

# 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 to what extent 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 birds, which suffers from two main drawbacks. The selectivity of the catch methods can lead to a biased representation of the underlying population structure. In practice, catching and releasing birds is also an invasive approach implying additional disturbances for endangered species or is simply forbidden for invasive alien species. In several 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 the recruitment and the adult survival in the population growth rate. 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:** fecundity - productivity - reproductive success - age ratio - vital rate - duck

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## <sup>1</sup> 1 Introduction

<sup>2</sup> Assessing population growth rate is a key step towards a better understanding of factors underlying the  
<sup>3</sup> dynamics of natural populations (e.g. Niel, 2005). It is also crucial for measuring the efficacy of management  
<sup>4</sup> actions **eventually** undertaken to help population recovery, control, or eradication (Shea & NCEAS Working  
<sup>5</sup> Group on Population Management, 1998). Among the approaches available to managers for reaching these  
<sup>6</sup> goals, those relying on the monitoring of the number of individuals are by far the most popular (Rintala  
<sup>7</sup> et al., 2022). In many instances, these methods even enable environmental factors underlying changes in  
<sup>8</sup> population size to be investigated and hence some mitigating actions to be implemented (Faillettaz et al.,  
<sup>9</sup> 2019). Unfortunately, relying on the monitoring of numbers of individuals alone **hinder** basic understanding  
<sup>10</sup> of the demographic mechanisms underlying changes in population growth rates. More specifically, based on  
<sup>11</sup> counts only, it is nearly impossible to assess **to what extent** population growth rate is affected by change in  
<sup>12</sup> survival rather than to variations in reproductive parameters (Austin et al., 2000). To assess the relative  
<sup>13</sup> sensitivity of population growth rate to factors affecting survival or reproductive parameters, demographers  
<sup>14</sup> most often rely on the monitoring of individuals by capture-mark-recapture (Lebreton et al., 1992). **In**  
<sup>15</sup> practice however, one cannot always rely on the capture and release of individuals owing to the legal status  
<sup>16</sup> of the species that precludes any additional disturbance, e.g. critically endangered species, or forbid the  
<sup>17</sup> release of alive individuals, e.g. invasive species or pests. **Indeed**, although highly efficient for assessing  
<sup>18</sup> demographic parameters, capture-mark-recapture methods have potential drawbacks such as being invasive  
<sup>19</sup> and hardly affordable when time and money are limiting. Genetic monitoring is a non-invasive alternative  
<sup>20</sup> to capture-mark-recapture approaches based on physical captures, but it suffers from being costly and time-  
<sup>21</sup> consuming and requires quite rigorous sampling schemes in the field.

<sup>22</sup> Most of the time therefore, managers do the best of a bad job using counts as the only viable option for  
<sup>23</sup> tracking population growth rates and assessing the efficiency of management actions. Counting the number  
<sup>24</sup> of immatures produced in addition to **alive** adults may enable adult survival and recruitment rate to be  
<sup>25</sup> estimated, and hence provides knowledge on which of adult survival and productivity has the most influence  
<sup>26</sup> on population growth rate. **Unfortunately**, this is only possible for a limited number of species in which  
<sup>27</sup> broodless adults and those with young display the same detectability. Alternatively, assessing the sex and  
<sup>28</sup> age structure in hunting bags has been used to infer the role of decreasing reproductive success in population  
<sup>29</sup> declines in a number of **games** species including ducks and geese (Fox & Cristensen, 2018). However, this  
<sup>30</sup> approach is not suited for protected/endangered species. Here we exemplify how, in dimorphic species,  
<sup>31</sup> delayed maturity of males can be exploited for estimating **productivity/recruitment** and adult survival by  
<sup>32</sup> differentiating male-like to female-like individuals in repeated winter counts. We **use** two non-native Ruddy  
<sup>33</sup> duck populations introduced in Europe as a study model. As numerous duck species, the Ruddy duck is  
<sup>34</sup> dimorphic, with newly born males looking like females until the pre-nuptial moult, which occurs in late  
<sup>35</sup> winter. This means that the apparent proportion of males increases over the course of the wintering season.  
<sup>36</sup> These changes in apparent proportions of males during this period are therefore directly related to the  
<sup>37</sup> proportion of immatures into the populations and hence to **the** reproductive success and **the** recruitment  
<sup>38</sup> rate. This study details the method to infer adult survival and recruitment rate from count data and an  
<sup>39</sup> application is developed to assess the impact of two different eradication strategies deployed in Great Britain  
<sup>40</sup> and in France respectively.

## <sup>41</sup> 2 Materials & methods

<sup>42</sup> The Ruddy duck is a stiff-tailed duck native from the Americas. From seven individuals initially acclimated  
<sup>43</sup> in the Slimbridge Wetland Centre in **the** Great Britain in the 40's (Gutiérrez-Expósito et al., 2020), a feral  
<sup>44</sup> population began to establish with the first observed reproductive attempts in the wild in the 60s (Figure  
<sup>45</sup> 1). This feral population rapidly grew and spread to the entire country to reach more than **5000** individuals  
<sup>46</sup> in the early 2000s. By the end of the 80s, a feral population began to establish also on the continent  
<sup>47</sup> in France, supposedly owing to the arrival of individuals born in Great Britain. Contrary to what was  
<sup>48</sup> observed in Great Britain, the French Ruddy duck population did not spread much, with the vast majority  
<sup>49</sup> of observations and breeding attempts clustering in Western France. In France, during winter, almost **none**

50 Ruddy duck is observed outside the lake of Grand Lieu ( $47.09^{\circ}\text{N}$ ,  $1.67^{\circ}\text{W}$ ), which is thus the exclusive  
 51 wintering site and greatly facilitates the monitoring of this population. The feral European populations of  
 52 Ruddy duck are considered as a major threat to the endangered native White-headed duck population of  
 53 the South-Western Mediterranean because of hybridization risks and thus an elevated potential for genetic  
 54 pollution and eventually genetic assimilation of the latter by the former (Muñoz-Fuentes et al., 2007). In  
 55 order to mitigate the risks of genetic pollution of the White-headed duck by Ruddy ducks, a European plan  
 56 of eradication of Ruddy ducks has been adopted by the European Commission. As a result, eradication  
 57 measures were taken both in Great Britain and in France from the late 90s (Gutiérrez-Expósito et al., 2020),  
 58 (Figure 1). The release of non-native species in the wild, including Ruddy ducks, is forbidden in countries  
 59 of the European Union, and the status of White-headed duck populations is highly unfavourable. The  
 60 use of capture-mark-recapture to monitor populations of these species is thus impossible. As a result, the  
 61 effectiveness of the eradication of Ruddy ducks and management actions intended to favour the recovery of  
 62 White-headed ducks were essentially checked through censuses. Censuses, however, prevented from assessing  
 63 the relative effects or variations in survival and reproductive success/recruitment on population growth rate,  
 64 which is a key towards a proper understanding of the efficiency of management actions.

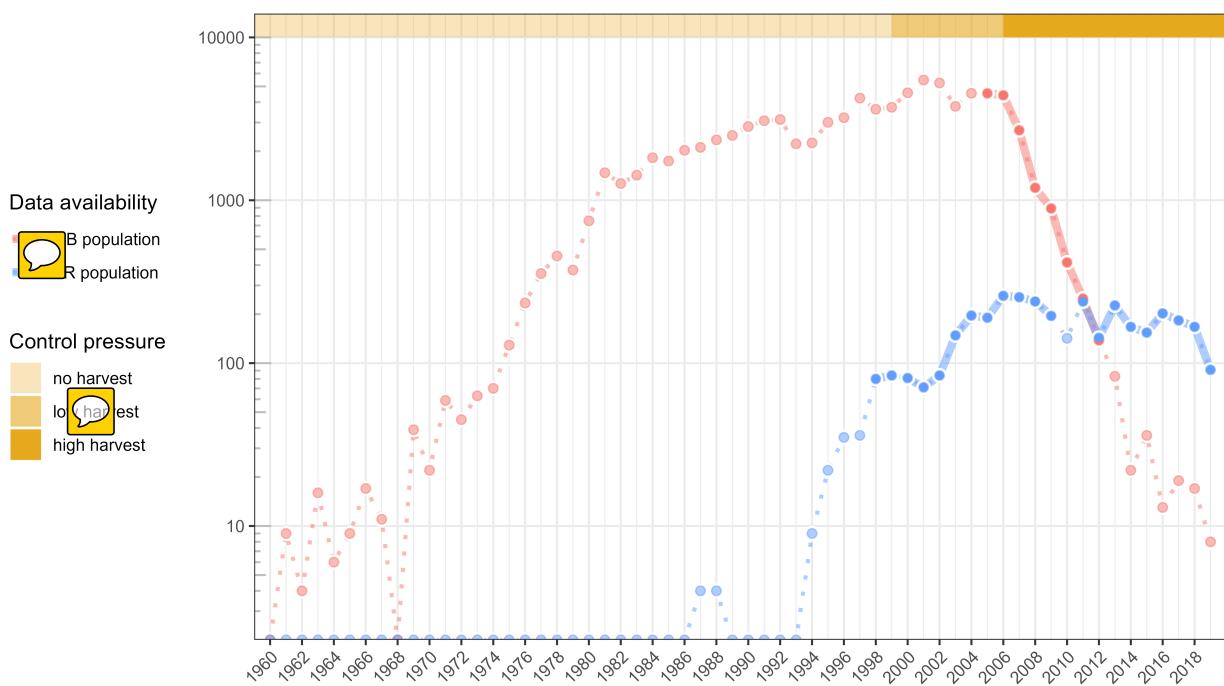


Figure 1: Evolution of the size of the two Ruddy duck populations; y-axis is on a log-scale; data availability refers to censuses that distinguished female-like from male-like individuals

65 Like many other ducks, Ruddy ducks and White-headed ducks both display delayed dichromatism. Thereby  
 66 immature males acquire the typical colourful plumage of their kind over the course of the interbreeding  
 67 season, which is typically in late winter. Immature males are thus confounded to immature and adult  
 68 females before their moult (Figure 2). The delayed dichromatism explains why the apparent proportion  
 69 of females in the winter counts is always higher than the true proportion of females that can be assessed  
 70 in winter hunting bags (Figure 3). Thus, it is possible to assess the proportion of immatures within a  
 71 population by monitoring the seasonal evolution of apparent sex ratio and assuming an even sex ratio at  
 72 birth, comparable mortality rates between females and males among juveniles, and unchanging adult sex  
 73 ratio over the monitoring period. Then, both adult survival rate and recruitment rate can be estimated by  
 74 combining the age ratio thus obtained with reliable counts over two successive winters.



Figure 2: Typical observation of a Ruddy duck flock in winter: 10 female-like individuals with a whitish cheek and a dark stripe across it, 4 male-like individuals with a white cheek and a black cap, 3 unidentified individuals © Jay McGowan - 3 February 2013 - Tompkins, New York, United States

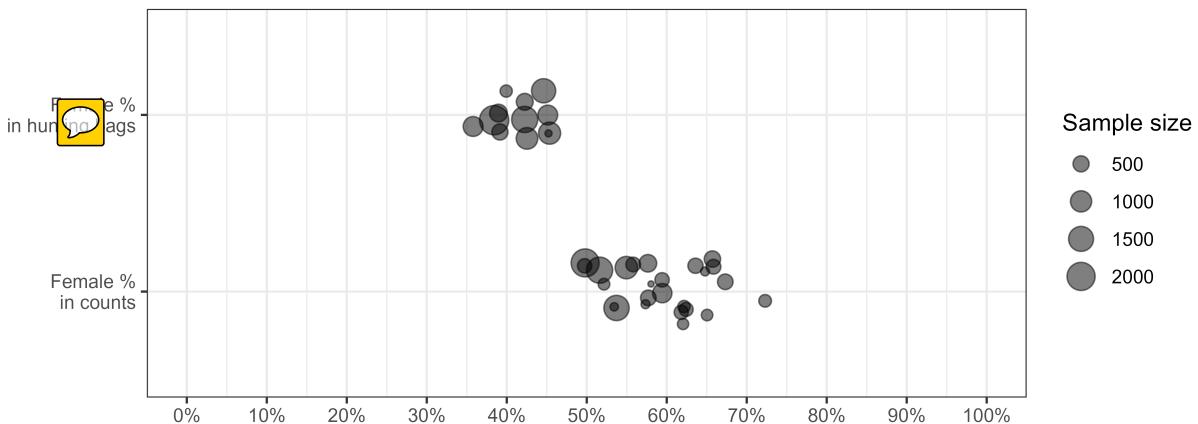


Figure 3: Female proportion in hunting bags vs in counts; For the first category, one point corresponds to the female proportion estimated from direct sex identification of the Ruddy ducks controlled over one year in a population; for the second category, one point is the proportion of female-like plumage in a population counted in winter; the difference is due to immature males that look like females before moult

We monitored the demography of Ruddy duck populations in both Great Britain and France thanks to exhaustive counts on the wintering grounds during the period between December 1 and January 31. In addition to these exhaustive counts, censuses that distinguished female-like from male-like individuals (Figure 1) were performed from 2006 to 2012 in Great Britain, which corresponded to a strong decline of the population. 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, which corresponds to a period with a strong control effort. During these years, the eradication effort, under control of the authorities in both countries, was recorded. Even if the age ratio in the hunting bag was uncertain before 2009 in France, we can qualify the harvest pressure on adults in three categories for both countries: “no harvest” before 1999, “low harvest” between 1999 and 2005, and “high harvest” from 2006 (see Figure 7 in Supplementary Materials).

## 86 2.1 Vital rates inference from count data

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

100 Assuming the additive property of the binomial distribution, the proportion of immatures can be deduced  
 101 from the cumulated counts of male-like individuals in the wintering population, see Equation (2). From this  
 102 proportion and the interannual variation of an abundance index of the population size, the adult survival  
 103 and the recruitment rate are straightforward, see Equation (3). If the absolute value of the population size  
 104 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 to be 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 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 $t$

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

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

$$s_{i,t} = \frac{N_{i,t}}{N_{i,t-1}} \cdot (1 - p(i)_{i,t}) \quad (3)$$

$$r_{i,t} = \frac{N_{i,t}}{N_{i,t-1}} \cdot p(i)_{i,t}$$

$$S_{i,t} = N_{i,t} \cdot (1 - p(i)_{i,t}) \quad (4)$$

$$R_{i,t} = N_{i,t} \cdot p(i)_{i,t}$$

## 105 2.2 Validation of the count-based method

106 The relevance of the method was assessed by testing the likelihood of the estimates of both vital rates. For  
 107 the adult survival rate, we checked if the values belonged to the expected interval [0; 1], and we compared the  
 108 values to literature data that are accessible because the adult survival is commonly assessed by capture-mark-  
 109 recapture (Lebreton, 2001). The maximum adult survival is defined as a uniform distribution on [0.7; 1]. The  
 110 lower limit corresponds to the upper range of survival rates observed in literature for waterfowl species of  
 111 similar weight, the upper limit was set to 1 because the survival rates of long-life waterfowl species are very  
 112 high (Buxton et al., 2004; Krementz et al., 1997; Nichols et al., 1997). The recruitment rate is more tricky  
 113 to validate because it is not upper bounded as it is defined on [0;  $\infty$ ] and is neither explicitly informed in  
 114 the literature. We then developed an approach to estimate the maximum recruitment rate expected without  
 115 exploitation and without negative density-dependence processes and we checked if all values were equal or  
 116 below this maximum recruitment rate. If the recruitment rate outputs of the model are significantly higher  
 117 than the maximum recruitment rate, it means that the method overestimates the recruitment rate, which  
 118 reflects that a part of adult males are not detected during count surveys. A null or negative recruitment  
 119 rate would mean that immature males moulted before the survey or/and the assumption on the stability of  
 120 the adult sex ratio is overrated.

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

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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 $t$

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

129 The maximum growth rate occurred for both populations during their expansion phase, when the evolution  
 130 of the population size was the steepest. To estimate robust maximum population growth rates for both  
 131 populations, we smoothed annual population growth rate over a consistent time period by using a linear  
 132 regression on the logarithm scale, see Equation (6). To do so, we rejected Great Britain data before 1972  
 133 since the size estimate of this population is noisy below 50 individuals (Figure 1). After reaching the  
 134 threshold of 1000 individuals, the Great Britain (GB) population growth observed a strong inflexion whereas  
 135 no harvest pressure was applied. This observation suggests that a negative density-dependence process  
 136 might occur beyond 1000 individuals and led to consider only the first sequence of the time series to infer on  
 137 the maximum growth rate in Great Britain, i.e. 1972-1981. For the French (FR) population, the sequence  
 138 without harvest 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 $\text{year}^{-1}$ )
$t \in J$	Index	Year index within the time interval $J$
$\sigma_{i,J}$	Parameter	Standard deviation of the regression model

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

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

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

149 **2.3 Impact of harvest strategies on vital rates**

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

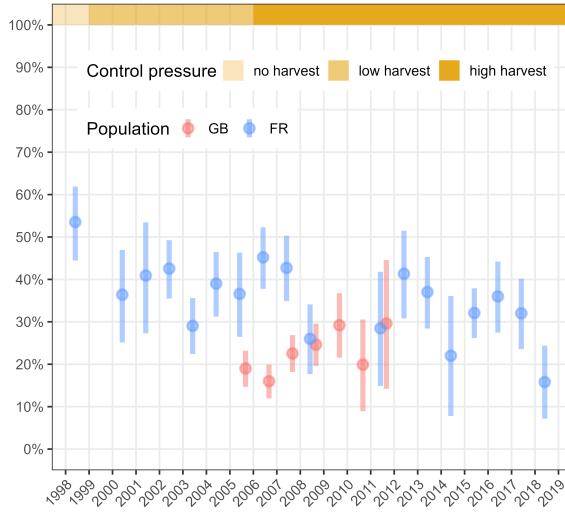
160 For all the sub-models in Section 2, the Bayesian framework was used for its efficiency and simplicity to  
161 propagate error through the parameters. We used uninformative priors on all parameters. As the maximum  
162 growth rate is an life history trait expected to be stable among populations of a same species, we used a  
163 uninformative hierarchical prior for this parameter. We generated three chains of length 500000, with a  
164 thinning of 10 to avoid autocorrelation in the samples, and we discarded the first 2000 samples as burn-in.  
165 Chain convergence was assessed using the Gelman and Rubin convergence diagnostic ( $R < 1.1$ , Gelman &  
166 Rubin (1992)). We fit the models using NIMBLE (de Valpine et al., 2017) run from R (R Core Team,  
167 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  
168 values  $\mathbf{X}[\mathbf{Y}; \mathbf{Z}]$  reported in results are the medians and the associated boundaries of the 95% confidence  
169 interval of posterior distributions. The median was preferred to the mean because of its robustness to skewed  
170 distribution.

171 **3 Results**

172 **3.1 Estimates of vital rates**

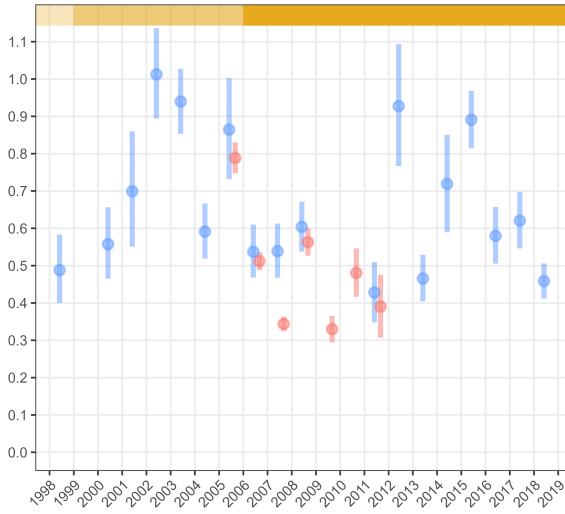
173 The method successfully provides estimates and associated uncertainty of immature proportion in both  
174 wintering populations. The adult survival rate and the recruitment rate, i.e. the two components of the  
175 population growth rate, are also successfully estimated by the method (Figure 4).

### Proportion of immatures in the population



### Survival rate

Proportion of breeders still alive after one year



### Recruitment rate

Number of recruits produced per breeder

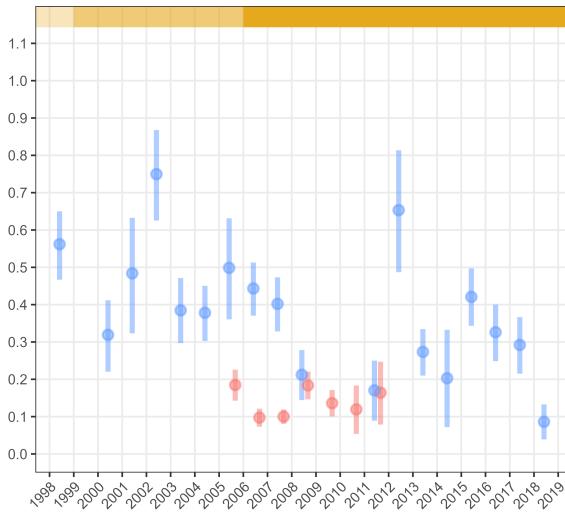


Figure 4: Evolution of the proportion of immatures in the population and the vital rates in light of the harvest pressure; bars define the 95% confidence intervals

176 The male proportion in adults, which is a prerequisite to infer on the immature proportion, is estimated at  
177 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  
178 are similar for the two populations, but the range of the immature proportions in the GB population is far  
179 more limited (upper value : 0.30 [0.14; 0.45]). Conversely from the FR population, there is no significant  
180 difference from a year to another because all estimates overlap each other. We can notice that the immature  
181 proportion for the GB population is quite stable over the time series available, but a slight decrease is  
182 observed for the FR population.

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

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

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

## 202 3.2 Likelihood of year-to-year variability in vital rates

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

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

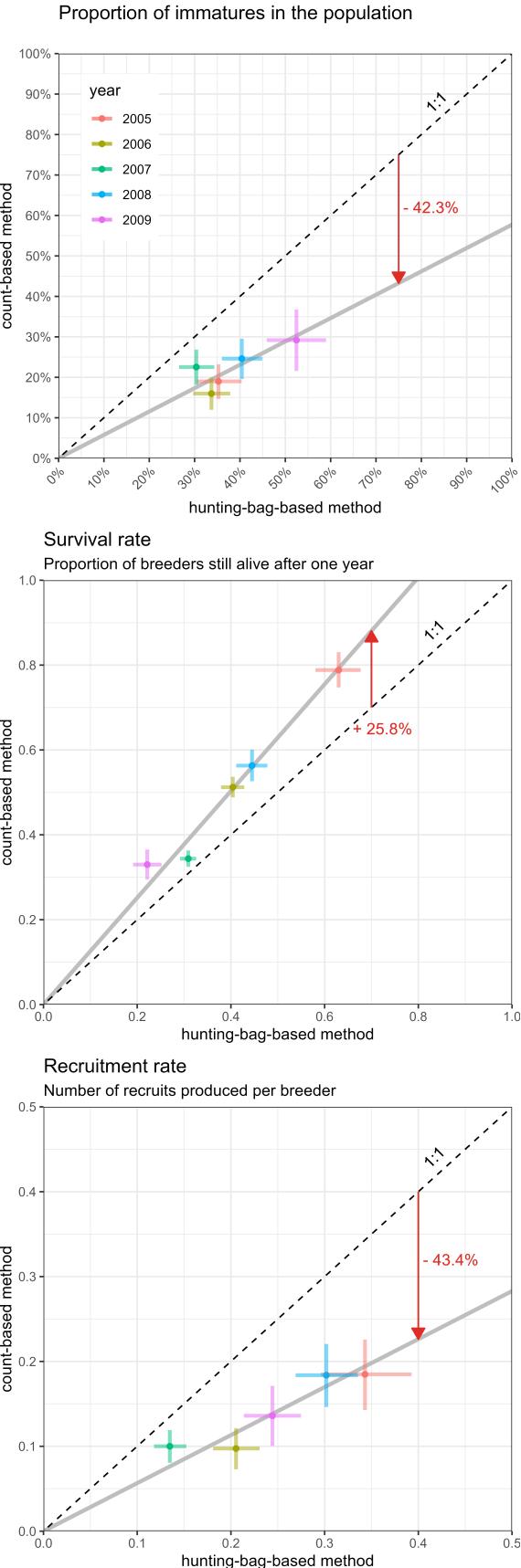


Figure 5: Comparison of the parameter estimates between the count-based method and hunting-bag-based method. Only 5 years for the GB population were available; bars define the 95% confidence intervals; the red arrow defined the average difference in proportion between the two methods

215 **3.3 Response of vital rates to the harvest strategy**

216 Under no harvest pressure, the maximum growth rates of the two populations are very similar (Figure 6),  
217 respectively 1.45 [1.36; 1.55] and 1.52 [1.25; 1.88] for the GB and the FR population. It corresponds to  
218 an increase of 45% per year and 52% per year respectively. Based on literature, we assumed a maximum  
219 survival rate similar for both populations 0.85 [0.7; 1]. We deduced a maximum recruitment rate of 0.60  
220 [0.42; 0.78] for the GB population and of 0.68 [0.36; 1.06] for the FR population.

221 Even if a significant part of culled individuals were not aged for some years, the proxies of the harvest  
222 pressure show significant shifts over time (Figure 7). This led to consider a high harvest pressure period  
223 from 2006 with no clear difference between the two populations because the signal is very noisy. Even if the  
224 harvest pressure seems comparable, the harvest strategies differ significantly between the two populations,  
225 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]  
226 for the GB and the FR population respectively, which corresponds to a decrease of 44% per year and 3%  
227 per year. This result shows that the GB population significantly decreases during the high harvest pressure  
228 whereas the FR population is stabilized.

229 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  
230 and FR populations respectively, when the recruitment rate decreases to 0.13 [0.11; 0.15] and 0.32 [0.29;  
231 0.34] respectively. The drop of the growth rate of the GB population corresponds to a similar average drop  
232 in adult survival rate (-0.41) and in recruitment rate (-0.47). The stabilisation of the FR population is  
233 more due to a decrease of the recruitment rate (-0.36) than from a drop of the adult survival (-0.23). For  
234 both populations, the response to the harvest pressure is significant, meaning that the compensation of the  
235 population to harvest mortality is limited if not null. Vital rates of the GB population are more affected  
236 than the FR population. Unsurprisingly, the FR harvest strategy focusing on the postbreeding period affects  
237 mostly the recruits. However, the prebreeding harvest strategy applied on the GB population that targets  
238 adults performs to deplete strongly the recruitment to a very low level (0.13 recruits produced per breeder).

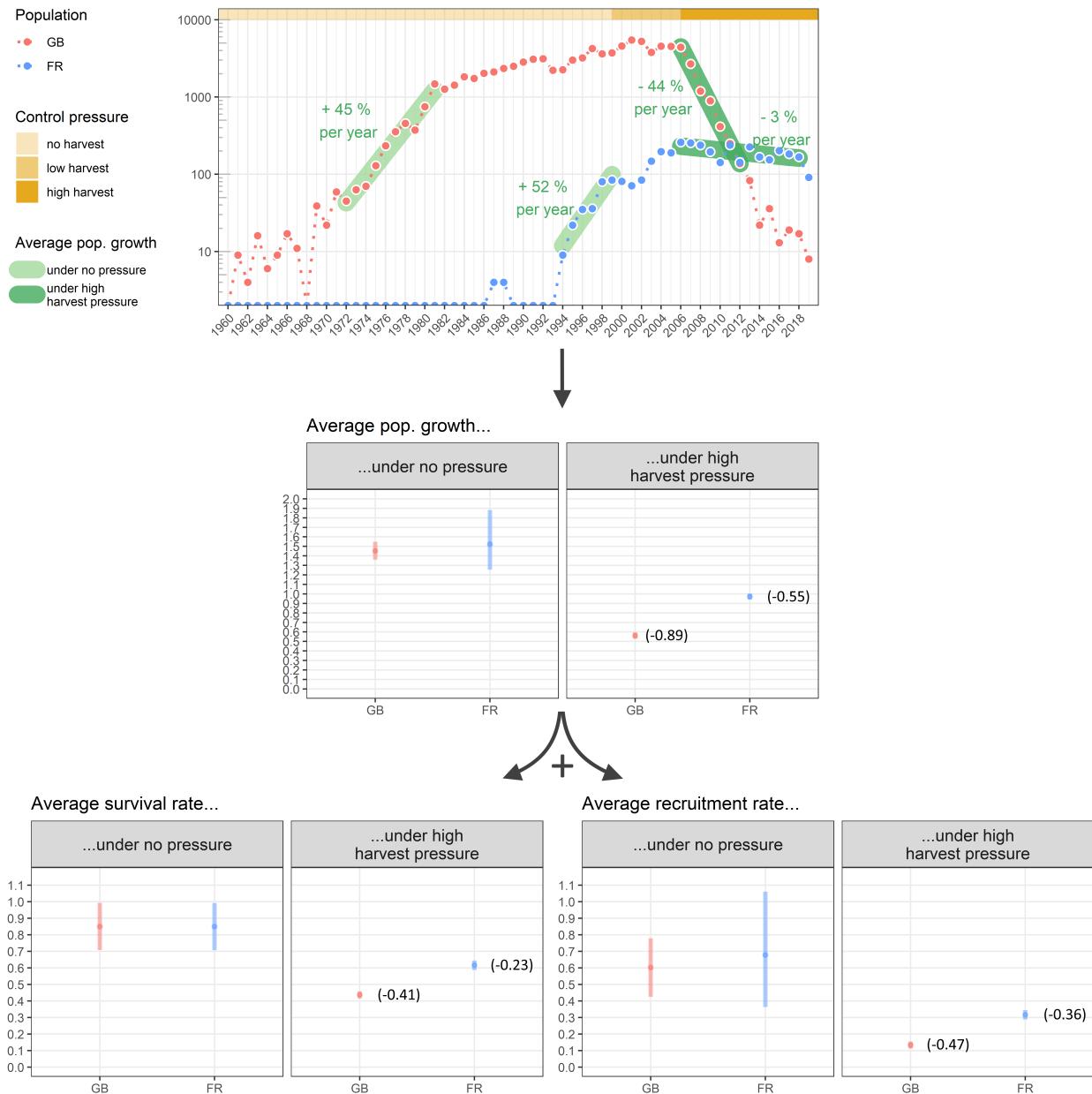


Figure 6: Comparison between average population growth rate under no pressure vs under high harvest pressure; The harvest effort for the GB population occurs mostly during the prebreeding period, whereas it focuses mostly during and after the breeding period for the FR population (see 2.3 for details);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

## 239 4 Discussion

240 The delayed sexual dichromatism in a waterfowl species is used here to develop and test the validity of a  
 241 new non-invasive method aiming to break down the apparent growth of a population into its two structural

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

## 250 4.1 Accuracy of the method to estimate vital rates

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

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

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

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

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

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

## 298 4.2 Population response to management measures

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

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

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

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

### 341 4.3 Implication for waterfowl management

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

351 The immature proportion, or age ratio, is commonly used to describe the renewal capacity of a waterfowl  
352 population and to track the changes of its productivity (Bellrose, 1980; Robertson, 2008; Rodway et al.,  
353 2015; Smith et al., 2001; Zimmerman et al., 2010). The recruitment rate remains however a better indicator  
354 than the immature proportion/age ratio, the latter having only the advantage to be more directly accessible.  
355 Indeed, the immature proportion/age ratio does not account for the dynamics of the population and reflects  
356 the population productivity only if the population growth is steady. For instance, let's consider a breeding  
357 population of 100 individuals reaching the next year 100 individuals, which then drops to 60 individuals the  
358 second year. If there is 50% of immature individuals each year, corresponding to a 1:1 age ratio, we may  
359 conclude that the productivity is stable over time. But it actually corresponds to a strong decrease of the  
360 productivity (-40%) because the recruitment rate evolved from 0.5 recruits per breeder the first year to 0.3  
361 recruits per breeder the second year. This demonstrates that the immature proportion/age ratio suffers from  
362 caveats that can be misleading for a manager. According to Blums & Clark (2004), the recruitment for diving  
363 ducks is not related to the fecundity, but depends mostly on the juvenile survival, the other component of  
364 the recruitment that is mostly driven by the weather conditions. Studies on other birds also conclude of the  
365 poor correlation between fecundity and recruitment (e.g. Murray, 2000). Fecundity alone does not provide  
366 all knowledge that is required for a manager to understand the dynamics of a population.

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

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### References

- Arnold, T. W. (2018). Using ring-recovery and within-season recapture data to estimate fecundity and population growth. *Ecology and Evolution*, 8(20), 10298–10305. <https://doi.org/10.1002/ece3.4506>

- Austin, J. E., Afton, A. D., Anderson, M. G., Clark, R. G., Custer, C. M., Lawrence, J. S., Pollard, J. B., & Ringelman, J. K. (2000). Declining scaup populations: Issues, hypotheses, and research needs. *Wildlife Society Bulletin*, 254–263.
- Bellrose, F. C. (1980). *Ducks, geese & swans of North America: 3rd. ed.* Stackpole Books.
- Blums, P., & Clark, R. G. (2004). Correlates of lifetime reproductive success in three species of European ducks. *Oecologia*, 140(1), 61–67. <https://doi.org/10.1007/s00442-004-1573-8>
- Buxton, N. E., Summers, R. W., & Peach, W. J. (2004). Survival rate of female *Boldeneye bucephala clangula*. *Bird Study*, 51(3), 280–281. <https://doi.org/10.1080/00063650409461365>
- Cooch, E. G., Guillemain, M., Boomer, G. S., Lebreton, J.-D., & Nichols, J. D. (2014). The effects of harvest on waterfowl populations. *Wildfowl*, 220–276.
- de Valpine, P., Turek, D., Paciorek, C. J., Anderson-Bergman, C., Lang, D. T., & Bodik, R. (2017). Programming with models: Writing statistical algorithms for general model structures with NIMBLE. *Journal of Computational and Graphical Statistics*, 26(2), 403–413. <https://doi.org/10.1080/10618600.2016.1172487>
- Dmitriew, C. M. (2010). The evolution of growth trajectories: What limits growth rate? *Biological Reviews*, 86(1), 97–116. <https://doi.org/10.1111/j.1469-185x.2010.00136.x>
- Dzus, E. H., & Clark, R. G. (1998). Brood survival and recruitment of mallards in relation to wetland density and hatching date. *The Auk*, 115(2), 311–318. <https://doi.org/10.2307/4089189>
- Failliettaz, R., Beaugrand, G., Goerville, E., & Kirby, R. R. (2019). Atlantic multidecadal oscillations drive the basin-scale distribution of atlantic bluefin tuna. *Science Advances*, 5(1). <https://doi.org/10.1126/sciadv.aar6993>
- Flint, P. (2015). Population dynamics of sea ducks: Using models to understand the causes, consequences, evolution, and management of variation in life history characteristics. In J.-P. L. Savard, D. V. Derksen, D. Esler, & J. M. Eadie (Eds.), *Ecology and conservation of North American sea ducks* (Vol. 46, pp. 63–96). CRC Press.
- Folliot, B., Caizergues, A., Barbotin, A., & Guillemain, M. (2017). Environmental and individual correlates of common pochard (*Aythya ferina*) nesting success. *European Journal of Wildlife Research*, 63(4). <https://doi.org/10.1007/s10344-017-1126-1>
- Folliot, B., Caizergues, A., Tableau, A., Souchay, G., Guillemain, M., Champagnon, J., & Calenge, C. (2022). Assessing spatiotemporal variation in abundance: A flexible framework accounting for sampling bias with an application to common pochard ( *< i>aythya ferina</i>* ). *Ecology and Evolution*, 12(4). <https://doi.org/10.1002/ece3.8835>
- Fox, A. D., Clausen, K. K., Dalby, L., Christensen, T. K., & Sunde, P. (2014). Age-ratio bias among hunter-based surveys of Eurasian wigeon *Anas penelope* based on wing vs. Field samples. *Ibis*, 157(2), 391–395. <https://doi.org/10.1111/ibi.12229>
- Fox, A. D., Clausen, K., Dalby, L., Christensen, T., & Sunde, P. (2016). Between-year variations in sex/age ratio bias in hunter wings of eurasian wigeon (*Anas penelope*) compared to field samples. *Ornis Fennica*, 93(1), 26.
- Fox, A. D., & Cristensen, T. K. (2018). Could falling female sex ratios among first-winter northwest european duck populations contribute to skewed adult sex ratios and overall population declines? *Ibis*, 160(4), 929–935. <https://doi.org/10.1111/ibi.12649>
- Gelman, A., & Rubin, D. B. (1992). Inference from iterative simulation using multiple sequences. *Statistical Science*, 7(4). <https://doi.org/10.1214/ss/1177011136>
- Gutiérrez-Expósito, C., Pernollet, C., Adriaens, T., & Henderson, I. (2020). Ruddy duck (*Oxyura jamaicensis* Gmelin, 1789). In *Invasive birds: Global trends and impacts* (pp. 200–205). CABI.
- Hochbaum, H. A. (1942). Sex and age determination of waterfowl by cloacal examination. *Transactions of the North American Wildlife Conference*, 7, 299–307.
- Johnsgard, P. A., & Carbonell, M. (1996). *Ruddy ducks & other stifftails: Their behavior and biology (animal natural history series)*. Univ of Oklahoma Pr.
- Krementz, D. G., Barker, R. J., & Nichols, J. D. (1997). Sources of variation in waterfowl survival rates. *The Auk*, 114(1), 93–102. <https://doi.org/10.2307/4089068>
- Lebreton, J.-D. (2001). The use of bird rings in the study of survival. *Ardea*, 89(1), 85–100.
- Lebreton, J.-D., Burnham, K. P., Clobert, J., & Anderson, D. R. (1992). Modeling survival and testing biological hypotheses using marked animals: A unified approach with case studies. *Ecological Monographs*, 62(1), 67–118. <https://doi.org/10.2307/2937171>

- Muñoz-Fuentes, V., Vilà, C., Green, A. J., Negro, J. J., & Sorenson, M. D. (2007). Hybridization between white-headed ducks and introduced ruddy ducks in Spain. *Molecular Ecology*, 16(3), 629–638. <https://doi.org/10.1111/j.1365-294x.2006.03170.x>
- Murray, B. G. (2000). Measuring annual reproductive success in birds. *The Condor*, 102(2), 470–473. <https://doi.org/10.1093/condor/102.2.470>
- Nichols, J. D., Hines, J. E., & Blums, P. (1997). TESTS FOR SENESCENT DECLINE IN ANNUAL SURVIVAL PROBABILITIES OF COMMON POCHARDS, *AYTHYA FERINA*. *Ecology*, 78(4), 1009–1018. [https://doi.org/10.1890/0012-9658\(1997\)078%5B1009:tfstdia%5D2.0.co;2](https://doi.org/10.1890/0012-9658(1997)078%5B1009:tfstdia%5D2.0.co;2)
- Nichols, J. D., & Williams, B. K. (2006). Monitoring for conservation. *Trends in Ecology & Evolution*, 21(12), 668–673. <https://doi.org/10.1016/j.tree.2006.08.007>
- Niel, J.-D., Colin & Lebreton. (2005). Using demographic invariants to detect overharvested bird populations from incomplete data. *Conservation Biology*, 19(3), 826–835. <https://doi.org/10.1111/j.1523-1739.2005.00310.x>
- Péron, G. (2013). Compensation and additivity of anthropogenic mortality: Life-history effects and review of methods. *Journal of Animal Ecology*, 82(2), 408–417. <https://doi.org/10.1111/1365-2656.12014>
- R Core Team. (2022). *R: A language and environment for statistical computing*. R Foundation for Statistical Computing. <https://www.R-project.org/>
- Rintala, J., Hario, M., Laursen, K., & Møller, A. P. (2022). Large-scale changes in marine and terrestrial environments drive the population dynamics of long-tailed ducks breeding in siberia. *Scientific Reports*, 12(1). <https://doi.org/10.1038/s41598-022-16166-7>
- Robertson, G. J. (2008). Using winter juvenile/adult ratios as indices of recruitment in population models. *Waterbirds*, 31(sp2), 152–158. <https://doi.org/10.1675/1524-4695-31.sp2.152>
- Rodway, M. S., Regehr, H. M., Boyd, W. S., & Iverson, S. A. (2015). Age and sex ratios of sea ducks wintering in the Strait of Georgia, British Columbia: Implications for monitoring. *Marine Ornithology*, 43, 141–150.
- Shea, K., & NCEAS Working Group on Population Management, the. (1998). Management of populations in conservation, harvesting and control. *Trends in Ecology & Evolution*, 13(9), 371–375. [https://doi.org/10.1016/s0169-5347\(98\)01381-0](https://doi.org/10.1016/s0169-5347(98)01381-0)
- Smith, C. M., Goudie, R. I., & Cooke, F. (2001). Winter age ratios and the assessment of recruitment of harlequin ducks. *Waterbirds: The International Journal of Waterbird Biology*, 24(1), 39. <https://doi.org/10.2307/1522241>
- Souchay, G., & Schaub, M. (2016). Investigating rates of hunting and survival in declining european lapwing populations. *PLOS ONE*, 11(9), e0163850. <https://doi.org/10.1371/journal.pone.0163850>
- Wood, K. A., Brides, K., Durham, M. E., & Hearn, R. D. (2021). Adults have more male-biased sex ratios than first-winter juveniles in wintering duck populations. *Avian Research*, 12(1). <https://doi.org/10.1186/s40657-021-00286-1>
- Zimmerman, G. S., Link, W. A., Conroy, M. J., Sauer, J. R., Richkus, K. D., & Boomer, G. S. (2010). Estimating migratory game-bird productivity by integrating age ratio and banding data. *Wildlife Research*, 37(7), 612. <https://doi.org/10.1071/wr10062>

## A Supplementary Materials

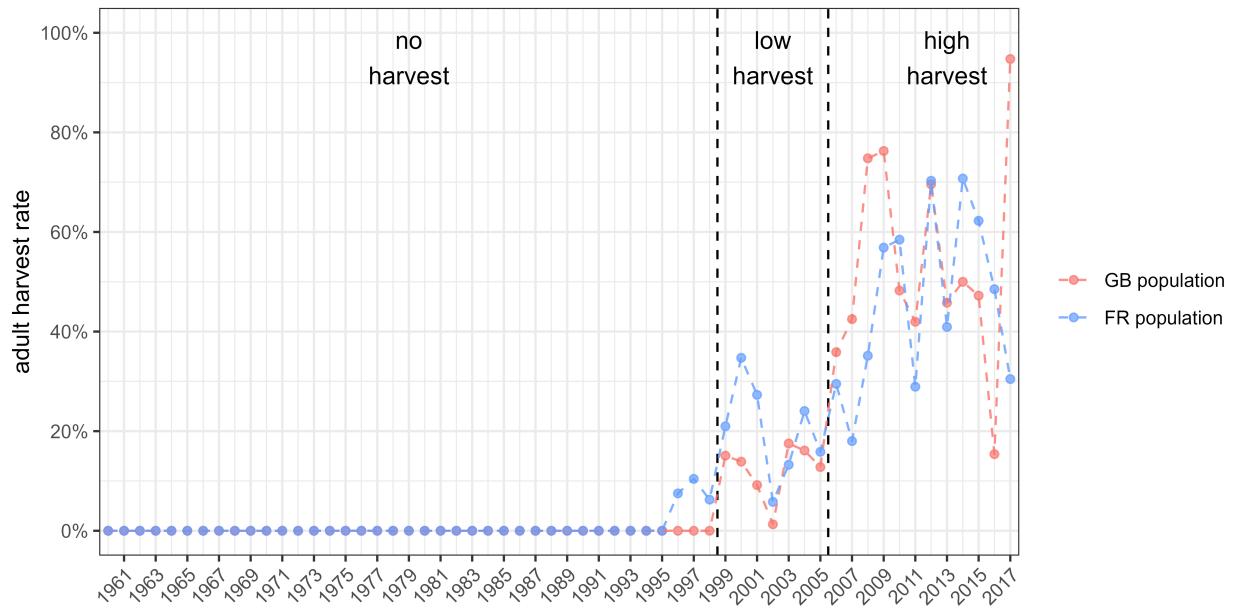


Figure 7: Definition of 3 periods of different harvest pressure from an index of harvest rate; as only half of the controlled individuals were aged in France before 2009, we applied the average age ratio over 2009-2019 on unaged individuals to provide an estimate of the number of adults in hunting bags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