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Differential mapping of ringed bird distributions from live resightings *versus* dead recoveries: an illustration using Eurasian Teal *Anas crecca*

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Abstract

Ringling and visual marking have long been used to delineate bird distribution ranges, but neither method is free from biases linked with differential re-encounter probabilities over the landscape, which may also differ among data collection methods. Modern statistical techniques enable two-dimensional smoothing of the capture/re-encounter information compared with earlier raw ring recovery location maps, improving geographical presentation of areas of greater bird encounter density. However, such technological tools do not solve the issue of the potential biases associated with different data collection methods. We used ring recovery and nasal saddle resighting data from over 14,000 Eurasian Teal *Anas crecca* ringed in France since 2002 to produce flyway-scale kernel distribution maps to highlight differences between distributions dependent on whether they were derived from recoveries or resighting information, despite abundant data in both cases. Results show that neither large datasets nor modern analytical tools are sufficient to overcome re-encounter probability biases, which require serious evaluation and future dedicated research.

Key words: flyway delineation, kernel, live resighting, nasal saddle, ring recovery.

Ringling has been the primary method to delineate flyways and draw bird distribution maps over the last century (*e.g.* Lincoln 1935; Perdeck & Clason 1980; Scott & Rose 1996), including in national ringling atlases (*e.g.*

Saurola *et al.* 2013; Dupuy & Sallé 2022; Spina *et al.* 2022). Geolocation and tracking devices nowadays provide alternatives (*e.g.* Robinson *et al.* 2010; Bridge *et al.* 2013; Kays *et al.* 2022), but their cost still restricts

their use to relatively few individuals per population. A few satellite-tagged individuals may be enough to discover unexpected migration pathways and distances, for instance for Ospreys *Pandion haliaetus* (Strandberg *et al.* 2009) and Lesser Black-backed Gulls *Larus fuscus* (Klaassen *et al.* 2012), yet ring recoveries remain the preferred method for drawing distribution maps at the continental population scale.

A caveat applied to results from ringing studies is that their results obviously depend upon an even probability of ring recoveries in time and space. This is rarely the case: no recoveries will be derived from areas devoid of people, or from those areas where it is less likely that people will encounter, recover and/or return rings to the ringing organisation. Care therefore must be exercised in drawing conclusions from the geographic distribution of populations based only on ring recovery data due to temporal and spatial heterogeneity in ring recovery probability (*e.g.* Perdeck 1977; Royle & Dubowsky 2001; Strandberg *et al.* 2009; Thorup & Conn 2009; Korner-Nievergelt *et al.* 2010; Thorup *et al.* 2014; Sallé *et al.* 2022). Moreover, even when the need for such caution is recognised it may prove very difficult or impossible to evaluate such potential bias (Busse 2001; see also the use of reward rings in Nichols *et al.* 1995), even more so retrospectively when analysing long-term ringing data sets (Korner-Nievergelt *et al.* 2010). Ring re-encounter distribution maps therefore generally remain biased to an unknown extent.

Hunted species are well suited to the study of geographic distribution through

ring recoveries because their rings are far more likely to be recovered and reported back to ringing centres than those of protected species, which more often die of natural causes without being found. The difference in recovery probabilities can be of up to two orders of magnitude between *c.* 10% in hunted waterfowl and *c.* 0.1% in swallows (Robinson *et al.* 2009), hence providing far more ring recovery locations in the former case. However, distribution maps of hunted species are highly dependent upon the distribution of hunting pressure, a factor that has generally not been evaluated at broad geographical scales since it depends both on the number of hunting licences in a given area (which may already be difficult to quantify, *e.g.* Aubry *et al.* 2020) and on the level of hunting pressure exerted by these hunters, which is generally totally unknown (see, however, McCulloch *et al.* 1992 for an attempt at measuring large-scale hunting pressure from ring recoveries). An alternative is to add visual marks to ringed birds, which can be read from a distance thus allowing distribution maps to be drawn from observations made by anyone, without the need to physically recapture or obtain dead individuals, potentially yielding many resightings per marked individual (Bairlein 2003). Such visual marks, again, have proved useful for drawing flyways or even sub-units for management within flyways (*e.g.* neck collars in Greylag Goose *Anser anser*, Bacon *et al.* 2019). However, this time the delineation of such geographic ranges may be strongly affected by available observation pressure from ornithologists, which is often totally unknown but would be required to conduct such an analysis properly.

Eurasian Teal *Anas crecca* (hereafter Teal) is among the species which have been ringed in greatest numbers over the last eight decades, with relatively high (though declining) proportions of rings later returned, mostly by hunters (Guillemain *et al.* 2011). Such ring recoveries have been used to study flyway delineation via various statistical means (Guillemain *et al.* 2005, 2017; Calenge *et al.* 2010). In addition, nasal saddles have been fitted to a significant proportion of these birds (55.0% of those ringed in France over the last 20 years). The Teal dataset hence offers the opportunity to draw wide re-encounter distribution maps based on two distinct information sources. While several earlier papers warned about the consequences of unknown heterogeneity in re-encounter probability when generating distribution maps of ring recoveries (see above), and some have produced maps plotting raw re-encounter ringing data from different sources to show differences (*e.g.* du Feu *et al.* 2016; Potvin *et al.* 2017; Nilsson 2017), new techniques now allow for such ring recovery data to be processed in order to provide more explicit kernel or heat maps with smoothed distribution of recovery likelihood, instead of mere dot clouds (*e.g.* Calenge *et al.* 2010 for waterfowl), but such elaborated maps have rarely been compared between sources of re-encounter data (see, however, Thorup *et al.* 2014). Our aim is to illustrate such problems in waterfowl, by comparing how different information modes (ring recoveries from hunting *vs.* saddle observations from birdwatchers) can provide contrasting results in terms of smoothed bird distribution maps.

Methods

Data collection

We analysed data from 14,360 Teal ringed throughout France between 2002 and 2023, of which 7,893 were also fitted with a plastic nasal saddle of the type described by Rodrigues *et al.* (2001) at ringing, with a model size adapted to the species (see Guillemain *et al.* 2007). This yielded 1,817 ring recoveries (12.7% of those initially ringed), of which 1,680 (92.5%) were shot birds reported by hunters, and constituted the dataset used here for ring recoveries (*i.e.* non-hunting recoveries were few and were discarded). A total of 5,322 physical recaptures of live birds were obtained, but the vast majority of these were multiple recaptures of the same individuals by the operators of the current programme, at initial ringing sites. Only 47 such physical recaptures were made elsewhere by foreign ringers, so this source of information was not used here. In total, 2,669 saddled Teal (33.8% of those initially marked) were visually resighted alive, generating 12,154 encounter events. However, many such dead recoveries and live resightings occur at or in close vicinity to the initial ringing sites, because of higher local hunting and observation pressure, including by operators of the programme themselves, as well as due to the accumulating knowledge of hunters and birdwatchers in the neighbourhood (*e.g.* du Feu *et al.* 2016). This can lead to spatial autocorrelation affecting later evaluation of ranges (*e.g.* Fleming & Calabrese 2017), especially when pseudo-replication due to multiple re-observations of the same individuals at the same place occurs, yielding

a biased weighting of the data towards such initial ringing places. To overcome the spatial autocorrelation issue, we first discarded all data from “communes” (the geographic territory of a city or village, which was the precision of recovery and resighting data) within a radius of 10 km from the ringing site, selected on the basis of earlier work undertaken on the nocturnal commuting flight distances recorded for Teal (Guillemain *et al.* 2008). To overcome the pseudo-replication issue we then only retained one location per individual per season (autumn–winter: August to January inclusive; spring–summer: February to July inclusive) per year. This resulted in 1,190 hunting dead recoveries (a 8.3% ring recovery rate) and 761 nasal saddle resightings from 560 of the 7,893 initially saddled birds (a resighting rate of 7.1% individual birds).

Data analysis

The distribution of Teal live resighting and dead recovery locations were mapped as kernel density probabilities using the `kde2d` function in the MASS package (Venables & Ripley 2002) in R version 4.2.2 (R Core Team 2022). A unique smoothing bandwidth was set up for all maps using the rule-of-thumb of the `bandwidth.nrd` function from the MASS package (Venables & Ripley 2002). A base map came from the `rnaturalearth` package (Massicotte & South 2023). It is important to note that `kde2d` does not distinguish between land and sea water, so the kernel areas extend slightly over sea areas albeit smoothed from only land points. Probability densities of the points were divided into three levels for the

sake of legibility: 1–5%, 5–25% and 25–100%.

Although the Teal are highly mobile (Guillemain *et al.* 2006), it may take some time for them to move around their entire flyway range. It is therefore common practice in migratory bird analyses to distinguish direct ring recoveries (those occurring during the year of ringing) from indirect recoveries during later years. This was undertaken here, based on a year extending from 1 August to the following 31 July. The same procedure was applied to nasal saddle resightings, so three maps are provided for the two sources of data: one comprising dead recoveries/nasal saddle resightings from all years, with the two additional maps using direct and indirect data.

Results

The live resighting map using data from all years is shown in Fig. 1. While the greatest probability densities were recorded in France, especially along the south and west coasts as well as along the Pyrenees, densities were also higher in a zone covering the Netherlands, Germany, Belgium, Switzerland, southern UK, southern Denmark and southern Sweden, as well as along the coasts of Spain and Portugal. At the European level, the annual distribution map derived from nasal saddle resightings thus indicates that Teal from France disperse primarily across northwest Europe.

The dead recovery map using data from across the year (Fig. 2) tells a different story. These data suggested that the annual range used by Teal, although still centred on France (especially along the coasts), did not reach the sea coasts of the Iberian

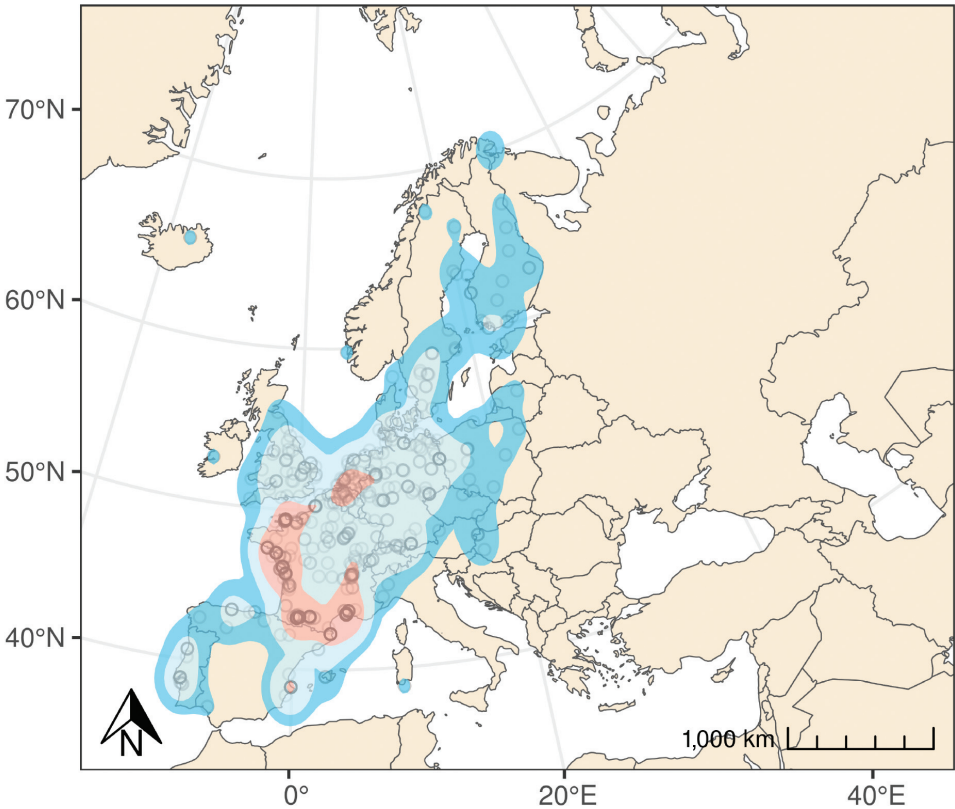


Figure 1. Probability density distribution of Teal inferred from nasal saddle resightings from 2002–2023 inclusive. Different colours indicate varying levels of probability: dark blue = 1–5%, light blue = 5–25% and pink = 25–100%. Circles indicate locations where at least one resighting occurred, based on $n = 761$ independent observations of Teal identified by their nasal saddles.

Peninsula. It was also far patchier in eastern Europe, but extended over a vast area (albeit in a sporadic manner) up to the Siberian border, with greatest densities in northern Italy, Denmark, the Baltic states and Finland. From this map, the Netherlands, Germany, Poland and other central European countries seemed to be devoid of Teal.

Maps comparing direct *vs.* indirect visual resightings yielded very similar distributions,

with the Teal again confined to northwestern Europe, albeit with the Baltic States and Central Europe slightly more represented when incorporating indirect recoveries (Fig. 3). For hunting recoveries, the difference between direct and indirect data was more straightforward. The main difference was the relative probability density for Finland and Russia, which was evidently greater (although still very patchy) on including the indirect data (Fig. 4).

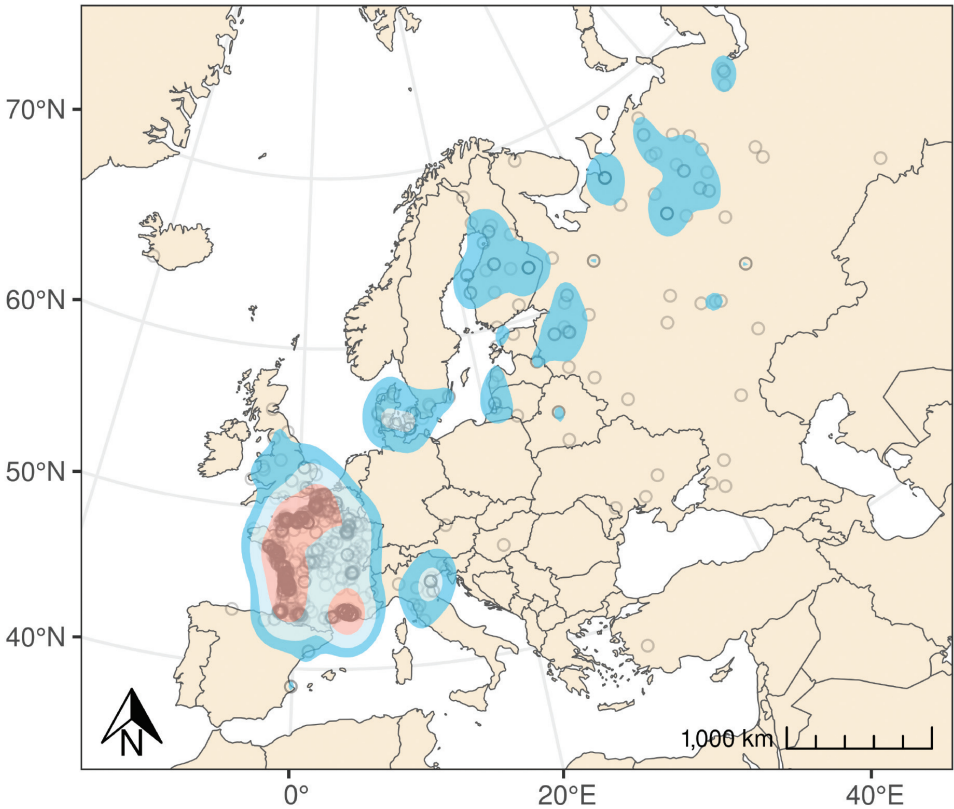


Figure 2. Probability density distribution of Teal inferred from ring recoveries of hunted birds from 2002–2023 inclusive. Different colours indicate varying levels of probability: dark blue = 1–5%, light blue = 5–25% and pink = 25–100%. Circles indicate locations where at least one ring recovery occurred, based on $n = 1,190$ ring recoveries.

Discussion

The maps presented here illustrate how reliance on different sources of bird ringing information can lead to distinct and differing patterns of geographic distribution. This is not a novel idea (see *e.g.* Perdeck 1977 also for Teal, or supplementary material in Fandos *et al.* 2021), but geographic data analyses summarise these patterns into a more visually comprehensible format based on

smoothing of data, distinguishing areas of different density (compare the raw maps of Teal ring recoveries in Guillemain *et al.* 2005 with the kernel estimates in Calenge *et al.* 2010). Despite this ease of data presentation, it is vital not to forget important biases in the underlying data. The kernel maps drawn here from visual resightings suggest that the Teal is mostly a northwest European bird, while hunting ring recoveries actually show that the range of this population extends

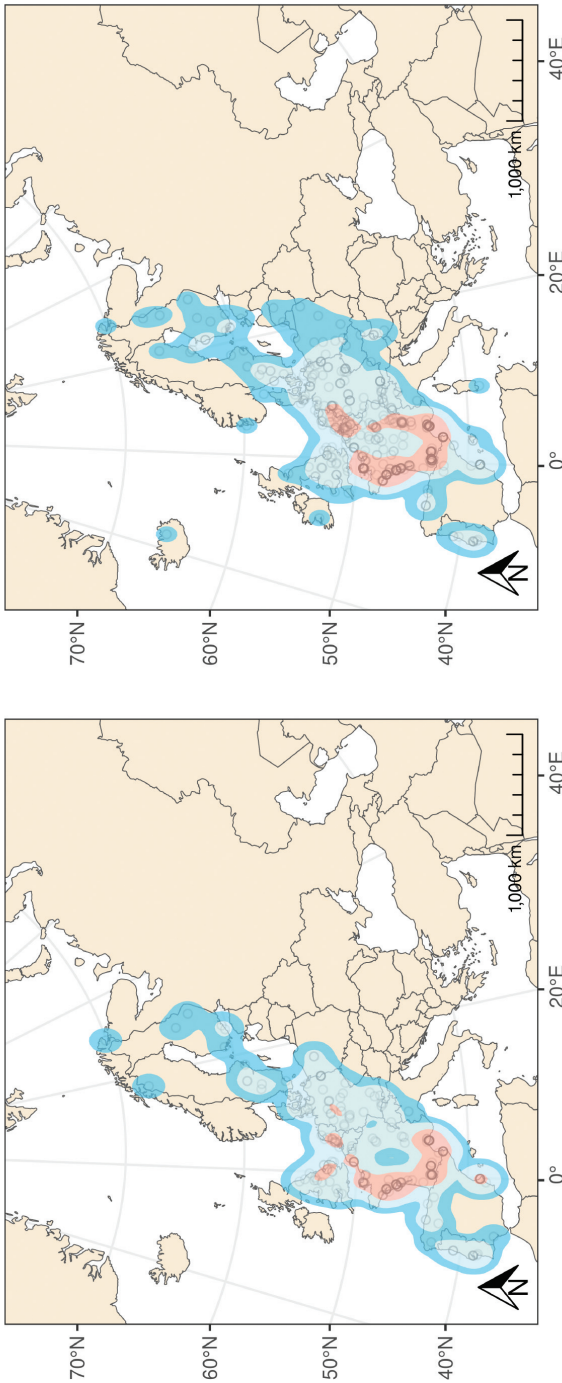


Figure 3. Probability density distribution of Teal inferred from nasal saddle resightings from 2002–2023 inclusive. Left: direct resightings during the year of ringing (*i.e.* up to the next 31 July, $n = 229$ individual locations). Right: indirect resightings, during years after the year of ringing (*i.e.* after the next 31 July, $n = 532$). Different colours indicate varying levels of probability: dark blue = 1–5%, light blue = 5–25% and pink = 25–100%.

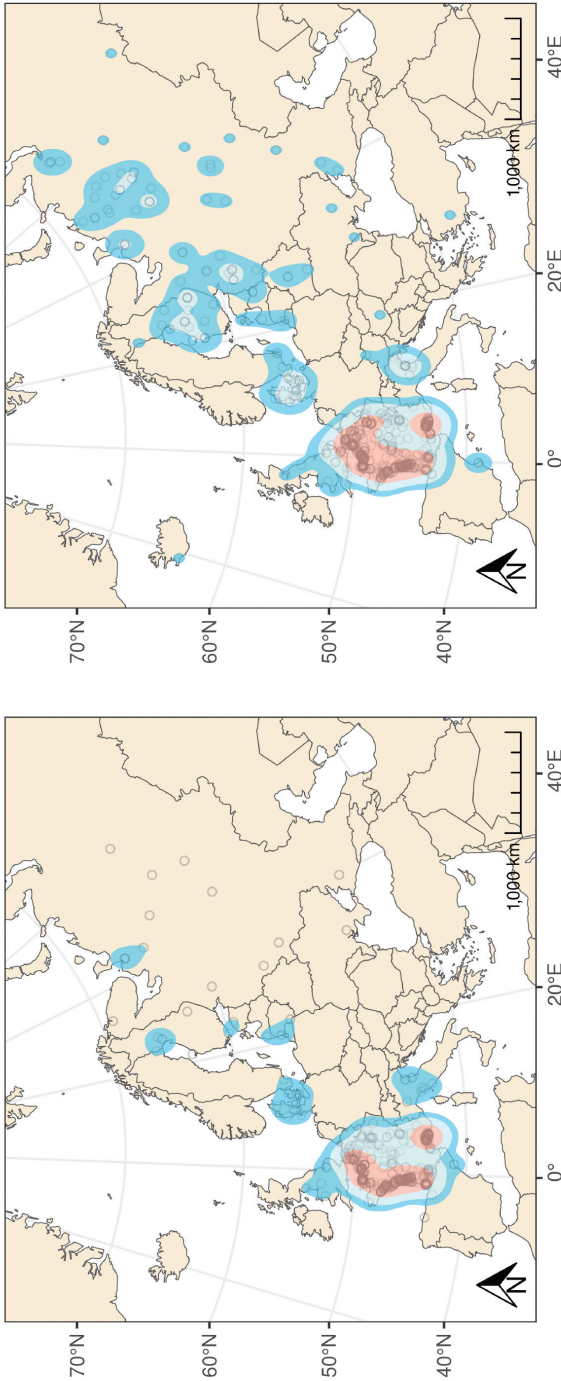


Figure 4. Probability density distribution of Teal inferred from ring recoveries of hunted birds from 2002–2023 inclusive. Left: direct recoveries during the year of ringing (i.e. up to the next 31 July, $n = 554$). Right: indirect recoveries, during years after the year of ringing (i.e. after the next 31 July, $n = 636$). Different colours indicate varying levels of probability: dark blue = 1–5%, light blue = 5–25% and pink = 25–100%.

several thousands of kilometres further to the east, to the Ural Mountains (from where no visual observations originate), but almost entirely overlooks its occurrence on the Iberian Peninsula. Results from hunting recoveries therefore confirm a substantially larger and more easterly geographical annual range for individual Teal emanating from western Europe, compared with the resightings data, not a reduced one as one might expect. Potvin *et al.* (2017) previously warned about the consequences of filtering out hunting-related ringing information to avoid the bias caused by differential ring reporting probabilities among geographic areas (owing to differences in human density and/or hunting pressure). The present results suggest that, while hunting data should definitely be used, these and all other sources of movement data have their own inherent geographic biases that need to be taken into account. For instance, the very high density probability inferred from nasal saddle resightings in the Netherlands (and to a lesser extent in southern UK) is likely biased high by the relatively intense birdwatching activity in these countries compared with elsewhere. Ideally, future analyses should weigh such results by observation effort, but such information is not currently available. Ongoing attempts to evaluate relative levels of local observation effort, by assessing relative numbers of multiple observations between different areas (A. Tableau & A. Caizergues, unpubl. data), was not possible here for Teal at the European scale because there are entire countries with no dead recoveries and/or live resightings data.

The maps presented here are the first to rely entirely on data from a new ringing

scheme initiated in 2002, based on many ringing sites across France, whereas earlier information was generally derived from older schemes *e.g.* in Denmark, United Kingdom and the Netherlands (Lebret 1947; Wolff 1966), or largely restricted to the Camargue in France (Guillemain *et al.* 2005; Calenge *et al.* 2010) before the 1970s. Although environmental conditions may have differed across such a time period, there were no major differences between these modern and the historic maps in terms of Teal distribution ranges or the main hunting areas for the species in Europe. Many recoveries are also obtained from Russia, Denmark or Finland, where large numbers of Teal are known to be harvested annually (Guillemain *et al.* 2016; Solokha & Gorokhovskiy 2017). The central role played by France illustrated by the maps presented here is partly due to the fact that birds were ringed in this country, and therefore were more likely to be at relatively short distance from the ringing sites, even with very local data (≤ 10 km from the ringing sites) being buffered. The relative importance of France compared with other countries, when it comes to dead recoveries, is also likely to result from the relatively high levels of wildfowling activity in the country (Guillemain *et al.* 2016), since the relative importance of France was great not only among direct recoveries (hence soon after ringing), but also for indirect ones, one or more years later. The main differences between the maps using direct *vs.* indirect ring recoveries were in areas at or close to breeding ranges (Finland, Russia), which are mostly used during summer and early autumn, hence could not be represented

in direct recoveries because ringing in France mostly occurred later (from October onwards). The same process could explain why there were slightly more nasal saddle observations in the Baltic States or central Europe among indirect resightings. However, maps for direct and indirect resightings were very similar, covering a consistent area in northwestern Europe, which is consistent with the rapid and broad movement of Teal soon after ringing (Guillemain *et al.* 2006).

The results shown here illustrate that even in a widely studied species where both hunting recovery and resighting data are numerous, the different methods of data collection come with their own biases and so present different patterns of distribution. To avoid drawing biased conclusions, it is vital to consider various sources of data, even in heavily hunted species like the Teal, and to take account of the known caveats associated with each method. Some earlier authors have developed maps of geographically explicit hunting pressure or re-encounter probabilities from the ringing datasets themselves, in order to correct for such biases when analysing ring recoveries (McCulloch *et al.* 1992; Korner-Nievergelt *et al.* 2010; Thorup *et al.* 2014). However, available data do not always allow such complex and information-demanding analyses. National harvest rates can also be evaluated through reward ring schemes (*e.g.* Boomer *et al.* 2013), but these take a long time to establish and are complex to put in place and maintain over time. It may also be possible to correct ring recovery (or visual resighting) maps by using completely independent information such as re-encounter probability inferred from

independent satellite-tagged bird tracks (*e.g.* Naef-Daenzer *et al.* 2017), hunting pressure maps built from bio-acoustic loggers recording gunshot frequency (Hedley *et al.* 2022), or maps of human population density and landscape features linked with the species' ecological niche (Tellería *et al.* 2014; Fandos & Tellería 2017). In a world where people tend (or have to) report information in real time on portable apps, one way forward could be to correct ring recoveries and visual observations by geographically explicit information on the number of users of such apps over time and space (*e.g.* eBird connections; apps used by hunters to report their bag). To date, such data are unfortunately not available for the Teal at the European scale.

Bayesian statistical methods now exist which can combine information from independent survey schemes with ring recovery and mark resighting data to take re-encounter likelihood into account and obtain a more realistic probabilistic mapping of bird distribution. This is clearly the way forward in the analysis of our precious bird ringing data sets (Korner-Nievergelt *et al.* 2010; Thorup *et al.* 2014): the challenge is not so much from a lack of statistical approaches, but more the current lack of reliable auxiliary data.

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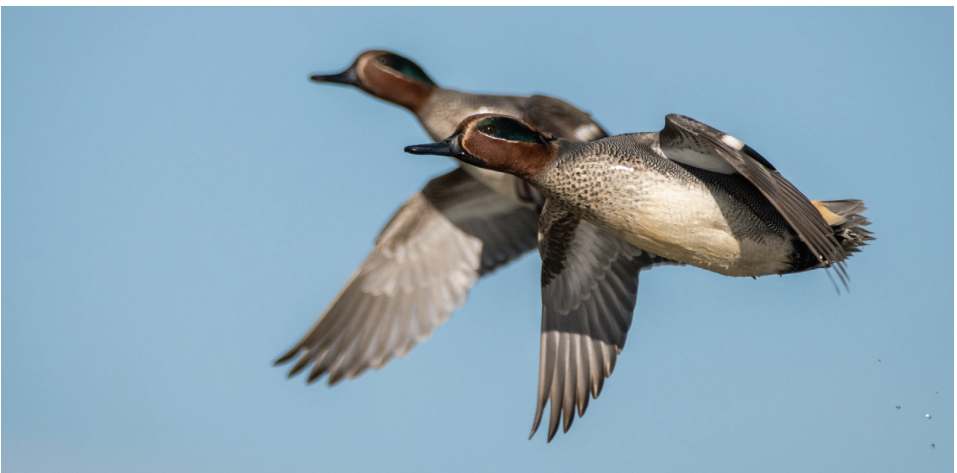
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Photograph: Teal in flight in the Camargue, by Pierre-Lou Chapot.



Photograph: Two male Teal, by Pierre-Lou Chapot.