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Source: Wildlife Biology, 16(1) : 12-24

Published By: Nordic Board for Wildlife Research

URL: https://doi.org/10.2981/08-071

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**Wildl. Biol. 16: 12-24 (2010)**
DOI: 10.2981/08-071
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**Original article**

# A comparison of green-winged teal *Anas crecca* survival and harvest between Europe and North America

**Olivier Devineau, Matthieu Guillemain, Alan R. Johnson & Jean-Dominique Lebreton**

The impact of waterfowl harvest on the dynamics of duck populations remains incompletely understood. While wide-scale monitoring and management programs have been set up in North America, far less has been done in Europe where populations and harvest are essentially managed at country level with a sole focus on population size. Hence, comparing North American waterfowl populations with European waterfowl populations could be useful in suggesting flyway-scale management options in Europe. In our paper, we analyse historical capture-recapture-recoveries data for the European teal *Anas crecca crecca* and we compare the computed survival and harvest rates to those obtained from a North American recovery data set for the green-winged teal *Anas crecca carolinensis*, its sister taxon. During 1960-1976, the annual probability of survival was slightly lower in Europe (average over sexes: 0.485 ± 0.101) than in North America (0.545 ± 0.010 for both sexes). Assuming a 30% ring reporting rate, our estimate of the annual harvest rate was about three times higher in Europe (average over sexes: 0.178 ± 0.051) than in North America (average over sexes: 0.071 ± 0.014). Although the European population increased over the study period and continues to do so, such a hunting pressure may potentially reduce our flexibility in managing this population due to uncertainties such as environmental changes, and have deleterious effects in the long term. We use our results to discuss waterfowl research and management in Europe. Initiating studies to estimate ring reporting rate would be an essential first step to properly evaluate the impact of harvest on the dynamics of the teal population in Europe.

*Key words: Anas crecca carolinenis, Anas crecca crecca, capture-mark-recapture, Eurasian teal, green-winged teal, harvest, population dynamics, recoveries, waterfowl*

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*Received 10 October 2008, accepted 30 October 2009*

*Associate Editor: Anthony D. Fox*

The impact of recreational harvest on population dynamics remains poorly understood for most species of waterfowl (Anderson & Burnham 1976, Elmberg et al. 2006). For example, whether harvest acts in a compensatory or additive way has been a contentious issue and is still unresolved (Nichols et al. 1995a, Nichols & Johnson 1996). In North America, this lack of knowledge gradually led to the setting up of monitoring programmes and, ultimately, to the implementation of an adaptive management scheme for waterfowl populations and harvest, in which information about population dynamics plays a central role (Nichols et al. 2006). On the contrary, the impact of harvest on the dynamics of exploited waterfowl populations has seldom been explored in Europe where, in accordance



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with directives from the European Union, waterfowl hunting regulations are implemented on a country-specific level with monitoring largely based on wintering numbers, which are of little help to understand future and past changes in population size (Elmberg et al. 2006). To this extent, waterfowl population dynamics are better known in North America than in Europe, and thus North American populations provide an interesting reference to which the dynamics of European waterfowl populations can be compared.

In our paper, we compare some basic demographic parameters between Europe and North America using the example of the green-winged teal *Anas crecca*. The green-winged teal is of great management interest because it is the second-most harvested duck species after the mallard *Anas platyrhynchos*, both in Europe and in North America (Baldassarre & Bolen 2006, Mooij 2005, Mondain-Monval & Girard 2000). However, while thousands of captive bred mallards are released every year for hunting purposes (Mondain-Monval & Girard 2000), there is no significant release of captive bred teal, thus potentially making the impact of harvest more acute for the teal population.

In addition, mid-January counts indicate that about 270,000 individuals winter in France, Italy, Spain and Portugal (Gilissen et al. 2002). By comparison, during 1998-1999, harvest was estimated to about 300,000 teal in France only (Mondain-Monval & Girard 2000). This seems to be a paradoxically high harvest, even if one considers that most hunting mortality likely occurs before the mid-January count. Nonetheless, the northwest European teal population is increasing while the western part of the Mediterranean population shows a slight decline (Delany & Scott 2006). Throughout our paper, we use the term 'teal' for both the European and the North American subspecies of the green-winged teal *Anas crecca crecca* and *A. c. carolinensis,* respectively.

Several hypotheses can be put forward to explain the apparent paradox of the European teal population. Firstly, counts are, sometimes strongly, influenced by differences between observers (Faanes & Bystrak 1981, Sauer et al. 1994, Cunningham et al. 1999), or by the site coverage (Delany & Scott 2006). The teal is a small bird that appreciates vegetation cover (Johnson 1995), which may lead to many birds being missed by observers. In addition, counts do not account for movements of individuals and thus, only produces an instantaneous, and potentially biased, snapshot of the status of a population (Frederiksen et al. 2004). In addition, there is often an important turnover on the wintering grounds and the number of birds counted on a given site at a given time generally represents only a fraction of the birds actually using this site (Pradel et al. 1997b, Devineau 2007). Bird counts are generally considered as underestimates of actual numbers (Delany & Scott 2006, Dervieux et al. 1980). Therefore, with an actually bigger teal population, harvest would comparatively not be as high as it seems.

Another explanation of the apparent paradox of the teal population could be density dependence mechanisms. Under this hypothesis, the reduction in density caused by harvest allow surviving individuals to have a higher survival and/or reproduction rate, which would compensate for the losses due to hunting. Although compensatory harvest has been widely discussed (Anderson & Burnham 1976, Burnham & Anderson 1984, Boyce et al. 1999), the importance or even the existence of such mechanisms is still under debate (Pöysä et al. 2004, Lebreton 2005).

Finally, the actual impact of harvest on the population could be concealed by some particularities in the population dynamics. Indeed, in Europe, hunting regulations vary from one country to another, and available information indicates that annual duck harvest varies as well (Mooij 2005). Hence, hunting could induce a source-sink functioning (see for example Novaro et al. 2005), in which low-hunting pressure areas would supply birds to the wintering grounds where hunting pressure is higher.

In our paper, we use a 20-year capture-recapture-recovery data set to provide robust estimates of important demographic parameters (survival and harvest rates) of the teal in Europe. Because population dynamics are difficult to analyse based on a single population study, we compare our results to those obtained from another, similar data set from North America. This may provide useful insights into the European teal population dynamics, which may eventually be translated into adequate management and conservation procedures.

## Methods

### Study area/species

In Europe, the teal breeds from Scandinavia and northern Russia to France, Switzerland, and the



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Table 1. Brief description of the European data. The European data were a mixture of live recaptures and dead recoveries. This table only presents the data distribution at time of ringing and at time of recovery. Juveniles and adults indicate the age of the birds at time of ringing. First-year birds were only considered as juveniles for the first time interval following ringing. They were considered as adults from the first encounter event following ringing and thereafter. Hence, numbers given for recoveries should be read as 'among the 18,849 female birds ringed during their first year, 2,484 were later recovered'. Counts given for recaptures represent the number of birds 'ringed as' that were recaptured alive at least once. The total number of recaptures was 5,315.

| | Females | | Males | | | Sex ratio | Age ratio |
|---|---|---|---|---|---|---|---|
| | Juveniles | Adults | Juveniles | Adults | Total | (♂:♀) | (Juv:Ad) |
| Ringed | 18849 | 6289 | 18322 | 11715 | 55175 | ~1.2:1 | ~2.0:1 |
| Recaptured at least once | 780 | 178 | 689 | 587 | 2234 | ~1.3:1 | ~1.9:1 |
| Recovered | 2484 | 788 | 2917 | 1727 | 7916 | ~1.4:1 | ~2.1:1 |

northern edge of the Black Sea (see distribution map in Scott & Rose 1996). Winter grounds cover most of southern Europe, North Africa (Nile region), and the Middle East (Cramp & Simmons 1977, Johnson 1995). Specific 'flyways' have been recognised, but no clear populations can be distinguished (Scott & Rose 1996), and evidence for a fairly large amount of exchange among these flyways has challenged these delineations (Guillemain et al. 2005). In North America, the teal breeds throughout much of Canada, and winters throughout the United States and Mexico. Migration occurs along four major flyways (Johnson 1995).

## Data

Duck ringing in France has been fairly intensive from the mid-1950s to the mid-1970s, but was then interrupted until new ringing programs were initiated in the early 2000s (e.g. Guillemain et al. 2007). However, this latter program has not yet provided enough data to adequately estimate demographic parameters, and we therefore used historical data from teal ringed during 1954/55-1975/76 during the internuptial season at the Tour du Valat biological station in the Camargue, southern France (43°30'28N, 04°40'07E). A large proportion of the French teal population winters in the Camargue (Hémery et al. 1979), which is a wetland of international importance according to the Ramsar criteria (i.e. $> 1\%$ of the considered population present in the area, Deceuninck et al. 2009). Because the Camargue is located at the limit between the northwest European and the Black Sea/Mediterranean regions, it attracts wintering birds from both sub-populations and as such, birds ringed in Camargue are fairly representative of the (western) European teal population. Our data consisted of a mixture of live recaptures and dead recoveries, with the latter mainly occurring in September-March, i.e. during the most common hunting season in southwestern Europe for the period of interest (nowadays, hunting season commonly ends in late January). Of recoveries, $> 95\%$ were from hunting and given the low number of other reported causes of mortality (e.g. predation), all reports were considered to be hunting mortalities in the analyses. Among the 55,175 individuals initially ringed, 2,234 were subsequently recaptured at least once by the same ringing crew (total 5,315 recaptures) and 7,916 were recovered by hunters (Table 1).

Dead recoveries of teal in North America were obtained between 1960/61 and 1997/98 at various ringing stations across North America (see Gustafson et al. 1997 for details). Ringings were carried out in January-February, i.e. at the very end or after the hunting season occurring from late September to February. Subsequent information was only composed of recoveries of dead animals (i.e. no live recaptures), with $> 99\%$ of reported recoveries being due to hunting. No capture-recapture event of any kind was recorded outside the September-February period. A total of 47,276 individuals were ringed, from which 2,381 were shot and reported (Table 2).

## Model structure

Traditional capture-recapture studies (Lebreton et al. 1992) imply that marked individuals are reported

Table 2. Brief description of the North American data. The data were based only on dead recoveries (i.e. no live recaptures). Given in North America ringing was carried out in January and February (as opposed to September-March in Europe), all ringed birds were at least in their second (calendar) year at time of ringing (i.e. second-year and after-hatching year birds), and were thus all considered as adults.

| | Females | Males | Total | Sex ratio (♂:♀) |
|---|---|---|---|---|
| Ringed | 12600 | 34676 | 47276 | ~2.7:1 |
| Recovered | 513 | 1868 | 2381 | ~3.6:1 |



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to the ringing laboratory when they are encountered, i.e. when they are recaptured alive. When the population of interest is exploited, marked individuals are encountered not only when recaptured alive, but also when harvested. It is thus possible to consider two states, alive and dead, and to consider the encounter of marked individuals within the context of multistate models (Lebreton & Pradel 2002). Traditional capture-recapture models (Lebreton et al. 1992) can then be considered as two-states models (i.e. birds can be alive or dead), in which only live birds can be encountered. Similarly, dead recoveries models (Brownie et al. 1985) can be considered as two-states models, in which only dead birds can be encountered. Both live recaptures and dead recoveries can be analysed as a mixture of information within the multistate framework (Lebreton et al. 1999). We applied this approach to the European data. The main advantage of including live recaptures in the analysis was to increase the number of releases, i.e. to increase sample size. This literally corresponds to a recovery analysis with a larger number of marked individuals, which improves the precision of estimates. To a lesser extent, live recaptures also contribute to the estimate of the probability of survival (J-D. Lebreton, unpubl. data).

In Europe, ducks were ringed from September to March, which roughly corresponded to the prevalent hunting season. A bird ringed early in the season was therefore more likely to be shot during the first hunting season than a bird ringed at the end of the season, which induced heterogeneity in survival estimates. In addition, spring hunting was common in Russia in the 1960s and 1970s, which lead to an appreciable number of recoveries to actually occur outside the September-March period. To account for these characteristics, we performed a combined analysis of live recapture and dead recoveries, and divided the year into three periods: fall-winter (hereafter FW: September-December), winter-spring (WS: January-March), and spring-fall (SF: April-August). The year was considered to start in September, with the beginning of the hunting season, and ringings occurred in FW and WS only. Most live recaptures actually occurred within a few months following ringing, and given that only one encounter event was possible for each period, live recaptures were limited to WS. Most recoveries occurred in FW and WS, but recoveries in period SF were also included in the analyses. Finally, ringing from September to March implied that first year birds were present in the data. Given most teal attempt breeding as soon as their second calendar year (Johnson 1995), these individuals were considered as juveniles for the first time interval only (i.e. from ringing to first re-encounter). The modelling of the first time interval as different from subsequent intervals is denoted by 'age' in the model notation.

Usual assumptions of ring recovery models (Brownie et al. 1985) were more closely met by North American data, which did not require any further model adjustments and were analysed using Brownie models for dead recoveries. The model applied to North American data was based on a 1-year interval starting in September, with recoveries occurring only between September and February. Given they had been ringed in January-February, i.e. when aged $\geq$ 5 months old, all individuals were considered as adults at time of ringing.

## Statistical methods

### *Goodness-of-fit*

Due to the particular structure of the European data, no appropriate goodness-of-fit test was available for a global model. Hence, we assessed the goodness-of-fit of our most general model recognising full temporal variation in survival and recapture/recovery rate using multistate goodness-of-fit tests 3G and M in software U-Care (Choquet et al. 2005a). When a lack of fit was detected, we modelled the first occasion after ringing separately from subsequent occasions, either for survival (transient model) or for capture (trap-dependence model), according to the main significant effect. Only the main effect was accounted for in the model structure and other significant components were used to calculate a variance inflation factor (Lebreton et al.1992) which was used to adjust Akaike information criterion (i.e. QAIC) for model selection (Burnham & Anderson 2003).

### *Model selection*

All models were fitted using program M-Surge (Choquet et al. 2004, 2005b), and models were selected based on their lowest $QAIC_c$ value. However, since our data were relatively sparse, we could not fit the full model, and thus, we rather started model selection from a simple model which we gradually made more complex. Effects were considered first on recapture/recovery parameters and then on survival parameters (Lebreton et al. 1992). Priority was given to biologically relevant models (e.g.



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different survival between sexes) but models adjacent to low-AIC ones were also considered in search of unexpected effects, or interactions between effects. A similar approach to model selection was used for the North American data, and example models for Europe and North America are given in Tables 3 and 4, respectively.

### *Parameterisation*

The parameterisation used in M-Surge was based on the probability ($\lambda$) that the ring was reported, conditional on the death of the bird with probability 1-S (Lebreton et al. 1999). This differed from the traditional parameterisation of Brownie et al. (1985), which provides an estimate of the ring recovery probability f, i.e. the probability that the bird was shot and reported. However, hunting is not the only source of mortality, and thus, $(1\text{-}S) > H$, with S being the probability of survival and H being the probability of mortality due to hunting. In this model only the product $H*\delta$, i.e. the probability that the bird was shot (H) and reported ($\delta$), is actually identifiable. The two parameterisations are then simply related by $H*\delta = (1\text{-}S)*\lambda = f$. For clarity, we hereafter discuss our results using the f notation. We also note that the Brownie parameterisation (based on the ring recovery probability f) can be modelled directly within the multistate framework (Gauthier & Lebreton 2008).

### *Obtaining annual estimates for European data*

While North American data produced yearly estimates directly, the specificities of the European data implied seasonal estimates, which had to be combined in order to obtain annual estimates.

The annual probability of recovery $f_{yr}$ was thus obtained as

$$f_{yr} = f_{FW} + (S_{FW}*f_{WS}) + (S_{FW}*S_{WS}*f_{SF})$$

indicating that a teal recovered in a given year was either shot and reported during FW with probability $f_{FW}$, or it survived FW (probability $S_{FW}$) but was shot and reported during WS (probability $f_{WS}$), or, it survived both FW and WS (probability $S_{FW}*S_{WS}$) but was shot and reported during SF (probability $f_{SF}$). Similarly, we calculated the annual probability of survival as the product of seasonal estimates $S_{yr} = S_{FW}*S_{WS}*S_{SF}$ because a bird that survived the whole year must have survived the three periods. The standard deviations associated with annual estimates were derived from empirical variances over years using the delta method, and corrected as suggested by Burnham et al. (1987).

Finally, the proportion of the population H that is harvested during a given period is related to the probability of recovery by the proportion $\delta$ of ringed birds taken by hunters that are reported to the ringing lab (Williams et al. 2002). Provided $\delta$ is known, it can be considered to compute an index of harvest rate as $H = f/\delta$, which becomes $h = f*(1+c)/\delta$ when accounting for crippling loss, i.e. for birds that were shot but not retrieved. To our knowledge, the ring reporting rate $\delta$ has only been estimated for mallard in North America (Henny & Burnham 1976, Nichols et al. 1991, Royle & Garrettson 2005), and no estimate is available for waterfowl in Europe. Given the time period over which our data were collected, the ring reporting estimate provided by Henny & Burnham (1976) may seem more appropriate, but methods used by Nichols et al. (1991) were actually more accurate. Hence, we used the value $\delta = 0.32 \pm 0.063$ (SE) provided by Nichols et al. (1991) to estimate harvest rate for North America as well as for Europe. We discuss below the use of this estimate to evaluate harvest rate in Europe, as well as how different values of $\delta$ may influence the evidence for a difference in harvest rate between Europe and North America.

### *Intra-annual comparison of survival in Europe*

The seasonal estimates obtained from the European data allowed us to compare the probability of survival between hunting and non-hunting seasons, as well as between males and females. In southwestern Europe, the most commonly observed hunting season during 1954-1976 ranged from early September to late March, which corresponds to periods FW and WS (for short, FW + WS = FS). The non-hunting season corresponded to period SF. Since these two periods (hunting season FS and non-hunting period SF) were not of equal length, the corresponding survival probabilities were scaled to the month for comparison. In addition, since the probability of survival was sex-dependent for SF but not FS, we used the average over sexes for SF for the comparison between periods.

### *Comparison of demographic parameters between Europe and North America*

A comparison of demographic parameters between Europe and North America was only possible



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during 1960/61-1975/76. Comparisons were realised on annual estimates, associated with their corresponding standard errors, using a Wald test (for an example of a Wald test in a capture-recapture context, see Lebreton et al. 1992: 90). Inter-annual variability was accounted for in the Wald test by using whole vectors of estimates for time-dependent parameters (e.g. annual probability of survival in Europe). However, estimates for North America were not sex-dependent, while those for Europe were sex-dependent (due to sex-dependence during SF period) and thus, the comparison was carried out using the average over sexes for Europe (variability was also accounted for when calculating this average).

Because spring hunting was common in former Soviet Union during the years covered by our European data, period SF included a fairly large number of recoveries due to hunting. On the contrary, the annual harvest rate obtained from North American data concerned the September to February hunting season only. Hence, for the comparison with North America, we only considered periods FW and WS to estimate the annual harvest rate in Europe.

### *Ring reporting rate when harvest rate is the same in Europe as in North America*

When using the ring reporting rate provided by Nichols et al. (1991) to estimate the harvest rate in Europe, we implicitly assumed that the ring reporting rate was the same for teal as for mallard and, more importantly, that the ring reporting rate was the same in Europe as in North America, i.e. we considered $\delta_{EU} = \delta_{US}$. In order to discuss this assumption as well as our estimate of the harvest rate, we also estimated what would be the minimum ring reporting rate in Europe for the harvest rate to be the same in Europe as in North America, i.e. what is the value of $\delta$ for $H_{EU} = H_{US}$.

## Results

### Goodness-of-fit tests

For the European data, almost all components of the goodness-of-fit tests were significant, indicating lack of fit of the $\{S_t, P_t\}$ model. Component 3G.SR (see Choquet et al. 2005a for details on test components) indicated that a large number of teal were ringed but never re-encountered again. This was accounted for by considering an age structure on survival parameters (Pradel et al. 1997a), i.e. by differentiating the first interval following ringing ($a_1$ in model notation hereafter) from subsequent ones (noted $a_2$). The variance inflation factor calculated with the other components was $\hat{c} = 1.682$. Table 3 presents the initial model, some example models and the best AIC model for the European data.

Given that the North American data did not include live recaptures, only the M component of the goodness-of-fit tests could be computed, and this test was not significant. In addition, there was no need to account for overdispersion. However, we detected a lack of direct recoveries due to the data structure. Indeed, in North America, teal were ringed in January and February, i.e. at the end of the hunting season. As a consequence, little chance existed for newly ringed birds to be shot by the end of the hunting season (i.e. direct recoveries), and these birds were more likely recovered in future hunting seasons (i.e. indirect recoveries). This lack of direct recoveries may result in overestimating the probability of survival. To account for this particularity,

Table 3. Model selection results for the European data. Only the initial model, three intermediate models and the best $QAIC_c$ model (bold) are presented. Main effects are in plain text, and supplementary details are provided in subscripts when necessary. For example, time: indicates year to year variation and $time_{\{FW\ Ad,\ SF\}}$ indicates that the time effect applies only to individuals ringed as adults for period FW, and to all individuals for period SF. Transience was accounted for in all models by considering direct recoveries (a1 in subscripts) separately from indirect recoveries (a2). Age at ringing was also included in all models presented here, although this effect was partially confounded with the model structure accounting transience, because first-year individuals were considered as juveniles only during the first time interval following ringing. For all models presented here both capture and survival parameters differed between periods FW, WS and SF. The number of parameters in each model is indicated by k.

| Model | Survival, S | Recovery, f | Deviance | k | $\Delta QAIC_c$ |
|---|---|---|---|---|---|
| Initial | sex | sex | 106750.9 | 30 | 1397.4 |
| Model 180 | $sex_{\{SF\ Ad\}}$ * $time_{\{FW\ Juv,\ WS,\ FW\ Ad\ a2\}}$ | $sex_{\{FW\ Ad,\ WS\ Ad,\ SF\ Ad\}}$ * $time_{\{FW\ Juv\}}$ | 103907.1 | 180 | 24.5 |
| Model 179 | $sex_{\{SF\ Ad\}}$ * $time_{\{FW\ Juv,\ WS,\ FW\ Ad\ a2\}}$ | $sex_{\{WS\ Juv,\ SF\ Ad\}}$ * $time_{\{FW\ Juv\}}$ | 104901.4 | 181 | 23.1 |
| Model 163 | $sex_{\{SF\ Ad\}}$ * $time_{\{FW\ Juv,\ WS,\ FW\ Ad\ a2\}}$ | $sex_{\{FW\ Ad,\ WS\ Ad,\ SF\ Ad\}}$ * $time_{\{FW\ Juv\}}$ | 103855.8 | 184 | 2.3 |
| **Model 172** | **$sex_{\{SF\ Ad\}}$ * $time_{\{FW\ Juv,\ FW\ Ad\ a2,\ WS\}}$** | **$sex_{\{FW\ Ad,\ WS,\ SF\ Ad\}}$ * $time_{\{FW\ Juv\}}$** | **103848.5** | **185** | **0.0** |



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Table 4. Summary of model selection results for the North American data. Only the initial model, three examples and the best $QAIC_c$ model (bold) are presented. Contrary to Table 3, transience was not accounted for in all models presented here, it is therefore denoted as transient when relevant. For the North American data, parameters were estimated on an annual basis (see text), thus there is no 'season' effect as in Table 3. Notation is otherwise the same as in Table 3, with main effects in plain text and additional details in subscripts. Time indicates a year to year variation.

| Model | Survival, S | Recovery, f | Deviance | k | $\Delta QAIC_c$ |
|---|---|---|---|---|---|
| Initial | sex | sex | 25645.1 | 4 | 21.4 |
| Model 15 | sex * $transient_{\{F\}}$ | sex * $transient_{\{M\}}$ | 25628.4 | 6 | 8.7 |
| Model 21 | sex | sex * $transient_{\{M\}}$ * time | 25467.4 | 121 | 77.7 |
| Model 49 | sex * $transient_{\{F\}}$ | sex * transient * $time_{\{M\ a1\}}$ | 25545.5 | 44 | 1.8 |
| **Model 42** | **transient** | **sex * $transient_{\{M\}}$ * $time_{\{M,\ a1\}}$** | **25545.7** | **43** | **0.0** |

the conditional probability of recovery (i.e. $\lambda$) was estimated separately for the first year following ringing. This is denoted $a_1$ in model notation below, with respect to $a_2$ for subsequent years. The model selection for the North American data is summarised in Table 4.

## Parameter estimates

### *Parameter estimates for Europe*

In the model best describing the European data (see Table 3), the annual probability of recovery f varied between sexes and seasons but was constant over years. When considering year-round recoveries, on average over years 1954-1976, the annual probability of recovery was 0.064 ± 0.018 (estimate ± standard error) for males and 0.084 ± 0.014 for females. These values were significantly different (Wald test, $z = 3.945$, $P < 0.001$). The average over years and across sexes, calculated while accounting for variability, was 0.074 ± 0.016. In Europe, the annual probability of survival varied from year to year as well as between sexes. On average over years 1954-1976, the probability of survival was significantly different between males (average over years: 0.525 ± 0.108) and females (average over years: 0.445 ± 0.092)(Wald test: $z=-5.367$, $P<0.001$). The average over years and across sexes was 0.485 ± 0.100.

Annual harvest rate was sex and time-dependent for European teal. On average over years 1954-1976, the annual probability of harvest was 0.201 ± 0.060 for males and 0.262 ± 0.046 for females, when considering the whole year (Wald test: $z = 14.312$, $P < 0.001$). The average over sexes for the period 1954-1976 was 0.227 ± 0.022.

Seasonal estimates obtained for European data were sex-specific only for period SF. The probability of survival during SF was thus 0.807 ± 0.018 for females and 0.952 ± 0.003 for males. These values were significantly different (Wald test: $z = 10.667$, $P < 0.001$). Within the model applied to European data, hunting season was represented by periods FW and WS (September-March), whereas period SF (April-August) represented the non-hunting season. Estimates of the probability of survival were scaled to the month in order to be compared between hunting and non-hunting seasons. The monthly probability of survival was significantly different (Wald test, $z = 6.360$, $P < 0.001$) between the hunting (average over sexes: 0.915 ± 0.034) and the non-hunting (0.975 ± 0.002) seasons.

### *Parameter estimates for North America*

In North America, the annual probability of recovery f was different for males and females but constant over years (see Table 4). During 1960-1998, the annual probability of recovery was 0.027 ± 0.002 for males and 0.019 ± 0.001 for females. These values were significantly different (Wald test: $z = -4.345$, $P < 0.001$). The average over sexes was 0.023 ± 0.001. Similarly, during 1960-1998, the annual probability of survival for North American teal was constant over years, and was 0.545 ± 0.010 for both sexes. The annual probability of harvest was constant over time and not significantly different between sexes (Wald test: $z = -1.229$, $P = 0.055$). For the period 1960-1998, it was 0.058 ± 0.012 for females, and 0.084 ± 0.017 for males. The average over sexes was 0.071 ± 0.014.

### *Comparison between Europe and North America*

As indicated earlier, recoveries were strictly restricted to September-February in North America, whereas in Europe, a significant amount of recoveries was actually observed during the spring/summer period. For the comparison between Europe and North America, these SF recoveries were discarded, and the annual probability of recovery $f_{yr}$ was estimated in Europe using periods FW and WS only. In addition, we considered only the overlap-



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ping period between the two data sets, i.e. during 1960/61-1975/76. Over this reduced period, the probability of recovery (average over sexes) was $0.057 \pm 0.019$ in Europe and $0.023 \pm 0.001$ in North America. These values were significantly different (Wald test: $z = 11.701$, $P < 0.001$).

To compare the annual probability of survival between Europe and North America, we used the weighted (using sex ratio) average over sexes ($0.492 \pm 0.101$) for Europe and the estimator provided by the best $AIC_c$ model for North America ($0.544 \pm 0.010$). The annual probability of survival was highly significantly different between Europe and North America (Wald test: $z = -3.130$, $P < 0.001$). However, the sex ratio among recoveries was 3.6 males per female in the North American data whereas it was more balanced (1.4 male per female) in Europe. Given that in Europe, the probability of survival was higher for males than for females, such a differential sex ratio may lead to a higher overall apparent probability of survival in North America. Nonetheless, applying a 3.6:1 sex ratio to the European data and estimating the weighted average of the annual probability of survival as $0.22*S_{\varphi} + 0.78*S_{\sigma}$, i.e. artificially increasing the probability of survival in Europe, did not change the conclusion. Even then, the annual probability of survival remained significantly lower (Wald test: $z = -1.982$, $P = 0.012$) in Europe (weighted average over sexes: $0.508 \pm 0.105$) than in North America ($0.544 \pm 0.010$).

For the period common to both data sets (1960-1976), the annual probability of harvest (average over sexes weighted using sex ratio) was estimated to $0.165 \pm 0.003$ in Europe, and to $0.071 \pm 0.014$ in North America, assuming the same ring reporting rate $\delta = 0.320 \pm 0.063$ for both locations. These two estimates were highly significantly different (Wald test, $z = 5.357$, $P < 0.001$).

### *Ring reporting rate when harvest rate is the same in Europe as in North America*

When considering that the harvest rates is the same in Europe as in North America, the null hypothesis of the Wald test used for the comparison becomes $H_{EU} = H_{US}$. Given the survival and recovery rate estimates we obtained for Europe and North America, this hypothesis would be rejected (i.e. $z \leq 1.96$) only if the ring reporting rate in Europe was $\geq 0.797$. We discuss the relevance of such a high value below.

## Discussion

### Results concerning Europe only

The particularities of the European data presented in our paper allowed us to estimate seasonal estimates of survival and harvest probabilities. Monthly survival was lower during the hunting period (i.e. periods FW and WS) than in the non-hunting period (SF), thus suggesting an impact of hunting on survival of the Eurasian teal. However, during the period considered in our paper, spring hunting was allowed in some European countries (Kostin 1996), and therefore period SF cannot be considered as an entirely non-hunting season. In addition, the hunting season we considered in our paper also included migration events, which can take a substantial toll on survival (Menu et al. 2005, Newton 2006), as well as winter and possible cold spells, to which teal are particularly sensitive (Lebreton 1973, Ridgill & Fox 1990, Bennett & Bolen 1978).

Our results indicated that annual probability of survival was sex-specific. However, seasonal survival was sex-specific only for period SF. This suggests that difference in annual survival between males and females is likely due to differential parental investment during the reproduction season. Indeed, males are known to desert immediately after eggs are layed, and females provide all parental care, thus comparatively increasing their energy demand and risk of predation while on the nest (del Hoyo et al. 1992).

In any case, our estimates of the annual probability of survival were similar to those obtained by Gitay et al. (1990) and by Boyd (1957), but slightly lower than estimates by Bell & Mitchell (1996), although the latter were derived from collected wings and population trends, and these methods are not as reliable as capture-recapture to estimate survival.

When calculated over the whole year, including the 'non-hunting' period SF, annual harvest rate was higher for females than for males, which suggests that females could be more sensitive to hunting, and the sex ratio of recoveries was skewed towards males. However, the data also included more males at time of ringing, reflecting the traditional skewed sex ratio in wintering populations, due to the differential parental investment during the reproduction season.

### Results concerning North America only

While one may expect the annual probability of survival to be sex-specific in North America, as in



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Europe, our estimate was constant over time and across sexes. It was similar to that obtained by Chu et al. (1995). Both the ring recovery rate and the harvest rate were nonetheless different between sexes and higher for males than for females. Although this could reflect an actual difference in report and/or kill rate, this is unlikely. It is worth noting that in our North American data, the sex ratio was strongly biased towards males, both at time of ringing and among recoveries. Hence, female-related data may not have been sufficient to properly estimate a separate probability of survival for females, although it was sufficient to estimate a sex-specific probability of recovery. These results could also be the result of an artifact in the data due to the post-season ringing.

**Comparison between Europe and North America**

According to our best $AIC_c$ models for both Europe and North America, the annual probability of recovery was higher in Europe than in North America. During the considered period, European hunters were possibly more inclined to report rings, or were actually killing more birds. However, our data do not allow us to conclude on this point.

Annual survival probability was significantly higher in North America than in Europe. This held true even when artificially biasing the sex ratio to 4:1 males in the European data, thus increasing the average survival across sexes due to the higher survival of males. This difference in survival between Europe and North America was thus fairly robust.

Although many factors could explain the difference in survival between Europe and North America, one possible explanation is the impact of harvest. During the years included in our study, the annual harvest rate was much higher in Europe than in North America. However, estimating the harvest rate is conditional on the availability of an estimate of the ring reporting rate. Although the ring reporting rate was estimated to ~50% in the 1970s (Henny & Burnham 1976), we used the value of 32% provided by Nichols et al. (1991) in our analyses. Hence, we assumed that the reporting rate was the same in Europe as in North America, and the same for teal as for mallard. While a potential difference between bird species should be adequately tested, it is known that within a species, the reporting rate varies geographically across North America (Nichols et al. 1995b), and is thus likely to be different between Europe and North America.

To our knowledge, no reward ring scheme has ever been carried out in Europe, and incentives to report rings have been being put in place in the last few years only. By comparison, reward ring studies are almost routinely carried out in North America, and a toll-free phone number which hunters can call to report rings has been engraved on rings for more than a decade (Royle & Garrettson 2005). Although we do not have any information for the 1950s and 1960s, we believe that the ring reporting rate is lower in Europe than in North America.

We acknowledge that our data are fairly old and may not adequately represent the current situation. In particular, one may argue that the harvest rate may have decreased substantially since the 1950s. Indeed, during the last 10-20 years, spring hunting has been banned, and hunting season length has been reduced in most European countries (Mooij 2005). Other European measures such as the Bird Directive or the recent ban of lead ammunition, as well as the loss of interest of younger generations for hunting, also contributed to reducing the annual waterfowl harvest. Similarly, the ring reporting seems to vary significantly across time. For example, the proportion of fitted rings that were returned (which is only an approximation of reporting rate, since it also includes kill rate) decreased from ~18% to ~10% between the 1950s and the 1970s in teal (Guillemain et al. unpubl. data), as it did in other bird species (Grantham 2009).

Could the harvest rate have decreased to a level similar to our estimates for North America? Instead of estimating the harvest rate in Europe $H_{EU}$ under the assumption that $\delta_{EU} = \delta_{US}$ (with $\delta$ being the ring reporting rate), it is also possible to estimate the ring reporting rate in Europe $\delta_{EU}$ under the assumption that $H_{EU} = H_{US}$. Based on our data, for the annual harvest rate to be the same in Europe as in North America (i.e. ~7%), at least 80% of rings would need to be actually reported by hunters. In the late 1980s in North America, such a high value could only be reached if a $40 reward was granted to hunters reporting rings (Nichols et al. 1991). Without a reward, this value was reached only recently in North America, after more than 10 years of use of a toll-free phone number engraved on the rings, and several advertisement/incitement campaigns (Royle & Garrettson 2005). Therefore, the ring reporting rate is very unlikely to be as high as 80% in Europe where virtually nothing has been done until very recently to incite hunters to report rings. This result



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validates the fact that the annual harvest rate is higher in Europe than in North America. Indeed, if, in Europe, the ring reporting rate is unlikely to be higher than 80%, then the annual harvest rate is equally unlikely to be lower than ~7%, and is therefore between 7% and 18%.

Assuming that harvest has an impact on survival, one may expect a stronger difference in annual probability of survival between the two continents, with respect to the observed difference in annual harvest rates. In addition, there is no noticeable difference in the reproductive output of the two subspecies. Although hatching success is not well documented, egg size, clutch size and brood size are about the same in Europe and in North America (~45 × 33 mm, 8-10 eggs and ~5 ducklings, respectively, Johnson 1995, Cramp & Simons 1977). Overall, teal is a 'fast' species that reproduces early in life, produces numerous offsprings and dies relatively young. Good reproduction probably plays an important role in the teal population dynamics, as it compensates for losses due to hunting (Kalchreuter 1996).

## Compensation

Our study does not rule out, nor allows testing for, the possible compensation of hunting mortality through density-dependent mechanisms, mostly because of year-round recoveries, which prevent us from estimating survival in absence of hunting. However, evidence for compensatory mortality is fairly elusive and the principle itself is still debated (e.g. Pöysä et al. 2004). In particular, the effects of compensation are confounded with those of harvest (Sedinger et al. 2007), which favours using additive models for management rather than compensatory models (Conn & Kendall 2004). Yet, this latter point is valid only when model-based management is implemented, which is far from being the case in Europe (see Elmberg et al. 2006). If compensation occurs, it is probably at a fairly low level (Lebreton 2005), which would be insufficient to compensate for 18% harvest, especially if we consider that our estimate of the harvest rate did not account for crippling (and lead poisoning) loss. It is also unclear how much harvest can be compensated for in the presence of other sources of mortality such as prolonged bad weather conditions, for example.

Little is known about the interaction between harvest and weather conditions, and its effects on the dynamics of waterfowl populations. Although we did not specifically test for the effect of cold winters on survival, we noticed that in Europe, the peaks of mortality corresponded to the worse winters on record (winters 1955/56 and 1970/71). The currently available information does not allow determining what was the relative contribution of hunting, cold spells and migration to the variation in survival.

Teal are particularly sensitive to cold spells, and they move towards southwestern Europe in case of adverse weather (Lebreton 1973, Ridgill & Fox 1990, Bennett & Bolen 1978). In addition, teal also frequently change flyways during migration events (Guillemain et al. 2005). As shown by simple population modelling (not presented in our paper, though see Devineau 2007), such movements may contribute to the apparent paradoxical increase of the population mentioned above.

With our estimates, the population crashes when it is modelled as whole, which is inconsistent with the observed stable/increasing trend (Delany & Scott 2006). Demographic parameters are probably not homogenous across Europe, and the population may present a source-sink dynamic. For example, the total number of harvested ducks is higher in western Europe than in eastern Europe (Mooij 2005), and other demographic parameters are likely spatially variable as well. Hence, when modelling the population as two sub-populations differing by their harvest rate, the population does not crash anymore. In particular, a small amount of exchange from the low-harvest region to the high-harvest region allows the high-harvest sub-population to maintain itself, whereas it would otherwise crash in absence of exchange. However, a higher rate of exchange from the low-harvest to the high-harvest sub-population eventually leads to the crash of the whole population, because immigration then does not allow the sink to sustain itself (Lebreton & Gonzalez-Davila 1993).

## Management implications

During the 1950s and 1960s, the harvest rate of teal in Europe was about three times higher than in North America. Survival was not so different, thus indicating that harvest has relatively little impact on the survival of a fast species such as the teal. Although only 15% of the juveniles produced a given year reach the wintering grounds (Guillemain et al. 2010), good reproduction seems to compensate, at least partially, for losses due to hunting.



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Other compensation mechanisms could not be ruled out from our study.

Because of the historical nature of our data, our results do not necessarily represent the current situation. New ringing programmes are carried out in various European countries since the early 2000s, which will help to update our results.

In particular, the annual harvest rate and the ring reporting rate have probably decreased since the 1950s (Grantham 2009). North America has a several decades-long history of science-based waterfowl population and harvest management, together with several incentives for hunters to report rings, whereas most European countries barely have any information at all on hunting statistics, let alone a proper management strategy. It is thus very unlikely that the current ring reporting rate reached in Europe will reach the level it now has in North America, i.e. about 80% (Royle & Garrettson 2005). In other words, the current harvest rate in Europe probably lies somewhere between our estimate for Europe (~18%) and our estimate for North America (~7%).

As a fast species, teal has a good capacity to withstand some level of harvest, and compensation mechanisms other than reproduction could not be ruled out with our study. However, it is unknown how much harvest the European teal population can stand, and how this compensation of hunting losses interact with other factors such as weather conditions, for example. In addition, the population is currently considered to be globally increasing (Delany & Scott 2006), but on the basis of counts, which are only moderately reliable as management tools. Stability may be apparent only, and the population may actually involve a source-sink system that maintains regions where harvest is high at the (hidden) expense of regions where harvest is lower.

As a conclusion, it seems clear to us that subtle population mechanisms, such as the intricacies of spatial heterogeneity in harvest intensity and movement, may seriously complicate attempts to progress towards scientifically-based management of harvested populations. Comparing populations and situations seem to us particularly relevant and worthwhile in such a context.

*Acknowledgements* - we are most grateful to Luc Hoffmann, Hubert Kowalski, Heinz Hafner and others who have ringed teal at the Tour du Valat for more than 25 years, and to all hunters and observers who reported rings. We would also like to thank Marc Lutz, Paul Isenmann and the Centre de Recherche sur la Biologie des Populations d'Oiseaux (Muséum National d'Histoire Naturelle, Paris) for their help while computerising the European teal data. In addition, we are particularly grateful to Jim Nichols and Jim Hines who provided us access to the North American ringing database as well as to the ringers who collected these data. Jim Nichols also provided useful comments on an earlier version of the manuscript. Our thanks also go to Roger Pradel, Rémi Choquet, Olivier Gimenez, Paul Doherty and others for their valuable suggestions regarding the data analysis and the manuscript. The analyses presented here were funded through a graduate stipend from the French Ministry of Research.

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