Becoming more sedentary? Changes in recovery positions of Mallard *Anas platyrhynchos* ringed in the Camargue, France, over the last 50 years

MATTHIEU GUILLEMAIN[1]*, JOCELYN CHAMPAGNON[2], GREGOIRE MASSEZ[3], CLAIRE A. PERNOLLET[1,2], THIERRY GEORGE[4], ANDRE MOMERENCY[5] & GERALDINE SIMON[2]

[1]Office National de la Chasse et de la Faune Sauvage, Unité Avifaune Migratrice, La Tour du Valat, Le Sambuc, 13200 Arles, France.
[2]Centre de recherche de La Tour du Valat, Le Sambuc, 13200 Arles, France.
[3]Les Marais du Vigueirat, Mas Thibert, 13200 Arles, France.
[4]Office National de la Chasse et de la Faune Sauvage, DIR Nor-Est, 41–43 route de Jouy, 57160 Moulins les Metz, France.
[5]Impression Nature Environnement, 2bis rue des Coudriers, 89290 Vaux, France.
*Correspondence author: E-mail: matthieu.guillemain@oncfs.gouv.fr

Abstract

Earlier studies from central and northern Europe have found a shortening of the ring recovery distance in Mallard *Anas platyrhynchos*, which was generally attributed to climate change leading to a northwards shift of the wintering range. Here we show that recovery distances for Mallard ringed during winter in the Camargue (southern France), at the southern end of their range, have also shortened over the last 50 years, from a mean of 417 km (s.e. ± 17.4) for birds ringed between 1950–1978 to 74 km (± 28.9) for birds ringed between 2002–2013. In contrast to the studies in other areas, however, the more recent recoveries of Mallard ringed in the Camargue were made to the south and west of where they were previously, and changes in ring recoveries were likely caused by a greater proportion of sedentary birds among the Camargue wintering population. Discarding unlikely methodological biases that may explain the pattern observed, we suggest three non-mutually exclusive hypotheses to explain such a change: a) increased attractiveness of Camargue habitats as a winter quarter, with migrant birds now staying for longer periods and allowing more local recoveries, b) hybridization between resident captive-bred and wild Mallards, and c) former migrants from northern Europe now foregoing long migration to this distant winter quarter due to climate change. Future studies combining genetic and isotope analyses may help in teasing these hypotheses apart, to provide a better understanding of the factors leading to such increased sedentarity.

Key words: *Anas platyrhynchos*, climate change, habitat quality, hybridization, restocking, ring recoveries, sedentarity.

Studies over the last couple of decades have repeatedly documented shifts in waterfowl geographic ranges and site occupancy, in response to fluctuations in local habitat quality and general climate change (Duncan *et al.* 1999; Švažas *et al.* 2001; Gunnarsson *et al.* 2012; Lehikoinen *et al.* 2013; Jónsson & Afton 2015; Guillemain *et al.* 2015). Climate change is expected to result in increasingly mild winter conditions and hot summers, gradually leading to migratory bird population ranges shifting north-eastwards in western Europe. Huntley *et al.* (2007) provided maps illustrating expected shifts of breeding ranges, based on the environmental needs for a range of bird species. Gunnarsson *et al.* (2012) showed that the mean recovery location during winter of Mallard *Anas platyrhynchos* ringed in southern Sweden shifted *c.* 300 km northeast between the 1960–1970s and the early 21st century (*i.e.* over the last 15 years). Similarly, by analysing ring recoveries from many European countries, Sauter *et al.* (2010) found that Mallard continued to move to the southwest during winter, but travelled increasingly short distances, which they attributed to climate change leading to fewer cold spells during more recent years.

The Mallard is a partial migrant in most of western Europe, with resident breeding birds being supplemented by migrants during the winter (Young 2005). This is the case of the population wintering in Camargue, which originates from the *c.* 5,000 local breeding pairs (Olioso 2009) supplemented by migrants from northern areas and countries (Tamisier & Dehorter 1999). There is no precise monitoring of the Camargue breeding population, but it is considered to have been stable in recent decades (Olioso 2009). The wintering population, which is monitored much more rigorously, showed no significant trend during the late 20th century (years 1964–2002 inclusive), with a mean number of *c.* 18,000 individuals (Tamisier 2004). However, these numbers have increased dramatically over the more recent 1984–2002 period. This has been especially the case for September counts (+27%), likely reflecting the development of releases of captive-bred Mallard for hunting purposes (Tamisier 2004), which occur during the summer. Again, there is no precise count of the number of such birds being released in the Camargue annually, but the most recent estimates suggest *c.* 50,000 individuals are released before the hunting season each year (Champagnon 2011), while the practice was considered virtually non-existent before the mid-1970s. Captive-bred Mallard released for hunting have poor or no migratory abilities (with only a few hundred meters between release and recovery site reported in Champagnon 2011; see Söderquist 2015 for a review), so the increase in this practice of releasing Mallard in Europe since the 1970s and subsequent genetic hybridization among wild and captive-bred conspecifics (Čížková *et al.* 2012; Champagnon *et al.* 2013) may have led to an increasingly sedentary behaviour in this population (Söderquist 2015).

In addition to the above potential changes in the composition of wintering Mallard populations in the Camargue, local habitat management practices have also changed over the last decades (Brochet *et al.* 2012), which may affect the habitat use and

distribution of birds at the flyway scale. For instance, an earlier study has shown that changes in Camargue habitat management have increased attractiveness of the region for migratory Eurasian Teal *Anas crecca* (Guillemain *et al.* 2015).

This paper aims to determine whether the recovery locations of Mallard ringed in Camargue during winter have changed over the last 50 years, analogous to the change in movements recorded for the species in other parts of Europe. It also proposes explanatory hypotheses for potential changes, new avenues for research on the composition of duck populations and possible changes in the migration strategies and geographic distribution of Mallard in Europe over time.

Methods

Recovery data recorded for 11,453 Mallard ringed in Tour du Valat, Camargue (43°30'N, 4°40'E) between 28 March 1950 and 17 January 1978, hereafter termed "historical Camargue data", and 1,789 Mallards ringed in the same region in the Marais du Vigueirat (43°31'N, 4°47'E) between 5 December 2002 and 5 December 2013 (hereafter "modern Camargue data") were analysed to determine any changes in recovery distances since the mid 20th century. To control for a change in hunting reporting rates between historical and modern dataset, we also studied the recovery locations of Mallard ringed over the recent years in the Bassin Parisien, northern France. Data for the Bassin Parisien came from 1,292 Mallard ringed in Arrigny (Marne department, 48°37'N, 4°42'E), Outines (Marne, 48°33'N, 4°39'E), Marolles-sur-Seine (Seine et Marne, 48°23'N, 3°02'E), Moutiers-en-Puisaye (Seine et Marne, 47°37'N, 3°11'E), Noyen-sur-Seine (Seine et Marne, 48°27'N, 3°21'E), Saint-Julien-du-Sault (Yonne, 48°02'N, 3°18'E) and Vergigny (Yonne, 47°58'N, 3°43'E), all ≤ 180 km to the south-east of Paris, between 16 September 2005 and 5 March 2015. From each study area, only individuals ringed between September and March were considered, restricting the analysis to birds that were already flying at ringing. We also used only ring recoveries of dead birds in the analyses (*i.e.* not live recaptures or re-sightings, of which there were only a handful away from the ringing site in the historical dataset). The cause of death was known for 1,726 (92.3%) of the recoveries. Of these, 88.9% were shot by hunters in the historical Camargue dataset, 93.8% in the modern Camargue dataset and 97.5% in the modern Bassin Parisien dataset; differences between time periods and sites in the proportion of birds found shot were not significantly different (all pair-wise Chi-squared tests: $\chi^2_1 < 0.48$, all $P > 0.83$, n.s. in each case). The other sources of mortality, which included birds caught in traps or nets, mortality at ringing and predators, therefore had marginal influence on the recovery data.

We plotted the recovery locations of the birds, and compared the mean latitude, longitude and recovery distance using non-parametric Mann-Whitney and Kruskal-Wallis tests in Statistica 10 (Statsoft 2011) because the residuals of preliminary ANOVAs were not normally distributed (Kolmogorov-Smirnov tests: all $P < 0.01$) and different forms of transformation failed to solve this problem. Because the hunting

seasons in European countries including France have shortened considerably since the 1950s (see Figure 9.8 in Guillemain & Elmberg 2014), an observed shorter recovery distance over time periods could be the consequence of fewer recoveries during spring migration in the modern dataset. The barycentre of the recoveries (mean latitude and mean longitude for all individuals from a ringing area during the historical or modern periods) and the mean recovery distances were thus computed both on considering all recoveries throughout the year and also when considering only recoveries made during the more restricted current hunting season, *i.e.* September–January inclusive.

A change in the median date of ringing within the winter between the historical and the modern years could lead to different exposure times to hunting, which in turn could result in a differential probability of the bird being recovered locally in the Camargue. Specifically, if the timing of ringing shifted to earlier periods in the autumn and winter, then a longer exposure to hunting at the Camargue wintering site and consequently shorter ring recovery distances would be expected. We therefore also compared within-winter ringing dates for the historical and modern Camargue birds. The first of January was calculated as day 0, with days from September to December each year having negative values (Guillemain *et al.* 2013).

An earlier study of ring recovery distance in Mallard found that first-year birds were recovered at greater distances than adults (*i.e.* after-hatch year birds) during the later stage of the first winter (January–February; Sauter *et al.* 2010). Because there were relatively few recovery data for Mallard ringed in recent years (*i.e.* in the modern datasets) we had to consider all recoveries in the analyses presented here, including those made after the year of ringing (*i.e.* combining the intra- and inter-annual recoveries). Only two age classes can be distinguished in dabbling ducks (first-year *vs.* after-hatch year individuals; *e.g.* Mouronval 2014), age at ringing may differ from age at recovery, and the recovery data were grouped into just two categories (historic and modern recoveries), so we did not attempt to test for any age differences in the distance travelled. Sauter *et al.* (2010) did not find any difference between the sexes in ring recovery distance for Mallard, but an earlier study of Eurasian Teal ringed in the Camargue showed that males generally move further afield than females (Guillemain *et al.* 2005). Within each period and ringing area we therefore compared the mean recovery distance between sexes, and also tested for temporal changes in recovery distance from the Camargue between time periods separately for males and for females. It should be noted that sex was not recorded for three of the historical Camargue Mallard on ringing.

Results

From a total of 14,534 ringed Mallard included in the study, we obtained 1,622 recoveries of historical Camargue birds from Tour du Valat (14.2% of the ringed birds from this period and area), 128 recoveries of modern Camargue birds from Marais du Vigueirat (7.1%) and 120 recoveries of modern Bassin Parisien

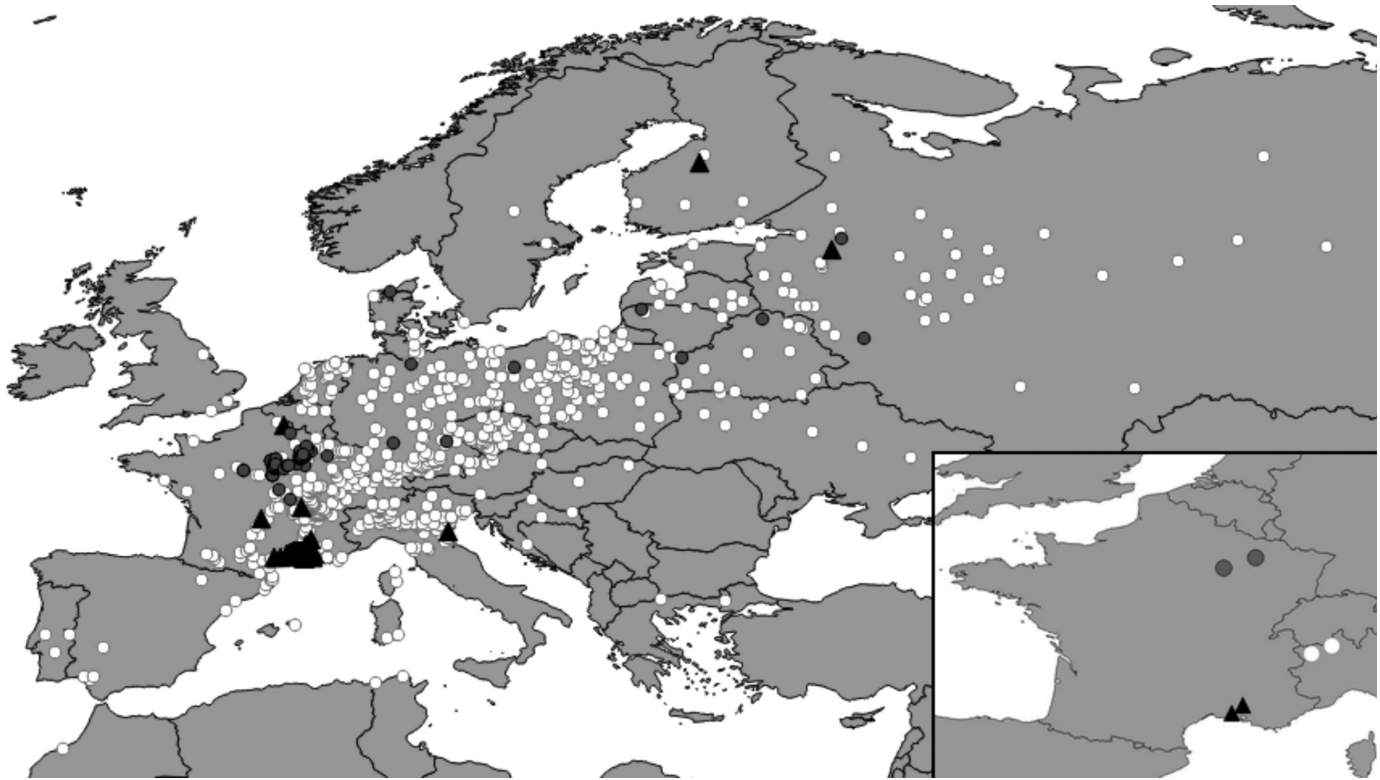


Figure 1. Recoveries of Mallard ringed in Camargue from 1950 to 1978 (white dots, "historical Camargue"), in Camargue from 2002 to 2013 (black triangles, "modern Camargue") and in the Bassin Parisien from 2005 to 2015 (grey dots). The small map to the bottom right shows the barycentre of the recoveries for each of these ringing areas and periods, depending on whether recoveries over the whole year or only from September–January were considered. The barycentre in the later case is consistently further to the southwest.

individuals (9.3%). The median ringing date of these birds was day –5 (*i.e.* 27 December, range = days –151 to +89, $n = 1{,}622$) for the historical Camargue dataset, and day 10.5 (*i.e.* 11 January, range = days –52 to +72, $n = 128$) for modern Camargue birds, which was significantly different (Mann-Whitney *U*-test: $Z = -5.00$, $P < 0.0001$).

Figure 1, which illustrates the ring recovery locations of birds from each ringing area and time period, shows that the historical Camargue birds were recovered throughout Europe, clearly delineating their flyway from southern France to western Russia across the Netherlands, Switzerland, northern Italy, Germany, Poland and the Baltic countries. Although less numerous, foreign recoveries in these countries were also obtained for the modern Mallard from the Bassin Parisien. Conversely, very few modern Camargue Mallard were recovered outside France, albeit this was technically possible since some Camargue birds were recently recovered in Finland ($n = 1$) and Russia ($n = 1$), > 2,500 km away. The mean latitude of recoveries was significantly lower in the modern than in the historical Camargue dataset (Mann-Whitney U test: $Z = 7.19$, $P < 0.0001$), while the mean longitude was just at the significance threshold ($Z = 1.91$, $P = 0.057$). This led to the barycentre of recoveries being much closer to the ringing site during modern than historical years, both when the whole year or when only September–January recoveries were considered (Fig. 1). The mean recovery distance differed between the three ringing areas and periods; historical Camargue: 416.6 km (s.e. ± 17.4, $n = 1{,}622$); modern Camargue: 74.1 km (s.e. ± 28.9, $n = 128$); modern Bassin Parisien: 126.0 km (s.e. ± 35.6, $n = 120$) (Kruskal-Wallis: $H_{2,1870} = 65.47$, $P < 0.0001$; Fig. 2). Multiple bilateral comparisons at $P < 0.05$ indicated that such differences were due to a greater recovery distance for the historical Camargue Mallard than in the two modern datasets, which did not differ significantly from each other (Fig. 2a). If only the recoveries between September and January were considered, the mean distances were slightly lower, but the differences between ringing sites and periods remained similar ($H_{2,1184} = 57.23$, $P < 0.0001$, Fig. 2b), although this time all three mean values differed from each other in multiple pairwise comparisons.

The comparison of ring recovery distances between sexes yielded non-significant results in the modern datasets (recoveries around the year considered; Camargue: $Z = 0.03$, $P = 0.98$; Bassin Parisien: $Z = -0.80$, $P = 0.42$, n.s. in each case), while in the historical Camargue dataset females were recovered further away than males (495.3 km, s.e. ± 30.0, $n = 599$ and 364.7 km, s.e. ± 20.7, $n = 1{,}020$, respectively; $Z = 3.60$, $P = 0.0003$). The reduction in ring recovery distance of Camargue-ringed Mallard was apparent both in males (mean modern recovery distance = 58.6 km, s.e. ± 25.3, $n = 106$; $Z = 3.59$, $P = 0.0003$) and in females (mean modern recovery distance = 148.7 km, s.e. ± 116.6, $n = 22$; $Z = 2.41$, $P = 0.02$).

Discussion

The recovery distance of Mallard ringed in Camargue during winter has shortened considerably over the last 50 years, declining from a mean of 417 km between the 1950s

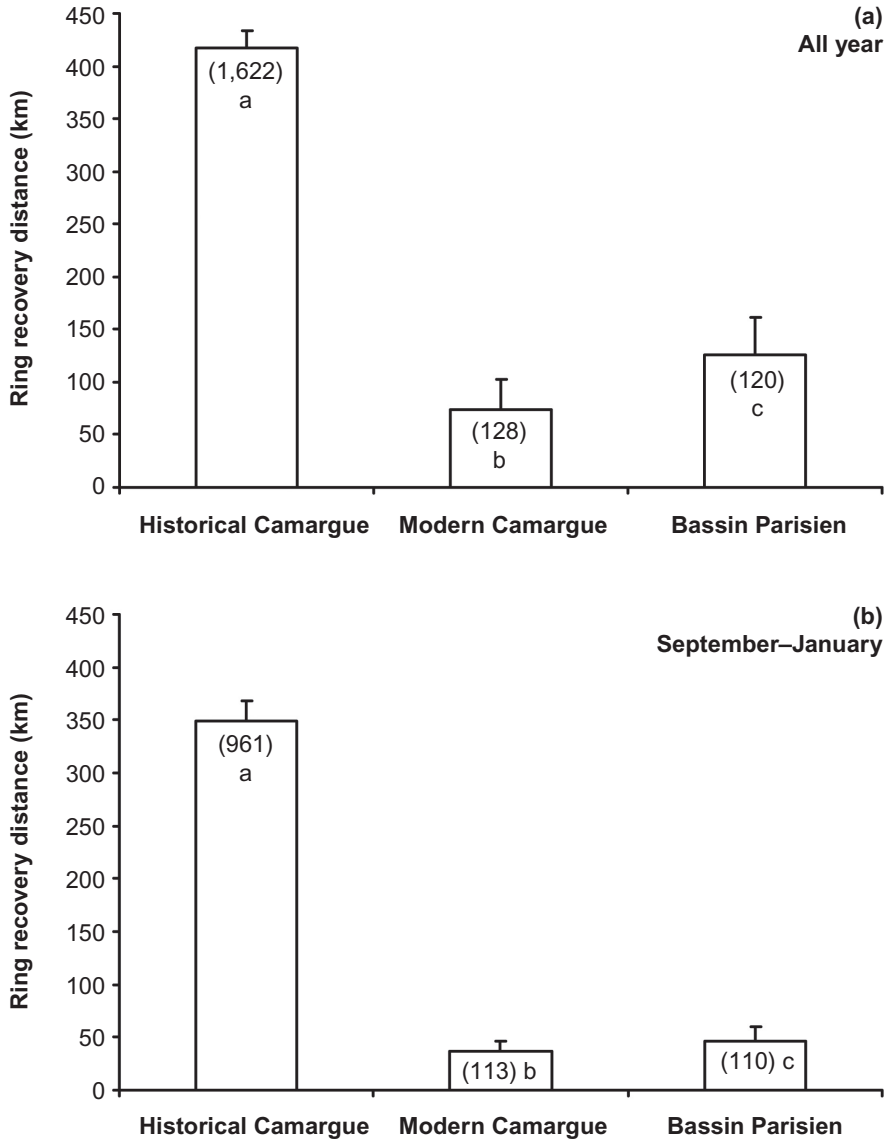


Figure 2. Mean recovery distance for Mallard ringed in Camargue from 1950–1978 ("historical Camargue"), in Camargue from 2002–2013 ("modern Camargue") and in the Bassin Parisien from 2005–2015. The top graph comprises all recoveries any time during the year, while the bottom graph is restricted to recoveries made from September–January inclusive. In both cases the mean value for historical Camargue Mallard was significantly greater than in the two other areas/periods (see text). Numbers in brackets are sample sizes, *i.e.* number of ring recoveries. Columns with different letters differed significantly in multiple pair-wise comparisons. Vertical bars show standard errors.

and 1970s to 74 km in more modern times. The decline in the ring recovery distance suggests that our sample of Camargue-wintering Mallard is increasingly composed of resident and short-distance migratory birds. The present recovery distance of Camargue-ringed Mallard is comparable to the 56 km for Mallard ringed in Great Britain or the 61 km in Italy in Sauter *et al.* (2010, note however that movements of < 5km were omitted from this later study), as well as being comparable although lower than the mean of 126 km for ducks ringed in the Bassin Parisien described here. Actually, 88% of the modern Camargue Mallard were recovered < 50 km from their ringing site, while this proportion was only 56% in the historical dataset. Several hypotheses could be put forward to explain such a pattern, as described below.

Methodological issues

First, it cannot be completely excluded that hunting pressure and reporting rates of ringed birds have changed at different rates in different parts of Europe. General hunting pressure and/or ring reporting rates have declined over time, resulting in the declining percentage of rings lately recovered, here and elsewhere (*e.g.* recovery rates for waterfowl ringed in Britain and Ireland have halved from *c.* 0.14 in the 1960s to 0.07 in the 1990s, Robinson *et al.* 2009). A differential rate of decline in hunting and/or reporting rates in different parts of the flyway therefore could have caused an apparent shift in the distribution of ring recoveries, as already acknowledged by Sauter *et al.* (2010), Gunnarsson *et al.* (2012) and Guillemain *et al.* (2015) for ducks. However, the Bassin Parisien results described in the current study show that French-ringed birds may still technically be recovered and reported from other countries. Moreover, the Camargue results suggest increasing proportions of recoveries to the south, while in contrast Sauter *et al.* (2010) and Gunnarsson *et al.* (2012) recorded increasing recoveries in northern areas. If local hunting pressure in and around the Camargue had increased sufficiently to bias the results towards more local recoveries, a similar shift of the recoveries towards the Camargue should also have been apparent for the Swiss Mallard studied by Sauter *et al.* (2010), since some of the Swiss ducks also wintered in southern France. There is therefore no indication that ring reporting probability has changed at different rates in different parts of the flyway, and should thus bias the results significantly in any of the Mallard studies listed above, nor the present one. Similarly, the current results for Camargue-ringed Mallard cannot be attributed to the general shortening of the hunting seasons in France and in other countries, since we obtained similar results when considering recoveries made only during the period of the current hunting season, *i.e.* September to January. Finally, there was a difference between historical and modern Camargue Mallard in the date on which birds were ringed during the winter, which could have affected their exposure to local hunting, and hence potentially their ring recovery distance. The historical birds were ringed slightly earlier than modern ones (late December *vs.* early January), however, resulting in them being exposed for longer

periods to local hunting, yet they were recovered further away from the ringing area.

Change in Camargue habitats

A second hypothesis could be that the habitat conditions have become so good for dabbling ducks in the Camargue that individuals formerly migrating from northern countries have become year-round residents, or arrive earlier during the season and spend more time in the area nowadays. An earlier study has shown that Eurasian Teal have become increasingly faithful to the Camargue as a winter quarter, likely owing to changes in water management making the wetlands more permanent and plant-productive than they once were, in addition to the large quantities of bait now being spread in some hunting estates (Guillemain *et al.* 2015). In the same way that such practices seem to attract Eurasian Teal from one winter to the next, they could also lead the Mallard discovering this region to remain in the area around the year to a greater extent than they did in the past. This is again highly unlikely, however, because dabbling duck females are strongly philopatric, returning year after year to the same breeding area (Oring & Sayler 1992; Blums *et al.* 1996). Our historical Camargue dataset showed that females apparently came from more distant sites than males; hence, many of these were true migrating birds. It seems very unlikely that changes in local habitat conditions in the Camargue would have been large enough to lead dabbling duck females to completely forego their philopatric habits. Furthermore, if this had been the case the local breeding population would have increased significantly. Although the monitoring of Camargue breeding ducks is poor, such a massive change would likely have been detected, whereas the breeding population is conversely considered to have been relatively stable over the last decades (Olioso 2009).

Climate change

Because the number of local breeding birds had not increased dramatically between the 1950s–1970s and more recent years (see above), such a pattern could have been due to a decline of the Nordic breeding populations, producing fewer migrants to fuel the Camargue wintering groups within which catching occurred, hence gradually leading to a greater share of local birds in the ringing sample. The most recent breeding population estimates do suggest long-term declines in countries with large Mallard breeding populations, such as the Netherlands, Lithuania, Estonia or Ukraine, but other countries important for this species such as Latvia, Poland or Germany show no trend or an increase in their populations, and the changes in the number of Russian breeding Mallards are simply unknown (Birdlife International 2015). It is therefore not possible at present to determine if the declining recovery distance of Camargue-ringed birds can be attributed to changes in abundance in different breeding areas across Europe and into Russia. What is likely, however, is that northern migrant Mallard increasingly forego long migrations to distant Camargue winter quarters (winter short-stopping, *sensu* Elmberg *et al.* 2014). Gunnarsson *et al.*

(2012) and Sauter *et al.* (2010) both found that Mallard were recovered at increasingly shorter distances from the ringing site over time. Gunnarsson *et al.* (2012) studied ducks ringed in Sweden, while Sauter *et al.* (2010) used ringing data from a variety of European countries (Great Britain, Denmark, Sweden, the Netherlands, Belgium, Germany, Switzerland and Italy) but not including France. In both cases, only winter recoveries were considered, and were consistently to the south or southwest of the ringing sites: shorter recovery distances therefore corresponded with recoveries gradually occurring further to the north and/or east, which Gunnarsson *et al.* (2012) attributed mainly to climate change leading to a general shift in the birds' wintering grounds. Sauter *et al.* (2010) considered this shift to be primarily a consequence of decreasing frequency of winter cold spells, resulting in Mallard being pushed less frequently to the southwest during winter. Both scenarios are consistent with our results because they would translate into fewer migrants from these areas within the Camargue wintering groups, hence a greater proportion of local birds wintering in southern France and consequently a shortening of their mean ring recovery distance.

Massive releases of captive-bred Mallard

The last hypothesis to explain such a shortening of the ring recovery distance is linked with the fact that the Mallard is the only duck species where releases of captive-bred birds are carried out for hunting purposes. This is practised at a massive scale in Europe, where an estimated 3 million individuals are released annually, of which 1.4 million are released in France alone (Champagnon 2011). Champagnon (2011) also estimated that *c.* 50,000 individuals are released annually in the Camargue, mostly during the summer, while this was virtually non-existent during the historical years of our study. Captive-bred birds usually do not disperse much (review in Söderquist 2015): the mean ring recovery distances of 861 released Mallards in Camargue were only 610 m in Champagnon (2011). It is possible that the winter catch for ringing in the Camargue is increasingly composed of these largely non-migrating released birds. Unfortunately, these birds are not marked and very much resemble their wild conspecifics in appearance, so the origin of an individual is impossible to tell when the bird is in the hand having been caught for ringing. Hybridization of the released Camargue Mallards with their wild conspecifics also does occur (Champagnon *et al.* 2013), and may have led the birds to remain in the Camargue throughout the year. Introgression of captive genes may lead to changes in migratory behaviour (Champagnon *et al.* 2012), as observed in different species of birds where wild populations were supplemented with more resident individuals, for instance Common Quail *Coturnix coturnix* (Derégnaucourt *et al.* 2005), Little Bustard *Tetrax tetrax* (Villers *et al.* 2010) or White Stork *Ciconia ciconia* (Massemin-Chalet *et al.* 2006).

Future research

Although the pattern of a decrease in the recovery distance for Mallard ringed in

Camargue during winter is very clear, it is not currently possible to tease apart the three main hypotheses proposed above (*i.e.* a change in attractiveness of Camargue habitats, a climate change effect, or the consequences of massive releases of captive-bred Mallard), which furthermore may not be mutually exclusive from each other. We suggest that a combination of genetic and isotope studies of wing feathers should be carried out while ringing Mallard in Camargue, along with testing museum specimens from a period corresponding to our historical data. This will provide an assessment of the proportion of birds produced locally while also determining whether they are of wild or captive origin. In addition to such laboratory approaches, annual surveys of the Mallard population breeding in this region would be very valuable, although unfortunately difficult and expensive to set up (Fouque *et al.* 2004; C. Tetrel, unpubl. data). Such information would help to quantify the relative proportion of sedentary birds in the population, which are likely responsible for the shortening of mean ring recovery distances in this species over the last 50 years, and determine whether such increased sedentarity is the consequence of bird releases.

Acknowledgements

We would like to thank the many fieldworkers who took part in the Mallard ringing programmes over the years, as well as the many people (mostly hunters) who sent the rings back. We also thank Eileen Rees, Tony Fox, Jón Einar Jónsson and two anonymous referees for useful comments on an earlier version of the manuscript.

References

BirdLife International 2015. *European Red List of Birds*. Office for Official Publications of the European Communities, Luxembourg City, Luxembourg. Accessible at http://www.birdlife.org/datazone/info/euroredlist (last accessed 3 August 2015).

Blums, P., Mednis, A., Bauga, I., Nichols, J.D. & Hines, J.E. 1996. Age-specific survival and philopatry in three species of European ducks: a long-term study. *The Condor* 98: 61–74.

Brochet, A.L., Mouronval, J.B., Aubry, P., Gauthier-Clerc, M., Green, A.J., Fritz, H. & Guillemain, M. 2012. Diet and feeding habitats of Camargue dabbling ducks: What has changed since the 1960s? *Waterbirds* 35: 555–576.

Champagnon, J. 2011. Conséquences des introductions d'individus dans les populations exploitées: l'exemple du canard colvert *Anas platyrhynchos*. Ph.D. thesis, Université Montpellier II, France.

Champagnon, J., Elmberg, J., Guillemain, M., Gauthier-Clerc, M. & Lebreton, J.D. 2012. Conspecifics can be aliens too: a review of effects of restocking practices in vertebrates. *Journal for Nature Conservation* 20: 231–241.

Champagnon, J., Crochet, P.A., Kreisinger, J., Čížková, D., Gauthier-Clerc, M., Massez, G., Söderquist, P., Albrecht, T. & Guillemain, M. 2013. Assessing the genetic impact of massive restocking on wild mallard. *Animal Conservation* 16: 295–305.

Čížková, D., Javůrková, V., Champagnon, J. & Kreisinger, J. 2012. Duck's not dead: Does restocking with captive bred individuals affect the genetic integrity of wild mallard (*Anas platyrhynchos*) population? *Biological Conservation* 152: 231–240.

Derégnaucourt, S., Guyomarc'h, J.C. & Belhamra, M. 2005. Comparison of migratory tendency in European quail *Coturnix c. coturnix*,

domestic Japanese quail *Coturnix c. japonica* and their hybrids. *Ibis* 147: 25–36.

Duncan, P., Hewison, A.J.M., Houte, S., Rosoux, R., Tournebize, T., Dubs, F., Burel, F. & Bretagnolle, V. 1999. Long-term changes in agricultural practices and wildfowling in an internationally important wetland, and their effects on the guild of wintering ducks. *Journal of Applied Ecology* 36: 11–23.

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.

Fouque, C., Corda, E., Tesson, J.-L., Mondain-Monval, J.-Y., Barthe, C., Dej, F. & Birkan, M. 2004. Breeding chronology of anatids (*Anatidae*) and coots (*Fulica atra*) in France. *Game and Wildlife Science* 21: 73–106.

Guillemain, M. & Elmberg, J. 2014. *The Teal*. T. & A.D. Poyser, London, UK.

Guillemain, M., Sadoul, N. & Simon, G. 2005. European flyway permeability and abmigation in Teal *Anas crecca*, an analysis based on ringing recoveries. *Ibis* 147: 688–696.

Guillemain, M., Green, A.J., Simon, G. & Gauthier-Clerc, M. 2013. Individual quality persists between years: individuals retain body condition from one winter to the next in Teal. *Journal of Ornithology* 154: 1007–1018.

Guillemain, M., Pernollet, C.A., Massez, G., Cavallo, F., Simon, G. & Champagnon, J. 2015. Disentangling the drivers of change in Common Teal migration phenology over 50 years: land use *vs.* climate change effects. *Journal of Ornithology* 156: 647–655.

Gunnarsson, G., Waldenström, J. & Fransson, T. 2012. Direct and indirect effects of winter harshness on the survival of Mallards *Anas platyrhynchos* in northwest Europe. *Ibis* 154: 307–317.

Huntley, B., Green, R.E., Collingham, Y.C. & Willis, S.G. 2007. *A Climatic Atlas of European Breeding Birds*. Lynx Edicions, Barcelona, Spain.

Jónsson, J.E. & Afton, A.D. 2015. Are wintering areas shifting North? Learning from Lesser Snow Geese banded in Southwest Louisiana. *Southeastern Naturalist* 14: 293–307.

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

Massemin-Challet, S., Gender, J.-P., Samtmann, S., Pichegru, L., Wulgue, A. & Le Maho, Y. 2006. The effect of migration strategy and food availability on White Stork *Ciconia ciconia* breeding success. *Ibis* 148: 503–508.

Mouronval, J.B. 2014. *Guide de Détermination de l'Age et du Sexe des Canards*. Office National de la Chasse et de la Faune Sauvage, Paris, France. [In French.]

Olioso, G. 2009. Canard colvert *Anas platyrhynchos*. *In* A. Flitti, B. Kabouche, Y. Kayser & G. Olioso (eds.), *Atlas des Oiseaux Nicheurs de Provence-Alpes-Côte d'Azur*, pp. 48–49. Ligue pour la Protection des Oiseaux PACA, Delachaux et Niestlé, Paris. [In French.]

Oring, L.W. & Sayler, R.D. 1992. The mating system of waterfowl. *In* B.D.J. Batt, A.D. Afton, M.G. Anderson, C.D. Ankney, D.H. Johnson, J.A. Kadlec & G.L. Krapu, G.L. (eds.), *Ecology and Management of Breeding Waterfowl*, pp. 128–189. University of Minnesota Press, Minneapolis, USA.

Robinson, R.A., Grantham, M.J. & Clark, J.A. 2009. Declining rates of ring recovery in British birds. *Ringing & Migration* 24: 266–272.

Sauter, A., Korner-Nievergelt, F. & Jenni, L. 2010. Evidence of climate change effects on

within-winter movements of European Mallards *Anas platyrhynchos*. *Ibis* 152: 600–609.

Söderquist, P. 2015. Large-scale releases of native species: the Mallard as a predictive model system. Ph.D. thesis, Faculty of Forest Sciences, Swedish University of Agricultural Sciences, Umeå, Sweden.

Statsoft 2011. *Statistica Version 10*. Accessible at www.statsoft.fr (last accessed 27 July 2015).

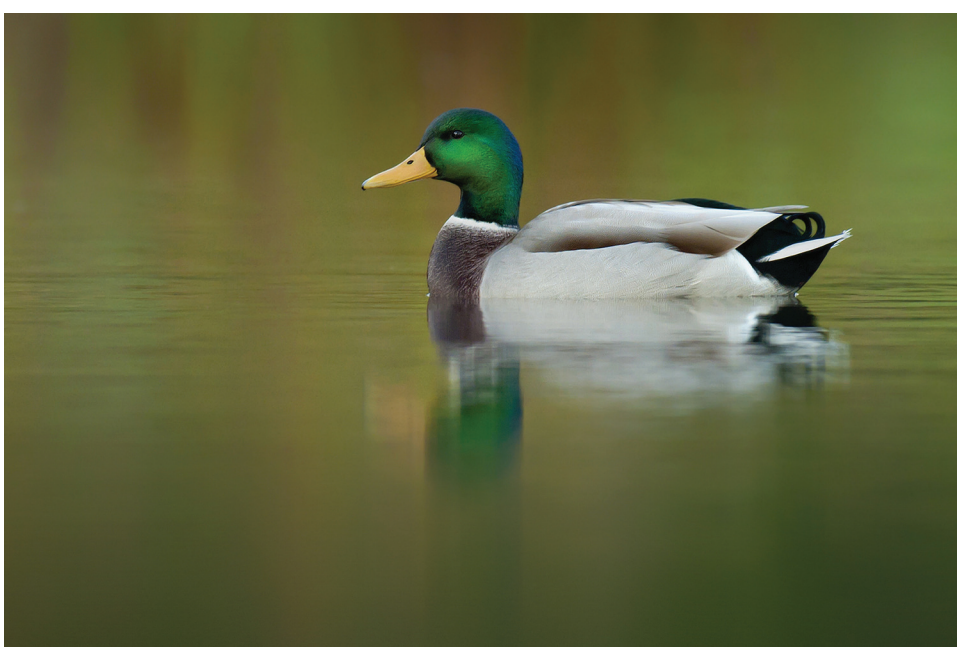
Švažas, S., Meissner, W., Serebryakov, V., Kozulin, A. & Grishanov, G. 2001. *Changes in Wintering Sites of Waterfowl in Central and Eastern Europe*. Oiseaux Migrateurs du Palearctique Occidental (OMPO) Special Publication. OMPO Vilnius & Lithuanian Institute of Ecology, Vilnius, Lithuania.

Tamisier, A. 2004. Camargue, quartier d'hiver de canards et de foulques. Modalités de fonctionnement, facteurs limitants et perspectives d'avenir. *In* P. Isenmann (ed.), *Les Oiseaux de Camargues et leurs Habitats. Une Histoire de Cinquante Ans 1954–2004*, pp. 149–204. Buchet/Chastel, Paris, France. [In French.]

Tamisier, A. & Dehorter, O. 1999. *Camargue, Canards et Foulques – Fonctionnement et Devenir d'un Prestigieux Quartier d'Hiver*. Centre Ornithologique du Gard, Nîmes, France. [In French.]

Villers, A., Millon, A., Jiguet, F., Lett, J.-M., Attié, C., Morales, M.B. & Bretagnolle, V. 2010. Migration of wild and captive-bred Little Bustards *Tetrax tetrax*: releasing birds from Spain threatens attempts to conserve declining French populations. *Ibis* 152: 254–261.

Young, G. 2005. Northern Mallard *Anas platyrhynchos*. *In* J. Kear (ed.), *Ducks, Geese and Swans*. *Volume 2*, pp. 513–517. Oxford University Press, Oxford, UK.



Photograph: Mallard, by Des Ong/FLPA.

