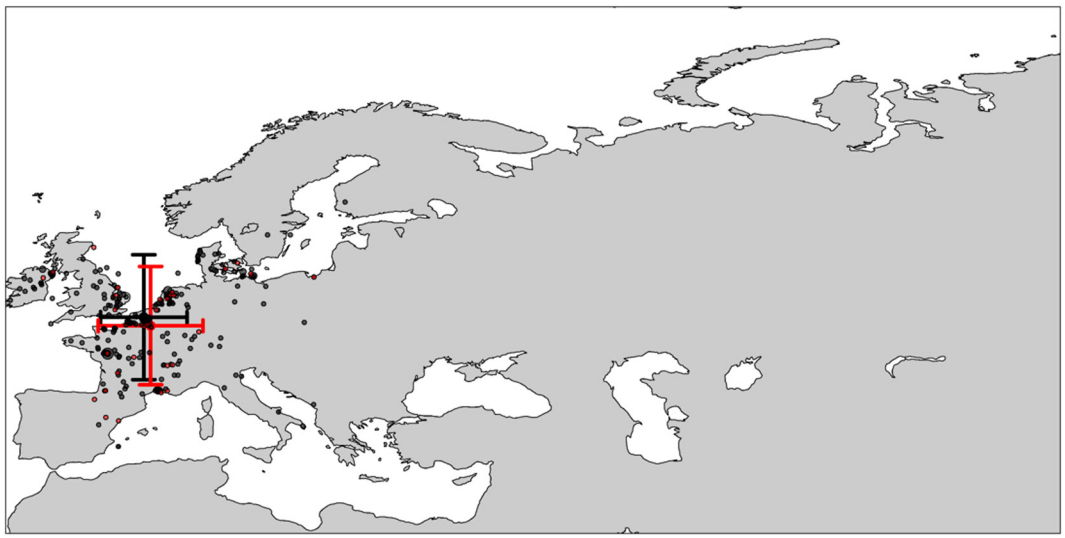


Figure 4. Average (± SE) autumn and winter recovery locations of pochards ringed in the former USSR and Latvia, and later recovered in western Europe in countries/months where hunting was allowed over the entire study period. Black and red colours stand for recoveries in the periods 1960–1990 and 1991–2001, respectively.

and the destination (wintering area) of those ringed during breeding were known for a limited number of individuals only, meaning that we did not assess flyway permeability/connectivity directly in most cases. Nevertheless, as suggested by our data about the probability of being recovered outside the NWE flyway, a substantial proportion of the individuals wintering in this flyway may have been originated from the CE or the SWA flyway, indicating a high degree of connectivity between the three putative flyways. Following previous findings based on ringing recoveries data (Hofer et al. 2006, Viksne et al. 2010), one can therefore recommend that treating common pochard populations of the Western Palearctic as three different management units/flyways should be considered carefully. The first scientists having delineating waterfowl flyways highlighted that these should not be regarded as perfectly closed (sub) populations (Isakov 1967, 1976, des Clers 1976). This led Scott and Rose (1996) to stress that "no discrete populations are identifiable, and it is very doubtful if any such populations exist". However, because it is so convenient for management, their flyway maps have gained foothold over the years (Kuijken 2006), and still serves as the only basis for the definition of managements units (Wetlands International 2017). Without disregarding the quality of their work and the usefulness of such a map, our message is that exchanges between putative flyways should not be neglected, and additional analyses at the scale of the entire species range should be conducted when relevant. As a recent study on pink-footed geese *Anser brachyrhynchus* suggests, the solution for defining management units may reside in the compilation of different sources of data (ring recoveries/CMR, population genetics, isotopes, Madsen et al. 2014). Concerning common pochard, currently available data include genetic markers (Sruoga et al. 2009, Liu et al. 2011), isotopes (Caizergues et al. 2016), and ring recoveries (Hofer et al. 2006, Keller et al. 2009, Viksne et al. 2010, Gourlay-Larour et al. 2012, 2013); all

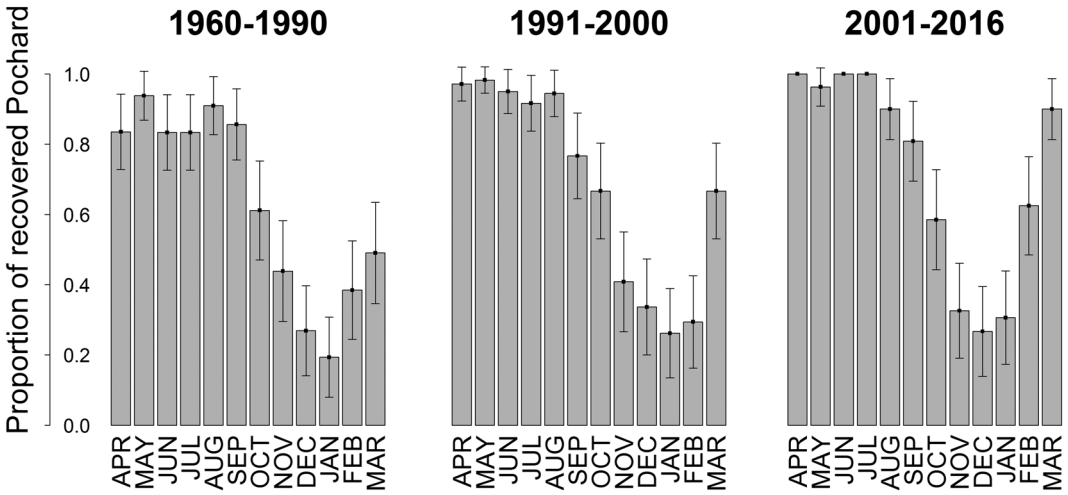


Figure 5. Average proportions (± SE) of pochards recovered more than 200 km eastwards from their ringing site, computed for each month and for the three study periods.

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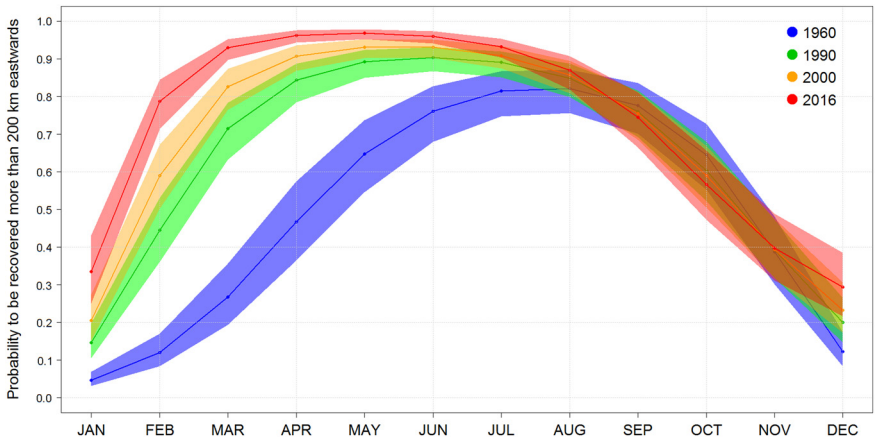


Figure 6. Predicted probabilities for a common pochard to be recovered more than 200 km eastwards from its ringing site over months and year, derived from the GLMM best model assessing the effects of months and periods on the proportions of migrants and taking into account the random effect of 'Ringing site'.

support extensive movements among populations in the Western Palearctic. Moreover, isotopes and ring-recoveries also suggest that the bulk of the population wintering in western Europe may originate from the northern and eastern parts of the species' range (Scandinavia, Kazakhstan, western parts of the Ural mountains) (Caizergues et al. 2016, present study).

We could be tempted to make the link between the temporal variations in the indirect recoveries probabilities in the SWA flyway and the observed variations in numbers of common pochard wintering in the NWE flyway. However, other factors such as changes in hunting pressure or ring-reporting rates, which could not be assessed in our study, may account for the observed patterns too. Nevertheless, one of the most interesting results of the present study was the large proportion of individuals recovered in the SWA flyway in the sample of indirect recoveries (up to 28%). Moreover, most of these recoveries were recorded in an area located at the East of the Ural mountains, close to the border between Russia and Kazakhstan, in a triangle formed by the Tobol and Irtysh rivers (northern parts of the river Ob catchment area, Fig. 1, Table 2). Interestingly, this area includes among the highest densities of ponds and floodplains found in the common pochard distribution range, but it is also characterised by much lower human densities than in western Europe (range 0.63 to 40 inhabitant km^{-2} against on average 114 inhabitant km^{-2} in France, <www.mapsofworld.com/russia/thematic-maps/population-density-map.html>) and probably a lower hunting pressure too. Therefore, we argue that studies relying on hunting recoveries, like the present one, may underestimate the true contribution to the wintering population of western Europe of individuals coming from such 'depopulated' areas. If this conjecture is true, one cannot rule out that the decrease in numbers of individuals in the NWE flyway, may be related to problems having affected this region of high duck productivity/density: intensification of irrigation, drought, changes in flooding regimes due to decreasing snowfall in the Altai mountains, water pollution due the intensification of gas/petroleum exploitation (Petr and Mitrofanov 1998, Hrkal et al. 2006, Papa et al. 2007, Bartsch et al. 2008). As all possibilities should be considered, ringing and counts effort therefore should be improved in this area, especially because common pochards are relatively abundant during the breeding season in this region (Ravkin 1978, Gavrilov 1999).

The lack of evidence for short-stopping

Due to the scarcity of ringing data from the eastern part of the Western Palearctic, especially during the 2001–2016 period, it was not possible to fully assess the short-stopping hypothesis as an explanation to the decline in wintering pochard numbers in western Europe. Nevertheless, we detected no change in the average longitude of individuals between the first two periods (1960–1990, 1991–2000), which had ample sample sizes. Moreover, there was no evidence that individuals tended to delay autumn migration, since the gradual decrease in the proportion of recoveries more than 200 km to the east of the ringing site was consistent over the three time periods. The results of our study therefore suggest that the decline in the numbers of common pochards counted during wintering in the NWE flyway is not the mere reflection of an increasing trend for these birds to winter further east, potentially into another flyway. One might be tempted to ask why we did not use the capture–mark–recapture (CMR) approach instead of comparing distances and departure dates, on the premises that it would have allowed tackling the problem of spatio–temporal differences in sampling effort (hunting pressure). Unfortunately, the CMR approach does not help tackling such problem of sampling effort. Indeed, although recoveries/recaptures may vary in space and time (Madsen et al. 2014), there is no simple way to assess if these variations reflect changes in hunting pressure rather than changes in the distribution of individuals. To tackle this problem, one must possess either data on numbers and spatial distribution of individuals (including on the breeding area, which is not available at this geographic scale for ducks) or data on numbers and spatial distribution of observers (hunters), which is not available either. Only under such conditions could the CMR approach prove more powerful and flexible than the approach we opted for in the present study. Moreover, the fact that ringing effort was not known concerning the bulk of the dataset available to us (Euring data, only comprising the ringing information of the

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birds that later were recovered) precluded using the CMR approach in a convenient way.

Concerning spring, there was conversely a trend towards an eastward shift of ring recoveries, as well as a significant advancement in migration. In many bird species, advanced spring migration have been recorded, which may directly or indirectly result from the effects of climate or habitat change (Hughes 2000, Walther et al. 2002, Crick 2004, see Guillemain et al. 2013 or Lehikoinen et al. 2013 specifically for ducks). Such changes may enhance intra-specific competition for the best breeding sites (Miller-Rushing and Lloyd-Evans 2008). Since breeding success is positively related to an earlier date of laying initiation in ducks, advancing spring migration may provide a substantial gain in terms of fitness (Dzus and Clark 1998, Elmberg et al. 2005, Öst et al. 2008, Folliot et al. 2017). We cannot ascertain that patterns of change in the distribution of ring recoveries only reflect changes in the distribution of common pochards, and are not partially affected by possible changes in hunting pressure over space and time. As explained in the methods section, we have taken a series of measures to limit such biases caused by ring recovery probability, in particular by only considering regions and months when hunting has remained a legal activity throughout the 56 years of our study period. Nevertheless, hunting pressure could still have increased in the eastern parts of the Western Palearctic (Tourenq et al. 2004), as a result of increases in human densities in relation with the rise of petroleum industry in these areas, and caused the increase in eastern recoveries we recorded over time periods. Alternatively, with the same effects (increase in the proportion of eastern recoveries), a decrease in ring reporting rates may have occurred in the meantime in western parts of the range (Potvin et al. 2017). However, the advancement in spring migration dates is harder to explain by such a potential bias. Indeed, explanations involving changes in hunting pressure for explaining the advancement in the date of migration would involve patterns of such complexity (simultaneous increase in hunting pressure in some areas while it would decrease in other ones) that the parsimony principle would not be on its side.

Altogether, our results add up to already existing concerns about the current status and decline of common pochard populations, particularly in northwest Europe. Indeed, even if birds ringed in the NWE flyway can be recovered into another flyway during the breeding season, they apparently generally come back during the following winters to their flyway of origin. Hence, the decrease in mid-January counts can neither be attributed to a hypothetical change of flyway nor to short-stopping. Therefore, not only does the decline in numbers of individuals counted in winter seems to reflect a genuine decrease in common pochard population size, but this decline is also likely an issue for breeding populations in central Europe (Fox et al. 2016) or in other, more distant major breeding area such as the river Ob watershed. One cannot rule out however that the decline of Pochard is part of a natural cyclic process; thereby population declines would naturally follow earlier major range expansions and population increases (Hanski 1990, Rodenhouse et al. 2003, Selivanova et al. 2017), similar to those experienced by this species two decades ago. The demographic mechanism behind such a population decline is currently being investigated through monitoring of reproduction and survival (Folliot et al. unpubl.).

Management implications

A declining breeding success in the former strongholds of Scandinavia and central Europe has recently been hypothesized to be among the main causes of the decline in wintering numbers of common pochard in the NWE flyway (Fox et al. 2016). Our results suggest that the large proportion of individuals originating from Siberia into the wintering population of the NWE flyway has been overlooked. One must therefore consider the possibility that extensive habitat degradation of wetlands in such areas (Petr and Mitrofanov 1998, Hrkal et al. 2006, Papa et al. 2007, Bartsch et al. 2008) may be involved in the decline of common pochard in the NWE flyway. It is important to notice that population trend estimates for the SWA flyway (Fig. 7) are associated with a very high uncertainty (–47%, CI: –81%, +34%), precluding a robust assessment of the current status of pochard populations in this area.

The high level of connectivity between flyways evidenced in our study suggests that it would be pertinent to consider all of them together when assessing the trend and status of common pochard populations in the Western Palearctic.

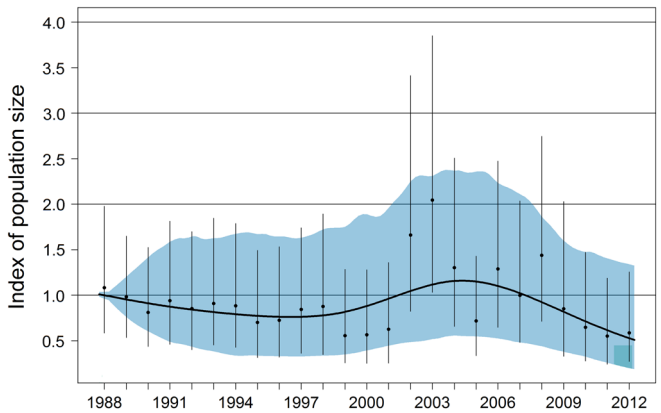


Figure 7. Estimated trend in number of pochards between 1988 and 2012, derived from the International Waterfowl Censuses, over the SWA. Only sites including a median number of Pochards greater than 100 birds were considered in the analyses. The black line shows the estimated trend, the blue area indicates the 95% confidence interval.

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A deeper analysis of pochard trends and their drivers is underway (Folliot et al. unpubl.), but using a generalized additive mixed model (GAMM) with the effects of site and year as random effects ('poptrend' R package, Knape 2016, <https://CRAN.R-project.org/package=poptrend>), we could already show that common pochard populations at the scale of the entire Western Palearctic have apparently experienced a significant decrease of ca –34% (CI 95%: –47%, –16%) over the period 1988–2012, and ca –35% (CI 95%: –49%, –20%) over the past 10 years, confirming the alarming conservation status assigned to this species by IUCN, which is hence far more worrying and much broader than would be a simple regional pattern. Given the probable large proportion of individuals pertaining to the SWA flyway for the overall trend in the Western Palearctic, it appears critical to strengthen census and ringing effort in this particular area.

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Supplementary material (available online as Appendix wlb-00427 at <www.wildlifebiology.org/appendix/wlb-00427>). Appendix 1.

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