BioOne COMPLETE

Emigration rates and population turnover of teal Anas crecca in two major wetlands of western Europe

Authors: Caizergues, Alain, Guillemain, Matthieu, Arzel, Céline, Devineau, Olivier, Leray, Gilles, et al.

Source: Wildlife Biology, 17(4) : 373-382

Published By: Nordic Board for Wildlife Research

URL: https://doi.org/10.2981/10-102

BioOne Complete (complete.BioOne.org) is a full-text database of 200 subscribed and open-access titles in the biological, ecological, and environmental sciences published by nonprofit societies, associations, museums, institutions, and presses.

Your use of this PDF, the BioOne Complete website, and all posted and associated content indicates your acceptance of BioOne's Terms of Use, available at www.bioone.org/terms-of-use.

Usage of BioOne Complete content is strictly limited to personal, educational, and non - commercial use. Commercial inquiries or rights and permissions requests should be directed to the individual publisher as copyright holder.

BioOne sees sustainable scholarly publishing as an inherently collaborative enterprise connecting authors, nonprofit publishers, academic institutions, research libraries, and research funders in the common goal of maximizing access to critical research.

Downloaded From: https://complete.bioone.org/journals/Wildlife-Biology on 29 Mar 2024
Terms of Use: https://complete.bioone.org/terms-of-use

Wildl. Biol. 17: 373-382 (2011)
DOI: 10.2981/10-102
© Wildlife Biology, NKV
www.wildlifebiology.com

Original article

Emigration rates and population turnover of teal *Anas crecca* in two major wetlands of western Europe

Alain Caizergues, Matthieu Guillemain, Céline Arzel, Olivier Devineau, Gilles Leray, Daniel Pilvin, Michel Lepley, Grégoire Massez & Vincent Schricke

During the winter of 2003/04, we studied emigration rates of teal *Anas crecca* in two major wetlands: the Camargue (southern France) and the Loire estuary (western France). We derived local survival probabilities as a step in ultimately estimating emigration rates from individual mark-resighting (visual recaptures) history of birds fitted with nasal saddles. In goodness-of-fit tests of time-dependent models for local survival, we only detected the presence of transients among young females in the Loire estuary, which indicated that this category of individuals includes an 'unstable compartment' continuing its migratory journey further to the south. We observed low monthly local survival and high emigration rates (range: 0.01-0.81) in both areas, which suggests high turnover rates. In the Loire estuary, temporal changes in emigration rates matched the post- and pre-nuptial migration peaks (i.e. October-November and February-March). By combining local survival probabilities and count data, we derived an estimate of the ratio between the winter peak count of teals in our study areas and the minimum number of birds that actually frequented the areas over the entire wintering period (October-March). In both cases, we estimated the number of teal visiting the two wintering sites be about twice as large as the maximum number of birds counted instantaneously.

Key words: Anas crecca, capture-mark-recaptures, ducks, local survival, population volume, teal, wintering

Alain Caizergues, Gilles Leray & Vincent Schricke, Office National de la Chasse et de la Faune Sauvage, Direction des Etudes et de la Recherche, CNERA Avifaune Migratrice, 39, Boulevard Einstein, CS 42355, F-44323 Nantes Cedex 3, France - e-mail: alain.caizergues@oncfs.gouv.fr
Matthieu Guillemain, Office National de la Chasse et de la Faune Sauvage, Direction des Etudes et de la Recherche, CNERA Avifaune Migratrice, La Tour du Valat, Le Sambuc, F-13200 Arles, France - e-mail: matthieu.guillemain@oncfs.gouv.fr
Céline Arzel, Office National de la Chasse et de la Faune Sauvage, Direction des Etudes et de la Recherche, CNERA Avifaune Migratrice, La Tour du Valat, Le Sambuc, F-13200 Arles, France, Department of Mathematics and Natural Sciences, Kristianstad University, SE-291 88 Kristianstad, Sweden, and Laboratoire d'Ecologie des Hydrosystèmes, Université Paul Sabatier, 118 route de Narbonne, F-31062 Toulouse, France - e-mail: celine_arzel@yahoo.fr
Olivier Devineau, Department of Fish, Wildlife and Conservation Biology, Colorado State University, Fort Collins, Colorado 80523-1474, USA - e-mail: olivier.devineau@gmail.com
Daniel Pilvin, Office National de la Chasse et de la Faune Sauvage, Direction de la Police, les Champs Neufs, F-44320 Frossay, France - e-mail: sd44@oncfs.gouv.fr
Michel Lepley, Centre de Recherche de la Tour du Valat, Le Sambuc, F-13200 Arles, France - e-mail: michel.lepley@cegetel.net
Grégoire Massez, Les Marais du Vigueirat, Mas Thibert, F-13200 Arles, France - e-mail: gestion.mdv@wanadoo.fr

Corresponding author: Alain Caizergues

Received 22 September 2010, accepted 14 April 2011

Associate Editor: Johnny Kahlert

Understanding patterns of stop-over and wintering-site use by migratory birds is essential from a management perspective. For example, assessing the actual number of individuals available to hunters in a particular area is a prerequisite for a better understanding of the impact of hunting

Downloaded From: https://complete.bioone.org/journals/Wildlife-Biology on 29 Mar 2024
Terms of Use: https://complete.bioone.org/terms-of-use

practices on wild bird populations. In western Europe, the relative importance of wintering quarters and staging areas for a bird population is mainly derived from instantaneous counts. For example, the importance of different wintering sites for a given species is inferred from the percentage of the entire biogeographical population which occupies each particular area in mid-January (e.g. Scott & Rose 1996). Conventionally, a wintering site is eligible to have the status of a site of international importance for a given migratory population if one of the instantaneous winter counts reaches 1% of the total biogeographical population. A major problem with such an approach is that censuses sometimes poorly reflect the number of birds actually using a given area, especially if there is a high turnover of individuals among wintering populations (see Pradel et al. 1997b). By using counts, the importance of areas that play key roles as stop-over (refuelling) sites might be underestimated too, because these areas host comparatively fewer individuals than most wintering sites at times other than during stop-overs. A measure of the individual turnover rate is therefore required to judge the quality and to assess the relative importance of the various sites used along any flyway.

The teal *Anas crecca* is the smallest wintering duck species in southwestern Europe (del Hoyo et al. 1992), and one of the most important quarry species (Mooij 2005). The species presents a good example of the poor reliability of counts used for estimating population size. In France, for example, the annual hunting bag is estimated to be > 330,000 individuals (Mondain-Monval & Girard 2000), whereas the mid-January simultaneous counts almost never exceeded 100,000 birds (Fouque et al. 2005). In the Camargue, 150,000 ducks and coots *Fulica atra* are harvested annually out of an estimated population of about the same size (Tamisier & Dehorter 1999). Such discrepancies between harvest bags and counts might partly be due to biases inherent to counts or unreliable hunting bag data. However, a likely alternative hypothesis is that immigrants continuously replace harvested individuals, i.e. that individual turnover rate is high.

Based on ringing data from the 1950s to the 1970s, Pradel et al. (1997b) were the first to demonstrate a high individual turnover in the wintering population of teal in the Camargue (southern France). Unfortunately, no data from other important European wetlands were available to these researchers for comparison. Moreover, they did not analyse sex and age categories separately, which might have provided useful insights into the understanding of teal stop-over and migration at the population scale. Finally, the fact that their analyses were based on a capture-recapture approach using only baited traps may have seriously biased their turnover estimates (essentially owing to trap dependence and a relatively low capture rate).

Using a similar capture-mark-recapture (CMR) approach, we modelled the local survival probabilities S (S = 1 - mortality - emigration; (Lebreton et al. 1992) of teal in two major wetlands of southwestern Europe to gather information on emigration rates and the number of individuals using these areas as stop-over or wintering sites (Frederiksen et al. 2001). To minimise the biases associated with trap dependence and low capture rates described above, we derived capture-recapture histories from visual recognition of individuals fitted with a nasal saddle, each bearing an individual alphanumeric code (Guillemain et al. 2007).

Methods

Study areas

Our study was conducted during the autumn-winter of 2003/04 in two of the most important wintering sites for teal in France: the Vigueirat marshes (4°38'E, 43°40'N) in the Camargue, southern France, and the Massereau reserve (1°54'W, 47°15'N) located in the Loire estuary, western France. The Camargue is one of the most important wintering areas for waterfowl in the Black Sea/Mediterranean migratory flyway, where the number of teal counted annually ranges between 750,000 and 1,375,000 individuals (Scott & Rose 1996; note that the existence of two distinct flyways has been challenged by Guillemain et al. 2005). The Vigueirat marshes are a protected area of 1,029 ha where up to 15,000 teals are counted (out of a total of about 38,000 in the Camargue). The Loire estuary belongs to the northwestern European flyway, in which the number of teals is estimated at 500,000 individuals (Wetlands-International 2006). The Massereau reserve (ca 400 ha) is used by up to 5,000 teals (out of a total of about 15,000 in the entire Loire estuary). The length of the hunting season (i.e. 1 September - 31 January) is the same in the two areas.

Downloaded From: https://complete.bioone.org/journals/Wildlife-Biology on 29 Mar 2024
Terms of Use: https://complete.bioone.org/terms-of-use

Field work procedures

In both areas, we captured the birds using funnel traps baited with wheat (i.e. in the Loire estuary) or rice (i.e. in the Camargue; Bub 1991). Traps were continuously active for five days/week in the Massereau, and all seven days/week in the Vigueirat. Birds were distinguished according to their age (first-year individuals vs adults) and sex using plumage criteria and cloacae examination. For simplicity, we term first-year birds 'young' in the following. All individuals included in the analyses were fitted with nasal saddles bearing a distinctive alphanumeric code (Rodrigues et al. 2001). This kind of marking enables identification of any bird up to a distance of 200 m using a 80×60 telescope (Rodrigues et al. 2001). No significant adverse effect of nasal saddles on dabbling duck behaviour or condition has formerly been detected when tested (Guillemain et al. 2007).

Identifications of birds based on the reading of the code on the nasal saddle will hereafter be called 'resightings' whereas 'capture' will refer to the first physical capture of the bird (which in our study corresponds to when the individual was marked). Captures and resighting sessions were carried out from October 2003 until the end of March 2004. Our efforts to obtain resightings of marked individuals were greater in the Camargue (12-20 hours/week) than in the Loire estuary (6-8 hours/week). The differences in capture effort between the two areas could entail differences in resighting probabilities and account for small differences in local survival probabilities. In practice, however, it proved much easier to find teal fitted with nasal saddles in the Loire estuary than in the Camargue, essentially because teals were usually clustered on a much smaller area in the former case. We did not look for or captured individuals outside the two study areas. Consequently, emigration rates estimated in our study may combine both long-distance emigration related to migratory movements and permanent local emigration. In each area, we counted teal each month using telescopes (during October-March) from permanent and mobile hides (i.e. three permanent hides in the Loire estuary and five permanent hides in the Camargue) situated on the ground or a couple of metres above it. We moved mobile hides to cover all water bodies presents in the areas. Usually, 4-5 mobile spots were necessary in each study site. Whenever possible, we performed counts on the 15th of each month and counts lasted < 3 hours. Counts and resighting sessions were independent (i.e. usually performed by different persons). As we performed no repetitions, we could not estimate the variance of the counts, and the number of teals counted has to be considered as a minimum, as is generally the case with waterbird counts.

Capture-resighting histories, local survival and emigration

To minimise heterogeneity due to, for example, trap dependence (individuals either attracted to or avoiding traps), we included only local resightings of the marked individuals in the analyses (i.e. we discarded physical recaptures of birds in the traps). We reconstructed capture-resighting histories for each individual. The initial capture (i.e. when the bird was seen for the first time, ringed and equipped with a nasal saddle) was coded 1. Then, for each resighting occasion, each individual was coded 1 or 0, depending on whether it was seen on that occasion (1) or not (0), respectively. We considered the calendar month as a capture-resighting occasion (see below). Therefore, our capture-resighting matrices included five capture occasions (October - February) and five resighting occasions (November - March).

Our sample size of newly caught individuals was not large enough to use a shorter time interval than the calendar month for the capture-resighting event. For this reason, our study might suffer from a slightly lower resolution than the Pradel et al (1997b). study, meaning that our results are not directly comparable. The strength of our study resides firstly in the fact that our investigations encompass a longer part of migration and wintering periods, and secondly, that possible biases due to trap dependences are minimised (see above).

We used individual capture-resighting histories to estimate local survival using CMR methods, which provide a range of models for the study of survival that takes into account possible variations in recapture probabilities (Lebreton et al. 1992). The major assumptions of CMR methods are that: 1) the probabilities of fates are identical for the different individuals, 2) marked individuals make up a random sample of the population, and 3) there are no behavioural effects of marking (Lebreton et al. 1992). We derived emigration rates from our local survival estimates and the same estimates of true survival probabilities as those used by Pradel et al. (1997b). Finally, we combined data on monthly counts and local survival estimates to compute the

Downloaded From: https://complete.bioone.org/journals/Wildlife-Biology on 29 Mar 2024
Terms of Use: https://complete.bioone.org/terms-of-use

total number of birds having used the area during the study period.

The local survival (φ) describes the probability that an individual survives and stays within the study area. In studies of open populations as in our study, local survival is therefore the product of the 'true' survival probability (S; equal to 1 - mortality rate) and the residence probability (R; equal to 1 - emigration rate, E). When S is known (e.g. from capture-recoveries models), E may therefore be estimated using the formula: $E = 1-\varphi / S$ (Pradel et al. 1997b). Following these researchers, we derived emigration rates assuming an average annual survival rate (S) of 45% (Pradel et al. 1997b) with all mortality concentrated during the study period, providing a monthly survival rate S' of $100 \times \sqrt[5]{0.45} = 85\%$ (^{5} indicates the number of intervals). We therefore assumed that all mortality was constant among months, which might be not true. For example, one might expect a decrease in mortality after the end of the hunting season, i.e. in February and March. This also means that an apparent decrease in local survival during this period would reflect the departure of individuals rather than an increase in mortality.

GOF tests, CMR modelling and parameter estimations

Before modelling local survival using the CMR approach, we performed goodness-of-fit (GOF) tests using U-CARE version 2.0 (Choquet et al. 2003). GOF tests assess whether the assumptions of the global CMR model (independence and identical fate of individuals) are met and allow determining possible sources of heterogeneity (e.g. trap happiness, trap shyness and transience). Detection of significant lack-of-fit (i.e. heterogeneity) means that the data do not follow, as they should, a multinomial distribution. Once sources of heterogeneity are properly identified, one can choose the 'umbrella' model that correctly fits the data. We used M-SURGE version 1.4.2 (Choquet et al. 2004) to model local survival starting from models taking into account all the suspected causes of variability detected using GOF tests. Model notations followed Lebreton et al. (1992) with: g = group (categories of individuals according to their sex and age classes), a = age (young vs adults), a2 = when newly marked individuals were treated differently than individuals marked at a previous capture occasion (our purpose of this parameterisation was to take into account transience), s = sex, t = time (capture occasion) as a discrete variable, T = time as a covariable (i.e. continuous variable), T^2+T = quadratic form of time as a covariate, g.t = interaction between group and time, g+t = the additive effects of the same variables and so on. P represents resighting probability and a dot in brackets (.) means that the parameter was held constant. We performed model selection using Aikake's Information Criterion corrected for small sample size (AIC_c; Lebreton et al. 1992). Models differing by < 2 AIC_c units were considered as being equivalent (Lebreton et al. 1992). In that case, we used model averaging of the set of competing models to derive the estimates and their unconditional confidence intervals (Buckland et al. 1997) including only models for which all parameters could be estimated. Model averaging was performed on Mark (version 5.1) software (White & Burnham 1999). Model selection was performed by starting with the global model and dropping the variables one by one. We included covariates (time taken as a quantitative variable) as any other parameter.

We computed estimates of the total number (volume V) of individuals using the area for at least part of the study period using the formula: $V = N_1 + \sum(N_{i+1} - N_i \times \varphi_{i \rightarrow i+1})$, where V = total number of individuals occupying the area from October to March, i = month, N_i = number of individuals counted in month I (N_1 being the first month of the period) and $\varphi_{i \rightarrow i+1}$ = survival from month i to month i+1 (Frederiksen et al. 2001). Assumptions of this approach are the same as for CMR methods, and the counts are unbiased estimates of the number of birds present.

Because our counts did not allow distinguishing the age and sex of individuals, we derived local survival probabilities incorporated in the formula from the best possible time-dependent models for local survival holding age and sex constant ($\varphi(T+T^2)$ for the Loire estuary and $\varphi(t)$ for the Camargue, respectively). By doing this, we therefore implicitly assumed that our marked samples were representative of populations occupying our study sites and that there were no differences in survival rates among age and sex classes (which was not necessarily true: see Table 2). In the Camargue, teal could not be counted in December 2003 due to flooding conditions. We then applied Frederiksen et al.'s (2001) formula by combining November-December and December-January survival probabilities (0.36 and 0.76, respectively). We computed variance of this combined survival probability as

Downloaded From: https://complete.bioone.org/journals/Wildlife-Biology on 29 Mar 2024
Terms of Use: https://complete.bioone.org/terms-of-use

suggested in Frederiksen et al. (2001). We could not derive any confidence interval for counts because the numbers of birds were estimated only once per month and bird counts in different places were pooled for each of the two sites. Nevertheless, we computed the variance of the total number of individuals V as

$$\mathrm{var}(V) = \sum_{i=1}^{k-1} (N_i^2 \times \mathrm{var}(\varphi_{i \to i+1})).$$

We then took the 95% confidence intervals of V as $\pm 1.96 \times \sqrt{\mathrm{var}(V)}$.

Results

We marked and monitored a total of 291 and 170 individuals in the Loire estuary and in the Camargue, respectively. The proportions of birds seen at least once after marking were similar in both areas (Table 1).

GOF tests

GOF tests did not reveal significant heterogeneity (all P values > 0.20), except in the Loire estuary where significant transience (excess of individuals never seen after initial capture) was detected in young females ($P < 0.026$). For this study area, we therefore analysed capture/resighting histories of young females separately from those of other classes (young males, adult males and adult females) starting with an 'umbrella' model φ(a2.t)p(t). This model takes transience into account by allowing newly captured individuals to display a different survivorship than from those captured for the second time or later on (Pradel et al. 1997a).

Local survival, resighting probabilities and emigration rates

In the Loire estuary, all best models included a quadratic effect of time (T^2+T) on local survival, except for young females for which one of the best two models included T^2+T and the other did not (Table 2). In this area, local survival exhibited a bell-like shape with lower values in the beginning and at the end of the wintering season (Fig. 1). Moreover, we detected a group effect (g1), suggesting that local survival probabilities of adult males were higher than those of young males and adult females (see Fig. 1). For young females, local survival probabilities derived from the model averaging of the two best models for which all parameters could be estimated (φ(a2+T^2+T) and φ(a2) p(t)), varied between 0.22 (95% CI: 0.04-0.63) and 0.43 (95% CI: 0.32-0.56) and between 0.47 (95% CI: 0.09-0.88)

Table 1. Proportions of teal resighted at least once (i.e. one month later or afterwards) after ringing in the Loire estuary and in the Camargue during the winter of 2003/04. Figures in brackets show the number of individuals in each case.

	Loire estuary	Camargue
Young females	0.34 (133)	0.21 (52)
Adult females	0.33 (33)	0.33 (15)
Young males	0.38 (98)	0.37 (56)
Adult males	0.55 (27)	0.40 (47)
Total	0.37	0.33

Table 2. Summary table of CMR models for local survival (φ) and capture (p) probabilities of teal in the Loire estuary and in the Camargue, France, during the winter of 2003/04. Models selected for model averaging are shown in italics, and umbrella models in bold italics. Only the bests models are shown; NP = number of identifiable parameters with number of mathematical parameters in brackets. The abbreviations include: AIC_c = Akaike information criterion corrected for small sample size and true number of parameters; g1 = group effect with two groups (adult males vs young males and adult females); g2 = group effect with two groups (adult males vs young males, young females and adult females; see the section Methods).

Model	NP	AIC_c	Δ AIC	AIC_c weight
Loire estuary				
Young females				
φ(a2+T2+T) p(.)	*5 (5)*	*338.73*		*0.45*
φ(a2) p(t)	*7 (7)*	*339.43*	*0.7*	*0.31*
φ(a2+T2+T) p(t)	9 (9)	341.66	2.93	0.10
φ(a2+t) p(.)	7 (7)	342.36	3.63	0.07
Φ (a2.t) p(t)	***13 (14)***	349.18	10.45	0.002
Adult males, adult females and young males				
φ(g1+T2+T) p(.)	*5 (5)*	*414.4*		*0.35*
φ(g1+T2+T) p(t)	*7 (7)*	*414.93*	*0.53*	*0.27*
φ(g+ T2+T) p(.)	7 (7)	416.47	2.07	0.12
φ(g+T2+T) p(t)	4 (4)	419.45	2.65	0.09
Φ(g.t) p(g.t)	***26 (30)***	437.59	30.4	-
Camargue				
All individuals				
φ(s+t) p(t)	10 (10)	411.41		0.16
φ(g2+t) p(t)	11 (12)	411.73	0.32	0.14
φ(g2) p(t)	*7 (7)*	*411.96*	*0.54*	*0.12*
φ(s) p(t)	*7 (7)*	*412.08*	*0.66*	*0.11*
Φ(g.t)p(g.t)	***33 (40)***	439.90	28.5	-

a = age (young vs adult), a2 = when newly-born individuals were treated differently than individuals marked at a previous capture occasion (taking into account transience), T = time as a covariate, T^2+T = quadratic form of time as a covariate, s = sex effect, a2.t = interaction term between a2 and time as a factor.

Downloaded From: https://complete.bioone.org/journals/Wildlife-Biology on 29 Mar 2024
Terms of Use: https://complete.bioone.org/terms-of-use

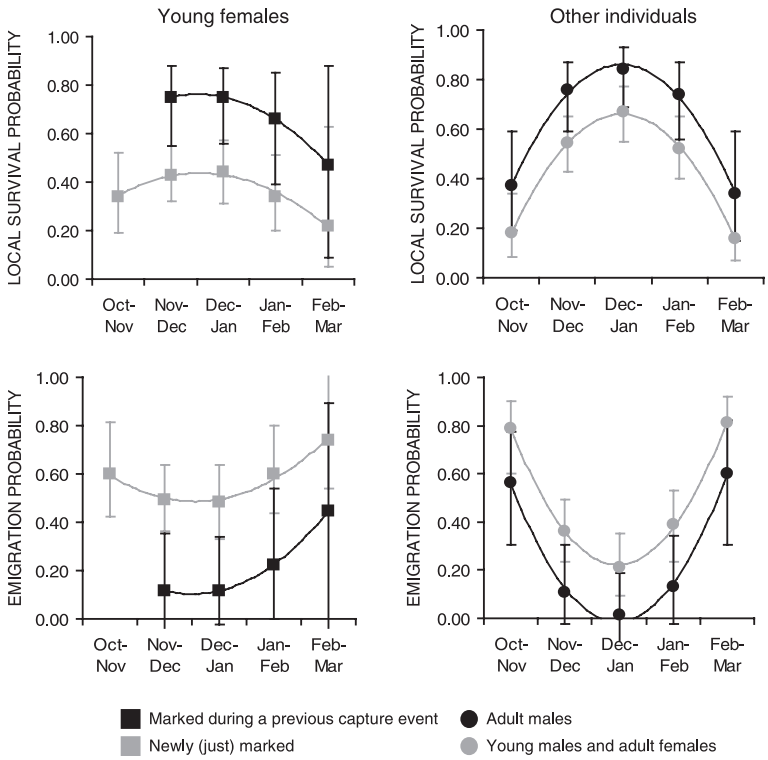


Figure 1. Local monthly survival (φ) and emigration probabilities (E) for teal in the Loire estuary during the wintering season of 2003/04, with bars indicating 95% confidence intervals. E = 1-φ/S, and the true monthly survival S = 0.85 are derived from the literature (see explanation in the text). Young females: grey squares are for individuals just marked (which includes transients) and black squares show individuals marked on a previous capture occasion.

and 0.75 (95% CI: 0.55-0.88) for individual just marked (which comprised transients) and individuals marked on a previous occasions (not affected by transience), respectively (see Fig. 1). Whatever the time interval, adult males exhibited higher local survival probabilities (minimum: 0.33 and 95% CI: 0.15-0.58, and maximum 0.84 and 95% CI: 0.68-0.92) than adult females and young males (minimum: 0.18 and 95% CI: 0.08-0.34, and maximum 0.67 and 95% CI: 0.55-0.77; values derived from model averaging of $\varphi(g1+T^2+T)\ p(.)$ and $\varphi(g1+T^2+T)\ p(t)$; see Fig. 1).

In the Camargue, local survival probabilities did not exhibit the 'bell-like' temporal patterns depicted above. Four models displayed similar AIC_c values (see Table 2) of which two included a time effect on survival but failed to provide an estimate for each parameter, and were therefore not considered further. Among the two models with estimable parameters, one φ(g2) p(t) included a group effect (g2) for local survival probability (see Table 2), indicating higher local survival for adult males than for young males and females; the other φ(s) p(t) included a sex effect suggesting higher local survival for males than for females. Local survival estimates averaged over the two models were 0.45 (95% CI: 0.34-0.56) for females, 0.53 (95% CI: 0.40-0.66) for young males and 0.61 (95% CI: 0.49-0.73) for adult males. Again, we could not determine whether the differences in local survival between groups were due to differences in mortality rather than due to differences in emigration rates.

In the Loire estuary, resighting probabilities derived from local survival estimates of the averaged models varied between 0.51 (95% CI: 0.09-0.91) in March and 0.78 (95% CI: 0.58-0.90) in December for young females and between 0.61 (95% CI: 0.39-0.79) in March and 0.82 (95% CI: 0.35-0.97) in October for the other individuals. In the Camargue, resighting probabilities were found to vary between 0.27 (95% CI: 0.11-0.52) in March and 0.95 (95% CI: 0.73-0.99) in January.

In the Loire estuary, depending on the category of individuals, we estimated monthly emigration probabilities to vary between 0.01 for adult males in December to 0.81 for adult females and young males in March, with the highest values perfectly matching the periods of migration (see Fig. 1). In the Camargue, we estimated the monthly emigration probabilities at 0.47 (95% CI: 0.34-0.60) for females, 0.38 (95% CI: 0.22-0.53) for young males and 0.28 (95% CI: 0.14-0.42) for adult males.

Downloaded From: https://complete.bioone.org/journals/Wildlife-Biology on 29 Mar 2024
Terms of Use: https://complete.bioone.org/terms-of-use

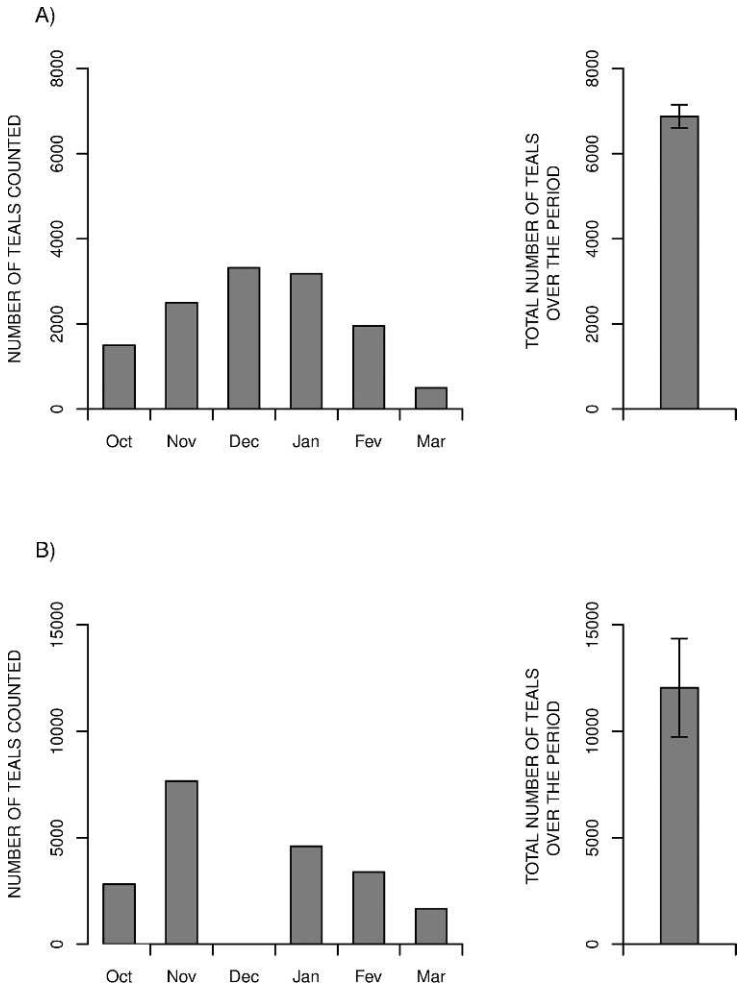


Figure 2. Monthly number of teals counted and the estimated total number of individual using the area over the whole period (V) with 95% confidence intervals indicated at the Massereau reserve (A) in the Loire estuary and at the Vigueirat marshes (B) in the Camargue during the winter of 2003/04. Data were not available for December in the Camargue.

Estimates of volumes (total number of teal in the two areas)

During the 2003/04 wintering season, the maximum number of teal counted at the Massereau reserve reached ca 3,300 individuals in December (Fig. 2A). In reality, the estimated volume (V) of individuals using the Frederiksen et al. (2001) formula was more than twice as large (6,872 individuals, 95% CI: 6,601-7,145; monthly local survival estimates derived from the model $\varphi(T+T^2)p(.)$). At the Vigueirat marshes in the Camargue, the difference between maximum winter counts (see Fig. 2B) and V was ca 1.6 of the maximum numbers of individuals counted in November = 7,700 and the estimated number taking into account a turnover of 12,042 (95% CI: 9,731-14,353; monthly local survival estimates derived from the model $\varphi(t)\ p(t)$).

Discussion

Pradel et al. (1997b) were the first to quantify emigration and turnover rates in teal wintering in the Camargue, based on relatively old ringing data. Such pattern has since then been corroborated by a present-day study relying on teal nasal saddles, but which dealt more specifically with local switches between adjacent day-roosts (Guillemain et al. 2010). Our study confirms the existence of such high turnover rates, not only in the Camargue, but also in another wintering region, and it brings new insights into the understanding of the teal wintering populations in southwestern Europe.

In CMR terminology, transients are individuals disappearing immediately after capture. Transience can therefore include both individuals dying before

Downloaded From: https://complete.bioone.org/journals/Wildlife-Biology on 29 Mar 2024
Terms of Use: https://complete.bioone.org/terms-of-use

the first recapture occasion and individuals permanently leaving the study area. We only detected transience for young females in the Loire estuary. It is well-known that first-year dabbling ducks have higher mortality rates than adults (Tamisier & Dehorter 1999, Devineau 2003), but generally, no major difference exists in survival rates between male and female teal outside the breeding season (Johnson 1995, Devineau 2003). In contrast, the fact that females may migrate further south than males, and young birds further south than adults, is commonly reported in ducks (e.g. Salomonsen 1968, Alexander 1983, Campredon 1983). This inter-sexual differential migration has been supported by recent analyses for teal by Guillemain et al. (2009), though no significant difference between age classes was apparent. In our study, transience may therefore be more likely to reflect permanent emigration rather than mortality (Pradel et al. 1997b). A large proportion of young females might 'disappear' after initial capture simply because their 'final' destination lies further to the south. As we made no effort to capture or search for marked individuals outside the study areas, we cannot totally rule out that part of the observed emigration rate was due to local movements to an alternative resting site nearby. Nevertheless, the fact that teals are usually faithful to their resting site (Guillemain et al. 2002) suggests that permanent local emigration may only be occasional (see also Guillemain et al. 2010). Our results therefore are more likely to support the hypothesis that transience was due to individuals leaving the study area through migration or, alternatively, that they died.

As did Pradel et al. (1997b), we confirm the presence of high individual turnover rates in the two studied wintering areas. In the Loire estuary, the most abrupt changes in the number of counted teal occurred during October-November and February-March (see Fig. 2), suggesting that migratory movements reached a peak during these two periods (see also Guillemain et al. 2006 for spring migration periods of teal). Our results seem to be robust, because the same pattern as we found was recorded in all classes of individuals, including young females, even though they were analysed separately from each other (see Fig. 2).

Because the true pattern of mortality was unknown, one may argue that variations in local survival rates reflected changes in mortality rates rather than in turnover. In fact, several lines of evidence suggest that the reverse is true. Firstly, to our knowledge variations in mortality rates of such an amplitude have never been reported before, even in heavily hunted species like teal (monthly local survival varied between $< 10\%$ and up to 85% depending on month and class of individual). Secondly, the abrupt changes in the local survival probabilities found in our study exactly match the known peaks of migratory movements for teal, as explained above. Thirdly, hunting is probably the major cause of mortality in teal, and since the end of the hunting season occurred by the end of January, the sharp decrease in local survival observed between February and March can only be attributed to emigration of teal departing to their breeding areas. Possible changes in the mortality pattern (due either to variations in hunting pressure or to changes in natural mortality) across the season may be affecting our estimates. However, theses fluctuations in mortality cannot fully account for our results.

Pradel et al. (1997b) reported sharp temporal changes in local survival due to emigration following a cold spell. When no such cold spells occurred, like during our study period, temporal changes in emigration rates in Pradel et al.'s (1997b) study exhibited a temporal trend similar to ours. In the Camargue, during the winters of 1955/56 (with a cold spell) and 1957/58 (with a mild winter), monthly emigration rates from December to February ranged from 30 to 89%, depending on how low the temperatures were (Pradel et al. 1997b). These values are of the same order of magnitude as ours in the same area even though the duration of capture occasions was three times shorter in the Pradel et al. (1997b) study.

Estimating the total number of individuals using our two study areas over the winter is an important contribution of our study. In both areas, this estimate was almost twice as large as the maximum instantaneous count number. This clearly demonstrates that the importance of a given area cannot simply be derived from instantaneous counts, especially if these are carried out only once a year in mid-January (Elmberg et al. 2006).

Concluding remarks

The CMR approach applied to visual detection of nasal marks is very promising as a means to characterise the patterns of wetland use by ducks in winter, which would be appropriate to apply to

Downloaded From: https://complete.bioone.org/journals/Wildlife-Biology on 29 Mar 2024
Terms of Use: https://complete.bioone.org/terms-of-use

stop-over areas that are used by many birds while instantaneous counts remain low. This is especially true for study areas where birds can be monitored easily through resighting of marked individuals. For example, monitoring of only 300 teals with nasal saddles has enabled us to obtain reasonably robust estimates of monthly emigration rates in the Loire estuary.

The Camargue and the Loire estuary are known to differ in terms of instantaneous wintering duck counts, including teal (e.g. Fouque et al. 2005). Our study refines this view by showing how many more individuals may actually use the areas. Until now, qualitative differences between these two areas concerned their status as a wintering area (i.e. Camargue) or as an intermediate staging area (i.e. Loire estuary). Our data do not directly contradict these definitions, but they do suggest that the more northern Loire estuary is not just a stop-over area. Resightings made further south confirm that some individuals marked in both areas travel further south, and also that the birds in the two areas show some degree of mixing (Guillemain et al. 2005).

Finally, according to Elmberg et al. (2006) current monitoring schemes of natural populations of ducks in Europe (mostly based on counts) would be "insufficient to address objectives of wise use and sustainability...". Our study exemplifies why and how designing monitoring schemes based on a CMR approach would help towards a better understanding of duck population dynamics, a prerequisite for improving management practices.

Acknowledgements - we would like to thank Kévin Pineau, Jonathan Fuster, Jean-Baptiste Nogues and Matthieu Chambouleyron for their help with capturing teal and identification of nasal saddles at the Vigueirat marshes. Also, many thanks to Henry Vergereau, Patrice Friconeau, Luc Drouillet and Denis Lacourtpaille for their help with fieldwork at the Massereau reserve. We are indebted to Hubert Dugué, who greatly helped to improve capture success. Remi Choquet provided invaluable advice concerning the use of M-SURGE software. Many thanks to Roger Pradel for statistical advice. Morten Frederiksen greatly helped improving the ms. Many thanks to Gunnar Gunnarsson, Hugues Santin-Janin and an anonymous referee whose comments helped improving the manuscript.

References

Alexander, W.C. 1983: Differential distribution of wintering diving ducks Aythyini in North America. - American Birds 37: 26-29.

Bub, H. 1991: Bird trapping and bird banding. A handbook for trapping methods all over the world. - Cornell University Press, New York, New York, USA, 300 pp.

Buckland, S.T., Burnham, K.P. & Augustin, N.H. 1997: Model selection: an integral part of inference. - Biometrics 53: 603-618.

Campredon, P. 1983: Sexe et age ratio chez le canard siffleur *Anas penelope* en période hivernale en Europe de l'Ouest. - Revue d'Ecologie (La Terre et la Vie) 37: 117-128. (In French).

Choquet, R., Reboulet, A-M., Pradel, R., Gimenez, O. & Lebreton, J-D. 2003: User's manual for U-CARE. - CEFE/CNRS, Montpellier, France, 26 pp.

Choquet, R., Reboulet, A-M., Pradel, R., Gimenez, O. & Lebreton, J-D. 2004: User's manual for M-SURGE 1.4. - CEFE/CNRS, Montpellier, France, 45 pp.

del Hoyo, J., Elliot, A. & Sargatal, J. (Eds.) 1992: Handbook of the Birds of the World. Vol .1: Ostrich to ducks. - Lynx Editions, Barcelona, Spain, 602 pp.

Devineau, O. 2003: Dynamique et gestion des populations exploitées: l'exemple de la Sarcelle d'hiver (*Anas crecca crecca*). - M.Sc. thesis, University of Montpellier II, Montpellier, France, 26 pp + Appendices. (In French).

Elmberg, J., Nummi, P., Pöysä, H., Sjöberg, K., Gunnarsson, G., Clausen, P., Guillemain, M., Rodrigues, D. & Väänänen, V-M. 2006: The scientific basis for new and sustainable management of migratory European ducks. - Wildlife Biology 12(2): 121-127.

Fouque, C., Guillemain, M., Leray, G., Joyeux, E., Mondain-Monval, J-Y. & Schricke, V. 2005: Distribution des effectifs hivernaux de Sarcelle d'Hiver (*Anas crecca*) en France et tendances d'évolution sur les 16 derniers hivers. - Faune Sauvage 267: 19-30. (In French).

Frederiksen, M., Fox, A.D., Madsen, J. & Colhoun, K. 2001: Estimating the total number of birds using a staging site. - Journal of Wildlife Management 65: 282-289.

Guillemain, M., Arzel, C., Mondain-Monval, J-Y., Schricke, V., Johnson, A.R. & Simon, G. 2006: Spring migration dates of teal *Anas crecca* ringed in the Camargue, southern France. - Wildlife Biology 12(2): 163-169.

Guillemain, M., Devineau, O., Brochet, A-L., Fuster, J., Fritz, H., Green, A.J. & Gauthier-Clerc, M. 2010: What is the spatial unit for a wintering Teal *Anas crecca*? Weekly day-roost fidelity inferred from nasal saddles in the Camargue, southern France. - Wildlife Biology 16(2): 215-220.

Guillemain, M., Hearn, R., King, R., Gauthier-Clerc, M., Simon, G. & Caizergues, A. 2009: Differential migration of the sexes cannot be explained by the body size hypothesis in Teal. - Journal of Ornithology 150: 685-689.

Guillemain, M., Poisbleau, M., Denonfaoux, L., Lepley, M., Moreau, C., Massez, G., Leray, G., Caizergues, A., Arzel, C., Rodrigues, D. & Fritz, H. 2007: Mutliple tests of the effect of nasal saddles on dabbling ducks: combining field and aviary approaches. - Bird Study 54: 35-45.

Downloaded From: https://complete.bioone.org/journals/Wildlife-Biology on 29 Mar 2024
Terms of Use: https://complete.bioone.org/terms-of-use

Guillemain, M., Fritz, H. & Duncan, P. 2002: The importance of protected areas as nocturnal feeding grounds for dabbling ducks wintering in western France. - Biological Conservation 103: 183-198.

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

Johnson, K. 1995: Green-winged Teal (*Anas crecca*). - In: Poole, A. & Gill, F. (Eds.); The birds of America. The Academy of Natural Sciences, Philadelphia and The American Ornithologist's Union, Washington D.C., USA, 20 pp.

Lebreton, J-D., Burnham, K.P., Clobert, J. & Anderson, D.R. 1992: Modelling survival and testing biological hypotheses using marked animals: a unified approach with case studies. - Ecological Monographs 62: 67-118.

Mondain-Monval, J-Y. & Girard, O. 2000: Le Canard colvert, la Sarcelle d'hiver et autres canards de surface. - Faune Sauvage 241: 124-139. (In French).

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

Pradel, R., Hines, J.E., Lebreton, J-D. & Nichols, J.D. 1997a: Capture-recapture survival models taking account of transients. - Biometrics 53: 60-72.

Pradel, R., Rioux, N., Tamisier, A. & Lebreton, J-D. 1997b: Individual turnover among wintering Teal in Camargue: a mark-recapture study. - Journal of Wildlife Management 61: 816-821.

Rodrigues, D.J.C., Fabiâo, A.M.D. & Figueiredo, M.E.M.A. 2001: The use of nasal markers for monitoring mallard populations. - In: Fields, R., Waren, R.J., Okarma, H. & Sievert, P.R. (Eds.); Wildlife, land, and people: priorities for the 21st century. Proceedings of the second International Wildlife Management Congress, Hungary, The Wildlife Society, Bethesda, Maryland, USA, pp. 316-318.

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

Scott, D.A. & Rose, P. 1996: Atlas of Anatidae populations in Africa and Western Eurasia. - Wetland International, Wageningen, The Netherlands, 336 pp.

Tamisier, A. & Dehorter, O. 1999: Camargue, canards et foulques - Fonctionnement et devenir d'un prestigieux quartier d'hivernage. - Centre Ornithologique du Gard, Nimes, France, 369 pp. (In French).

Wetlands-International 2006: Waterbird population estimates. - Wetlands International, Wageningen, The Netherlands, 239 pp.

White, G.C. & Burnham, K.P. 1999: Program MARK: survival estimation from populations of marked animals. - Bird Study 46(Supplement): 120-129. Available at: http://www.phidot.org/software/mark/

Downloaded From: https://complete.bioone.org/journals/Wildlife-Biology on 29 Mar 2024
Terms of Use: https://complete.bioone.org/terms-of-use