

# Exploiting delayed dichromatism to disentangle the effects of adult survival and recruitment on the population dynamics of waterfowl

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## Abstract

Monitoring the number of individuals is by far the most popular strategy for investigating the environmental factors ruling the population dynamics and for measuring the efficacy of management actions targeting population recovery, control or eradication. Unfortunately, it is insufficient for the basic understanding of the demographic mechanisms and more specifically to assess the extend to which population growth rate is affected by changes in adult survival rather than to variations in reproductive parameters. Usual methods to inform survival and recruitment (capture-mark-recapture, game-hunting bag) rely on catching animals in a way or another, which suffers from three main drawbacks. First, the selectivity of the catching methods can lead to a biased representation of the underlying population structure. In practice, catching and releasing animals is also an invasive approach implying additional stress to the individuals. Furthermore releasing may simply be forbidden for invasive alien species. In many waterfowl species, a sexual dichromatism is observed in adults whereas immatures of both sexes display a cover-up plumage similar to adult females. From populations of Ruddy duck, a species displaying this pattern, this study introduces a non-invasive method based on count data to estimate the respective contribution of recruitment and adult survival on population growth rate. Relying on matricial models shows that performing count survey during the appropriate time window to differentiate both plumage types is sufficient to provide long-term time series of the two main demographic components of the population growth rate.

**Keywords:** reproductive success - fecundity - productivity - age ratio - vital rate - duck - *Oxyura jamaicensis*

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# 1 Introduction

Assessing population growth rate is a key step towards a better understanding of factors underlying the dynamics of natural populations (e.g. Niel, 2005). It is also crucial for measuring the efficacy of management actions potentially undertaken to help population recovery, control, or eradication (Shea & NCEAS Working Group on Population Management, 1998). Among the approaches available to managers for reaching these goals, those relying on the monitoring of the number of individuals are by far the most popular (Rintala et al., 2022). In many instances, these methods even enable environmental factors underlying changes in population size to be investigated, and hence some mitigating actions to be implemented (Faillietaz et al., 2019). Unfortunately, relying on the monitoring of numbers of individuals alone generally hinders basic understanding of the demographic mechanisms underlying changes in population growth rates. More specifically, based on counts only, it is nearly impossible to assess the extent to which population growth rate is affected by change in survival rather than to variations in reproductive parameters (Austin et al., 2000). To assess the relative sensitivity of population growth rate to factors affecting survival or reproductive parameters, demographers most often rely on the monitoring of individuals by capture-mark-recapture (Lebreton et al., 1992). In practice, however, one cannot always rely on the capture and release of individuals owing to the legal status of the species that precludes any additional disturbance, e.g. critically endangered species, or forbid the release of alive individuals, e.g. invasive species or pests. Furthermore, capture and handling may also be so stressful to individuals that their behaviour and/or the very parameters under study may be altered. Indeed, although highly efficient for assessing demographic parameters, capture-mark-recapture methods have potential drawbacks such as being invasive and hardly affordable when time and money are limiting. Genetic monitoring is a non-invasive alternative to capture-mark-recapture approaches based on physical captures, but it suffers from being costly and time-consuming, and requires quite rigorous sampling schemes in the field (Caniglia et al., 2011).

Most of the time therefore, managers do the best of a bad job using counts as the only viable option for tracking population growth rates and assessing the efficiency of management actions. Counting the number of immatures produced in addition to live adults may enable adult survival and recruitment rate to be estimated, and hence provides knowledge on which of these components has the most influence on population growth rate. The recruitment rate, defined as the average number of immatures per breeder reaching the sexual maturity, is the product of two main sub-parameters: the fecundity followed by the juvenile survival (Arnold, 2018; Etterson et al., 2011). The recruitment rate is sometimes also called annual fertility (e.g. Koons et al., 2014), reproductive rate (e.g. Cooch et al., 2014), reproductive success (e.g. Etterson et al., 2011), or productivity (e.g. Hagen & Loughin, 2008; Johnson et al., 1987). Unfortunately, assessing the respective contribution of the adult survival and the recruitment rate is only possible for a limited number of species in which broodless adults and those with young display the same detectability. Alternatively, assessing the sex and age structure in hunting bags has been used to infer the role of decreasing reproductive success in population declines in a number of game species including ducks (e.g. Fox & Cristensen, 2018). However, this approach is not suited for protected/endangered species with no harvest. Here we exemplify how, in dimorphic species, delayed maturity of males can be exploited for estimating adult survival and recruitment rate by differentiating male-like to female-like individuals in repeated winter counts. We used two non-native Ruddy duck, *Oxyura jamaicensis*, populations introduced in Europe as a study model. As numerous duck species, the Ruddy duck is dimorphic, with newly born males looking like females until the pre-nuptial moult, which occurs in late winter. This means that the apparent proportion of males increases over the course of the wintering season. These changes in apparent proportions of males during this period are therefore directly related to the proportion of immatures into the populations and hence to reproductive success and recruitment rate of the previous spring/summer. This study details the method to infer adult survival and recruitment rate from count data, and an application is developed to assess the impact of two different eradication strategies deployed in Great Britain and in France, respectively.

## 2 Materials & methods

The Ruddy duck is a stiff-tailed duck native from the Americas. From seven individuals initially acclimated in the Slimbridge Wetland Centre in Great Britain in the 40's (Gutiérrez-Expósito et al., 2020), a feral population began to establish with the first observed reproductive attempts in the wild in the 60s (Figure 1). This feral population rapidly grew and spread to the entire country to reach more than 5,000 individuals in the early 2000s. By the end of the 80s, a feral population began to establish also on the continent in France, supposedly owing to the arrival of individuals born in Great Britain. Contrary to what was observed in Great Britain, the French Ruddy duck population did not spread much, with the vast majority of observations and breeding attempts clustering in Western France. In France, during winter, almost no Ruddy duck is observed outside the lake of Grand Lieu (47.09°N, 1.67°W), which is thus the exclusive wintering site and greatly facilitates the monitoring of this population. The feral European populations of Ruddy duck are considered as a major threat to the endangered native White-headed duck, *Oxyura leucocephala*, population of the South-Western Mediterranean, because of hybridization risks and thus an elevated potential for genetic pollution and eventually genetic assimilation of the latter by the former (Muñoz-Fuentes et al., 2007). In order to mitigate the risks of genetic pollution of the White-headed duck by Ruddy ducks, eradication measures were taken both in Great Britain and in France from the late 90s (Gutiérrez-Expósito et al., 2020), (Figure 1), and a European Ruddy duck eradication plan has been initiated by the European Commission in 1999 (Hughes et al., 1999). The release of non-native species in the wild, including Ruddy ducks, is forbidden in countries of the European Union, and the status of White-headed duck populations is highly unfavourable. The use of capture-mark-recapture to monitor populations of these species is thus impossible. As a result, the effectiveness of the eradication of Ruddy ducks and management actions intended to favour the recovery of White-headed ducks were essentially assessed through censuses. Censuses, however, prevented assessment of the relative effects or changes in survival and recruitment rate on population growth rate, which is a key towards a proper understanding of the efficiency of management actions.

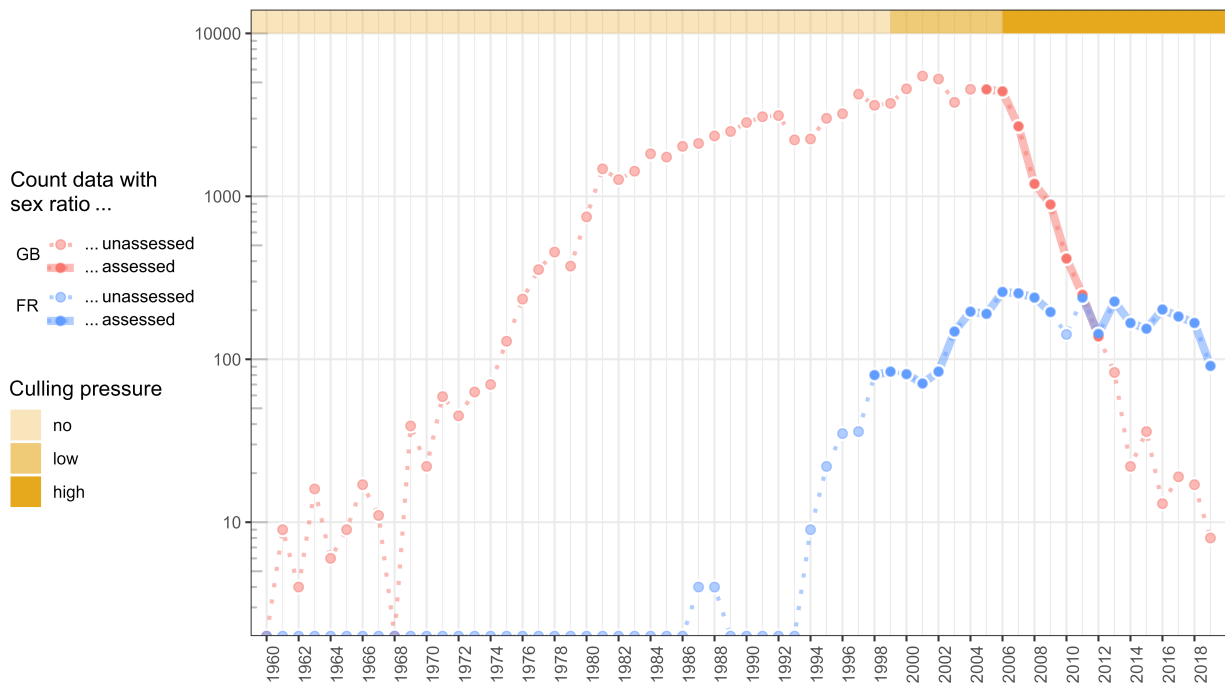


Figure 1: Changes in the size of the two Ruddy duck populations; y-axis is on a log-scale; sex ratio refers to censuses that distinguished female-like from male-like individuals

Like many other ducks, Ruddy ducks and White-headed ducks both display delayed dichromatism. Thereby immature males acquire the typical colourful plumage of their kind over the course of the interbreeding season,

which is typically in late winter. Immature males are thus confounded to immature and adult females before their moult (Figure 2). Delayed dichromatism explains why the apparent proportion of females in the winter counts is always greater than the true proportion of females that can be assessed in removals (Figure 3). Thus, it is possible to assess the proportion of immatures within a population by monitoring the seasonal evolution of apparent sex ratio and assuming an even sex ratio at birth (Bellrose et al., 1961; Blums & Mednis, 1996), comparable mortality rates between females and males among juveniles (Ramula et al., 2018; Wood et al., 2021), and unchanging adult sex ratio over the monitoring period (Devineau et al., 2010). Then, both adult survival rate and recruitment rate can be estimated by combining the age ratio thus obtained with reliable counts over two successive winters.



Figure 2: Typical observation of a Ruddy duck flock during winter: 10 female-like individuals with a whitish striped cheek, 4 male-like individuals with a white cheek and a black cap, 3 unidentified individuals (1<sup>st</sup>, 4<sup>th</sup>, and 10<sup>th</sup> from left) © Jay McGowan - 3 February 2013 - Tompkins, New York, United States

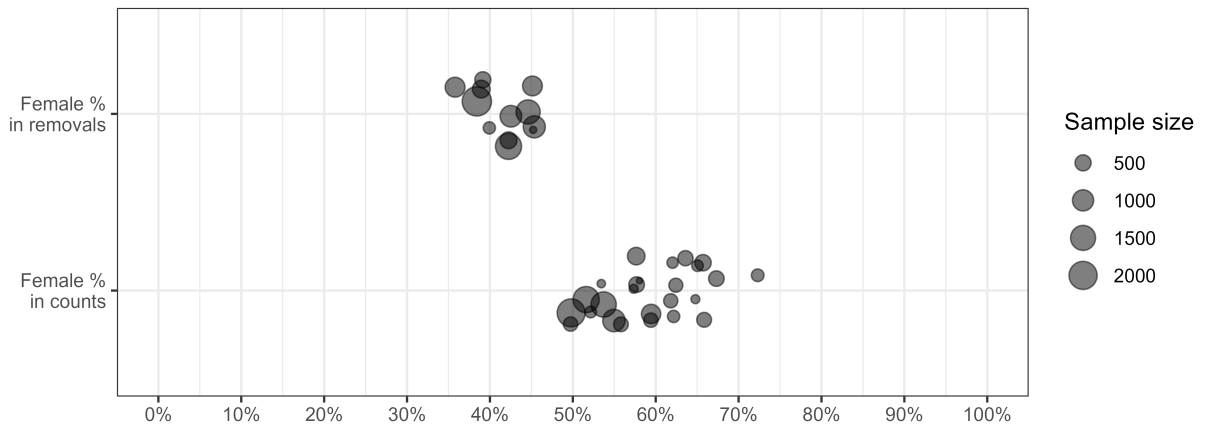


Figure 3: Proportion of females in removals vs in counts; For the first category, one data point corresponds to the female proportion estimated from direct sex identification of the Ruddy ducks culled over one year in a population; for the second category, one data point corresponds to the proportion of individuals wearing female-like plumage in a population counted in winter; the difference of female proportion between the two approaches is due to immature males that look like females before moulting; this difference is at the root of the method introduced inhere to disentangle survival from recruitment

We monitored the demography of Ruddy duck populations in both Great Britain and France using exhaustive counts on the wintering grounds during the period between December 1 and January 31. In addition, counts that distinguished female-like from male-like individuals were performed from 2006 to 2012 in Great Britain,

which corresponded to a period of strong decline of the population (Figure 1). In France, the monitoring spread over 1999, 2001-2009, and 2012-2019. This population grew rapidly during the first years of the monitoring and then stabilized from 2006 onwards, which corresponds to a period with a high culling effort, which was performed under control of the authorities in both countries. Even if the age ratio in the removals was uncertain before 2009 in France, it is possible to grossly qualify the culling pressure in three categories for both countries: “no culling” before 1999, “low culling” between 1999 and 2005, and “high culling” from 2006 (see Figure 7 in Supplementary Materials).

## 2.1 Vital rates inference from count data

In waterfowl, survival rate is commonly higher in adult males than in adult females (Baldassarre, 2014). Adult sex ratio is then generally biased towards males (Figure 3, Székely et al. (2014)). As a consequence, deducing the proportion of immatures within a population from the observed proportion of adult males is not straightforward because the proportion of adults is not just twice as much as the observed proportion of adult males. There were no counts differentiating male-like from female-like individuals during the breeding period to properly estimate adult sex ratio. But sex identification in adults from removals was available for both Ruddy duck populations. However, the small population size in France prevented from getting precise adult sex ratios. A comparison over months in Great Britain showed no difference in proportion of males in adults, so data from adults collected over the whole year were used to estimate the proportion of males in adults. A comparison of proportion of males in adults among years with more than 500 samples did not show significant interannual differences. Even if the adult sex ratio may vary over a long time range, it is relatively stable over a few years (Wood et al., 2021). As a consequence, removal data from all adults were pooled to estimate the proportion of males in adults, see Equation (1).

Assuming the additive property of the binomial distribution, the proportion of immatures can be deduced from the cumulated counts of male-like individuals in the wintering population, see Equation (2). From this proportion and the interannual variation of an abundance index of population size, adult survival and recruitment rate are straightforward, see Equation (3). If the absolute value of population size is accessible, numbers of adults and recruits can be estimated, see Equation (4).

Name	Class	Description
$AM$	Data	Total number of adult males in hunting bags
$AF$	Data	Total number of adult females in hunting bags
$p(m a)$	Parameter	Proportion of males in adults (or probability of being a male knowing it is an adult)
$CML_{i,t}$	Data	Cumulated number of male-like individuals counted in population $i$ in year $t$ , which are assumed to all be adult males
$C_{i,t}$	Data	Cumulated number of individuals counted in population $i$ in year $t$
$p(a \cap m)_{i,t}$	Parameter	Proportion of adult males in population $i$ in year $t$
$p(a)_{i,t}$	Parameter	Proportion of adults in population $i$ in year $t$
$p(i)_{i,t}$	Parameter	Proportion of immatures in population $i$ in year $t$
$N_{i,t}$	Data	Size of the population $i$ in year $t$ (maximum number of individuals counted in the wintering population)
$s_{i,t}$	Parameter	Adult survival rate, i.e. proportion of individuals in year $t - 1$ still alive in year $t$
$r_{i,t}$	Parameter	Recruitment rate, i.e. number of recruits in population $i$ in year $t$ per individual in year $t - 1$
$S_{i,t}$	Parameter	Number of adults in population $i$ in year $t$
$R_{i,t}$	Parameter	Number of recruits in population $i$ in year $t$

$$p(m|a) \sim \text{Beta}(AM, AF) \quad (1)$$

$$\begin{aligned}
CML_{i,t} &\sim \text{Binom}(p(a \cap m)_{i,t}, C_{i,t}) \\
&\sim \text{Binom}(p(m|a) \cdot p(a)_{i,t}, C_{i,t}) \\
&\sim \text{Binom}(p(m|a) \cdot (1 - p(i)_{i,t}), C_{i,t})
\end{aligned} \tag{2}$$

$$\begin{aligned}
s_{i,t} &= \frac{N_{i,t}}{N_{i,t-1}} \cdot (1 - p(i)_{i,t}) \\
r_{i,t} &= \frac{N_{i,t}}{N_{i,t-1}} \cdot p(i)_{i,t}
\end{aligned} \tag{3}$$

$$\begin{aligned}
S_{i,t} &= N_{i,t} \cdot (1 - p(i)_{i,t}) \\
R_{i,t} &= N_{i,t} \cdot p(i)_{i,t}
\end{aligned} \tag{4}$$

## 2.2 Validation of the count-based method

The relevance of the method was assessed by testing the likelihood of the estimates of both vital rates. For adult survival rate, we checked if the values belonged to the expected interval  $[0; 1]$ , and we compared the values to literature data on ducks that are accessible because adult survival is commonly assessed by capture-mark-recapture (Lebreton, 2001). Maximum adult survival is defined as a uniform distribution on  $[0.7; 1]$ . The lower limit corresponds to the upper range of survival rates in literature for waterfowl species of similar weight, the upper limit was set to 1 because survival rates of long-life waterfowl species are very high (Buxton et al., 2004; Kremetz et al., 1997; Nichols et al., 1997, 1992). Recruitment rate is more tricky to validate because it is not upper bounded as it is defined on  $[0; \infty[$  and is neither explicitly informed in the literature. Only some components of the recruitment rate are generally described, such as nesting rate, nesting success, clutch size, hatching success, early stage survival, but rarely survival between the juvenile stage and the first breeding season, which is necessary to inform recruitment rate (e.g. Baldassarre, 2014). We then developed an approach to estimate the maximum expected recruitment rate without exploitation and without negative density-dependence processes, and we checked if all values were equal or below this maximum recruitment rate. If the recruitment rate outputs of the model are significantly higher than maximum recruitment rate, it means that the method overestimates such rate, which reflects that a part of adult males are not detected during count surveys. A null or negative recruitment rate would mean that immature males moulted before the survey or/and the assumption on the stability of the adult sex ratio is overrated.

Practically, maximum recruitment rate is deduced by using its relationship to maximum growth rate and maximum adult survival rate, see Equation (5). This relationship comes from a simple reasoning for a closed population: population size in year  $t$  is equal to the number of adults that survived over year  $t - 1$  plus the offspring produced in year  $t - 1$  that survived until the reproduction period of year  $t$ , i.e. the recruitment in year  $t$ . The growth rate of a population is thus the sum of adult survival rate plus recruitment rate (Flint, 2015). For an open population, adult survival and recruitment rates are confounded to adult and recruit migrations, respectively. This relationship becomes more complex if a species with delayed maturity is considered, see Robertson (2008).

Name	Description
$N_t$	Number of adults in year $t$
$D_t$	Number of adults dead during year $t$
$R_t$	Number of recruits in year $t$
$s_t$	Adult survival rate, i.e. proportion of individuals in year $t - 1$ still alive in year $t$
$r_t$	Recruitment rate, i.e. number of recruits in year $t$ produced per individual in year $t - 1$
$\lambda_t$	Growth rate of the population between year $t - 1$ and year $t$

$$\begin{aligned}
N_t &= N_{t-1} - D_{t-1} + R_t \\
N_t &= N_{t-1} - (1 - s_t) \cdot N_{t-1} + r_t \cdot N_{t-1} \\
N_t &= s_t \cdot N_{t-1} + r_t \cdot N_{t-1} \\
\frac{N_t}{N_{t-1}} &= s_t + r_t \\
\lambda_t &= s_t + r_t \\
r_t &= \lambda_t - s_t
\end{aligned} \tag{5}$$

The maximum growth rate occurred for both populations during their expansion phase, when change in population size was the steepest. To estimate robust maximum population growth rates for both populations, we smoothed annual population growth rate over a consistent time period by using a linear regression on the logarithm scale, see Equation (6). To do so, we discarded Great Britain data before 1972 since the size estimate of this population was noisy below 50 individuals (Figure 1). After reaching the threshold of 1,000 individuals, the Great Britain (GB) population growth showed a strong inflexion whereas no culling pressure was applied. This observation suggests that a negative density-dependence process might occur beyond 1,000 individuals and led to consider only the first sequence of the time series to infer on the maximum growth rate in Great Britain, i.e. 1972-1981. For the French (FR) population, the sequence without culling effort spread over the period 1994-1999.

Name	Class	Description
$N0_{i,J}$	Parameter	Intercept of the regression model
$\lambda_{i,J}$	Parameter	Average population growth rate over a restricted time interval $J$ for a population $i$ (in $year^{-1}$ )
$t \in J$	Index	Year index within the time interval $J$
$\sigma_{i,J}$	Parameter	Standard deviation of the regression model

$$\log(N_{i,t}) \sim \text{Norm}(N0_{i,J} + \log(\lambda_{i,J}) \cdot t, \sigma_{i,J}) \tag{6}$$

Even if both vital rates vary in a likely range following the validation methodology previously described, this does not prove that the interannual variability is properly tracked. In order to validate this aspect, we compared the outputs of the count-based method, i.e. the proportion of immatures and both vital rates, to outputs based on data from removals. Only data from years with more than 100 individuals culled in winter were selected. It covers 5 years of the count time series of the GB population. The presence of the bursa of Fabricius enables immature to be identified with certainty (Hochbaum, 1942). The estimation of the proportion of immatures in removals is then straightforward, see Equation (7). Adult survival and recruitment rates were then estimated by combining this proportion and Equation (3). We discussed the ability of the count-based method to accurately track the interannual variability by comparing the outputs of the two methods.

Name	Class	Description
$SI_{i,t}$	Data	Number of immatures sampled in the wintering population $i$ in year $t$
$S_{i,t}$	Data	Number of individuals sampled in the wintering population $i$ in year $t$

$$SI_{i,t} \sim \text{Binom}(p(i)_{i,t}, S_{i,t}) \tag{7}$$

## 2.3 Impact of culling strategies on vital rates

Over the high culling period, i.e. from 2006 onwards, strategies differed between Great Britain to France. In Great Britain, culling mostly occurred in winter, i.e. before the breeding period (53.4% of adults were shot before the 30<sup>th</sup> May), whereas it was mostly done in summer in France, i.e. during and after the breeding period (81.6% of adults were shot after the 30<sup>th</sup> May). We compared the population growth of the two populations in light of the difference between the two strategies and we assessed the respective response of the vital rates by comparing the average values over the high culling period to proxies of maximum vital rates estimated when both populations reached their maximum growth (see Section 2.2). In France, a LIFE project was implemented from early 2019 to intensify the culling pressure, especially during winter and spring. We therefore excluded the FR time series from 2019 in order to provide a comparison of homogeneous culling strategies.

For all the sub-models in Section 2, the Bayesian framework was used for its efficiency and simplicity to propagate error through the parameters. We used uninformative priors on all parameters. As the maximum growth rate is a life history trait expected to be stable among populations of a given species, we used an uninformative hierarchical prior for this parameter. We generated three chains of length 500,000, with a thinning of 10 to avoid autocorrelation in the samples, and we discarded the first 2,000 samples as burn-in. Chain convergence was assessed using the Gelman and Rubin convergence diagnostic ( $R < 1.1$ , Gelman & Rubin (1992)). We fit the models using NIMBLE (de Valpine et al., 2017) run from R (R Core Team, 2022). Data and code are available here: [https://github.com/adri-tab/Ruddy\\_duck\\_vital\\_rates](https://github.com/adri-tab/Ruddy_duck_vital_rates). The values  $\mathbf{X}[\mathbf{Y}; \mathbf{Z}]$  reported in Section 3 are the medians and the associated boundaries of the 95% confidence interval of posterior distributions. The median was preferred to the mean because of its robustness to skewed distribution.

## 3 Results

### 3.1 Estimates of vital rates

The method successfully provided estimates and associated uncertainty of immature proportion in both wintering populations. Adult survival rate and recruitment rate, i.e. the two components of the population growth rate, were also successfully estimated by the method (Figure 4).



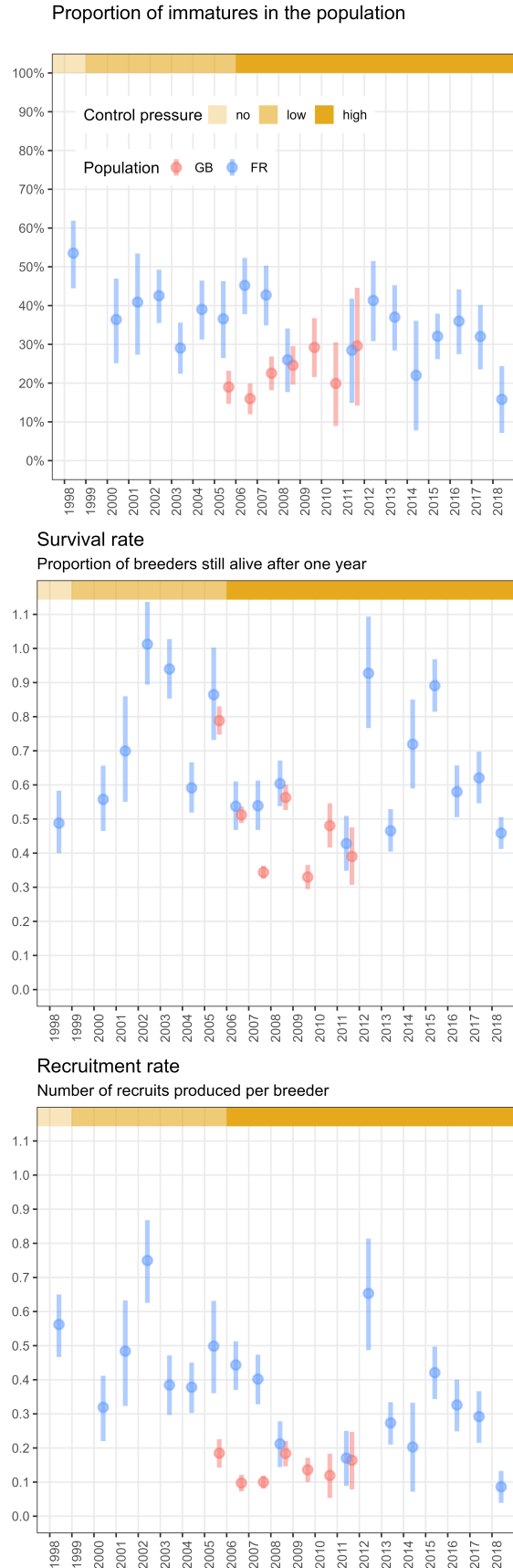


Figure 4: Evolution of the proportion of immatures in the population and the vital rates in light of the culling pressure; bars define the 95% confidence intervals

The male proportion in adults, which is a prerequisite to infer on the immature proportion, is estimated at 0.60 [0.59; 0.61]. The immature proportion varies from 0.16 [0.07; 0.24] to 0.54 [0.44; 0.62]. The lower values are similar for the two populations, but the range of the immature proportions in the GB population is far more limited (upper value : 0.30 [0.14; 0.45]). Conversely from the FR population, there is no significant difference from a year to another because all estimates overlap each other. We can notice that the immature proportion for the GB population is quite stable over the time series available, but a slight decrease is observed for the FR population.

The adult survival rate varies from 0.33 [0.29; 0.37] to 1.01 [0.89; 1.14]. All estimates are not significantly outside the range of a survival rate defined without immigration [0; 1]. There is no trend in adult survival for both populations, but we can notice two main differences. The GB population has the lowest values of adult survival rate, and even if there are significant difference among years for both populations, the variability for the GB population is a bit lower.

The recruitment rate varies from 0.09 [0.04; 0.13] to 0.75 [0.63; 0.87]. All estimates are above 0, meaning there is no senseless estimation. The maximum recruitment rate being 0.68 [0.36; 0.78] (see Section 3.3), all estimates are not significantly outside the range of a recruitment rate defined without immigration [0; 0.78]. Similarly to the immature proportion, there is no trend for the GB population, but a decrease is observed for the FR population even if it is more noisy than for the immature proportion. Similarly to the survival rate, the GB population has low values of recruitment rate, and even if there are significant difference among years for both populations, the variability for the GB population is far lower than for the FR population.

The lower variability of both vital rates for the GB population explains its steady population growth over the considered time series compared to the FR one (Figure 1). In the FR population, the range of the recruitment rate (min/max difference: 0.66) is higher than the range of the survival rate (min/max difference: 0.58). Conversely, the range of the survival rate (min/max difference: 0.46) in the GB population is far higher than the range of the recruitment rate (min/max difference: 0.08). This reflects that the variability of the population growth rate for the FR population is mostly driven by the recruitment rate whereas the main source of variability is the adult survival for the GB population.

### 3.2 Likelihood of year-to-year variability in vital rates

From the 5 years available in the GB population, immature proportions estimated from the count-based method is positively correlated to estimates from hunting-bag data (Figure 5). The hypothesis that the proportion of female-like individuals in the wintering populations reflects the age structure of these populations is then supported by this result. This correlation is even stronger when considering vital rates (Figure 5). This result is expected since the two methods estimating these vital rates have a component in common, the growth rate of the population (see Equation (3)).

It is noticeable that a 1:1 correlation is never obtained. Immature proportion is lower in counts than in hunting bags. This result is not surprising because immature individuals are expected to be more vulnerable to hunting than adults and might then be over represented in hunting bag data. As a consequence, the correlation coefficients for both vital rates differ also from 1. This difference between the two approaches does not question the previous validation of the ability of the count method to track the interannual variability of the vital rates.

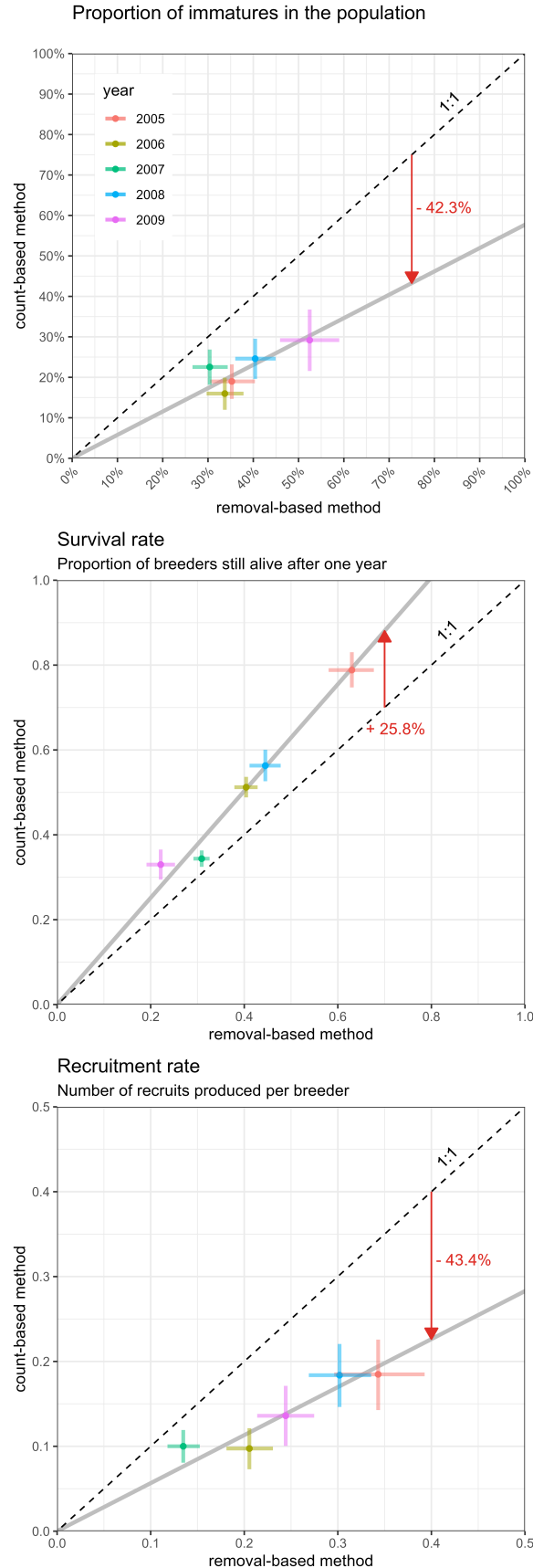


Figure 5: Comparison of the parameter estimates between the count-based method and removal-based method; only 5 years for the GB population were available; bars define the 95% confidence intervals; the red arrow defined the average difference in proportion between the two methods

### 3.3 Response of vital rates to the harvest strategy

Under no harvest pressure, the maximum growth rates of the two populations are very similar (Figure 6), respectively 1.45 [1.36; 1.55] and 1.52 [1.25; 1.88] for the GB and the FR population. It corresponds to an increase of 45% per year and 52% per year respectively. Based on literature, we assumed a maximum survival rate similar for both populations 0.85 [0.7; 1]. We deduced a maximum recruitment rate of 0.60 [0.42; 0.78] for the GB population and of 0.68 [0.36; 1.06] for the FR population.

Even if a significant part of culled individuals were not aged for some years, the proxies of the harvest pressure show significant shifts over time (Figure 7). This led to consider a high harvest pressure period from 2006 with no clear difference between the two populations because the signal is very noisy. Even if the harvest pressure seems comparable, the harvest strategies differ significantly between the two populations, see Section 2.3. Under high harvest pressure, the growth rate drops to 0.56 [0.53; 0.59] and 0.97 [0.94; 1.00] for the GB and the FR population respectively, which corresponds to a decrease of 44% per year and 3% per year. This result shows that the GB population significantly decreases during the high harvest pressure whereas the FR population is stabilized.

The adult survival rate under high harvest pressure is 0.44 [0.42; 0.46] and 0.62 [0.59; 0.64] for the GB and FR populations respectively, when the recruitment rate decreases to 0.13 [0.11; 0.15] and 0.32 [0.29; 0.34] respectively. The drop of the growth rate of the GB population corresponds to a similar average drop in adult survival rate (-0.41) and in recruitment rate (-0.47). The stabilisation of the FR population is more due to a decrease of the recruitment rate (-0.36) than from a drop of the adult survival (-0.23). For both populations, the response to the harvest pressure is significant, meaning that the compensation of the population to harvest mortality is limited if not null. Vital rates of the GB population are more affected than the FR population. Unsurprisingly, the FR harvest strategy focusing on the postbreeding period affects mostly the recruits. However, the prebreeding harvest strategy applied on the GB population that targets adults performs to deplete strongly the recruitment to a very low level (0.13 recruits produced per breeder).

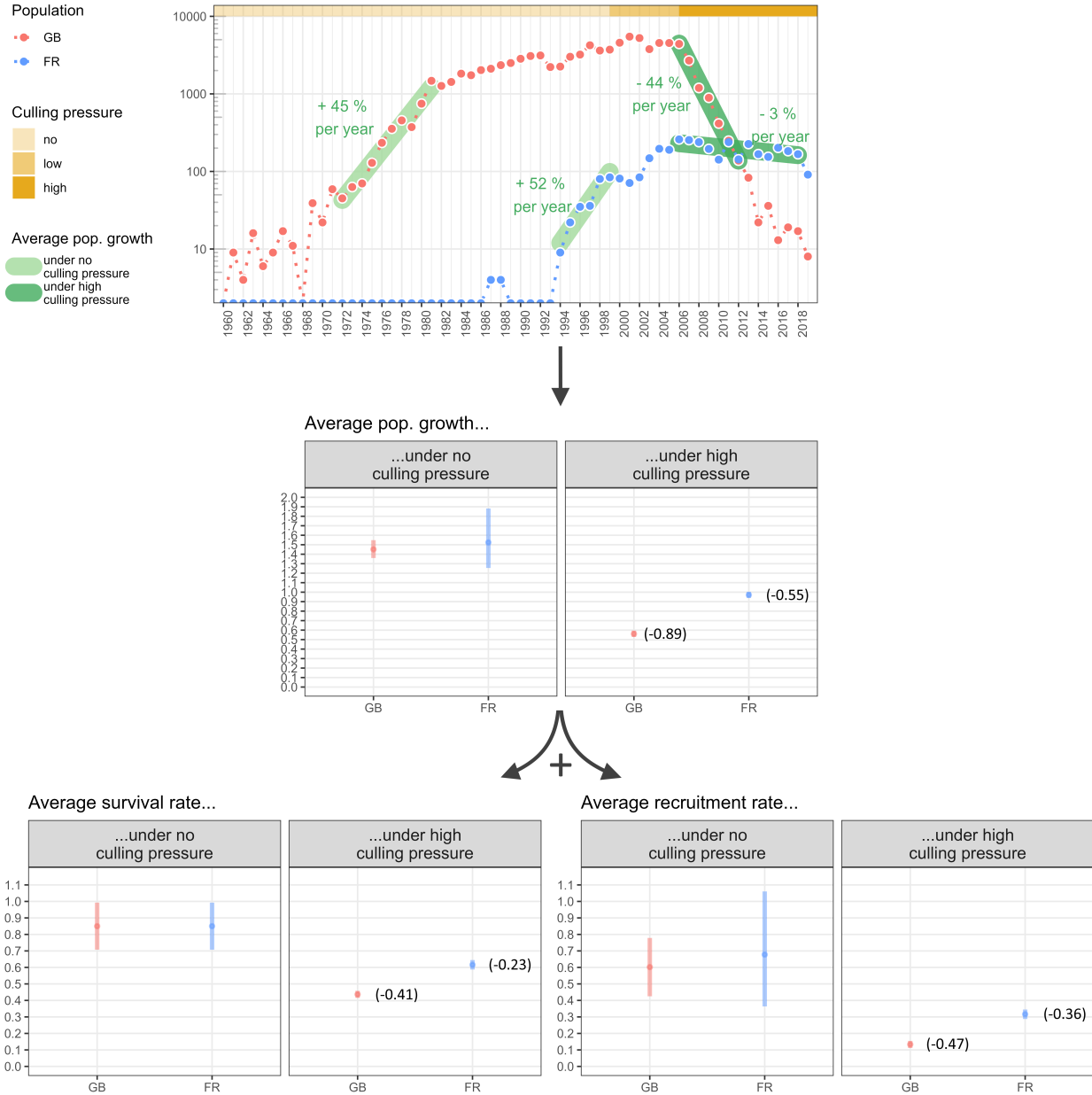


Figure 6: Comparison between average population growth rate under no pressure vs under high culling pressure; the culling effort for the GB population occurs mostly during the prebreeding period, whereas it focuses mostly during and after the breeding period for the FR population (see 2.3 for details); the average vital rates during the maximum growth time period are proxies deduced literature and estimates of maximum population growth estimates (see 2.2 for details); the vital rates under high culling pressure are average values over a time period observing a consistent culling pressure; bars define the 95% confidence intervals

## 4 Discussion

The delayed sexual dichromatism in a waterfowl species is used here to develop and test the validity of a new non-invasive method aiming to break down the apparent growth of a population into its two structural components: the adult survival rate and the recruitment rate. Disentangling the contribution of these two

vital rates is a key to understand the response of a population to management measures. The development of the method holds on a unique dataset of two comparable populations of a same species, the Ruddy duck. Both populations were tracked from their introduction in a similar environment to a period of intense harvest pressure. This common history trajectory enables to evaluate the maximum growth of this species, but also its response to harvest pressure. As the harvest strategy differs between the two populations, we detail the similarities and the discrepancies of the responses of the vital rates, and open the discussion to the generalization of this method and its implications for waterfowl management.

#### 4.1 Accuracy of the method to estimate vital rates

The vital rate estimates of the two populations belongs to the same range, which demonstrate a certain consistency in the results obtained from the method. The higher variability observed in France is not unexpected because the FR time series covers a larger spectrum of harvest pressure than the GB time series. There is no temporal correlation between the two populations, suggesting that fluctuations of the vital rates are more likely influenced by regional factors than large-scale ones. This is consistent with the literature because both nesting/hatching success and juvenile survival are conditional to the onset of laying, which is tightly related to local weather parameters, e.g. spring temperature, cumulative rainfall, and water levels (Blums & Clark, 2004; Dzus & Clark, 1998; Folliot et al., 2017).

The estimates of adult survival rates correspond to values observed in the literature on species of similar weight (Buxton et al., 2004; Krementz et al., 1997; Nichols et al., 1997). This reflects that there is no apparent scaling issue of this method based on count data. The assumption that male-like individuals correspond only to adult males is then acceptable. This result supports that the count-based method is poorly biased if it is. However, some adult survival rate values are outside the range of expected values even if they are never significantly over 1. A likely reason to these extreme values is a corruption of the closed population assumption on some years. Indeed, if there is an arrival from another Ruddy duck population, the true recruitment cannot explain by itself the population growth and leads to an adult survival combining true adult survival and adult immigration. For the FR population, upper outliers of recruitment rates and survival rates are observed in 2002 and 2012, suggesting immigration events on these years.

The theoretical maximum of the population growth rate is a potential which is determined by intrinsic life history traits of a species (Dmitriew, 2010). This potential is expected to be similar to all Ruddy duck populations anywhere in the world. Realised maximum growth rates that are observed in this study are very close for the two populations. It suggests that the Ruddy duck species reached its intrinsic biological reproduction limit, at least given the environmental conditions of the western Palearctic, i.e. about 0.6 recruits per breeder. The consistency of this intermediate result suggests that the population size estimation is quite accurate for both populations and demonstrates that their changes are well tracked even with a few individuals. The average recruitment rates estimated from the count-based method, with and without harvest, are never higher to the proxies of maximum recruitment rate for both populations. The assumption on the accuracy of the count-based method is then again not excluded from the consistency of this result.

Assuming that hunting-bag data provide a good picture of the year-to-year variability of age structure of a population, the strong correlation with the outputs of our method demonstrates its ability to track interannual fluctuations. This result is robust because such correlation is obvious despite being based on a short time series. This strong relationship is also satisfying because it demonstrates that the assumption of a constant adult sex ratio is not corrupted. The temporal autocorrelation of the adult sex ratio might be explained because it integrates many age-cohorts, which makes it structurally strong. Even if significant variations of the adult sex ratio can still occur over long time periods, this result demonstrates that it is not necessary to monitor and update it on a yearly base. The adult sex ratio found here on a restricted time period is in line with the Ruddy duck in its native area (0.62 in Bellrose, 1980) and with other duck species (Wood et al., 2021). The count-based method always provides recruitment rates significantly lower than the method based on hunting-bag data by a factor close to two, a result that is in line with the hypothesis that the harvest is generally selective towards immature individuals in waterfowl because they are more vulnerable than adults to hunters (Bellrose, 1980; Fox et al., 2014). The gap of vulnerability among ages

observed here is realistic because the harvest-induced mortality on first-year immatures compared to adults is higher by a factor ranging from 1.3 to 2.6 for hunted duck species in North America (Bellrose, 1980).

Overall, even if the true values of vital rates are not known to test properly the accuracy of the count-based method, a beam of arguments supports that the method is not heavily biased. This consists in a big difference with the method based on hunting-bag data as demonstrated in Fox et al. (2014), even when one considers an age structure picture that is limited to the end of the hunting season to limit the bias (Fox et al., 2016).

## 4.2 Population response to management measures

Both populations respond to the harvest pressure by a large drop of their growth, meaning that the harvest effort is efficient to control this species. The response of the GB population differs from the FR one because it displays a strong decrease when the FR population is stabilized. The analysis of the growth alone does not provide clues to understand the mechanisms explaining the difference of the responses between the two populations. Indeed, the bigger drop of growth of the GB population might be explained either by a decrease of the adult survival or of the reproduction success, or even of both components.

The vital rates that are estimated thanks to the count-based method developed in here demonstrates that the harvest pressure affects on average negatively both the adult survival and the recruitment rate for the two populations. The harvest pressure occurring mostly before the breeding period for the GB population targets by definition future breeders, and consequently induces mortality on these individuals and prevent them from reproducing. We observe that adult survival and recruitment rate decrease equally, which is a result in line with the expectation of this harvest strategy. For the FR population, the harvest pressure occurs mostly during the postbreeding period. This strategy should induce a higher mortality on immatures as they are expected to be more vulnerable to hunting (Bellrose, 1980; Fox et al., 2014). However, this anthropogenic mortality on immatures might be compensated by a higher survival of the future recruits because the competition for resources decreased (Cooch et al., 2014). The recruitment rate of the FR population being more affected by 50% than the adult survival, the results support the hypothesis that no or only a limited compensation occurs. This conclusion is even strengthened by the result on the GB population. Indeed, we should expect a decrease of the recruitment rate lower than the adult survival rate if immatures would take advantage of additional resources that unexploited by culled adult individuals. The equal decrease of the two vital rates supports then that there is no compensation. This might be explained because the population size is far lower than the carrying capacity of the available habitats, so there is no competition for resources that potentially enhances the survival of the remaining immature individuals (Péron, 2013).

Considering a population following a compensatory functioning, the FR strategy is counter-productive. As studied Ruddy duck populations are expanding, it seems that the postbreeding harvest strategy still provides some results to control such populations. However, the analysis of the year-to-year variability of the recruitment rate demonstrates that the prebreeding strategy buffers strongly the recruitment and maintains it to a low level every single year whereas the recruitment rate of the postbreeding strategy is highly variable. This might be because harvesting future breeders ensures to avoid the production of potential recruits whereas the postbreeding harvest strategy cannot prevent and dampen exceptional reproduction events. The postbreeding strategy relies also on a detectability of immatures highly variable because these individuals spread over many reproduction habitats more or less accessible whereas the prebreeding strategy targets individuals that are more easily localized because they usually gather in open water on a limited number of wintering spots (Johnsgard & Carbonell, 1996).

The response to the harvest pressure of the two Ruddy duck populations demonstrate that it is necessary to account for the time window over which the harvest occurs to produce proper predictions. Predicting the impact of a harvest pressure on a waterfowl population is then not only a question about how big is the harvest effort, but also mostly when this effort occur within a year. More generally, disentangling the adult survival to the recruitment rate brings capital information to understand the process of harvest on population dynamics and brings key knowledge to improve the conservation of hunted species or the control of invasive species.

### 4.3 Implication for waterfowl management

Tracking variations in abundance is a common tool to determine the conservation status of a population (e.g. Folliot et al., 2022). However, the abundance alone does not provide information on the mechanisms behind the changes of population growth. Identifying the determinants requires to dig into the components structuring the population growth to provide relevant tools to managers (e.g. Austin et al., 2000). Gaining knowledge on adult survival and the recruitment rate often involves capture mark recapture surveys (e.g. Arnold, 2018). However, tracking fine time-scale variability of the vital rates requires to mark a minimum number of individuals (e.g. Souchay & Schaub, 2016) and prevents from implementing such method to small populations with a poor conservation status for instance. The method introduced in here bypasses these caveats to provide annual estimates of vital rates.

The immature proportion, or age ratio, is commonly used to describe the renewal capacity of a waterfowl population and to track the changes of its productivity (Bellrose, 1980; Robertson, 2008; Rodway et al., 2015; Smith et al., 2001; Zimmerman et al., 2010). The recruitment rate remains however a better indicator than the immature proportion/age ratio, the latter having only the advantage to be more directly accessible. Indeed, the immature proportion/age ratio does not account for the dynamics of the population and reflects the population productivity only if the population growth is steady. For instance, let's consider a breeding population of 100 individuals reaching the next year 100 individuals, which then drops to 60 individuals the second year. If there is 50% of immature individuals each year, corresponding to a 1:1 age ratio, we may conclude that the productivity is stable over time. But it actually corresponds to a strong decrease of the productivity (-40%) because the recruitment rate evolved from 0.5 recruits per breeder the first year to 0.3 recruits per breeder the second year. This demonstrates that the immature proportion/age ratio suffers from caveats that can be misleading for a manager. According to Blums & Clark (2004), the recruitment for diving ducks is not related to the fecundity, but depends mostly on the juvenile survival, the other component of the recruitment that is mostly driven by the weather conditions. Studies on other birds also conclude of the poor correlation between fecundity and recruitment (e.g. Murray, 2000). Fecundity alone does not provide all knowledge that is required for a manager to understand the dynamics of a population.

Applying the method implemented in this study to any other waterfowl species implies that the adult males can be distinguished from the other individuals at distance. The latter in the season the dichromatism is observable, the better it is to ensure a relevant picture of the age structure of the population and then good estimates of the adult survival and the recruitment rate. Modifying standard monitoring protocols to distinguish male-like from female-like individuals is almost costless but provides substantial increases in the efficiency and usefulness of monitoring results in conservation (Nichols & Williams, 2006).

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## A Supplementary Materials

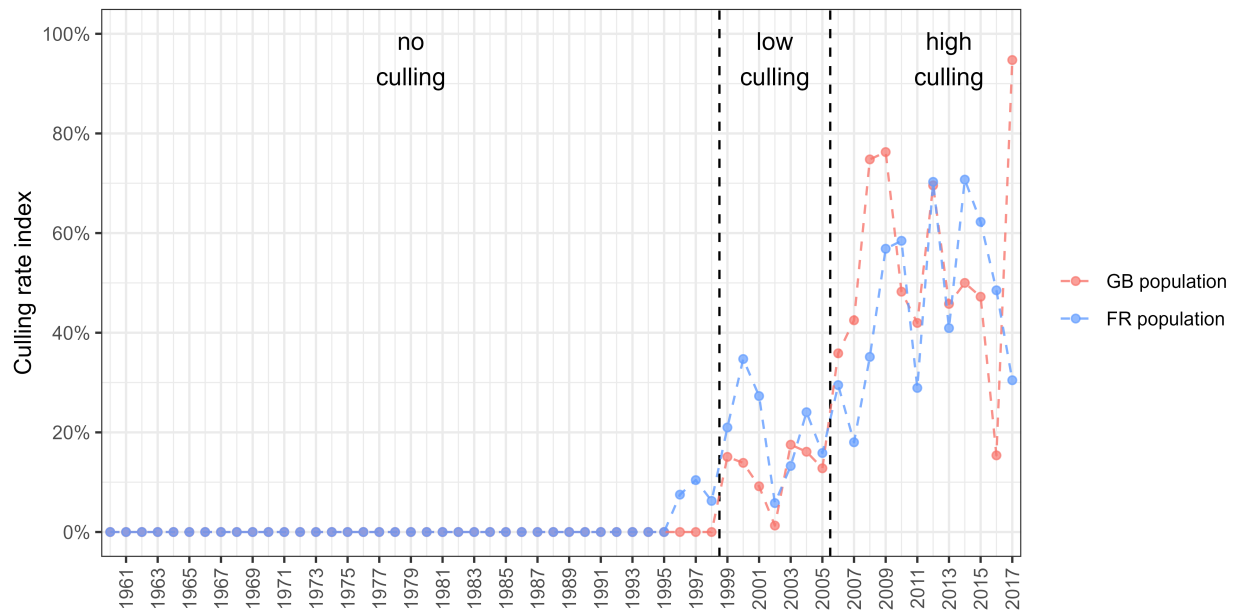


Figure 7: Definition of 3 periods of different culling pressures from an index based on an estimation of the adult culling rate; as only half of the culled individuals were aged in France before 2009, we applied the average age ratio over 2009-2019 on unaged individuals to provide an estimate of the number of adults in removals before 2009; the culling rate increased over time, we then split the time series in 3 categories : we defined a “no culling” period before 1999 because the culling rate for both countries was mostly null and always below 10%, we defined a “low culling” between 1999 and 2005 because the culling rate varies around 20% for both countries, the culling rate then raises significantly for both countries, so we defined a “high culling” period from 2006