Movement patterns of diving ducks *Aythya* sp. in western Europe

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Abstract

Millions of birds have been ringed worldwide over the past 100 years to provide a better understanding of their movements and demography. Yet despite this impressive effort, knowledge of migration patterns and strategies, including the location of stopover sites and migratory connectivity, remains incomplete because recapture and ring recovery rates are often extremely low. Using re-encounter records for ringed birds found dead or recaptured, and visual sightings reported for individuals ringed and fitted with nasal saddles, we investigated the patterns of post-nuptial movements of Common Pochard *Aythya ferina* and Tufted Duck *A. fuligula* caught in France during the breeding season. So far, most ringing effort for these diving duck species has focussed on populations in northeast Europe, whilst migration patterns for the declining populations which breed in southwest European countries, including France, remain almost entirely unknown. Surprisingly, a large proportion of the individuals re-encountered at least once after capture were either resident birds or had initiated post-breeding movements to the north or east, to wintering sites spread over a large area encompassing northern France, Belgium, the Netherlands and Great Britain, as well as to the Alpine lakes (Lake Geneva and Lake Constance). The relatively large proportion of residents and short-distance migrants among the ringed individuals highlights the importance of harvest management schemes being assessed at the local scale, in the same manner as for more sedentary species.

Key words: *Aythya* sp., Common Pochard, migration, residency, Tufted Duck.

Migratory behaviour is widely recognised as an adaptation to spatio-temporal fluctuations of resources and a response to environmental adversity (Berthold 2001; Newton 2008). In order to optimise habitat selection at each moment in their life cycle, migratory wildfowl in the northern hemisphere usually move seasonally from breeding sites at high latitudes to wintering areas at lower latitudes. However, some parts of northwest Europe, where winter conditions are neither extremely harsh nor especially benign (*e.g.* Great Britain and Ireland), can be used as both wintering and breeding grounds (Newton 2008). Overall, knowledge of migration patterns often remains sketchy, particularly for the diving duck *Aythya* sp. because individuals are relatively difficult to identify in the field from their ring codes or other markings, in comparison with larger or more terrestrial species. Yet repeat locations recorded for individual birds is crucial for describing migratory connectivity, for instance to determine the location where individuals breed in a given area spend the wintering season and *vice versa*. As a result, the extent to which individuals from different breeding or wintering areas occur together at different stages of the migratory cycle is poorly documented (Webster *et al.* 2002).

Assessing patterns of seasonal dispersal and migration is also a crucial step towards obtaining a better understanding both of the drivers (and evolution) of bird movements (Newton 2008; Chapman *et al.* 2011) and of the epidemiology (particularly the spread) of zoonotic diseases (*e.g.* highly pathogenic avian influenza (HPAI) viruses; Gaidet *et al.* 2010; Takekawa *et al.* 2010). Populations occurring in different parts of a species' range may experience radically different selection pressures and, as a result, could display very different migration strategies (Newton 2008). Furthermore, populations or species breeding at high latitudes may respond to global warming by delaying their migration (*e.g.* Common Pochard *Aythya ferina*; Folliot *et al.* 2018), reducing the time spent at their wintering sites (short-staying; Nuitjen *et al.* 2020), and/or by remaining closer to their breeding grounds during winter (migratory short-stopping; Elmberg *et al.* 2014).

Two diving duck species – the Common Pochard and the Tufted Duck *A. fuligula* – are considered to be partial migrants; *i.e.* some individuals which nest in temperate regions of western Europe would remain on their breeding grounds year-round, whereas northern populations are migratory and usually spend the winter in central, western and southern Europe (Scott & Rose 1996). Increasing numbers of Tufted Ducks are being counted in Scandinavia during winter, indicating that they may be short-stopping on migration in response to increasing winter temperatures (Lehikoinen *et al.* 2013; Nilsson & Hermansson 2021). The northern half of France forms the southern limit of the Tufted Duck's breeding range, whereas the Common Pochard can breed at more southerly latitudes including North Africa (Cherkahoui *et al.* 2017). To date, studies of the movements of these two diving ducks have focussed either on birds caught during the wintering season (Evans & Day 2001; Korner-Nievergelt *et al.* 2009; Gourlay *et al.* 2012; Caizergues *et al.* 2016), or on breeding populations from the north-eastern parts of the Northwest European Flyway (Blums *et al.* 2003a, b). Whether individuals breeding in southern parts of the range depart, or stay on their breeding grounds during winter, is less well documented (but see Gourlay-Larour *et al.* 2014).

Here we therefore investigate the post-nuptial movements of Common Pochard and Tufted Duck, using re-encounter data for birds which were ringed and fitted with nasal saddles in France during the breeding season. In particular, we aim to determine: (1) the direction of movements (migration) in relation to the ringing location (which can fall into two flyways – the Northwest European and the Central-European/Mediterranean-Black Sea flyways; Fig. 1), and (2) the levels of residency, which would in turn illustrate the extent to which winter visitors and non-migratory individuals occur in the same areas during the wintering season.

Methods

From 2003–2011 inclusive, we captured Common Pochard and Tufted Duck in western France (on Grand-Lieu Lake: 47°05'N, 1°39'W, and in the Mayenne region: 48°11'N, 0°26'W) and in eastern France (in the Dombes and Lac du Der areas, at 46°00'N, 5°01'E and 48°35'N, 4°43'E, respectively), using baited barrier traps and drop-door nest traps (Haramis *et al.* 1982; Blums *et al.* 1983) (Fig. 1). At capture, each individual was ringed and fitted with a nasal saddle bearing an individual code, visible at up to 250 m using a 20–60 x 80 spotting scope (Rodrigues *et al.* 2001). The database consisted of encounter histories, comprising recaptures of these birds at the Grand-Lieu Lake ringing site (from 15 April–30 June and 15 October–15 February), visual sightings of nasal-saddled birds, and recoveries of hunter-shot individuals. Sightings and ring recoveries could potentially be recorded anywhere throughout the ranges of the two species, although it is highly likely both sources of information are subject to differential regional bias. The probability of birds being re-encountered through ring recoveries is likely to be higher in countries where hunting pressure is high (*e.g.* in France, Spain, Italy, Denmark and the United Kingdom; Guillemain *et al.* 2016; Hirschfeld *et al.* 2019), but this potential bias was at least partly offset by the much higher re-sighting probability, with *c.* 10% of individuals re-encountered through ring recoveries, against

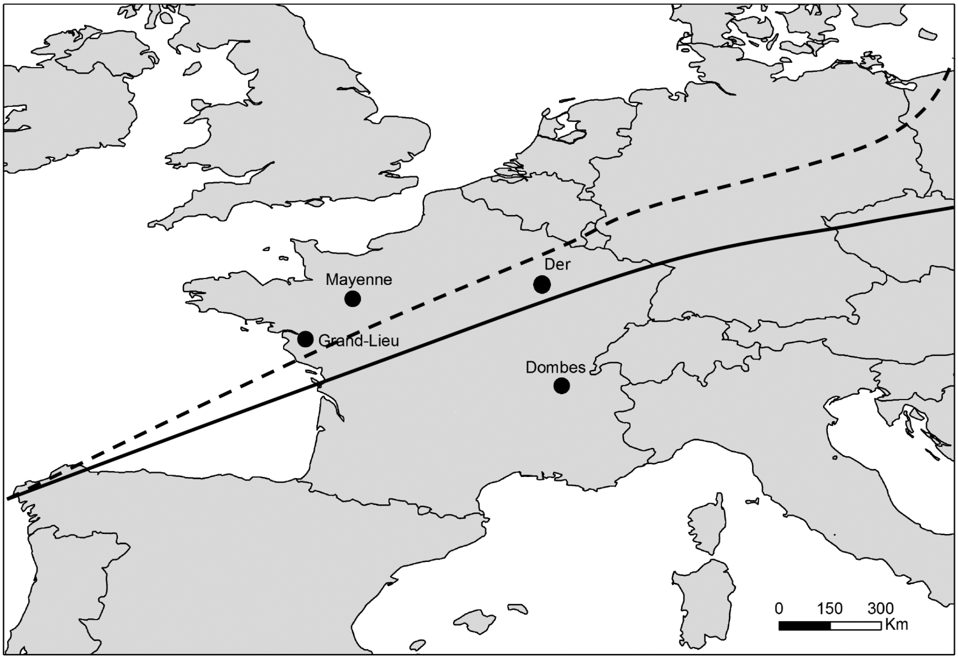

Figure 1. Location of Common Pochard and Tufted Duck ringing sites in France together with the southern limits of the range for the Northwest European population of each species (— Common Pochard, --- Tufted Duck). According to the literature, ringing sites in western France would be within the flyway of the Northwest European population for both species, whereas the two sites in eastern France would be within the flyway of the Central-European/Mediterranean-Black Sea population (for Tufted Duck) or within the zone where two Northwest European and Central-European/ Mediterranean-Black Sea flyways overlap (at Der, for Common Pochard).

c. 40% through observers reading and reporting the codes on their nasal saddles.

The dataset included only adults that had been caught during the breeding season, defined as between 15 April and 15 July each year. The analysis focussed on populations (rather than individuals), and used monthly encounters (*i.e.* physical and visual recaptures, as well as ring recoveries). To avoid pseudo-replication (which would give too much weight to individuals observed many times, or to areas with high observation effort), we randomly selected one encounter per month/year/individual for inclusion in the analyses, with the data being analysed on a monthly temporal scale (see below). The study also focussed primarily on females; thus, data on males were scarcer. Preliminary inspection of the data did not show any difference between the sexes in their distribution patterns, however, and only for Common Pochard ringed at Grand-Lieu did males comprise a substantial proportion (24.5%) of the species captured at a site, so data for male birds were retained in the analyses.

We described the movements for each species and for individuals caught in western *versus* eastern France separately ("populations"), by drawing maps displaying the spatio-temporal variations of the probability densities of encounters estimated with the product kernel algorithm (Keating & Cherry 2009). Individuals ringed in western France belonged to the Northeast/Northwest European population described for Common Pochard and to the Northwest European population described for Tufted Duck (defined by Wetlands International 2022), whereas those captured in eastern France were in the overlap zone between these populations and the Central & Northeast Europe/Black Sea & Mediterranean population (for both species) (see Fig. 1). We chose a smoothing parameter of > 1° for latitude and longitude coordinates because the resolution of the spatial coordinates reported by birdwatchers or hunters were often rounded to the nearest minute of latitude and longitude. Because data were quite scanty, we also opted for a temporal smoothing parameter equal to one month in the range estimations. All estimates were derived from the kernelkc function in the adehabitat package (Callenge 2006; Callenge *et al.* 2010), within Program R (R Development Core Team 2006).

We assessed the proportions of migratory *versus* resident individuals on the basis of the locations of individuals during winter (15 November–15 January). An individual was classed as being migratory when it was encountered > 10 km from its capture site but not within a 10 km radius of the site during winter, and reciprocally as being resident when it was encountered ≤ 10 km from its capture site and never observed further away during winter.

Results

Overall, 616 Common Pochard (480 in western France; 181 in eastern France) and 215 Tufted Duck (145 in western France; 70 in eastern France) were caught during the 2003–2011 breeding seasons. These individuals provided 2,506 encounters for Common Pochard (from 346 birds marked in western France; 148 from eastern France) and 1,227 for Tufted Duck (from 106 in birds marked in western France; 57 from eastern France).

Timing and directions of movements

Common Pochard ringed in western France during the breeding season initiated movements as early as July, and encounters of these "early movers" were mostly located at more northerly latitudes than the actual ringing/breeding sites, with individuals reported along major rivers such as the Seine and Somme in northern France, as well as in Belgium, the Netherlands and Great Britain (Fig. 2a). This propensity to move towards the north/northeast persisted into October and November but increasing proportions of encounters also occurred both at lower latitudes (in southern France, northern Spain) and to the east (in eastern France, Switzerland and southwest Germany) at this time. As a result, by mid-winter (in December), birds that had bred in western France were evenly distributed over a large area, encompassing wintering grounds in all possible directions including Great Britain, Belgium/the Netherlands, western and eastern France, Switzerland and Spain.

Tufted Duck ringed in western France initiated movements two months later than Common Pochard ringed in the same area (*i.e.* in September, Fig. 2b). However, in contrast to patterns observed in Common Pochard (Fig. 2a), most individuals were encountered at a more northerly latitude than their breeding and ringing location (Fig. 2b).

Data for both Common Pochard and Tufted Duck ringed in eastern France were quite limited compared to those from the western part of the country (Fig. 2a, b and Fig. 3a, b). Nevertheless, both species initiated movements as early as July although August and September were characterised by much extensive movements (Fig. 3a, b). Whereas Common Pochard moved in all directions (to northern France, UK, Germany and the Alpine lakes in Switzerland, Fig. 3a), Tufted Duck tended to favour more northerly latitudes, as well as the Alpine lakes (*e.g.* Lake Leman, Fig. 3b). Individuals of both species were distributed over a quite large area in more or less all directions during the mid-winter season (November–January, Fig. 3a, b).

Residency

For both species and in all months when observation coverage was greater than zero (noting that observations were not made at Grand-Lieu Lake in August and September each year), a substantial proportion of individuals ringed in western France were encountered within 10 km of their ringing/breeding sites (16% of Common Pochard; 19% of Tufted Duck) suggesting a high propensity for residency. This propensity for residency was less evident in the density distribution maps for individuals of both species ringed in eastern France, albeit no less real with proportions of residents ranging from 19% to 26% for Common Pochard and Tufted Duck, respectively. It should be noted, however, that because we used a 10 km radius to distinguish residents from migratory individuals, our estimates of residency are very conservative.

Discussion

Migration routes of obligate (long distance) migratory duck populations usually display quite simple patterns in terms of the direction and distances covered (Newton 2008). Here, we describe somewhat counterintuitive patterns of post-breeding movements in diving duck populations for birds nesting in the southern parts of the species' breeding ranges, including movements in unexpected directions (*e.g.* to wintering sites further north or east) and much more complex (*e.g.* in terms of the variable distances travelled) than previously suspected.

Direction of movements

Many post-nuptial movements of both Common Pochard and Tufted Duck, ringed in both western and eastern France during the breeding season, were in a northerly direction, suggesting that sites located along major rivers and wetlands (such as the River Seine and River Somme in northern France, as well as in Belgium, the Netherlands and Great Britain), provided suitable refuelling and/or wintering areas for the species. Three non-mutually exclusive hypotheses may explain this

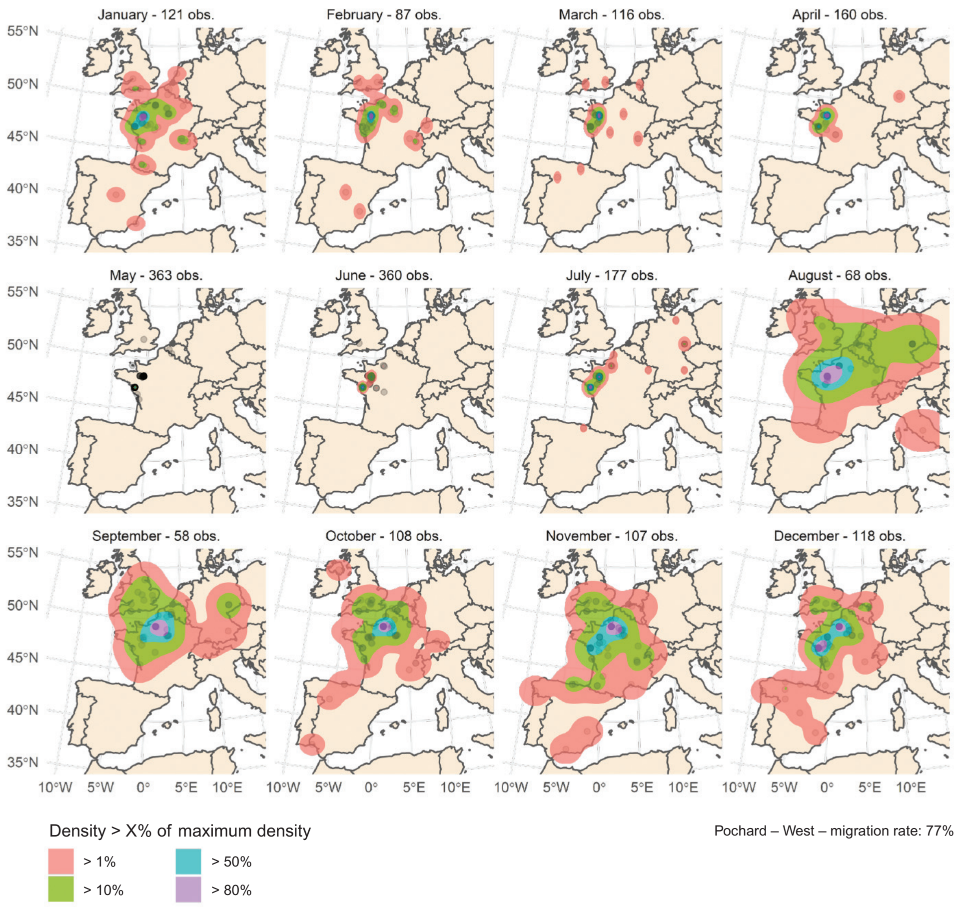

Figure 2a. Monthly changes in the distribution of Common Pochard breeding in western France (Grand-Lieu), determined using the density probability algorithm (kernelkc function in the adehabitat package). Migration rate (77% for Common Pochard) is the percentage of individuals encountered > 10 km from the ringing site during winter (15 November–15 January; see Methods).

unusual (northerly) direction of post-breeding movements. Firstly, creation of gravel-pits over the last 50 years may have provided favourable habitat for diving ducks, in non-riverine areas as well as along the major rivers of western Europe (Santoul *et al.* 2004). Secondly, it may have become beneficial for the ducks to move into more northern countries because of the lower hunting pressure experienced in these regions relative to those in southern Europe (Mooij 2005; Hirschfeld *et al.* 2019). Finally, northward migration could be becoming more prevalent because of increasing winter temperatures resulting from global warming (see also Strebel 2019; Marchowski *et al.* 2020). It should be noted however, that large numbers of Tufted

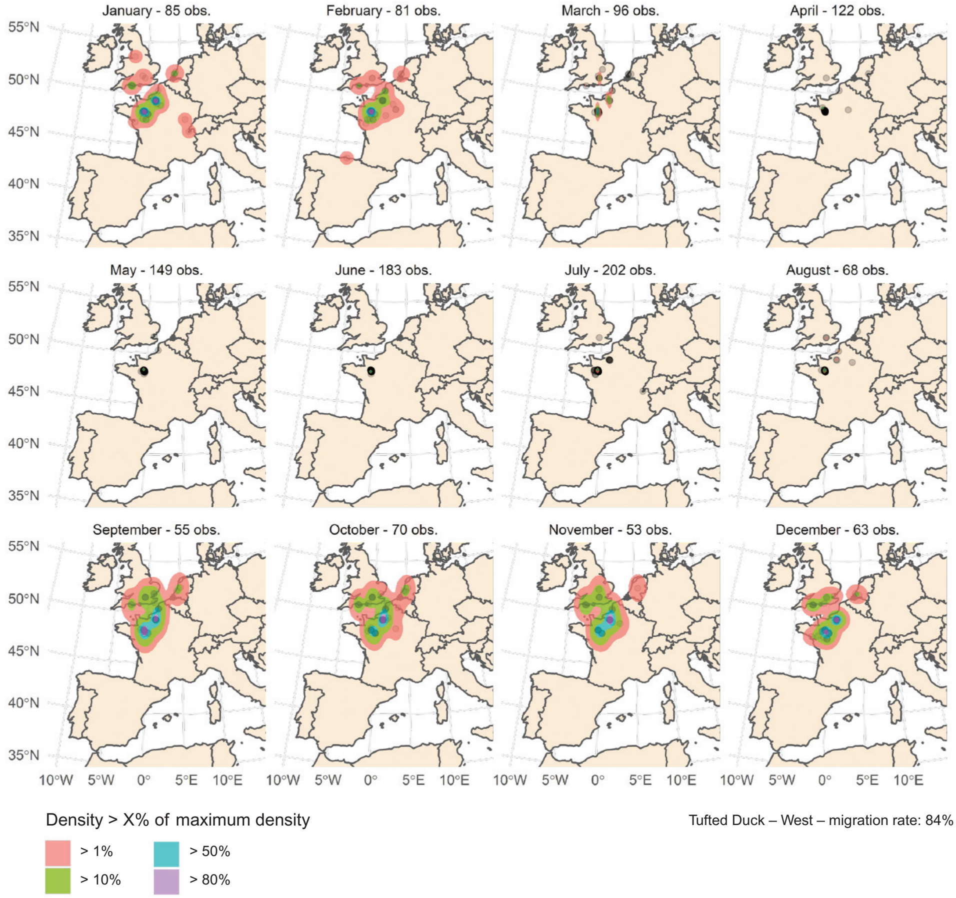

Figure 2b. Monthly changes in the distribution of Tufted Duck breeding in western France (Mayenne), determined using the density probability algorithm (kernelkc function in the adehabitat package). Migration rate (84% for Tufted Duck) is the percentage of individuals encountered > 10 km from the ringing site during winter (15 November–15 January; see Methods).

Duck have wintered in the Netherlands, Denmark and Sweden (Nilsson 1975; Lehikoinen *et al.* 2013) for many years, indicating that northern Europe has offered suitable wintering conditions for this species at least since the mid-20th century.

In both species, a large proportion of the individuals which were fitted with nasal saddles at their breeding sites in eastern France, as well as a substantial proportion of the Common Pochard from western France, were later encountered on Alpine lakes such as Lake Geneva and Lake Constance. These lakes may have become particularly favourable to wintering diving ducks over the past century, as a result of their colonisation by the Zebra Mussel *Dreissena*

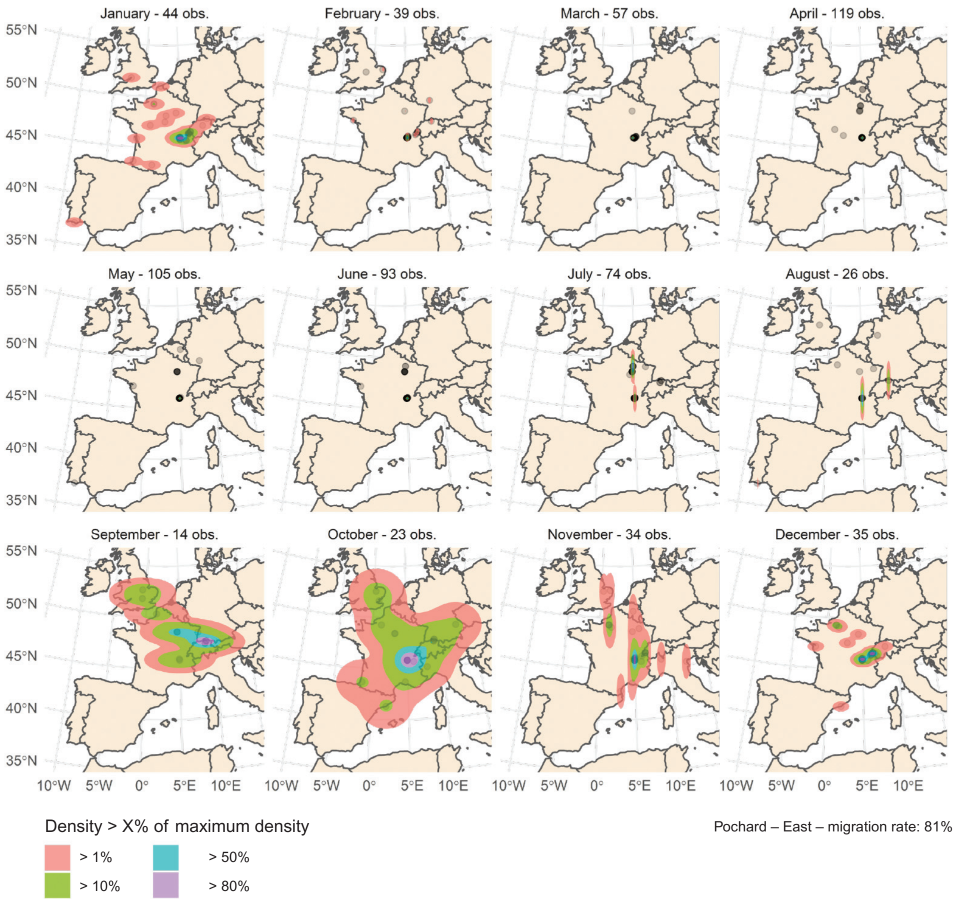

Figure 3a. Monthly changes in the distribution of Common Pochard breeding in eastern France (Dombes), determined using the density probability algorithm (kernelkc function in the adehabitat package; see Methods). Migration rate (81%) is the percentage of individuals encountered > 10 km from the ringing site during winter (15 November–15 January).

polymorpha, a preferred food of Tufted Duck (Olney 1963; Werner *et al.* 2005). In any case, the pattern of movements found in our study are consistent with the results of long-term waterbird censuses, which highlight these alpine lakes as being among the most important wintering areas for diving ducks in western Europe (Ridgill & Fox 1990; Strebel 2019).

Moult or wintering migration?

In our study, we did not analyse movements at the individual level because multiple records for single individuals were scarce. It therefore was not possible, at this stage, to characterise different types of movements, such as breeding dispersal, vagrancy, moult migration, and obligate *versus* facultative migration. Moult migration (the movements

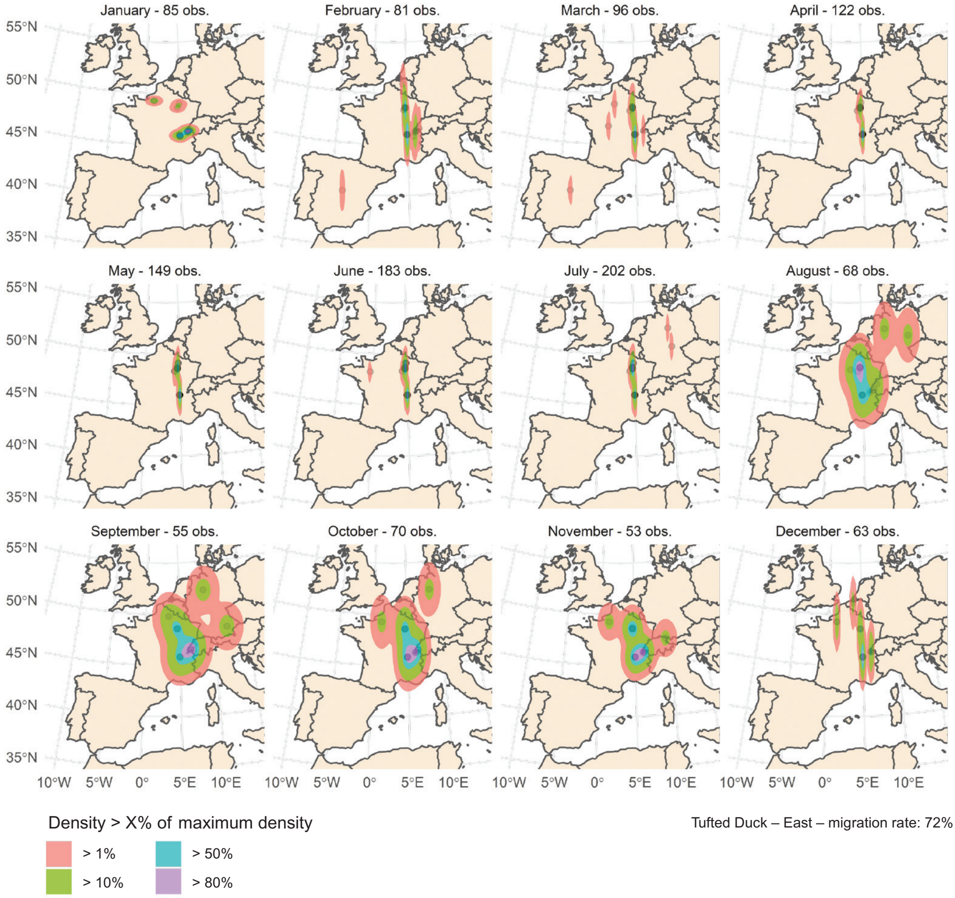

Figure 3b. Monthly changes in the distribution of Tufted Duck breeding in eastern France (Dombes/Der), determined using the density probability algorithm (kernelkc function in the adehabitat package; see Methods). Migration rate (72%) is the percentage of individuals encountered > 10 km from the ringing site during winter (15 November–15 January).

of individuals between breeding grounds and moulting sites), which is a well-documented phenomenon in ducks and geese (Salomonsen 1968; Jehl 1990), could account for quite large proportions of encounters in July and August. Indeed, males left Lake Grand-Lieu as early as June, and some of these, as well as females without broods, were encountered as early as July on moulting sites in eastern France (*e.g.* the Lindre fishponds in Moselle), Germany and the Netherlands. Eastward and northward encounters did not represent moult migration movements only, however, as the few individuals included in the present analysis that could be monitored over several breeding and wintering seasons, were encountered at the same location in mid-winter (*i.e.* outside the moulting season) in several consecutive years. If confirmed using larger datasets, these individuals can be considered obligate migrants, even though their breeding and winter grounds were sometimes separated by only a few tens of kilometres.

Residency

The estimated probability density functions displayed in various shades of colours in Figs 2 & 3, together with our very conservative estimates of residency (*i.e.* based on a 10 km radius), indicate a substantial degree of annual residency by Tufted Duck and Common Pochard breeding in both western and eastern France, albeit lower than that reported by Wernham *et al.* (2002) for the same species in Great Britain and by Gourlay *et al.* (2014) for Common Pochard breeding at Grand-Lieu (up to 43% residency estimated for Grand-Lieu individuals using multi-event capture-mark-recaptures/ recoveries models with the same dataset). Together, these results confirm that, in Europe (including France, Great Britain, Belgium, the Netherlands and also Switzerland), migratory and resident birds (local breeders) can spend the winter in the same areas as those used for breeding, although at much larger densities than observed during the breeding season (see Chapman *et al.* 2011; Gourlay *et al.* 2014). In these areas, the habitat therefore seems capable of sustaining many more individuals than are currently observed during the breeding season, suggesting that: (1) food shortage is probably not the main driver of migration, and (2) food availability may not be a factor limiting breeding diving duck populations in these areas. In any case, such propensity for residency (and/or short-distance obligate migration) implies that managers should pay greater attention to the monitoring of local harvest rates because they could have a significant effect on the local breeding populations, as may also be the case for purely sedentary species.

Limitations of the approach

The encounter probabilities of marked individuals depend on the presence of bird-watchers and hunters, as well as on their willingness to report their data. Because encounter and reporting rates vary in space and time, possible biases may affect the results of such analysis (Korner-Nievergelt *et al.* 2010; Thorup *et al.* 2014). However, because our study included the simultaneous collection of visual recaptures and ring recoveries, such possible biases were likely reduced. Moreover, we showed previously that there was no substantial heterogeneity in the distribution of the resightings reports, nor of hunting pressure, detectable in France (Gourlay-Larour *et al.* 2012). Thus we can assume our results are sufficiently robust to provide reasonable depictions of the ducks' post-nuptial distributions.

Conclusion

We show that diving ducks breeding in the temperate regions of western Europe (here France) are likely to move towards the north (to northern France, Belgium, Great Britain or Switzerland) during the post-nuptial period, and that coexistence of individuals with different migratory behaviours can occur on the breeding and non-breeding grounds in these areas. Managers should consider these seasonal patterns of movements by resident and migratory individuals when designing protected area networks and deriving hunting schemes for these species at both the local and flyway scales. The patterns in timing and directions of movements described in our study also may provide valuable insight into the spread and maintenance of emerging zoonotic diseases, such as the highly pathogenic influenza viruses.

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References

Berthold, P. 2001. *Bird Migration. A General Survey*. Oxford University Press, Oxford, UK.

Blums, P.N., Reders, V.K., Mednis, A.A. & Baumanis, J.A. 1983. Automatic drop-door traps for ducks. *Journal of Wildlife Management* 47: 199–203.

Blums, P., Nichols, J.D., Hines, J.E., Lindberg, M.S. & Mednis, A. 2003a. Estimating natal dispersal movement rates of female European ducks with multistate modelling. *Journal of Animal Ecology* 72: 1027–1042.

Blums, P., Nichols, J.D., Lindberg, M.S., Hines, J.E. & Mednis, A. 2003b. Factors affecting breeding dispersal of European Ducks on Engure Marsh, Latvia. *Journal of Animal Ecology* 43: 292–307.

Caizergues, A., Van Wilgenburg, S.L. & Hobson, K.A. 2016. Unraveling migratory connectivity of two European diving ducks: a stable isotope approach. *European Journal of Wildlife Research* 62: 701–711.

Calenge, C. 2006. The package "adehabitat" for the R software: a tool for the analysis of space and habitat use by animals. *Ecological Modelling* 197: 516–519.

Calenge, C., Guillemain, M., Gauthier-Clerc, M. & Simon, G. 2010. A new exploratory approach to the study of the spatio-temporal distribution of ring recoveries: the example of Teal (*Anas crecca*) ringed in Camargue, Southern France. *Journal of Ornithology* 151: 945–950.

Chapman, B.B., Bronmark, C., Nilsson, J.A. & Hansson, L.A. 2011. The ecology and evolution of partial migration. *Oikos* 120: 1764–1775.

Cherkaoui, S.I., Selmi, S. & Hanane, S. 2021. Ecological factors affecting wetland occupancy by breeding Anatidae in the southwestern Mediterranean. *Ecological Research* 32: 259–269.

Elmberg, J., Hessel, R., Fox, A.D. & Dalby, L. 2014. Interpreting seasonal range shifts in migratory birds: a critical assessment of 'short-stopping' and a suggested terminology. *Journal of Ornithology* 155: 571–579.

Folliot, B., Guillemain, M., Champagnon, J. & Caizergues, A. 2018. Patterns of spatial distribution and migration phenology of Common Pochards *Aythya ferina* in the Western Palearctic: a ring-recoveries analysis. *Wildlife Biology* 2018: 1–11.

Gaidet, N., Cappelle, J., Takekawa, J.Y., Prosser, D.J., Iverson, S.A., Douglas, D.C., Perry, W.M., Mundkur, T. & Newman, S.H. 2010. Potential spread of highly pathogenic avian influenza H5N1 by wildfowl: dispersal ranges and rates determined from large scale satellite telemetry. *Journal of Applied Ecology* 47: 1147–1157.

Gourlay-Larour, M.-L., Schricke, V., Sorin, C., L'Hostis, M. & Caizergues, A. 2012. Movements of wintering diving ducks: new insights from nasal saddled individuals. *Bird Study* 59: 266–278.

Gourlay-Larour M.-L., Pradel R., Guillemain M., Guitton J.-S., L'Hostis M., Santin-Janin H. & Caizergues A. 2014. Movement patterns in a partial migrant: A multi-event capture-recapture approach. *PLoS ONE* 9: e96478.

Haramis, G.M., Derleth, E.L. & McAuley, D.G. 1982. Techniques for trapping, aging, and banding wintering canvasbacks. *Journal of Field Ornithology* 53: 342–351.

Hirschfeld A., Attard G. & Scott L. 2019. Bird hunting in Europe. *British Birds* 112: 153–166.

Jehl J.R. 1990. Aspects of the molt migration. *In*: E. Gwinner (ed.), *Bird Migration*, pp. 102–113. Springer, Berlin/Heidelberg, Germany.

Keating, K.A. & Cherry, S. 2009. Modeling utilization distributions in space and time. *Ecology* 90: 1971–1980.

Korner-Nievergelt, F.R., Hofer, J., Sauter, A. & Jenni, L. 2009. Measuring within-winter movement rates of Tufted Duck *Aythya fuligula* and Common Pochard *A. ferina* based on ring re-encounter data. *Wildfowl* (Special Issue 2): 24–41.

Korner-Nievergelt, F., Sauter, A., Atkinson, P.W., Guélat, J., Kania, W., Kéry, M., Köppen, U., Robinson, R.A., Schaub, M., Thorup, K., van der Jeugd, H. & van Noordwijk, A.J. 2010. Improving the analysis of movement data from marked individuals through explicit estimation of observer heterogeneity. *Journal of Avian Biology* 41: 8–17.

Lehikoinen, A., Jaatinen, K., Vähätalo, A., Clausen, P., Crowe, C., Deceuninck, B., Hearn, R., Holt, C.A., Hornman, M., Keller, V., Nilsson, L., Langendoen, T., Tománková, I., Wahl, J. & Fox A.D. 2013. Rapid climate driven shifts in winter distributions of three common waterbird species. *Global Change Biology* 19: 2071–2081.

Mooij, J.H. 2005. Protection and use of waterbirds in the European Union. *Beiträge zur Jagd- und Wildforschung* 30: 49–76.

Newton, I. 2008. *The Migration Ecology of Birds*. Academic Press, Amsterdam, the Netherlands.

Nilsson, L. 1975. Midwinter distribution and numbers of Swedish Anatidae. *Ornis Scandinavica* 6: 83–107.

Nilsson, L. & Hermansson, C. 2021. Changes in numbers and distribution of wintering waterbirds around Gotland 1969–2020. *Ornis Svecica* 31: 78–93.

Nuijten, R.J.M., Wood, K.A., Haitjema, T., Rees, E.C. & Nolet, B.A. 2020. Concurrent shifts in wintering distribution and phenology in migratory swans: individual and generational effects. *Global Climate Change* 26: 4263–4275.

Olney, P.J.S. 1963. The food and feeding habits of Tufted Duck *Aythya fuligula*. *Ibis* 105: 55.

R Development Core Team. 2006. *R: a Language and Environment for Statistical Computing*. R Foundation for Statistical Computing, Vienna, Austria.

Ridgill, S.C. & Fox, A.D. 1990. *Cold Weather Movements of Waterfowl in Western Europe*. International Waterfowl Research Bureau Special Publication No. 13. IWRB, Slimbridge, UK.

Rodrigues, D.J.C., Fabio, A.M.D. & Figueiredo, M.E.M.A. 2001. The use of nasal markers for monitoring Mallard populations. *In* R. Field, R.J. Waren, H. Okarma & P.R. Sievert (eds.), *Wildlife, Land, and People: Priorities for the*

21st Century. Proceedings of the 2nd International Wildlife Management Congress, pp. 316–318. The Wildlife Society, Bethesda, Maryland, USA.

Salomonsen, F. 1968. The moult migration. *Wildfowl* 19: 5–24.

Santoul, F., Figuerola, J. & Green, A.J. 2004. Importance of gravel pits for the conservation of waterbirds in the Garonne River floodplain (southwest France). *Biodiversity and Conservation* 13: 1231–1243.

Scott, D.A. & Rose, P.M. 1996. *Atlas of Anatidae Populations in Africa and western Eurasia*. Wetlands International, Wageningen, the Netherlands.

Strebel, N. 2019. *Monitoring Hivernal des Oiseaux d'Eau en Suisse: Résultats des Recensements des Oiseaux d'Eaux 2018/2019*. Station Ornithologique Suisse, Sempach, Switzerland. Available online at https://www.vogelwarte.ch/en/projects/population-trends/state-of-birds/winter-visitors/ (last accessed 29 June 2022).

Takekawa, J.Y., Newman, S.H., Xiao, X., Prosser, D.J., Spragens, K.A., Palm, E.C., Yan, B., Li, T., Lei, F., Zhao, D., Douglas, D.C., Muzaffar, S.B. & Ji, W. 2010. Migration of waterfowl in the East Asian flyway and spatial relationship to HPAI H5N1 outbreaks. *Avian Diseases* 54(s1): 466–476.

Thorup, K., Korner-Nievergelt, F., Cohen, E.B. & Baillie, S.R. 2014. Large-scale spatial analysis of ringing and re-encounter data to infer movement patterns: a review including methodological perspectives. *Methods in Ecology and Evolution* 5: 1337–1350.

Webster, M.S., Marra, P.P., Haig, S.M., Bensch, S. & Holmes, R.T. 2002. Links between worlds: unraveling migratory connectivity. *Trends in Ecology and Evolution* 17: 76–83.

Werner, S., Mortl, M., Bauer, H.G. & Rothhaupt, K.O. 2005. Strong impact of wintering waterbirds on Zebra Mussel (*Dreissena polymorpha*) populations at lake Constance, Germany. *Freshwater Biology* 50: 1412–1426.

Wernham, C., Toms, M., Marchant, J., Clark, J., Siriwardena, G. & Baillie, S. 2002. The Migration Atlas: Movements of the Birds of Britain and Ireland. T. & A.D. Poyser, London, United Kingdom.

Wetlands International. 2022. *Waterbird Populations Portal*. Wetlands International, Wageningen, the Netherlands. Available at wpp.wetlands.org (last accessed 29 June 2022).

Photograph: Tufted Duck in France, by Ralph Martin/AGAMI.

