

Delayed dichromatism as a convenient tool to disentangle the effects of survival and productivity on the population dynamics in waterfowl

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Abstract

Monitoring the number of individuals is by far the most popular strategy for investigating the environmental factors ruling population dynamics and for measuring the efficacy of management actions targeting population recovery, control or eradication. Monitoring numbers is unfortunately inefficient for assessing the mechanisms underlying demographic processes and more specifically to assess the extent to which population growth rate is affected by changes in adult survival rather than fluctuations in reproductive parameters. Usual methods to inform adult survival and productivity, such as capture-mark-recapture and analysis of game-hunting bag, rely on catching animals which suffers from three main drawbacks. Firstly, the selectivity of the catching methods can lead to a biased representation of the underlying population structure. Secondly, catching and releasing animals is quite invasive, which generates stress, and is thus an additional threat to often already endangered species. Thirdly, releasing may simply be impossible especially for invasive alien species that represent a threat to native taxa. 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. Using the case of alien Ruddy duck populations of Western Europe (a species displaying this pattern), we introduce a non-invasive method based on count data distinguishing plumage types that allows estimating the respective contribution of adult survival and productivity (also called recruitment rate) to population growth rate. We exemplify how, based on count surveys, changes in apparent male proportion (due to female-like immature males progressively acquiring adult male plumage) can be exploited to decompose population growth rate into adult survival and recruitment rates, greatly helping to understand the demographic impact of two different eradication strategies.

Keywords: intrinsic growth rate - vital rate - reproductive success - fecundity - sex ratio - age ratio
- *Oxyura jamaicensis*

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¹ 1 Introduction

² Assessing population growth rate is a first step towards a better understanding of factors underlying the
³ dynamics of natural populations (e.g. Niel & Lebreton, 2005). It is also crucial for measuring the efficacy
⁴ of management actions potentially undertaken to help population recovery, control, or eradication (Shea &
⁵ NCEAS Working Group on Population Management, 1998). Among the approaches available to managers
⁶ for reaching these goals, those relying on the monitoring of the number of individuals (counts) are by far the
⁷ most popular (Rintala et al., 2022). In many instances, these methods enable investigating environmental
⁸ factors underlying changes in population size, and hence help implementing mitigating actions (Faillettaz
⁹ et al., 2019). Unfortunately, relying on the monitoring of population abundance alone generally hinders
¹⁰ basic understanding of the demographic mechanisms underlying changes in population growth rates. More
¹¹ specifically, based on counts only, it is nearly impossible to assess the extent to which population growth rate
¹² is affected by changes in adult survival rather than to variations in productivity (Austin et al., 2000), which is
¹³ defined as the product of all reproductive parameters. To assess the relative sensitivity of population growth
¹⁴ rate to factors affecting adult survival or reproductive parameters, demographers most often rely on the
¹⁵ monitoring of individuals by capture-mark-recapture (CMR, Lebreton et al., 1992). In practice, however,
¹⁶ one cannot always rely on the capture and release of individuals owing to the legal status of the species
¹⁷ that precludes any additional disturbance (e.g. critically endangered species) or forbid the release of alive
¹⁸ individuals (e.g. invasive species or pests). Furthermore, although highly efficient for assessing demographic
¹⁹ parameters, capture-mark-recapture methods suffer from potential drawbacks such as being invasive (and
²⁰ may affect behaviour and hence survival or breeding success) and hardly affordable when time and money
²¹ are limiting. Genetic monitoring is a non-invasive alternative to capture-mark-recapture, but it suffers from
²² being costly and requires large samples (Caniglia et al., 2011).

²³ Most of the time therefore, managers do the best of a bad job using counts as a viable option for tracking
²⁴ population size changes and then population growth rate, in order to assess the relevance of management
²⁵ actions. Distinguishing immatures from adults in counts enables estimating adult survival rate, i.e. the
²⁶ proportion of breeders that survived over one year, and productivity/recruitment rate, i.e. the number
²⁷ of immatures produced per breeder that reach sexual maturity, which are, by definition, recruited in the
²⁸ breeding population. This additional effort makes it possible to assess the relative influence of each of these
²⁹ components on population growth rate. Alternatively, assessing the age structure in hunting bags has been
³⁰ used to infer the role of decreasing reproductive success in population declines in a number of game species
³¹ including ducks and geese but suffers from intractable biases (Fox & Cristensen, 2018). Of course, the latter
³² approach is not suited for protected/endangered species.

³³ Here we exemplify how, in dimorphic species, delayed maturity of males can be used for estimating adult
³⁴ survival and recruitment rate by differentiating male-like from female-like individuals in repeated winter
³⁵ counts. We used two non-native Ruddy duck (*Oxyura jamaicensis*) populations introduced in Europe as
³⁶ a study model. As numerous duck species, Ruddy duck is dimorphic, with newly born males looking like
³⁷ females until the prenuptial moult, which occurs in late winter. As a result of this late prenuptial moult
³⁸ of immatures, the apparent proportion of males increases over the course of the wintering season. These
³⁹ changes in apparent proportions of males during this period are therefore directly related to the proportion
⁴⁰ of immatures in the populations and thus to the reproductive success of the previous breeding season. We
⁴¹ estimated adult survival and recruitment rates and assessed the impact of two different eradication strategies
⁴² deployed in Great Britain and in France, respectively.

⁴³ 2 Materials & methods

⁴⁴ The Ruddy duck is a stiff-tailed duck native from the Americas. From seven individuals initially acclimated
⁴⁵ in the Slimbridge Wetland Centre in the 1940's (Gutiérrez-Expósito et al., 2020), a feral population began
⁴⁶ to establish in Great Britain with the first observed reproductive attempts in the wild in the 1960's (Figure
⁴⁷ 1). This feral population rapidly grew and spread to the entire country to reach more than 5,000 individuals
⁴⁸ in the early 2000s. By the end of the 1980's, a feral population began to establish also on the continent,

especially in France, supposedly owing to the arrival of individuals born in Great Britain. But contrary to what was observed in Great Britain, the Ruddy ducks did not spread much in France, with the vast majority of observations and breeding attempts clustering in the North-West of the territory. In France, during winter, almost no Ruddy duck is observed outside the lake of Grand Lieu (47.09°N , 1.67°W), which greatly facilitates the monitoring of this population. Ruddy ducks are considered as a major threat to the endangered native White-headed duck (*Oxyura leucocephala*) of the South-Western Mediterranean, because of hybridization and thus an elevated risk for genetic pollution and 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 implemented in the late 1990's both in Great Britain and in France (Gutiérrez-Expósito et al., 2020), and were followed by a European Ruddy duck eradication plan in 1999 (Hughes et al., 1999) (Figure 1).

The trends and status of populations of both White-headed duck and Ruddy duck are being assessed through population censuses only. It is thus impossible to assess the factors that impair recovery of the former and the efficacy of the eradication program for the latter. In particular, based on censuses alone, one cannot assess the relative effects of changes in adult survival and recruitment rates on population growth rates which are prerequisites to identifying limiting factors.

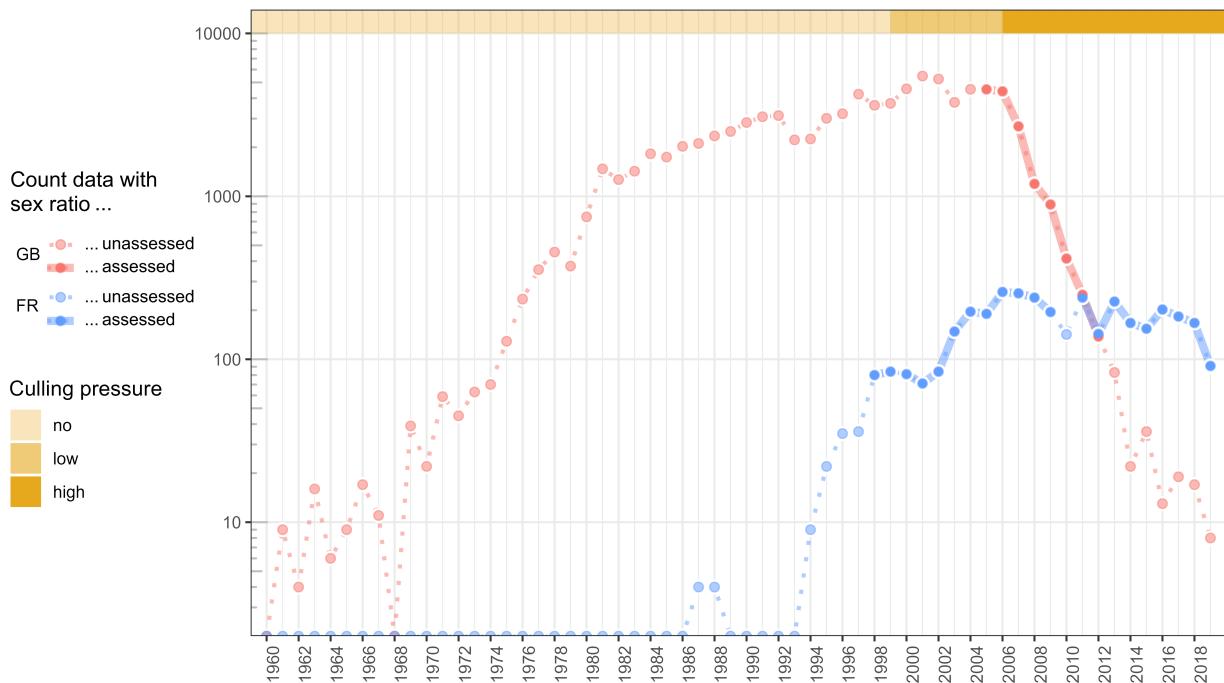


Figure 1: Temporal changes in the number of Ruddy ducks (log scale) in Great Britain (GB) and France (FR) from 1960 to 2019, with indications of periods when apparent sex ratios were also recorded

- Like many other ducks, Ruddy ducks and White-headed ducks both display delayed dichromatism thereby young males acquire the typical colourful plumage of their kind, and hence can be distinguished from females, over the course of the interbreeding season, typically by mid-winter for the earliest individuals (Baldassarre, 2014). Delayed dichromatism generally explains the discrepancies in the estimates of apparent proportions of males counted in winter vs counted in spring, or vs males determined from individuals culled in winter (Figures 2 & 3).
- Interestingly, delayed dichromatism enables estimating adult survival and recruitment/productivity by monitoring the seasonal evolution of apparent sex ratio and by making few and reasonable assumptions (see next section).



Figure 2: A Ruddy duck flock observed in winter including ten female-like individuals with a whitish striped cheek (some of which are immature males), four male-like individuals with a white cheek and a black cap (all adult males), three unidentified individuals (1st, 4th, and 10th from left) © Jay McGowan - 3 February 2013 - Tompkins, New York, United States

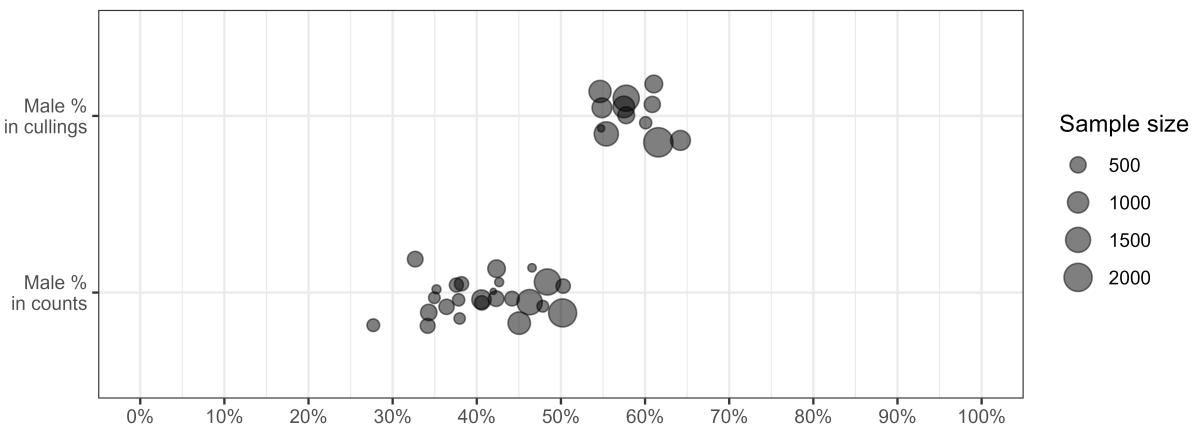


Figure 3: Proportions of males estimated through the internal examination of individuals shot as part of the eradication programme over one year in a population (Male % in cullings) and proportions of individuals displaying a male-like plumage in a population counted in winter (Male % in counts); discrepancies between the two estimates are due to delayed dichromatism (immature males looking like females before moulting); we exploited these discrepancies for estimating survival and productivity/recruitment

⁷⁴ We monitored the demography of Ruddy duck populations in both Great Britain (GB) and France (FR)
⁷⁵ using exhaustive counts on the wintering grounds during the period between December 1 and January 31.
⁷⁶ In addition, apparent sex ratios in winter could be accessible from counts that distinguished female-like from
⁷⁷ male-like individuals in winter. Such counts were performed from 2006 to 2012 in Great Britain, which
⁷⁸ corresponded to a period of strong decline of the population (Figure 1). In France, a monitoring accounting
⁷⁹ for apparent sex was performed in 1999, 2001-2009, and 2012-2019. The French population observed a
⁸⁰ rapid growth during the first years of the monitoring and then stabilized from 2006 onwards as a result of a
⁸¹ high culling pressure. In both countries, shooting was performed under the strict control of the authorities,
⁸² meaning that the exact number of individuals culled was known. Therefore, despite the age ratio in birds
⁸³ shot was not ascertained before 2009 in France, it is possible to grossly qualify the culling pressure in three
⁸⁴ categories for both countries: “no culling” before 1999, “low culling” between 1999 and 2005, and “high
⁸⁵ culling” from 2006 (see Figure 8 in Supplementary Material).

86 **2.1 Inferring adult survival and recruitment rates from changes in population
87 size and proportion of immatures**

88 The proportion of immature males is the difference between the proportion of female-like individuals between
89 winter and spring. The proportion of all immature individuals is twice this value if we assume an even
90 sex ratio at birth (Bellrose et al., 1961; Blums & Mednis, 1996) and comparable mortality rates between
91 immature females and immature males (Ramula et al., 2018; Wood et al., 2021). However, counts in spring
92 suffer from inextricable issues, such as a differential detectability between females and males. Fortunately,
93 the proportion of immatures can also be estimated only from winter counts by making the assumption of a
94 known and unchanging adult sex ratio over the monitoring period (Devineau et al., 2010).

95 The adult sex ratio is a prerequisite to estimate the proportion of immatures. No counts differentiating males
96 from females were available during the breeding period to estimate adult sex ratios, but we determined the
97 sex of each adult that was shot as part of the eradication programme both in Great Britain and in France.
98 Nevertheless, the small number of culled individuals in France prevented from getting robust adult sex ratios.
99 In Great Britain, the adult sex ratio estimated from the analysis of birds shot did not differ among months,
100 so data from adults collected over the whole biological cycle were pooled to estimate adult sex ratios. The
101 proportion of males did not statistically differ between the different years with more than 500 adults shot.
102 This is consistent with previous findings showing that adult sex ratios in ducks are usually highly stable over
103 the short-term (Wood et al., 2021) but may vary over the long-term. Therefore, we pooled data from all
104 adults shot as part as the control programme to estimate the adult sex ratio, see Equation (1).

105 Assuming the additive property of the binomial distribution, the proportion of immatures in a population
106 can be deduced from the proportion of males in adults (alternatively the adult sex ratio) and the proportion
107 of male-like individuals in the different count surveys in winter (assuming all these individuals are adult
108 males), see Equation (2). By combining the population growth rate, which is derived from the year-to-year
109 variation of an index of abundance of population size, to the proportion of immatures, one can derive adult
110 survival and recruitment rates, see Equation (3) and Figure 4. A key concept is that if the absolute value of
111 population size is known, numbers of adults and recruits can be estimated, see Equation (4).

Variable name	Description
<i>Observation (input)</i>	
AM	Total number of adult males shot as part of the eradication programme
AF	Total number of adult females shot as part of the eradication programme
$CML_{i,t}$	Number of male-like individuals counted in population i in year t
$C_{i,t}$	Number of individuals counted in population i in year t
$N_{i,t}$	Size of the population i in year t (maximum number of individuals counted in the wintering population)
<i>Parameter (output)</i>	
$p(m a)$	Proportion of males in adults (or probability of being a male knowing it is an adult)
$p(a \cap m)_{i,t}$	Proportion of adult males in population i in year t
$p(a)_{i,t}$	Proportion of adults in population i in year t
$p(re)_{i,t}$	Proportion of immatures/recruits in population i in year t
$s_{i,t}$	Adult survival rate, i.e. proportion of individuals in year $t - 1$ still alive in year t
$r_{i,t}$	Recruitment rate, i.e. number of recruits in population i in year t per individual in year $t - 1$
$S_{i,t}$	Number of adults in population i in year t
$R_{i,t}$	Number of recruits in population i in year t

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

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

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

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

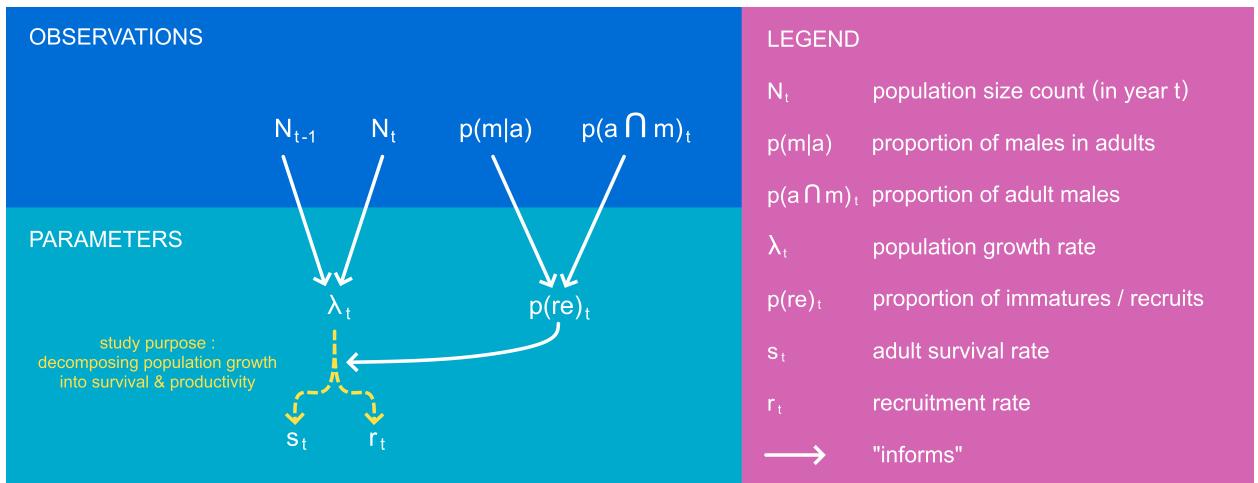


Figure 4: Outline of the method to disentangle the population growth into survival (adult survival rate) and productivity (recruitment rate)

112 2.2 Validating the method

113 Nevertheless, we developed an indirect approach to estimate the maximum expected recruitment rate without
 114 exploitation and assuming that the observed density levels did not affect components of the recruitment
 115 process. Estimated values above that maximum recruitment rate would reflect failure in detection of adult
 116 males. On the other hand, null or negative recruitment rates would reflect either that immature males had
 117 acquired the male plumage before the survey, or violation of the assumption about the stability of the adult
 118 sex ratio.

119 Practically, maximum recruitment rate is estimated from the difference between maximum growth rate and
 120 maximum adult survival rate, see Equation (5). This relationship comes from a simple reasoning for a closed
 121 population: population size in year t is equal to the number of adults that survived over year $t-1$ plus the
 122 offspring produced in year $t-1$ that survived until the reproduction period of year t , i.e. the recruitment in
 123 year t (Flint, 2015). For an open population, adult survival and recruitment rates are confounded to adult
 124 and recruit migrations, respectively, but this does not corrupt the equation. This relationship becomes more
 125 complex if a species with delayed maturity is considered, see Robertson (2008).

Variable 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 $t - 1$
λ_t	Growth rate of the population between year $t - 1$ and year t

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

126 Maximum adult survival was defined as a uniform distribution on the [0.7; 1] interval. The lower limit
127 corresponded to the upper range of survival rates observed in waterfowl species of similar weight, and the
128 upper limit was set to 1 because survival rates of long-lived waterfowl species are very high (Buxton et al.,
129 2004; Koons et al., 2014; Krementz et al., 1997; Nichols et al., 1992, 1997).

130 In both populations, the maximum growth rates occurred during their geographical expansion phase before
131 shooting operations (Figure 1). To estimate robust maximum population growth rates for both populations,
132 we smoothed annual growth rate values over a consistent time-period by using a linear regression on the
133 logarithm scale, see Equation (6). We discarded Great Britain data before 1972 as the estimates were
134 probably noisy when the population was low (below 50 individuals) (Figure 1). After reaching the threshold
135 of 1,000 individuals, the Great Britain (GB) population growth showed a strong inflexion despite culling
136 had not begun (Figure 1). This observation suggests that a negative density-dependence process might
137 occur beyond 1,000 individuals and led to consider only the first sequence of the time series to infer on
138 the maximum growth rate in Great Britain, i.e. 1972-1981. For the French (FR) population, the sequence
139 without culling pressure spread over the period 1994-1999.

Variable 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

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

140 Estimating vital rates within an acceptable range, as defined above, would not prove that our modelling
141 approach correctly tracked their year-to-year variability. In order to ascertain this aspect, we check the
142 correlation between the proportions of immatures and both survival and recruitment rates derived from
143 counts, to estimates derived from cullings, i.e. from individuals shot as part of the eradication programme.
144 As we restricted the dataset to years with more than 100 individuals shot in winter for sake of precision,
145 the analysis covered only five years of the time series of the GB population. Proportions of immatures were

¹⁴⁶ estimated from culled individuals by checking the presence of the bursa of Fabricius, which is present in
¹⁴⁷ immature individuals only (Hochbaum, 1942); see Equation (7). Adult survival and recruitment rates were
¹⁴⁸ then estimated by combining the proportion of immatures and Equation (3).

Variable name	Class	Description
$SI_{i,t}$	Observation	Number of immatures culled in the wintering population i in year t
$S_{i,t}$	Observation	Number of individuals culled in the wintering population i in year t

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

¹⁴⁹ 2.3 Assessing the impact of culling strategies

¹⁵⁰ During period when culling pressure was high (i.e. from 2006 onwards), eradication strategies differed between
¹⁵¹ Great Britain and France. In Great Britain, culling mostly occurred in winter (53.4% of adults were shot
¹⁵² before the 30th May), whereas it was mostly done during the breeding period in France (81.6% of adults
¹⁵³ were shot after the 30th May). We assessed whether or not these strategies had a different impact on
¹⁵⁴ populations by comparing growth rates and the relative contributions of both recruitment and survival on
¹⁵⁵ them (by comparing the average values over the high culling pressure 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 by early 2019 to intensify the culling pressure, especially during winter and spring.
¹⁵⁸ We therefore excluded the FR time series from 2019 onward in order to provide a comparison of homogeneous
¹⁵⁹ culling strategies.

¹⁶⁰ 2.4 Statistical framework

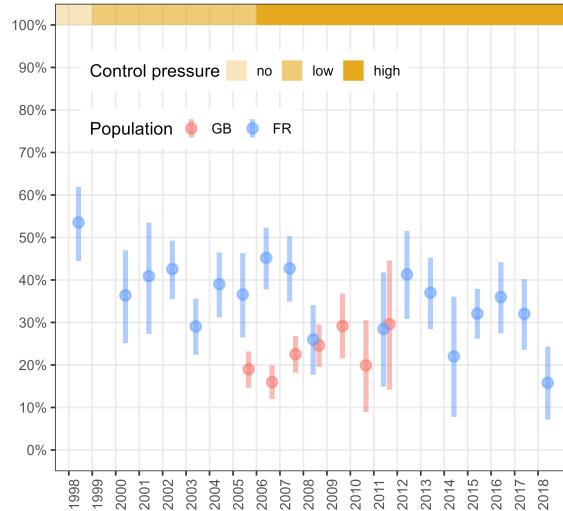
¹⁶¹ We used the Bayesian framework to implement all sub-models presented in Section 2. The Bayesian frame-
¹⁶² work is both straightforward and efficient to propagate error through the parameters. We used uninformative
¹⁶³ priors on all parameters. As the maximum growth rate is a life history trait expected to be stable among
¹⁶⁴ populations of a same species, we used an uninformative hierarchical prior for this parameter. We generated
¹⁶⁵ three chains of length 500,000, with a thinning of 10 to avoid autocorrelation in the samples, discarding
¹⁶⁶ the first 2,000 samples as burn-in. We assessed chain convergence using the Gelman and Rubin convergence
¹⁶⁷ diagnostic ($R < 1.1$, Gelman & Rubin (1992)). Models were fitted using NIMBLE (de Valpine et al., 2017) run
¹⁶⁸ from R (R Core Team, 2022). The values $\mathbf{X}[\mathbf{Y}; \mathbf{Z}]$ reported in Section 3 are the medians and the associated
¹⁶⁹ boundaries of the 95% confidence interval of posterior distributions. We preferred the median to the mean
¹⁷⁰ because of its robustness to skewed distribution.

¹⁷¹ 3 Results

¹⁷² 3.1 Estimating vital rates

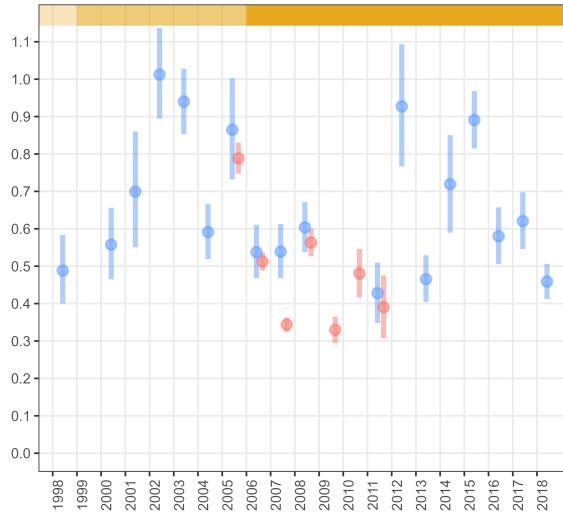
¹⁷³ The method successfully provided estimates and associated uncertainty for the proportion of immatures
¹⁷⁴ in both wintering populations. Similarly, adult survival and recruitment rates, i.e. the two components
¹⁷⁵ accounting for population growth rate, were also properly estimated (Figure 5).

Proportion of immatures in the population



Survival rate

Proportion of breeders still alive after one year



Recruitment rate

Number of recruits produced per breeder

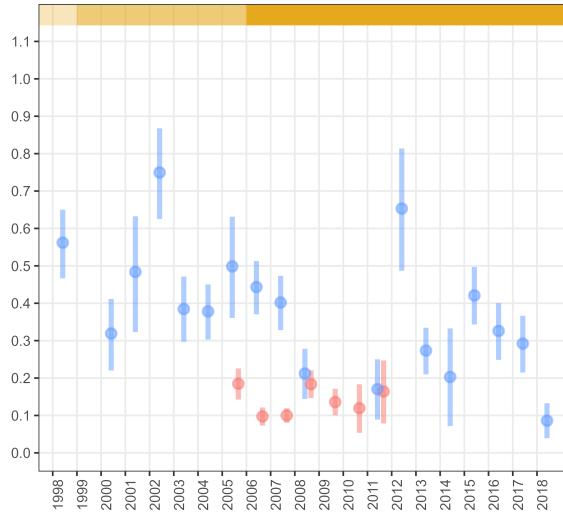


Figure 5: Temporal changes in the proportions of immatures and the vital rates following the culling pressure on Ruddy duck populations of Great Britain (GB) and France (FR); vertical bars represent the 95% confidence intervals.

176 The proportion of males in adults, which is a prerequisite to infer the proportion of immatures, was estimated
177 at 0.60 [0.59; 0.61]. The proportion of immatures ranged from 0.16 [0.07; 0.24] to 0.54 [0.44; 0.62], depending
178 on population and year. The lowest values were similar for the two populations, but the range of the
179 proportion of immatures in the GB population was far more limited (upper value GB: 0.30 [0.14; 0.45] &
180 FR: 0.54 [0.44; 0.62]). The proportion of immatures was stable over time in the GB population, while a
181 slight but significant decrease was observed for the FR population.

182 Adult survival rate ranged from 0.33 [0.29; 0.37] to 1.01 [0.89; 1.14]. None of the estimates was significantly
183 outside the range of a survival rate defined without immigration [0; 1]. No trend in adult survival rate could
184 be evidenced in any of the two populations, but patterns differed: adult survival in GB was both lower and
185 displayed a weaker inter-annual variability than in FR.

186 Recruitment rate ranged from 0.09 [0.04; 0.13] to 0.75 [0.63; 0.87]. All estimates were above 0, that is not
187 incompatible with reality. Moreover, the maximum recruitment rate was 0.68 [0.36; 0.78] (see Section 3.3),
188 and no estimates were significantly outside the range of recruitment rates defined without immigration [0;
189 0.78]. No trend was observed for the GB population, but recruitment rate decreased for the FR population
190 even if it was more noisy than for the proportion of immatures. Like for survival, the GB population had
191 lower values of recruitment rate with weaker variability than the FR one.

192 Lower values and weaker variability of both adult survival and recruitment rates estimated in GB than in FR
193 likely explained the differing trajectories of the two Ruddy duck populations, a sharp and constant decline for
194 the former vs slow and variable decline for the latter (Figure 1). In the FR population, the range in recruitment
195 rates (min/max difference: 0.66) was higher than the range of survival rates (min/max difference: 0.58).
196 Conversely, the range of survival rates (min/max difference: 0.46) in the GB population was far higher than
197 the range of recruitment rate (min/max difference: 0.08). This suggests that the variability of population
198 growth rate was mostly driven by recruitment in FR whereas it was mainly driven by changes in adult
199 survival in GB.

200 3.2 Examining the reliability of the estimates

201 In Great Britain, proportions of immatures derived from the count-based method were positively correlated
202 to those observed from culled individuals (Figure 6). Therefore, this result supports the hypothesis that the
203 proportion of female-like individuals in the wintering populations is efficient for assessing age structure and
204 hence reproductive output. The correlation was even stronger when considering vital rates (Figure 6), but
205 this was expected because the two methods estimating these vital rates shared a component, the growth rate
206 of the population (see Equation (3)). Interestingly, a 1:1 correlation is never reached for any parameters. The
207 proportion of immatures derived from counts is always lower than those observed in culled individuals. The
208 discrepancy between these two estimates is due to the fact that immatures are probably more vulnerable to
209 culling than adults and might then be over-represented in culling samples. As a consequence, the correlation
210 coefficients for both vital rates also differed. However, the differences between the two approaches do not
211 question the ability of the count method to track the interannual variability of the vital rates.

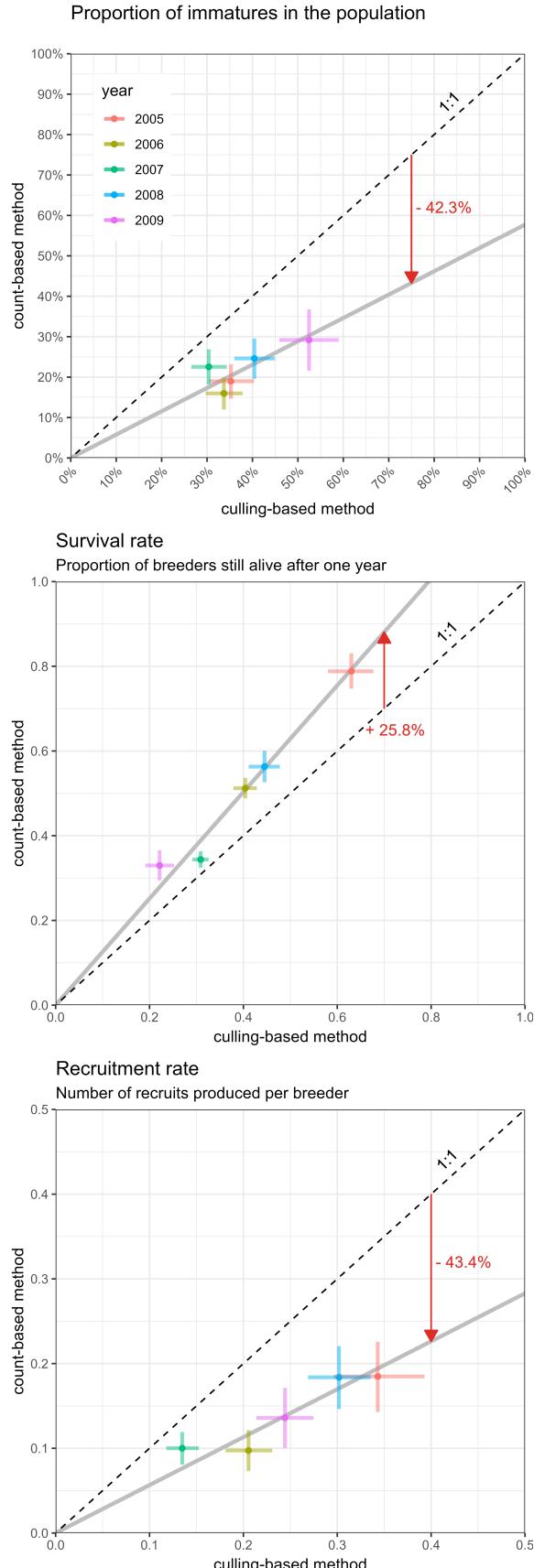


Figure 6: Relationship between parameter estimates derived from counts (count-based method) and those obtained from culled individuals (culling-based method).¹¹ only five years were available for the GB population; bars represent 95% confidence intervals and the red arrow indicates the direction and average differences between the two methods

212 **3.3 Assessing the demographic response to culling strategies**

- 213 When culling pressure was nil, maximum growth rates were very similar for the two populations (Figure 7),
214 respectively 1.45 [1.36; 1.55] and 1.52 [1.25; 1.88] for GB and FR. These values corresponded to a population
215 increase of 45% and 52% per year, respectively. Assuming a maximum adult survival rate of 0.85 [0.7; 1]
216 identical for both populations, we deduced maximum recruitment rates of 0.60 [0.42; 0.78] and 0.68 [0.36;
217 1.06] respectively for GB and FR.
- 218 Despite low sample sizes of sexed and aged culled individuals, proxies of the culling pressure exhibited
219 significant changes over time (Figure 8). We thus ranked the culling pressure according to this intensity.
220 High culling pressure occurred from 2006 onwards in both populations (although the signal was noisy).
221 However, despite similar levels of culling pressure, the culling strategies differed significantly between the
222 two populations, see Section 2.3. Under high culling pressure, the growth rate dropped to 0.56 [0.53; 0.59]
223 and 0.97 [0.94; 1.00] for GB and FR, respectively, which corresponded to a decrease of 44% per year and 3%
224 per year. This result showed that the GB population significantly decreased during the high culling pressure,
225 whereas the FR population was just stabilized.
- 226 Adult survival rate under high culling pressure was 0.44 [0.42; 0.46] and 0.62 [0.59; 0.64] for GB and FR,
227 respectively, and recruitment rates decreased to 0.13 [0.11; 0.15] and 0.32 [0.29; 0.34], respectively. The
228 resulting drop in growth rate of the GB population corresponded to a similar average drop in adult survival
229 rate (-0.41) and in recruitment rate (-0.47), whereas the stabilisation of the FR population was more caused
230 by a decrease of recruitment rate (-0.36) than by a drop in adult survival (-0.23). Overall, culling strategy
231 adopted in GB was more effective in affecting both adult survival and recruitment rates than that adopted
232 in FR.

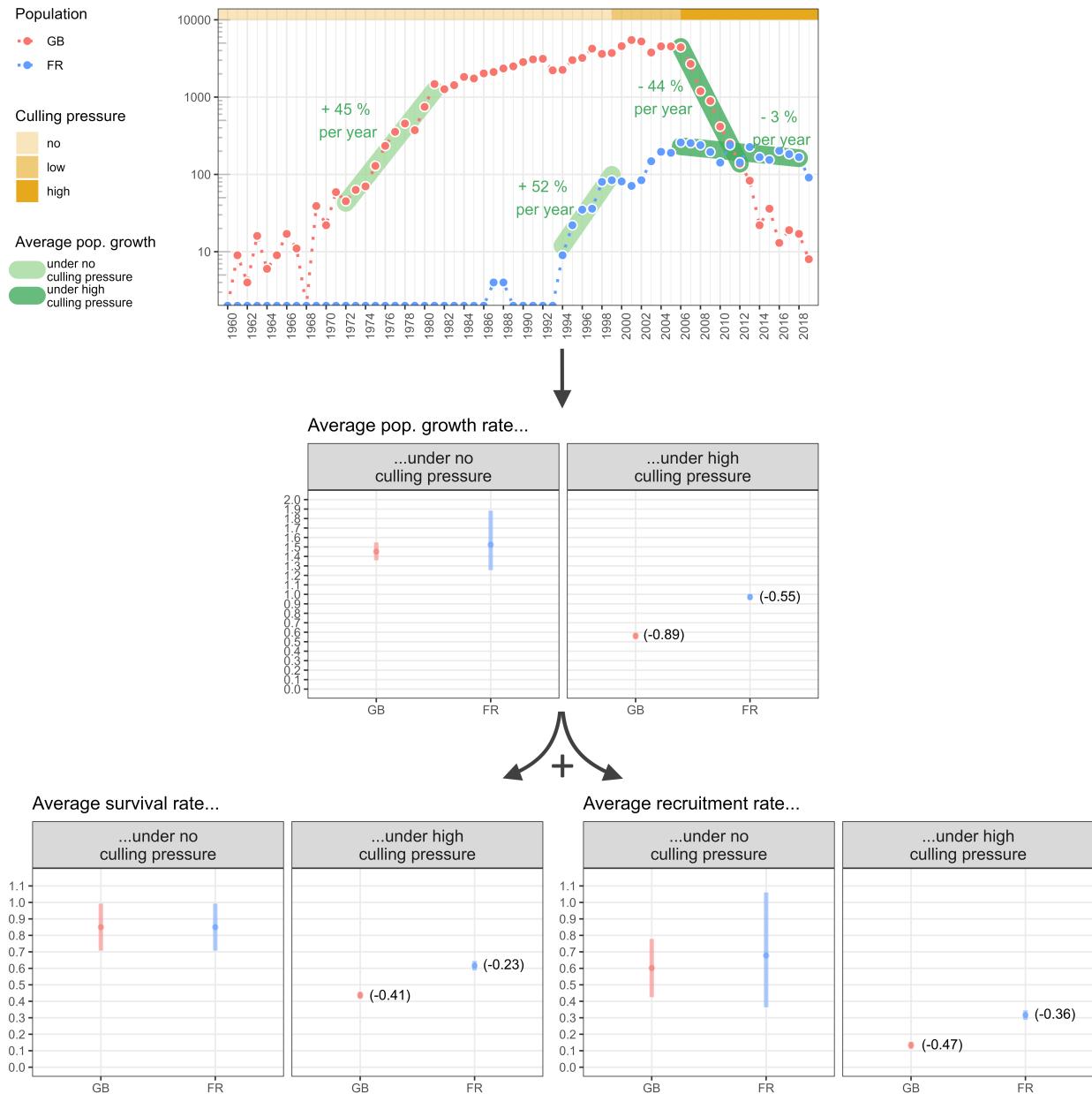


Figure 7: Average effects of culling pressure and different culling strategies (GB vs FR) on population growth rates (derived from counts only), and on adult survival and recruitment rates (derived from counts and apparent sex ratios); the culling pressure for the GB population mostly occurred during the prebreeding period, whereas it mostly focused during and after the breeding period for the FR population (see 2.3 for details); adult survival and recruitment rates under high culling pressure were averaged over a time-period observing a consistent culling pressure; vertical bars show 95% confidence intervals

233 4 Discussion

234 Disentangling the contribution of the vital rates to population growth rate is a key step towards a better
 235 understanding of the response of a population to management actions (Williams et al., 2002). We exploited
 236 delayed sexual dichromatism to develop a new approach based on counts to breakdown the apparent growth

rate of a population into two of its main structural components: adult survival and recruitment rates. The development of the “apparent sex ratio” method holds on a unique dataset of two comparable populations of the same species, the Ruddy duck. Both populations were monitored in a similar way from their introduction to a period of intense culling pressure, but the culling strategies differed sharply. The very similar demographic trajectories and properties of both populations in similar ecological setup enabled evaluating the response to both culling pressure and culling strategies.

4.1 Monitoring adult survival and recruitment rates

For the two populations, the vital rate estimates were within the same range, which demonstrates a certain consistency in the results obtained from the method. The greater variability observed for the FR population was expected because the time series covered a larger spectrum of culling pressure than the GB one. We did not detect temporal correlation in the demographic parameters between the two populations, suggesting that regional (e.g., weather) rather than large-scale factors (e.g., climate) prevailed. This is consistent with previous findings showing for example that in waterfowl, both breeding success and juvenile survival are conditional to the onset of laying, which is tightly related to local weather (e.g. spring temperature, cumulative rainfall, water levels) (Blums & Clark, 2004; Dzus & Clark, 1998; Folliot et al., 2017), and to local changes in predation pressure (Jaatinen et al., 2022).

Count surveys used to implement our model occurred in mid-winter, that is when some immature males might initiate their moult. This could partially violate the assumption that male-like individuals were adult males only, and hence potentially bias our estimates. Nevertheless, as survival estimates are within the range of those reported for similar species (Buderman et al., 2023; Buxton et al., 2004; Krementz et al., 1997; Nichols et al., 1997), the assumption seems reliable. Therefore, the time window of the count surveys must be chosen with care to fit the time preceding the initiation of moult of immature males.

In some years, the estimated values of adult survival were outside the range of expected values even if they never significantly exceed 1. One possible explanation for these discrepancies is a violation of the “closed population” assumption. Indeed, despite ringing data suggest that Ruddy ducks do not undertake long-distance seasonal movements in GB (Henderson, pers. com.), one cannot totally rule out that immigration occurred. The out of range outliers of both recruitment and survival rates that were observed in 2002 and 2012 in FR suggest then significant immigration events during these years.

The theoretical maximum population growth rate is an inherent trait related to the demographic characteristics of a species (Dmitriew, 2010; Niel & Lebreton, 2005). This trait is expected to be similar in all Ruddy duck populations anywhere in the world. In our study, we observed maximum growth rates that were very close for the two populations, which was expected because both populations experienced similar ecological conditions with an absence of harvesting and similar breeding conditions. Moreover, before the launch of the eradication programmes, the two populations also expressed a population growth much closer to the maximum expected values than any other native ducks species at the same period in the same areas. In the absence of culling, both populations expressed survival rates in the upper range of those observed in other diving ducks species (e.g. ~0.8 for Common pochard (Folliot et al., 2020; Nichols et al., 1997)). Ruddy duck tend to breed latter than both Common pochard and Tufted duck, yet nest predation has been found to decrease over the breeding season in a French fishpond complex (Bourdais et al., 2015). Therefore, both enhanced survival and nesting success might have accounted for high population growth rates of Ruddy duck populations in the absence of culling. Besides providing estimates of adult survival and recruitment rates that were consistent with observed increasing population sizes, our method also provided estimates consistent with both the decreasing phases occurring after the implementation of eradication programmes and the observed differences in populations growth rates under differing culling strategies. As expected, higher values of survival and recruitment rates were observed when the culling strategy focused on post-breeding season rather than the pre-breeding one.

Assuming that culling data provide a good picture of the year-to-year variability of age structure (Fox et al., 2014), the strong correlation between estimates derived from counts and those derived from culled individuals demonstrates the ability of the “apparent sex ratio” method introduced here to properly track

286 inter-annual fluctuations in demographic parameters such as survival and recruitment rates. The fact that
287 the observed correlation was strong despite being based on a short time series strengthens its robustness.
288 Furthermore, the strength of the relationship between parameters obtained through the two approaches also
289 supports that important assumptions of our model were met, such as constant adult sex ratio. The temporal
290 autocorrelation of the adult sex ratio might be explained by the fact that it integrates many age-cohorts,
291 which makes it structurally strong. Significant variations of the adult sex ratio can occur over the long term,
292 but our results suggests that it is not necessary to monitor and update it on a yearly basis. Proportions of
293 males in adults estimated in the present paper (i.e. 0.60) are within the range of those observed in native
294 Ruddy duck populations of North America (0.62 in Bellrose (1980)) and in other duck species (Wood et
295 al., 2021). The “apparent sex ratio” method always provided recruitment rates significantly lower than the
296 method based on culling data by a factor close to two, a result that is compatible with a higher vulnerability
297 of the immatures to shooting (Fox et al., 2014). For instance, in North America, immatures have been found
298 to be 1.3 to 2.6 times more vulnerable to hunting than adults in waterfowl (Bellrose, 1980).

299 Because estimates of survival were not available in the literature (see Buderman et al. (2023)), we could not
300 properly assess the accuracy of the “apparent sex ratio” method for estimating this parameter. Nevertheless,
301 circumstantial evidence support that the method is not heavily biased as detailed above. Thus the “count-
302 changing sex ratio” method would be much more efficient for monitoring key demographic parameters than
303 alternative methods such as those based on culling/hunting bag data that proved unreliable (Fox et al.,
304 2014), even when they focused on the end the hunting season to limit possible biases (Fox et al., 2016).

305 4.2 Assessing eradication strategies

306 Both populations responded to culling pressure by a significant decrease in their growth rate, meaning
307 that increasing mortality due to culling was neither compensated by increasing natural survival nor by
308 improved breeding success. The culling effort was therefore efficient to affect the demographic trajectory
309 of Ruddy duck in both contexts. However, the decrease in population growth was much stronger in GB,
310 where the population displayed a sharp decrease, than in FR where the increase was stopped and population
311 size remained more or less stable. The greater decline in population growth observed in GB compared to
312 FR was due to greater decline in both adult survival and recruitment rates. Overall, in both countries,
313 adult survival and recruitment rates seemed significantly affected by culling. However, the culling pressure
314 occurring before the breeding season, which affect only future breeders (pre-breeding culling strategy applied
315 in GB), seemed much more efficient in limiting both survival and recruitment rates than the culling pressure
316 occurring during nesting and young raising, which targets breeders and newly born individuals (breeding
317 culling strategy applied in FR).

318 As expected, the pre-breeding culling strategy had the same effect on adult survival and recruitment rates
319 because a bird killed before the breeding period reduces the breeding population (lower adult survival rate)
320 and prevents this bird from reproducing (lower recruitment rate). When the breeding culling strategy was
321 applied, the recruitment rate was more affected than adult survival. This was probably due to immatures
322 being much more vulnerable to shooting than adults (Bellrose, 1980; Fox et al., 2014). The compensation
323 hypothesis suggests that the higher harvest mortality of immatures can be compensated by increasing natural
324 survival (Cooch et al., 2014) but it is not supported by the observations. Overall, there was no evidence for
325 any compensation mechanism in either context. This might result from the fact that both populations were
326 far of reaching carrying capacity meaning that competition for resources was relaxed (Péron, 2013).

327 For more or less comparable culling pressure, the pre-breeding culling strategy proved much more effective.
328 This does not mean however, that the breeding culling strategy was not so. On the contrary, it proved
329 rather efficient for stopping both the population increase and range expansion in a first time, and in second
330 time to trigger a significant population decline by slightly increasing culling pressure. Thus when winter
331 culling is not possible, which was the case in FR, culling during the breeding season is effective for stopping or
332 reversing population increases in such species. The breeding culling strategy is however affected by the highly
333 variable detectability of immatures, as these individuals colonise new ponds. This results in fluctuations of
334 the recruitment rate and then threatens the long term efficiency of such strategy. The winter culling strategy

335 does not face such problem because of the habit of Ruddy ducks to gather in a limited number of sites during
336 winter (Johnsgard & Carbonell, 1996).

337 The response of the two Ruddy duck populations to culling pressure demonstrates the necessity to account for
338 the culling season to produce proper predictions. Predicting the impact of a harvest pressure on a waterfowl
339 population is then not only a question about how big is the harvesting effort, but also when harvesting occurs
340 (Kokko et al., 1998). Counter-intuitively, our results suggest that harvesting waterfowl during breeding has
341 far less impact on population growth rate than harvesting during winter. As a result, a target for effective
342 management of harvested waterfowl should be earlier onsets and endings of hunting seasons.

343 4.3 Waterfowl management implications

344 One major implication of our study concerns the timing of harvesting for limiting its impact on populations
345 growth rate. Counter-intuitively, our results show that the persistence of waterfowl populations should
346 benefit from earlier openings and closings of the hunting seasons (see above).

347 Tracking variations in abundance is a common tool to determine the conservation status of a population (e.g.
348 Folliot et al., 2022). But tracking abundance alone does not provide enough information for assessing the
349 underlying mechanisms behind the changes of population growth (Williams et al., 2002). In order to do that,
350 one must “dig deeper” (Austin et al., 2000), for example by monitoring individuals to assess parameters like
351 survival and recruitment rates (e.g. Arnold, 2018). However, monitoring individuals is time consuming (e.g.
352 Souchay & Schaub, 2016) and not always possible in endangered species. The method proposed here allows
353 circumventing these drawbacks in dichromatic species with delayed maturity of males. Among these species,
354 one can mention the White headed duck in Southern Spain, which is highly endangered and cannot be safely
355 monitored through capture-mark-recapture. Thus by improving census strategies and teasing apart the
356 effects of variations of adult survival and productivity on population growth through the approach presented
357 here, one could gather much more invaluable information about the pertinence of management strategies.

358 Finally, we want to stress the fact that the main aim of our approach was to decompose population growth
359 into its two main components and not to provide unbiased estimates of adult survival or recruitment rates.
360 However, if needed, censuses could be designed in such a way that would make this possible, at least in theory,
361 and in species presenting an observable delayed dichromatism. This property concerns most stiff-tailed
362 duck species (Johnsgard & Carbonell, 1996), as well as numerous other duck species, among which Tufted
363 duck, *Aythya fuligula*, Black scoter, *Melanitta nigra americana*, Common Goldeneye, *Bucephala clangula*
364 (*Bellrose*, 1980; Johnsgard, 1978). Modifying standard monitoring protocols to distinguish male-
365 like from female-like individuals is almost costless but worth the bet because it would provide substantial
366 increases in the efficiency of conservation/management actions (Nichols & Williams, 2006).

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A Supplementary Materials

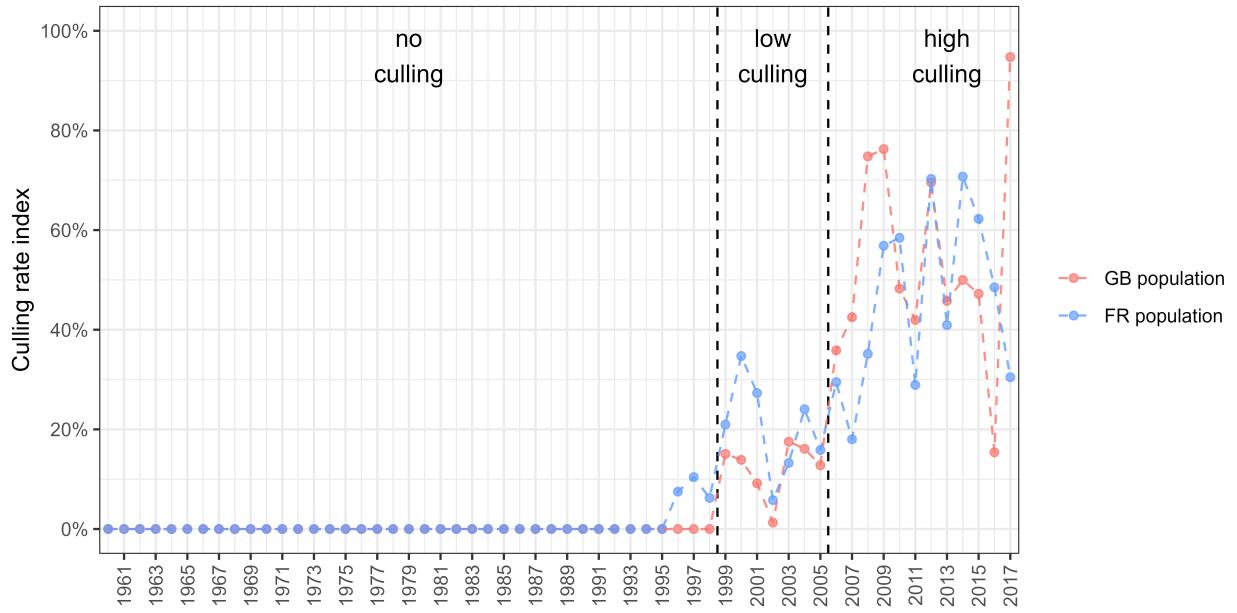


Figure 8: Definition of three periods of different culling pressures from an index based on an estimation of adult culling rate; as only half of the culled individuals were aged in France before 2009, we applied the average age ratio over 2009-2019 on unaged individuals to provide an estimate of the number of adults in cull data before 2009; culling rate increased over time, we therefore split the time series in three 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 varied around 20% for both countries, the culling rate then raised significantly for both countries, so we defined a “high culling” period from 2006 onwards