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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.

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Abstract We use a new method named "product kernel estimator" to explore the the spatial and temporal distribution of 9,114 recoveries of Teal (*Anas crecca*) ringed in Camargue, southern France, and recovered over the whole Europe. This method allows to explore the changes in time of the probability density to recover a ringed

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bird over a grid covering the study area. We thus identified two migration corridors for this species, to the North and the South of the Alps, while earlier analyses mostly suggested a Southern route from Camargue, especially in spring. The Northern route seems used to a greater extent in autumn than in spring, indicating a frequent abmigration (animals switching from one corridor to the other). Moreover, migration of the population seems faster in spring than in autumn. The simultaneous presence of Teal recoveries in many distinct geographical areas in spring is consistent with the idea that these ducks are not limited by their migratory speed in spring, nor do they wait until favourable environmental conditions before colonizing their breeding areas.

Keywords product kernel algorithm · spatial distribution · time effect · Eurasian Teal · ring recoveries

1 Introduction

The ringing of migratory birds has long been used to study the the movements and spatial distribution of a bird population, e.g. to determine where individuals of a given breeding population wintered or, conversely, where the individuals of a known wintering population were breeding (e.g. Schüz and Weigold 1931, see also the work carried out by HCC Mortensen, compiled by Jespersen and Veden Tåning 1950), or to define their flyways (e.g. Scott and Rose, 1996).

Purely spatial smoothing techniques have been used to explore the continuous variation in space of the probability of recoveries (Wand and Jones, 1995; Atkinson et al., 2007), but accounting for the time dimension in the analysis of such data may bring essential information on the temporal changes in the spatial distribution of the ringed animals. Recently, Keating and Cherry (2009) proposed an approach relying on the kernel method to smooth a distribution of points in both space and time. They developed the method to estimate the probability density distribution of presence of an animal monitored using GPS in both time and space, using relocation data. In the present paper, we test this method to assess if it could also be used valuably as an exploratory approach of the distribution of bird ring recoveries. We apply the technique to the very large Teal ring recovery dataset as an example, to assess if this can provide new insights into the migration patterns of this species throughout Europe. Our main aims were 1) to assess how many different routes these ducks use during spring and autumn migrations, 2) the extent and the rate at which they disperse from their ringing site during a given winter, 3) the consequences of known switches between wintering quarters from a winter to the next (abmigration) in terms of routes used during the migration journeys, and 4) if some areas are used markedly less than others by the species, at the continental scale.

2 Methods

Teal were caught at Tour du Valat in Camargue, southern France (43 ° 30' N, 04 ° 40'E) between January 1952 and February 1978 using standard dabbling duck funnel traps hidden in the vegetation (Bub, 1991). In total, 59,187 Teal were captured and ringed, of which most (96%, N=56,697) were so between November and March of each year, and constituted the dataset used in the present study. These ringing operations led to 9,114 recoveries (15% of the total number of ringed Teal), among which 4,652 (51%) were intra-annual recoveries, i.e. birds recovered before the month of November following the season of capture, and 4462 were inter-annual recoveries, i.e. birds recovered after this date. The different age and sex classes were not distinguished in the present exploratory analyses of this ring recovery dataset.

Each ring recovery is characterized by a set of spatial coordinates (X and Y), as well as a date of recovery. The whole set of recoveries therefore defines a point pattern in space and time. We aimed at identifying the changes of areas with the highest probability of recovery with time, which was expected to be a proxy for the migration corridor(s) of Teal. For this purpose, we used the product kernel algorithm (Wand and Jones, 1995) recently introduced in Ecology by Keating and Cherry (2009) to draw maps showing the distribution in space of this probability density at a given time t, and to combine the maps drawn for different times t into a movie to show the changes with time of this probability density. The method is described precisely in a document presented as Supplementary Electronic Material. The combination of maps into movies has the advantage, compared to maps, of easily providing the information relative to the speed of movements of animals.

All the estimations were carried out with the function `kernelkc` from the adehabitat package (Calenge, 2006) for R software (R Development Core Team, 2008). Note that a subsample of the analysed data (slightly modified, to preserve copyright) is available as an example dataset of the adehabitat package (dataset “teal”), and that the analysis displayed here is reproduced in the “example” section of the function `kernelkc` help page, to allow the reader to reproduce the computations.

In our estimations of the probability density function (pdf) of recovery, we distinguished the first year following ringing of the bird from subsequent years. Indeed, because all animals were captured and ringed at the same point (i.e. Tour du Valat), it follows that the migration of the first year following ringing had a constrained departure. Furthermore, an earlier study with the same dataset suggested that, at least in terms of probability to switch from a supposed flyway to another (abmigration rate), the behaviour of the birds differed between the year of ringing and subsequent years (i.e. intra-versus inter-annual recoveries), but then did not change with time among inter-annual recoveries (Guillemain et al., 2005). Therefore: (i) we estimated the pdf of recovery of ringed birds during the first year following the capture using the product kernel algorithm (i.e. intra-annual recoveries); (ii) we estimated this pdf in the years following the first year after the ringing (i.e. pooling all inter-annual recoveries). For the latter estimation, we considered the time as a circular variable.

3 Results and Discussion

3.1 The Teal migration

The two estimated pdfs are displayed in Figures 1, 2 and 3 (the movies are available as Supplementary electronic material). These pdfs clearly show distinct migration routes used by migratory Teal in spring and autumn (Figures 1 and 2), which was also suggested by earlier analyses (e.g. Guillemain et al., 2009). Camargue Teal are considered as showing partial loop migration, using a route (South of the Alps) in spring and another one to some extent (North of the Alps) during the autumn, as other migratory birds do (reviews of loop migration studies in Newton, 2008). Interestingly, our visualization method indicates clearly that not all birds migrate via the South of the Alps in spring, even when only intra-annual recoveries are considered, i.e. only those birds which spent at least a part of the previous winter in Camargue are considered (Figure 1). In autumn, too, Teal apparently rely on two distinct routes, one via the Baltic states and the Netherlands, one via central Europe, to reach their winter quarter in Southwestern Europe (Figure 2). It is clear that the route North of the Alps is used to a greater extent in autumn than in spring (see comparison of Figures 1 and 2). Whether apparent loop migration in other bird species may also be the consequence of simultaneous use of multiple migratory routes remains to be tested and could be so with the product kernel algorithm.

A surprising result is that the spring migration of the population terminates earlier for intra- than for inter-annual recoveries (e.g. May 15th maps in Figure 1). On the other hand, autumn migration seems to occur over a long period of time, since some individuals are still in the Northern parts of Europe very late in the season (e.g. Figures 2 and 3). This gives some indications regarding a previous hypothesis: analysing the Tour du Valat Teal ring dataset in an independent capture-recapture demographic manner, Devineau (2007) suggested that the Teal population should theoretically be declining (annual population growth rate λ being < 1). Conversely, the analysis of duck counts suggests the opposite both at the national (Fouque et al., 2005) and the international (Delany and Scott, 2006) scales. Devineau (2007) attributed this pattern to the fact that the population of Teal wintering in Western Europe, though heavily hunted, was regularly renewed by individuals arriving late in the season from more Eastern and Northern countries (the population therefore being more "open" than thought in the past), which seems to be confirmed by the present maps. A non-negligible number of Teal is still present there, e.g. around the Baltic Sea or in some areas of Central Europe even in mid-November.

Abmigration patterns are especially explicit if one compares the autumn migration for intra- and for inter-annual recoveries (Figure 2): from the early beginning of the autumn the northern migration route along the Baltic Coast and the Netherlands is used to a far greater extent for inter- than for intra-annual recoveries, leading to a greater use of the Atlantic and Northern coasts of France in mid-winter (Figure

3). Later on, this translates into a greater use of the same Northern migratory route during spring migration in inter- than in intra-annual recoveries (Figure 1). The high abmigration rate recorded from the very same dataset for Teal, with birds switching from the so-called "Mediterranean" to the so-called "North-Western European" flyways (Guillemain et al., 2005), can now be approached in a more dynamic fashion. Abmigration in ducks is generally believed to result from the pairs forming in winter, the male following its mate to her breeding area (e.g. Alerstam, 1990; Anderson et al., 1992). The present visualization suggests that abmigration may also be the result of individuals switching to a new target wintering area while migrating in the autumn, not only later while pairing in winter: although relatively few Teal apparently disperse to the French Atlantic coast during the winter of ringing (intra-annual recoveries in Figure 1), and birds from different origins therefore have few opportunities to meet during this first winter pairing period, many birds use the Northern and the Atlantic coasts of France right from their first autumn after being ringed in the Camargue (cf. intra-annual recoveries in Figure 2), suggesting that the switch between wintering areas may occur before pairing.

The examination of the movies did not highlight any geographic area that is completely devoid of recoveries, i.e. avoided or flew-over by Teal during migrations, which accords with the acknowledged plasticity of this species in terms of habitat choice (e.g. Johnson, 1995). However, the early spring maps clearly show that the recoveries do not progress gradually to the North-East over time along a clear front but, rather, that many distinct geographical areas get used by Teal simultaneously at the onset of the breeding season (e.g. April and May maps in Figure 1). Though this may reflect discontinuous human settlement distribution in these geographic areas (see below), this is also consistent with the idea that these ducks are not limited by their migratory speed in spring, nor have to wait until environmental conditions get favourable before colonizing their breeding areas (which supposedly occurs gradually with climate at least along a latitude gradient in spring). Rather, birds may try to get advantage from getting to or close to their breeding areas and start to nest as soon as possible, according to Elmberg et al. (2005).

3.2 Hypotheses underlying the visualization of ring recoveries

It has to be kept in mind that the kernel estimation of the probability density to recover a Teal at a given place and a given date is not the probability density that a Teal is present at that given place. Although we were interested in the latter, our dataset only allowed to estimate the former, like ring recoveries always do. Actually, the former is equal to the product of: (i) the probability density that a Teal is present at this place and this date or a few days before this date; (ii) the probability density that a Teal dies at this place and this date or a few days before this date, given that it is present there; (iii) the probability that the dead Teal is found by someone at this date (which is relatively close to one when the bird is killed during hunting); and (iv) the probability that this person reports the recovery to the national ringing centre.

Although we need to assume that the first probability is adequately reflected by the data to draw reliable conclusions on the migration corridors of Teal in Europe, the other three are likely to vary in both space and time, a problem inherent to the use of ring recoveries in general, including in demographic studies (Gauthier et al., 2001). The probability that a Teal dies at a given place depends on many factors that vary in both space and time (greater mortality of the Teal during the hunting period as opposed to the breeding season due to the apparent higher effect of hunting versus natural mortality causes, Devineau, 2010). This may indeed have affected our results, but the fact that hunting seasons were generally very long in European countries during the period when these data were collected (much longer than today, e.g. see Ogilvie, 1983) suggests that the results may not be too biased, at least at the national scale. It remains of course that the hunting pressure may be higher in some regions than in others.

The probability that a Teal is found by someone also varies in space and time, and is of course higher during the autumn-winter hunting season than when birds die of natural causes in remote breeding areas with scarce human population. This explains of course why we may have failed to identify a clear migration corridor above the Baltic sea, since recovery probability is zero over seas. The probability that a shot game is killed but not retrieved by a hunter, termed the "crippling loss", has been estimated to be around 20% in ducks (Anderson and Burnham, 1990). However, we see little reasons to believe that the probability to retrieve a killed duck by a hunter varies markedly over the season, or differ strongly between geographic areas. We think that the influence of this non-uniform probability was proabbly smaller that in other studies, as Teal has traditionally been the second most harvested species in Europe after Mallard Anas platyrhynchos (e.g., Mooij, 2005), and because the species was hunted in most European countries (e.g., Lampio and Michaelis, 1972). In addition, ring recovery rate for Teal was far higher during our study period than it is nowadays (Guillemain et al. Unpub. data, see Robinson et al., 2009, for a similar 25% decline in Teal ring recovery rate per decade since the 1960s).

Finally, the probability to report a ring may also vary in space and time, depending on sociological factors characterizing local human populations (degree of information concerning ringing studies, national hunting rules, etc). As far as we know, ring reporting rate for ducks has only been estimated in Mallard *Anas platyrhynchos* in North America, by means of reward ring studies (Nichols et al., 1991). Such studies have shown that ring reporting rate may well vary geographically (Nichols et al., 1995). The extent to which differences in reporting rates between geographic areas (varying reporting rate across the year being less likely) biases the present results remains to be addressed. This remains a general question for the analysis of duck ring recoveries, also for demographic studies, and strongly calls for the development of reward ring studies in Europe (as also suggested by Devineau, 2007).

To conclude, the use of a method smoothing a point pattern in both space and time, such as the kernel product algorithm, allows to take into account the time-related nature of the data in their exploration. It also provides a smoother display of the data than simply movies of the occurrence of ring recoveries (as it "borrows" strength from the neighbouring recoveries in space and time for the estimation of the pdf at a given place and a given date). This gives a smoother aspect to the resulting maps and a more dynamic aspect to resulting movies, an essential feature for visual exploration of data (Cleveland, 1993). The kernel product algorithm appears as a promising method to the dynamic analysis of other bird ring recovery datasets.

Zusammenfassung

Ein neuer Forschungsansatz zur Untersuchung der räumlich-zeitlichen Verteilung von Ringwiederfunden am Beispiel von in der südfranzösischen Camargue beringten Krickenten (*Anas crecca*)

Wir benutzen eine neue Methode namens "product kernel estimator", um die räumliche und zeitliche Verteilung von 9114 in der südfranzösischen Camargue beringten Krickenten (*Anas crecca*), die in ganz Europa wiedergefunden wurden, zu un-

tersuchen. Diese Methode ermöglicht es, zeitliche Veränderungen der Wahrscheinlichkeitsdichte, einen beringten Vogel über ein das Untersuchungsgebiet abdeckende Raster wiederzufinden, zu untersuchen. Auf diese Weise haben wir zwei Zugkorridore für diese Art identifiziert, nördlich und südlich der Alpen, während frühere Analysen meist eine von der Camargue nach Süden führende Route vorgeschlagen haben, insbesondere im Frühling. Die nördliche Route scheint in größerem Maße im Herbst als im Frühling genutzt zu werden, was auf eine häufige Abmigration hindeutet (Tiere wechseln von einem Korridor zum anderen). Außerdem scheint die Wanderung der Population im Frühling schneller zu sein als im Herbst. Der gleichzeitige Wiederfund von Krickenten in vielen verschiedenen geographischen Bereichen im Frühling steht mit der Idee im Einklang, dass diese Enten nicht durch ihre Zuggeschwindigkeit eingeschränkt sind. Sie warten auch nicht auf günstige Umweltbedingungen, bevor sie ihre Brutgebiete besiedeln.

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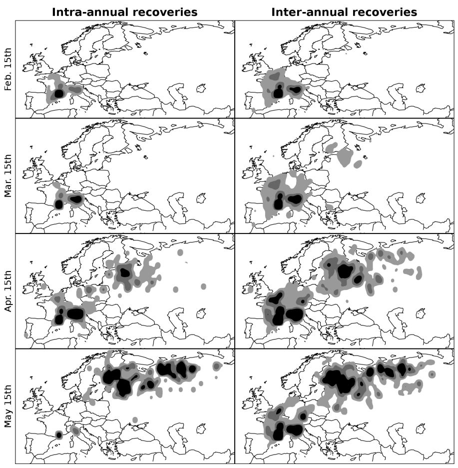

Fig. 1 Sample of maps for intra- (left column) and inter-annual recoveries (right column) of Teal ringed in the Camargue for the spring migration period. The black areas correspond to the smallest area where the probability of recovering a ring, given that it is recovered at this date, is equal to 0.5. The dark grey areas correspond to the smallest area where this probability is equal to 0.7. The light grey areas correspond to the smallest area where this probability is equal to 0.9.

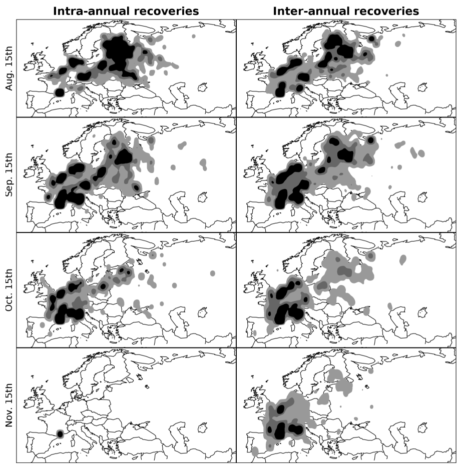

Fig. 2 Sample of maps for intra- (left column) and inter-annual recoveries (right column) of Teal ringed in the Camargue for the autumn migration period. The black areas correspond to the smallest area where the probability of recovering a ring, given that it is recovered at this date, is equal to 0.5. The dark grey areas correspond to the smallest area where this probability is equal to 0.7. The light grey areas correspond to the smallest area where this probability is equal to 0.9.

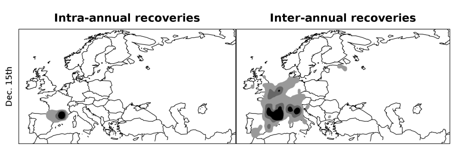

Fig. 3 Ring recovery probability by mid-December for intra- (left column) and inter-annual recoveries (right column) of Teal initially ringed in the Camargue. The black areas correspond to the smallest area where the probability of recovering a ring, given that it is recovered at this date, is equal to 0.5. The dark grey areas correspond to the smallest area where this probability is equal to 0.7. The light grey areas correspond to the smallest area where this probability is equal to 0.9.