Spring migration dates of teal *Anas crecca* ringed in the Camargue, southern France

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The policy of the European Commission prohibits hunting of migratory birds while they travel to their breeding grounds. To date, spring migration dates of ducks have mainly been determined using bird counts, but the validity of this sometimes disputed method has never been tested. We used ring-recovery data from close to 9,000 teal *Anas crecca* ringed in the Camargue, southern France, to determine the onset of spring migration. This method makes it possible to avoid potential biases linked to duck counts, and was used to test the validity of spring migration dates inferred from such counts. Depending on the type of analysis (intra- or inter-annual recoveries), teal appeared to start migrating from the Camargue during the first or second 10-day period of January, with no significant differences between years, and no effect of the bird's age or sex. However, when taking potential winter dispersion into account, we suggest that a conservative estimate for the onset of spring migration is the first 10-day period of February. Migration dates inferred from ring-recovery analyses were consistent with earlier results from duck counts, and provide a firm basis for policy making related to hunting. Though ringing data should be preferred when available, our study suggests that determining migration dates from bird counts may be a reliable method for teal, and potentially for other dabbling and diving ducks as well.

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Spring migration is a crucial part of the annual cycle for many birds, due to the high energy costs associated with long flights at a period of the year when individuals, especially females, prepare for reproduction. In capital-breeding species, this migration has to be completed while already carrying large amounts of reserves, thus incurring higher costs of flight and potentially higher predation risk (Pennycuick 1975, Witter et al. 1994, Kvist et al. 2001). In income-breeding species, individuals have to migrate at exactly the right dates, in order to ensure sufficient foraging opportunities at stopover sites and at the breeding grounds, while at the same time avoiding to arrive too late in the breeding area (assuming a general negative relationship between arrival date and breeding success; Dzus & Clark 1998). Due to their relatively low body mass, most dabbling duck species belong to the category of income breeders (Klaassen 2002), and are therefore likely to encounter these strong, and potentially opposing, selection pressures in spring. However, the ecology of ducks during this part of the year has so far received very little attention. This is unfortunate since a good knowledge of species ecology in spring is required for proper management, especially in the case of hunted species. In particular, following the European Directive 79/409/CEE, member states should not allow hunting of migratory species "during their period of reproduction or during their return to their rearing grounds".

So far, duck migration periods in Europe have mainly been estimated based on bird counts, considering either massive increases, massive decreases, or peaks in the number of individuals as indicative of migratory activity (e.g. Muséum National d'Histoire Naturelle (MNHN) & Office National de la Chasse (ONC) 1989 for France). However, apart from a few species that are never present in winter at their migration stopovers (e.g. garganey *Anas querquedula* in the south of France; Guillemain et al. 2003b), one could always argue that these changes in numbers reflect either a dispersion of the birds, or a modification in the carrying capacity of sites used, rather than a true migration event, because individual birds are not recognisable and the direction of their movements therefore cannot be fully ascertained. Ringing data, on the other hand, permit us to analyse such movements, thus providing a basis for a firm determination of migration dates.

In this paper, we use information from close to 60,000 teal *Anas crecca* ringed in winter in the Camargue, southern France, of which > 9,000 were subsequently recovered, to determine the date at which these birds leave the area in spring. In addition, we assess whether these dates differ between first-year and adult birds, between males

and females, and vary over years. Finally, we discuss the way these results compare with previous migration dates inferred from duck count analyses, to test the validity of the latter method.

Methods

Data collection and data used in the analyses

Teal in the Camargue were caught at the Domaine de la Tour du Valat (43°30'28N, 04°40'07E) between January 1952 and February 1978 using standard dabbling duck funnel traps hidden in the vegetation (for details of the Camargue technique see Bub 1991:103). Catching of the ducks was performed every day, mostly from the beginning of September to the end of March. Ducks were sexed and aged using plumage criteria, as well as by inspection of the cloaca and the bursa of Fabricius. A total of 59,187 teal were thus captured and ringed; of these 9,279 were subsequently recovered (i.e. deliberately killed, or found dead) all over Europe. Only data with precise date and location of ringing were considered. We also discarded data from years in which < 100 teal were recovered, both in the case of intra- and of inter-annual recoveries (birds recovered during the year of ringing and in subsequent years, respectively), and all individuals for which sex or age at the date of ringing could not be ascertained. Eventually, the data set used in the analysis included 3,167 individuals recovered intra-annually between the winters of 1955/56 and 1970/71, excluding the winter of 1969/70 when only 48 teal were recovered, and 5,586 individuals recovered inter-annually between the winters of 1956/57 and 1974/75. No such data set exists for comparison nowadays, but a new teal ringing scheme has recently been launched in order to fill this gap.
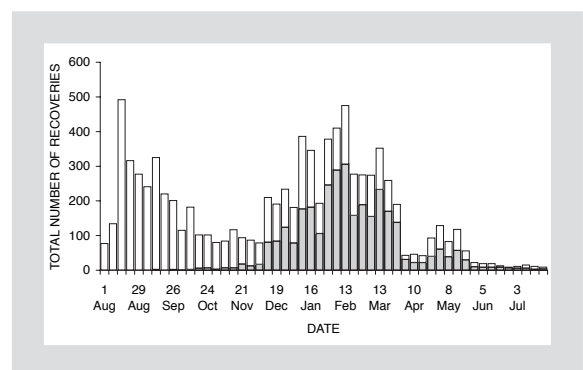

Figure 1. Total number of teal ringed in the Camargue and recovered per week. The grey part of each column represents the share of intra-annual recoveries among the total, the white part the share of inter-annual recoveries.

A 'year' or 'season' in this paper refers to the period from 1 August to the next 31 July. Data were considered on a weekly basis starting in week 1 for 1-7 August until week 52 (25-31 July). In all analyses, intra- and inter-annual recoveries were treated separately. The total number of recoveries per week ranged within 9-492 birds (Fig. 1). Seasonal variation in the number of recoveries per week was very clear, and the two peaks more or less corresponded to the general bi-annual migration periods (in the broad sense, i.e. autumn and spring) of ducks.

Determination of migration dates

The Camargue is a wintering area for teal, and the species is mainly present from September to February (Tamisier & Dehorter 1999). Given that the area is located in the southwestern part of the species' range, a bird ringed in the Camargue was considered to be migrating between wintering and breeding areas, or being recovered in a breeding area, if it was recovered in any French region or foreign country to the northeast of the Tour du Valat. By northeast we mean all countries and regions in this direction, up to the Siberian part of the former USSR. However, to avoid considering as migrants the birds that simply moved short distances from the ringing site, all recoveries from within a 200-km square centred on the Tour du Valat were considered as 'local' and analysed separately.

Two methods could be used to determine the onset of spring migration:

1) Migration can be considered to commence when the proportion of recoveries in the northeast of the Camargue starts to increase gradually in spring (both for intra- and inter-annual recoveries). After examining the overall shape of the curve describing the variation in the proportion of recoveries in the northeast over weeks, we isolated this period of spring increase and analysed, through General Linear Models, whether the migration events differed temporally between years, ages and sexes. Ages were only compared for intra-annual recoveries, since all birds recovered inter-annually were necessarily adults (i.e. > 1 year old). Proportions were arcsine-transformed for these analyses (Sokal & Rohlf 1995), but data are presented as proportions in figures to facilitate interpretation. The onset of spring migration was then determined by the intercept of the fitting linear regression through the dots of the migration period, and later expressed in 10-day periods.

2) Apart from true migration, wintering birds may also disperse during the winter, switching from one wintering quarter to another (hence leading to turn-over

in wintering populations; Pradel et al. 1997), or may also move in response to winter weather. These phenomena may confound the above analysis, especially if some dispersion to the northeast occurs. Another way of analysing spring migration is therefore to consider migration to start only when the proportion of recoveries in the northeast of the Camargue exceeds the proportion of recoveries in, e.g. the southwest of this area. This should be relevant both for intra- and inter-annual recoveries. In the case of inter-annual recoveries, this allows us to take into account the fact that some birds may winter northeast of the Camargue (e.g. in the Rhône or the Rhine Valleys) in the years after having been ringed in the south of France.

Results

Recoveries in the northeast over weeks

For intra-annual recoveries, the pattern was very clear since virtually none were made northeast of the Camargue in the first half of the winter, then a gradual increase was observed (corresponding to the increasing proportion of birds moving to their breeding grounds), before virtual-
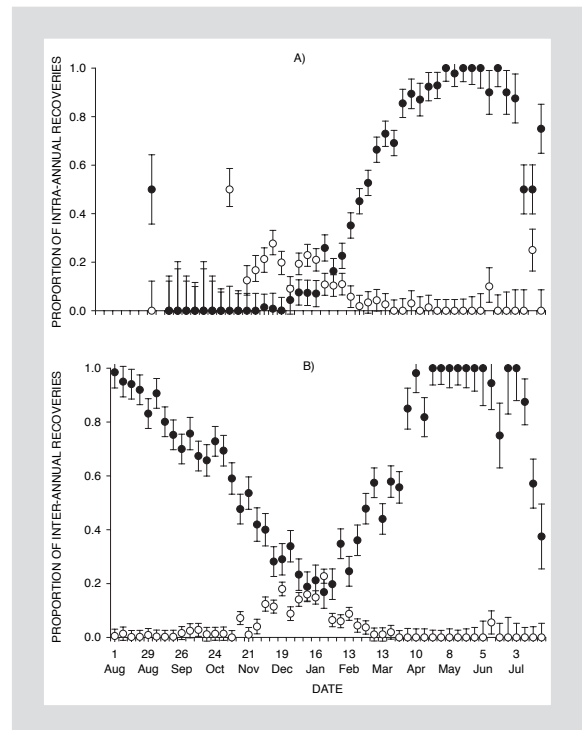

Figure 2. Average proportion (± SE) of intra-annual (A) and inter-annual (B) teal ring recoveries in the northeast (●) and in the southwest (○) of the Camargue over weeks, from 1 August to 31 July. Averages were computed over all years, summing female and male, first-year and adult data.

ly all recoveries were in the northeast in the last part of the season (when they all are in breeding areas; Fig. 2A). The high value in week 7 was linked to low numbers of intra-annual ring recoveries during this period (two recoveries in total, one in the northeast; see Fig. 1). When isolating the broad period of increase in the proportion of recoveries in the northeast (i.e. weeks 25-41), and analysing the effect of sex, age, year, week plus the interaction of these factors with week (to detect potential effects on the slope), only week had a significant effect in the GLM model (Table 1). Neither the interaction of sex, age or year with week had a significant effect, indicating that the rate of increase in the proportion of recoveries in the northeast did not differ between sex or age classes, nor between years. When using arcsine-transformed proportions, and the average value over all years for each week, the equation of the linear regression of the proportion of recoveries in the northeast on week was: $y = 5.3626x - 123.85$ ($r^2 = 0.97$, N = 17 weeks, P < 0.0001). The intercept of the curve with the X-axis was therefore reached for week = 23.09, or 2-9 January. Using this method, one could therefore say that from the second 10-day period of January teal are starting to migrate from the Camargue to the northeast (see Fig. 2A).

For inter-annual recoveries, the pattern was also very clear, with 1) a large proportion of recoveries in the northeast at the beginning of the year (birds still being on their breeding grounds or on their way to wintering areas), 2) a gradual decrease in the proportion of recoveries in the northeast in the autumn (post-nuptial migration), 3) a new increase in the proportion of recoveries in the northeast corresponding to spring migration before a plateau in late spring when all birds are in breeding areas (see Fig. 2B). The broad period of increase in the proportion of recoveries in the northeast took place during weeks 25-39. Also for this period, only week had a significant effect on the proportion of recoveries in the northeast, after a GLM analysis had been performed to test the effect

Table 1. Result of the GLM model to explain the variations in the proportion of intra-annual recoveries in the northeast of the Camargue depending on week, sex, age, year, plus all 2-way interactions of these factors with the variable week (complete model: $r^2 = 0.51$, $F_{33,567} = 18.24$, P < 0.0001).

Effect	Sum of squares	df	F	Type III P-value
Sex	316.5	1	0.43	0.5100
Age	68.2	1	0.09	0.7597
Year	7727.2	14	0.76	0.7152
Week	330768.7	1	454.25	< 0.0001
Sex*Week	240.9	1	0.33	0.5654
Age*Week	2.5	1	0.01	0.9530
Year*Week	7362.5	14	0.72	0.7528

Table 2. Result of the GLM model to explain the variations in the proportion of inter-annual recoveries in the northeast of the Camargue depending on week, sex, year, plus all 2-way interactions of these factors with the variable week (complete model: $r^2 = 0.40$, $F_{39,355} = 5.95$, P < 0.0001).

Effect	Sum of squares	df	F	Type III P-Value
Sex	381.8	1	0.46	0.4994
Year	13940.2	18	0.93	0.5455
Week	131494.3	1	157.45	< 0.0001
Sex*Week	210.8	1	0.25	0.6157
Year*Week	12923.7	18	0.86	0.6284

of sex, year, week, sex*week and year*week (Table 2). When using arcsine-transformed proportions, and the average value over all years for each week, the equation of the linear regression of the proportion of recoveries in the northeast on week was: $y = 5.1135x - 115.82$ ($r^2 = 0.89$, N = 15 weeks, P < 0.0001). The intercept of the curve with the X-axis was therefore reached for week = 22.65, or the week 26 December - 2 January. Using this method, one could therefore say that from the first 10-day period of January teal are migrating from the Camargue to the northeast (see Fig. 2B).

The patterns were very similar between intra- and inter-annual recoveries: an Analysis of Covariance to test the effect of the type of recovery (intra- or inter-annual) on the increase of the proportion of northeast recoveries over weeks (weeks 25-39) showed that the type of recovery did not have a significant effect *per se* ($F_{1,26} = 0.40$, P = 0.5324), i.e. the absolute proportion of recoveries a certain week did not differ significantly between intra- and inter-annual recoveries. The analysis also revealed that the interaction between type of recovery and week did not have a significant effect either
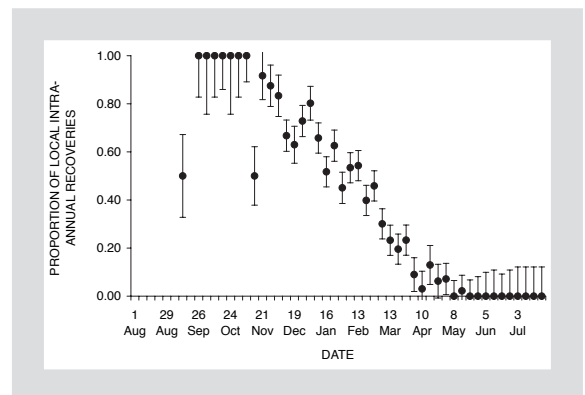

Figure 3. Average proportion (± SE) of local (i.e. Camargue) intra-annual teal ring recoveries over weeks, from 1 August to 31 July. Averages were computed over all years, summing female and male, first-year and adult data.

($F_{1,26} = 0.28$, $P = 0.6039$), i.e. the rate of increase of the proportion of recoveries in the northeast did not differ between recovery types (see Fig. 2). Here again, only week had a significant effect ($F_{1,26} = 254.93$, $P < 0.0001$), and the complete model fitted the data ($r^2 = 0.91$, $F_{3,26} = 85.31$, $P < 0.0001$).

Taking winter dispersion into account

A large share of the birds ringed in winter dispersed from their capture site within the same season, as shown by the early decrease of the proportion of local recoveries in intra-annual data throughout the season (Fig. 3): the onset of this decrease was week 15, i.e. 7-14 November, which cannot be considered as spring migration. Indeed, from week 15 the proportion of recoveries in the southwest of the Camargue (mainly in the Iberian Peninsula) increased, suggesting that some teal switched between these winter quarters (see Fig. 2A). From week 27 onwards (i.e. 30 January - 6 February) the proportion of intra-annual recoveries in the northeast consistently exceeded that in the southwest, indicating that spring migration had started in the first 10-day period of February while excluding potential biases linked to dispersion between wintering quarters.

When the same approach was applied to inter-annual recoveries, week 27 (i.e. 30 January - 6 February) again was the time after which the proportion of recoveries in the northeast exceeded the proportion of recoveries in the southwest. After that week, the former proportion consistently increased, while the latter consistently decreased (see Fig. 2B). As opposed to intra-annual recoveries, the proportion of inter-annual recoveries in the southwest was hardly larger than that in the northeast throughout the whole year.

Discussion

Apart from a few species only observed during migration, spring migration periods of ducks have until now mainly been explored through analyses of bird counts, identifying migration periods through the observation of clear changes in numbers (e.g. MNHN & ONC 1989). However, these dates could often be debated, since in some cases changes in numbers may only reflect changes in the carrying capacity of a site, or dispersion. Such debates especially occurred in ducks and other migratory game species, because according to European Directive 79/409/CEE those species should not be hunted while on their way back to their breeding grounds. Because ringed birds can be individually recognised, and their movements therefore can be determined with confidence, the

analysis of ring recoveries provides a powerful and reliable tool to determine the precise dates of spring migration in ducks.

Data from teal ringed at the Tour du Valat show that, when considering only the proportion of recoveries in the northeast, the onset of spring migration takes place between the first and the second 10-day period of January. This result is apparently robust, since no significant differences could be observed between years. The fact that no difference could be detected between males and females is consistent with the ecology of the species, as dabbling ducks are known to pair in winter (Cramp & Simmons 1977, Guillemain et al. 2003a). Observations in the Camargue revealed that the vast majority of individuals (especially females) are paired by the end of January (M. Guillemain & M. Lepley, unpubl. data). On the other hand, the determination of migration dates from duck counts never allowed us to test whether teal of different ages migrate at the same date, because in teal it is virtually impossible to differentiate between first-year birds and adults in the field. Our analysis fills this gap and, interestingly, shows that the two age classes leave for their breeding grounds at the same dates. This most likely is linked to the fact that teal are able to breed at one year of age (Cramp & Simmons 1977), adults and first-year birds therefore being subjected to the same selection pressures. This would also suggest that only a short time window is optimal for spring migration and initiation of breeding in the north of Europe, whatever the age of the bird. Such a pattern is consistent with the fact that duck breeding success, including in teal, has been found to decrease with time across the breeding season (Dzus & Clark 1998, Elmberg et al. 2005).

In addition to 'true' migration, teal can move from one site to another during the winter period, as shown by the gradual decrease in the proportion of local intra-annual recoveries starting in the first half of November. At this time, the proportion of recoveries in the southwest of the Camargue started to increase, indicating that teal left southern France, mainly heading for the Iberian Peninsula. The Iberian Peninsula is well known as a refuge for ducks, especially teal, in the case of cold weather (Lebreton 1973, Ridgill & Fox 1990), and it is possible that a category of individuals unable to cope with cold temperatures in the Camargue headed for milder areas in November and December. However, this may also indicate some nomadism of the birds, which has already been described especially in first-year male dabbling ducks (Anderson et al. 1992; Guillemain et al. 2005). In this case, it cannot be ruled out that such movements also take place to the northeast, and therefore that the increase in the proportion of recoveries in that direction

represented winter dispersion in addition to migration. By considering the date at which the proportion of recoveries in the northeast exceeds the proportion in the southwest, we believe that we were able to get rid of this potential bias (assuming that dispersion, if it exists, takes place at the same rate in all directions), and that the migration dates provided by this method are more robust and conservative. That date was the first 10-day period of February, with no significant difference between intra- and inter-annual recoveries. It is very unlikely that this result was biased because of differential hunting periods in the southwest and in the northeast (e.g. if hunting stopped earlier in the southwest, then the apparent onset of migration would be biased towards earlier dates): until the end of the 1960s, hunting was allowed until mid-February in Portugal, until the end of February in Spain, whereas it lasted until the end of March in France, and until the end of January to the end of February in northern countries like the Netherlands, Belgium or Denmark (Lampio & Michaelis 1972).

We have already mentioned the potential biases linked to estimating migration dates through duck counts. However, when comparing studies using this type of data and our study, it is obvious that the results of the analyses are broadly similar: apart from an early analysis by Schricke (1989) suggesting that the average spring migration period of teal takes place in February-March in France, all other sources agreed to consider late January - early February as the onset of spring migration (MNHN & ONC 1989, MNHN & ONC 1993, Fouque et al. 1997). Finally, the most recent analysis of duck counts suggests that teal spring migration starts between the last 10-day period of January and the first 10-day period of February in France (C. Fouque, pers. comm.). The fact that the results of duck counts and our ring recovery analyses are similar should not minimise the importance of the latter type of method. However, since recovery data sets such as ours are exceptional for ducks in Europe, this suggests that duck counts are valuable sources of information if no other data are available.

The aim of our study was not to determine the dates at which hunting of teal should be prohibited in France, but instead to provide scientifically based information needed by policy-makers to make their decision. Of course, and despite the size of the data set, our results hold for one wintering quarter (the Camargue) and the period at which information was collected (> 30 years ago). It is possible that migration dates changed over time due to long-term changes in climate and transformation of duck habitats, though such potential changes are unlikely to be of large time scales. However, we hope that our analysis will motivate similar studies in the future, and a large-scale programme on teal has been launched to collect the same type of data for the present period (Guillemain et al. 2002).

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