

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 juveniles of both sexes display a cover-up plumage similar to adult females. From two 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 - duck

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1 Introduction

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

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

Definitions

One defines the *recruitment rate* of a breeding population as the average number of recruits produced per each breeder (Flint, 2015). This parameter might sometimes be called *annual fertility* (Koons et al., 2014), *reproductive rate* (Cooch et al., 2014), *reproductive success* (Etterson et al., 2011), or *productivity* (Hagen & Loughin, 2008; D. H. Johnson et al., 1987). If one considers a species reaching its sexual maturity as early as its first year, all individuals are mature at the reproduction season. The recruitment rate is thus the ratio of the number of young adults at the reproduction season of year t , i.e. the recruits, to the number of all individuals at the reproduction season of the previous year, $t - 1$. The declination for species with delayed maturity follows the same process (see Robertson, 2008). The recruitment rate parameter is complex because it is composed of two main sub-parameters: the fecundity followed by the juvenile survival (Arnold, 2018; Etterson et al., 2011). Both sub-parameters can be split into other sub-parameters. The fecundity can be defined by the product of the nesting success, the average clutch size, and the hatching success. The

juvenile survival can be defined as the product of the post-hatching survival and the post-fledging survival, both critical life periods (Blums & Clark, 2004; Hill & Ellis, 2008). The recruitment rate as defined in the present study is thus a parameter integrating multiple life steps from the egg production to the young adult attempting to breed for its first time (Koons et al., 2017).

The use of recruitment rate in population management

Population conservation, harvesting, and control require tools in population management in order to reach quantitative targets, such as a population size for example (F. A. Johnson et al., 2021; Shea & NCEAS Working Group on Population Management, 1998). To do so, a first blind strategy is to test iteratively management rules to reach progressively an optimum. Such approach can be time-consuming given the intrinsic variability of the population response to its changing environment. It might also suffer from a rejection of the stakeholders because of the lack of transparency of an arbitrary process (Williams & Madsen, 2013). Another approach is to try to predict the growth rate of the population as a function of the harvest rate and other environment inputs. Such modelling approach can provide clues on the recovering time of a population upon a variety of management rules (Otis, 2006). These decision-support tools are then key inputs to status on the best management rules to implement. The growth rate of a population depends on the adult survival rate and the recruitment rate, see Equation (6) in Section 2.4. The adult survival is generally estimated by mark recapture/recovery methods (Lebreton, 2001). If the harvest pressure behaves as an additive mortality to the natural mortality for adults (e.g. Iverson et al., 2013), it is quite straightforward to predict its impact on the adult survival. The recruitment rate is thus a key parameter to build management scenarios. According to Blums & Clark (2004), the recruitment for diving ducks is poorly related to fecundity, but depends mostly on juvenile survival, which is driven by weather conditions. Studies on other birds concludes also on the weak correlation between fecundity and recruitment (e.g. Murray, 2000). The difficulty to track juvenile survival (Schmidt et al., 2008) demonstrates the interest to focus on the recruitment rate when accessible. The key to predict the growth rate of a population is then to estimate the value of the recruitment rate and its variability, potentially influenced by the harvest pressure (Anders & Marshall, 2005).

The variability of the recruitment rate

A waterfowl species that is released in a favourable habitat will naturally expand (Malthus, 1872). The growth of such a population reflects that the recruitment rate parameter is higher than the adult mortality rate. This expansion is limited by the carrying capacity of the habitat (Sayre, 2008). When a waterfowl species is endemic of an ecosystem and evolves in stable environmental conditions, the population size varies around the carrying capacity because the individuals compete for space or/and food (Nummi et al., 2015), which prevents the population from expanding indefinitely. This competition commonly induces a lower fecundity or/and a higher juvenile mortality. The population renewal is slowed down because the recruitment rate parameter is affected by density-dependent effects (Gunnarsson et al., 2013). For an endemic species evolving in stable environmental conditions, the recruitment rate compensates on average the adult mortality rate, which explains the stabilization of the number of individuals (Flint, 2015).

Waterfowl hunting induces adult and juvenile mortality (Bellrose, 1980). Intuitively, one expects that such a hunted population would observe lower adult survival and recruitment rate and then would rapidly deplete to its extinction. However, hunting waterfowl has a long history, and most of these species have persisted over time (Cooch et al., 2014). So paradoxically, hunting immature individuals does not always induce a decrease of recruitment rate. The heterogeneity of quality among immature individuals might explain this by inducing a compensation process if the harvest selects mostly individuals with a low reproductive potential (Gimenez et al., 2017; Lindberg et al., 2013). The recruitment rate can even increase because the harvest pressure reduces the densities and potentially the competition for space and food (Nummi et al., 2015; Péron et al., 2012). In conclusion, a limited exploitation of a population observing heterogeneity and/or density-dependent process might paradoxically increase or at least not affect the recruitment rate. Under moderate exploitation, a new balance between recruitment rate and adult mortality can be theoretically reached (Tsikliras & Froese, 2018). The size of a newly exploited population in stable environmental conditions should thus reach a different equilibrium, which is expected to be lower than the size without exploitation. This process explains why the exploitation of many waterfowl species is sustainable and has been lasting over a long time.

The fecundity and the juvenile survival, the two components of the recruitment rate, are very sensitive to

weather conditions (Blums & Clark, 2004; Folliot et al., 2017). The environment conditions are thus an additional source of variability of the recruitment rate. The response of the recruitment rate to a harvest pressure is thus not straightforward. It is noisy because of its sensitivity to environmental factors. It also depends directly on the intensity of harvest on the immature individuals and indirectly on the mitigation of the density-dependent effects.

What part of the recruitment rate gradient is necessary for population management?

In population management, a common question for a threaten or an invasive species is to determine the measure that will allow to reach a targeted population size/density in a limited time period (Shea & NCEAS Working Group on Population Management, 1998). For such question, the carrying capacity of the habitat is theoretically not reached. Any manager should then mostly focus on collecting knowledge on the maximum recruitment rate and its variability by removing the potential density-dependent effects occurring only for the highest theoretical densities (Eraud et al., 2021; Péron, 2013).

What is the ideal biological model to explore the gradient of the recruitment rate?

Waterfowl hunting has a long history, but the biological effects of long-term moratorium have been poorly surveyed (Martínez-Abraín et al., 2013). So there are few opportunities to explore the response of the recruitment rate to a gradient of pressure for such species. Alien vertebrate species are commonly introduced during release events (Saul et al., 2016) and usually observe a first period of colonisation on new territories without management measures. Since its presence might impact the balance of the colonized ecosystem, it happens that managers take strong control measures to restrict the growth of these populations or to eradicate them (Oficialdegui et al., 2020). Such species are then a good biological model to overcome density-dependent effects and explore the effects of a harvest gradient on recruitment rate.

How to estimate recruitment rate?

The recruitment rate parameter of a population can be assessed first by evaluating the fecundity of the breeding population and then by monitoring the survival from the egg life stage to the first-breeding event. To do so, it is necessary to monitor nests in habitats representative of the considered population (Blums & Clark, 2004). The survival of a chick to its recruitment can be done by capture mark recapture methods that are quite tricky to set up (Arnold, 2018; Blums & Clark, 2004; Schmidt et al., 2008). Even if such approach provides valuable information on the dynamics of the recruitment and can highlight the bottlenecks of survival, the fieldwork required to estimate both components is too time-consuming to generalize such approach for waterfowl population management on a long-term horizon.

In waterfowl, it is generally impossible to differentiate immatures from adults without examining birds at hand. Ageing individuals from samples coming from hunting bags is thus another opportunity to estimate the recruit proportion. Such approach suffers from two caveats. First, it is impossible to assess the recruitment rate when there is no harvest whereas it is necessary to predict what would happen if a moratorium seems required to allow a population to recover, or to calibrate a priori the harvest effort necessary to control an invasive species (G. C. Smith et al., 2005). Secondly, like any predation action, hunting is selective and provides a biased picture of the population age structure in favour of the immatures (Bellrose, 1980; A. D. Fox et al., 2014). The hunting bag analysis might then lead to overestimate the recruitment rate and consequently the maximum sustainable harvest rate, with adverse consequences on population conservation (A. D. Fox et al., 2014). Inferring recruitment rate from the proportion of immature birds trapped during tagging studies is also promising (Arnold, 2018), but the author admits that immatures might be more naïve and are then more likely caught in traps (Rguibi-Idrissi et al., 2003).

In waterfowl, it is common that adult males display brighter colours than adult females and immatures of both sexes, which display cover-up plumage similar to adult females (K. P. Johnson, 1999). This discrepancy is valuable because it can be observed and quantified from distance. Knowing adult sex ratio, such approach is promising because it requires only to count the proportion of birds of the two plumage kinds to infer the recruitment rate (C. M. Smith et al., 2001). Unlike the two previous methods, this one is non-invasive and requires an acceptable time investment, which allows to collect long time series and consequently to track recruitment rate variability.

Methodology of this study

From two populations of ruddy duck, a species introduced in Europe in the 40's, this study introduces a simple Bayesian model to infer recruitment rate from count data. A large part of this study focuses on assessing the viability of such approach. The comparison between two populations is a first step in testing the consistency of the method. A comparison to the common approach using samples from hunting bags aims at checking if the recruitment rate variability is well tracked and if the hypothesis stating that the recruitment rate is overestimated when using sample data is consistent with the results. Using two other approaches using population growth rates, one tests the consistency of the order of magnitude of the recruitment rate estimated from the counting method. Studying two populations is also an opportunity to discuss the response of the recruitment rate to a gradient of harvest pressure.

2 Materials & methods

2.1 Biological model

The ruddy duck is a diving duck species introduced in the United Kingdom in the 40's (Gutiérrez-Expósito et al., 2020). The first reproduction was observed in the 60's. The population rapidly grew to reach more than 5000 individuals spread over the entire country. A new population set up in France from the 90's, likely because of an arrival of a few individuals from the United Kingdom (UK). Unlike the UK population, the French one set up around a single wintering spot, the Grand Lieu Lake (47.09°N, 1.67°W), which facilitates the monitoring of this population. Since this species is considered as a threat to the white-headed duck because of the risk of a genetic introgression (Muñoz-Fuentes et al., 2007), an European plan of eradication has been adopted and control measures were taken in both countries (Gutiérrez-Expósito et al., 2020).

Just before the reproduction period on wintering spots, one can distinguish from shore individuals with male-like plumage from female-like individuals (Figure 1).



Figure 1: Typical observation of a ruddy duck flock in winter: 4 male-like individuals with a white cheek and a black cap, 10 female-like individuals with a whitish cheek and a dark stripe across it, 3 unidentified individuals © Jay McGowan - 3 February 2013 - Tompkins, New York, United States

It is noticeable that the apparent proportion of males in the counts from shore is far below the proportion of males in the samples from hunting bags (Figure 2). Assuming sex identification of samples is very accurate, such observation demonstrates that the counting method misses the identification of a significant part of males in the population. In many waterfowl species, immature individuals of both sexes display cover-up plumage similar to adult females (Reeber, 2015). Consequently, the counts in winter allows adult males to be distinguished from all other individuals (adult females, immature females, and immature males). This feature can be valuable to estimate the recruitment with two conditions. The season when adult males can be distinguished from all other individuals is sufficiently close to the breeding period to consider this age structure picture to be representative of the age structure of the breeding population. The adult sex ratio is known and stable over the considered time period.

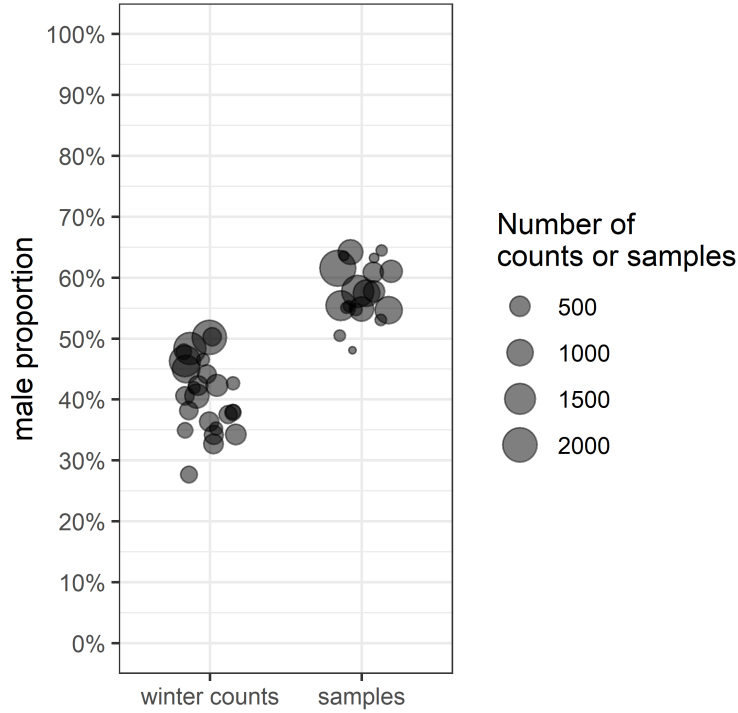


Figure 2: Apparent male proportion in winter counts vs male proportion in samples; for the first category, one point corresponds to the proportion of male-like plumage in a population counted in winter; for the second category, the male proportion is estimated from all ruddy ducks sampled over one year

The demography of both ruddy duck populations has been tracked thanks to exhaustive counts on the wintering spots during the period between December 1 and January 31. Controlled individuals between the counting date and the beginning of the reproduction period (set up to May 1 upon field observations of nests and Bellrose (1980)) were subtracted from the winter count to get a proxy of the breeding population size. Time series show that the two populations follow similar demographic histories (Figure 3). They grew freely in both countries until 1999. Control measures have been then applied from 1999 to 2005 in the UK and from 1999 to 2018 in France. In both countries, these management measures led to stop the expansion of the ruddy ducks. From 2005 in the UK and from 2018 in France, higher control effort led to a rapid depletion in both populations. This history underlines that both populations observed a large spectrum of harvest effort, from no pressure to very high pressure. For sake of interpretation, the time period 2001-2004 was classified in the *no harvest* category in France because the harvest pressure applied over this period was very limited with no effect on the population growth.

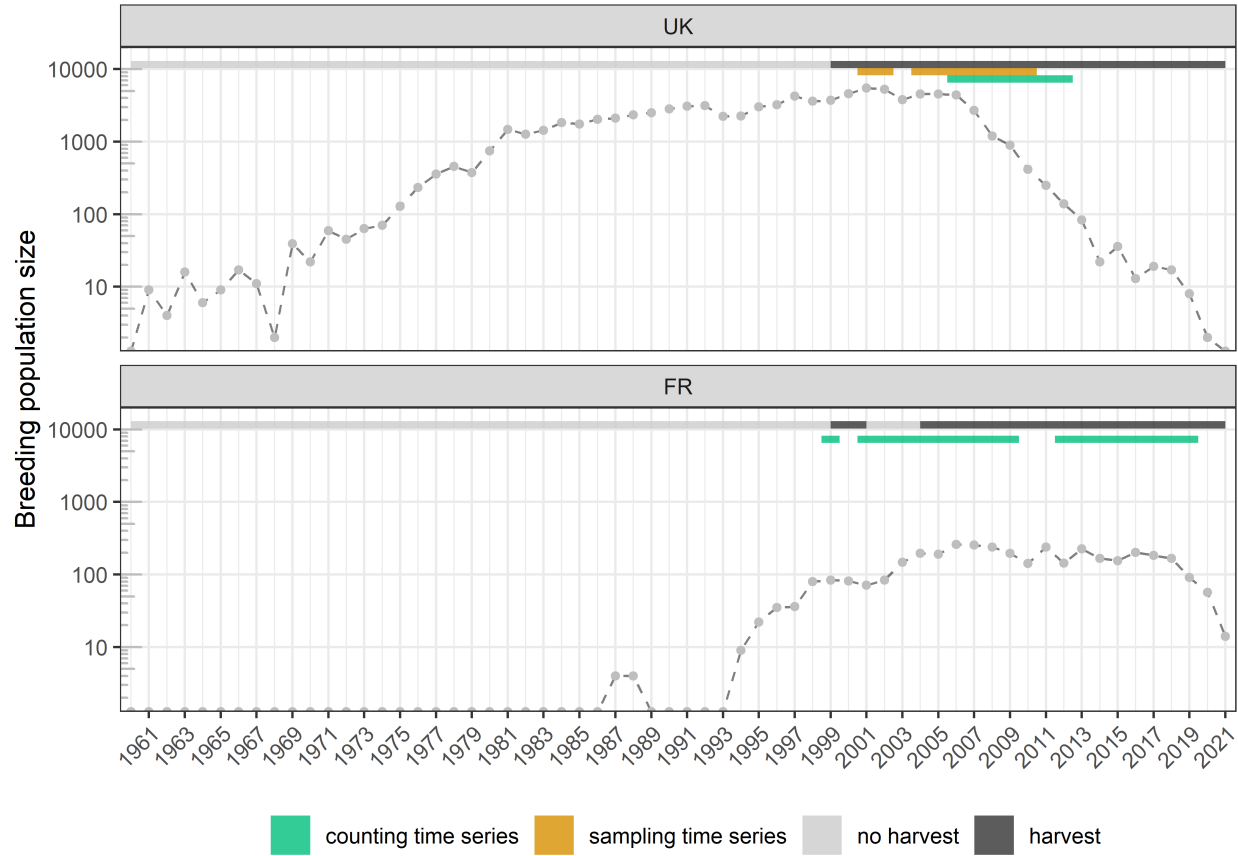


Figure 3: Evolution of the size of the two ruddy duck populations in light of the harvest pressure and the data time series

The counting dataset, which differentiates the male-like from the female-like individuals in winter, covers 7 years and 19 years in UK and France respectively (Figure 3). Combined together, the counting datasets cover different population dynamics corresponding to a gradient of harvest pressure. In France, data before 2004 correspond to a period of population growth with (almost) no harvest pressure, whereas data in the following years correspond to a stabilized population size with a significant level of harvest pressure (Figure 3). In UK, the counting data correspond to a quick population depletion associated to a high level of harvest pressure, especially before the reproduction period. In parallel, the sampling dataset, which corresponds to individuals shot in winter during control operations, covers 9 years only in UK, with 5 years in common with the corresponding counting time series.

2.2 Recruitment rate inference from count data

Adult sex ratio in waterfowl is generally biased towards males (Figure 2, Wood et al. (2021)). As a consequence, deducing the immature proportion from the adult male proportion is not straightforward because the adult proportion is not just twice as much as the male-like proportion. Even if the adult sex ratio may vary over a long time range, it is relatively stable over a few years (Wood et al., 2021). Sex identification in adult samples from hunting bags was available for both ruddy duck populations. However, the small population size in France prevents from getting precise adult sex ratios. A comparison over months in UK showed no difference in male proportion, so adult samples collected over the whole year were used to estimate the male proportion. A comparison of male proportion among years with more 500 samples did

not show significant interannual differences. As a consequence, all adult samples were pooled to estimate the male proportion in adults, see Equation (1).

Assuming the additive property of the binomial distribution, the proportion of immature individuals can be deduced from the cumulated counts of male-like individuals in the wintering population, see Equation (2). Only years with more than 100 individuals were selected. From this proportion and abundance index of breeding population sizes, the recruitment rate is straightforward, see Equation (3). If the absolute value of the breeding population size is accessible, the recruitment can be estimated, see Equation (4).

Name	Class	Description
SAM	Data	Total number of adult males in samples
SAF	Data	Total number of adult females in samples
$p(m a)$	Parameter	Proportion of males in adults (or probability to be a male knowing it is an adult)
$CAM_{i,t}$	Data	Cumulated number of type-male 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 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	Proxy of the size of the breeding population i in year t (maximum number of individuals counted in the wintering population minus removals before reproduction)
$r_{i,t}$	Parameter	Recruitment rate, i.e. number of recruits in population i in year t per breeder in year $t - 1$
$R_{i,t}$	Parameter	Number of recruits in population i in year t

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

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

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

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

2.3 Comparison with the sampling method

A direct estimation of the immature proportion can be made using samples from hunting bags, see Equation (5). By combining estimates of immature proportion and Equation (3), recruitment rates from samples were estimated to check the consistency of the counting method to track the recruitment variability. One selected only years with more than 100 individuals controlled in winter, which correspond to a 9-year period in UK. This sampling time series covers 5 years of the UK counting time series.

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

$$SI_{i,t} \sim \text{Binom}(p(i)_{i,t}, S_{i,t}) \quad (5)$$

2.4 Result validation using population growth rates

The simple relationship (a bit more complex if a species with delayed maturity is considered, see Robertson (2008)) between population growth rate, adult survival, and recruitment rate can be used to test the accuracy of the order of magnitude of recruitment rates estimated from the counting and the sampling methods, see Equation (6). This relationship comes from a simple reasoning for a closed population: the population size in year t is equal to the number of breeders that survived over year $t - 1$ plus the offspring produced in year $t - 1$ that survived until the reproduction period of year t , i.e. the recruitment in year t . The growth rate of a population is thus the sum of the adult survival rate and the recruitment rate (Flint, 2015).

Name	Description
N_t	Number of breeders in year t
D_t	Number of breeders dead after reproduction in year t
R_t	Number of recruits in year t
s_t	Adult survival rate, i.e. proportion of breeders in year $t - 1$ still alive in year t
r_t	Recruitment rate, i.e. number of recruits in year t produced per breeder in year $t - 1$
λ_t	Growth rate of the population between the reproduction periods of year $t - 1$ and year t

$$\begin{aligned}
N_t &= N_{t-1} - D_{t-1} + R_t \\
N_t &= N_{t-1} - (1 - s_t) \cdot N_{t-1} + r_t \cdot N_{t-1} \\
N_t &= s_t \cdot N_{t-1} + r_t \cdot N_{t-1} \\
\frac{N_t}{N_{t-1}} &= s_t + r_t \\
\lambda_t &= s_t + r_t
\end{aligned} \quad (6)$$

From the evolution of the breeding population size, population growth rate can be assessed every year to catch the variability range (6), or can be smoothed over a consistent time period to provide average population growth rate, see Equation (7), which is a linear regression on the logarithm scale.

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

$$\log(N_{i,t}) \sim \text{Norm}(N0_{i,J} + \log(\lambda_{i,J}) \cdot t, \sigma_{i,J}) \quad (7)$$

2.4.1 Analysis of the adult survival

The adult survival is commonly assessed by capture mark recapture (Lebreton, 2001). Combined to annual population growth rate, adult survival rate allows recruitment rate to be estimated each year, and then compared with the outputs of the counting method. Unfortunately, no tagging study was performed on the two ruddy duck populations. However, the relationship (6) could still produce annual adult survival estimates that can be discussed. To do so, annual population growth rates overlapping the counting time series were estimated.

Inconsistency on recruitment rate output, which is defined on $[0; \infty]$, would either lead to survival output < 0 , which points out an overestimation of the recruitment rate, or > 1 , which reflects that the recruitment rate cannot support the observed population growth and is thus underestimated. In between the two limit values, one still discuss the survival outputs by comparison with survival values published in the literature.

2.4.2 Comparison to a proxy of maximum recruitment rate

When population growth is not limited by a harvest pressure and/or by density-dependent effects, both recruitment rate and adult survival are close to their maximum potential. Given a conservative assumption on the maximum adult survival of ruddy ducks and maximum population growth rate estimated during no harvest time period, one can provide a proxy of the maximum recruitment rate. If the recruitment rate outputs of the model are significantly superior to this proxy, it means that the method overestimates the recruitment rate, which may reflect that some adult males are not detected during count surveys. By splitting the recruitment rate outputs upon populations and harvest categories, one can discuss of the impact of the harvest on the recruitment rate.

To do so, one estimates maximum population growth rates over time periods observing no harvest using Equation (7). Since the estimate of the UK population size is noisy below 500 individuals, one rejected data before 1972 (Figure 4). After reaching the threshold of 1000 individuals, the UK population growth observed a strong inflexion whereas no harvest pressure was applied. This observation led to split the analysis into two time series for the time periods used in the maximum growth rate inference in UK (Figure 4).



Figure 4: Evolution of the size of the two ruddy duck populations in light of the harvest pressure; on time periods without harvest, maximum population growth rates can be estimated (slopes in red for the UK and in blue for France)

To get proxies of maximum recruitment rate from Equation (6), one uses a very conservative prior on the adult survival by setting a uniform distribution on $[0.7; 0.9]$ (Buxton et al., 2004; Krementz et al., 1997; the lower limit corresponds to the upper range of survival rates observed in literature for species of similar weight, the upper limit corresponds to the range of survival rates of long-life species, Nichols et al., 1997). The average recruitment rates from the count data are estimated for each population and for each harvest category and compared to the maximum recruitment rates.

For all the sub-models in Section 2, the Bayesian framework was used for its efficiency and simplicity to propagate error through the parameters. One used uninformative priors on all parameters. One generated three chains of length 500000, with a thinning of 10 to avoid autocorrelation in the samples, and one discarded the first 2000 samples as burn-in. Chain convergence was assessed using the Gelman and Rubin convergence diagnostic ($R < 1.1$, Gelman & Rubin (1992)). One fit the models using NIMBLE (de Valpine et al., 2017) run from R (R Core Team, 2020). Data and code are available here: https://github.com/adri-tab/Ruddy_duck_recruitment_rate. The values $\mathbf{X}[\mathbf{Y}; \mathbf{Z}]$ reported in results are the medians and the associated boundaries of the 95% confidence interval of posterior distributions. The median was preferred to the mean because of its robustness to skewed distribution.

3 Results

3.1 Recruitment rate variability

The male proportion in adults, which is necessary to infer on the recruitment rate from count data, is estimated at 0.60 [0.59; 0.61]. The counting method provides estimations of the recruitment rate, see Figure 5A. In UK, values vary from 0.06 [0.05; 0.07] to 0.27 [0.20; 0.34] recruits per breeder, and in France, 0.08 [0.04; 0.12] to 0.76 [0.64; 0.88] recruits per breeder. There are significant year-to-year variations with a maximum amplitude of 0.68 recruits per breeder in France (9.5-time variability). On the available period, recruitment rate in UK is smaller than in France. Recruitment rates are estimated in both populations over 5 years, and no correlation is observed between the two populations. The lowest recruitment rate observed in France, which is in 2019, corresponds to the start of the depletion of the population. It is noticeable that it is in the same range than the UK values, also estimated during a strong population depletion.

Recruitment rates estimated from UK sample data are consistently higher than estimates from the corresponding count data, Figure 5A. The correlation between the two methods is strong and points out that the sampling method overestimates the recruitment rate by 44% compared to the counting method, Figure 5B. Estimation precision is similar for the two methods. The UK population started to deplete from 2006, but no significant shift is observed between the two periods.

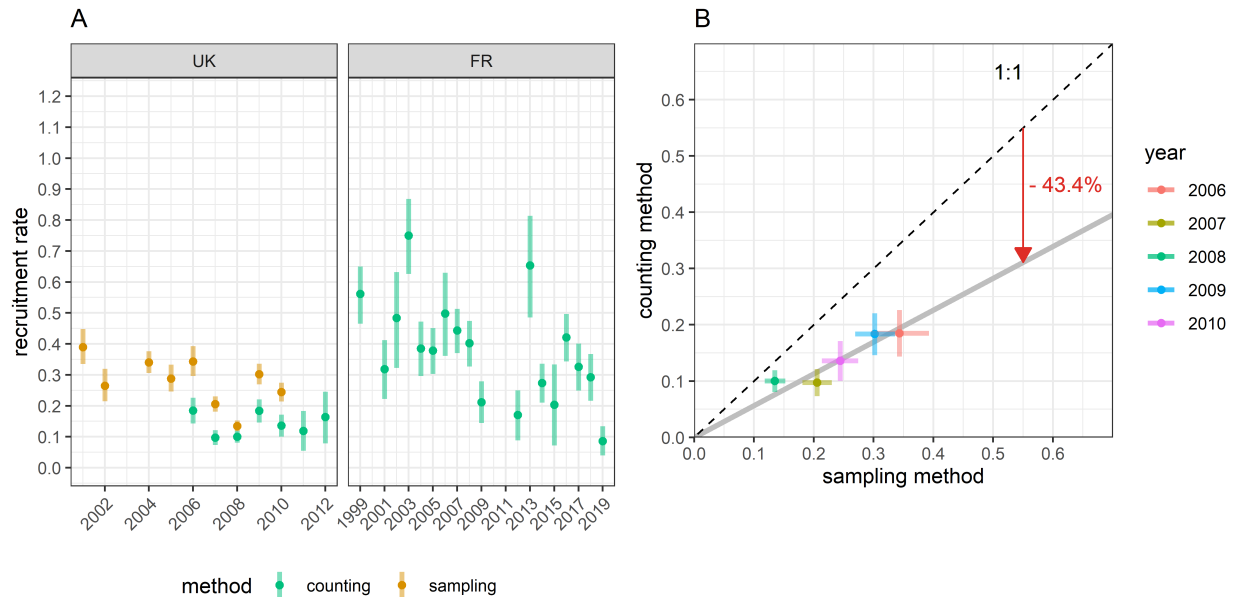


Figure 5: (A) Estimates of recruitment rate, i.e. average number of recruits produced per breeder; (B) Comparison of the recruitment rate values between the two estimation methods; bars define the 95% confidence intervals

3.2 Consistency of the corresponding adult survival

Adult survival rates were deduced from the recruitment rate estimates and the observed population growth rates, see Figure 6A. In UK, values that are obtained from the counting method ranged from 0.21 [0.20; 0.22] to 0.68 [0.65; 0.72]. In France, survival rates vary from 0.39 [0.34; 0.44] to 1.08 [0.98; 1.17]. Like recruitment rates, there is significant year-to-year variability without clear temporal structure in both populations with a maximum amplitude of 0.69 in France (2.8-time variability). Unlike the recruitment rate, the survival rate in 2019 in France is not a low outlier.

As expected, survival rates estimated from UK sample data are consistently lower than estimates from the corresponding count data, Figure 6A. The correlation between the two methods points out that the sampling method underestimates the survival rate by 32% compared to the counting method, Figure 6B. Estimation precision is similar for the two methods. The sample time series shows that the adult survival is significantly lower after 2006, which corresponds to the start of the depletion of the UK population.

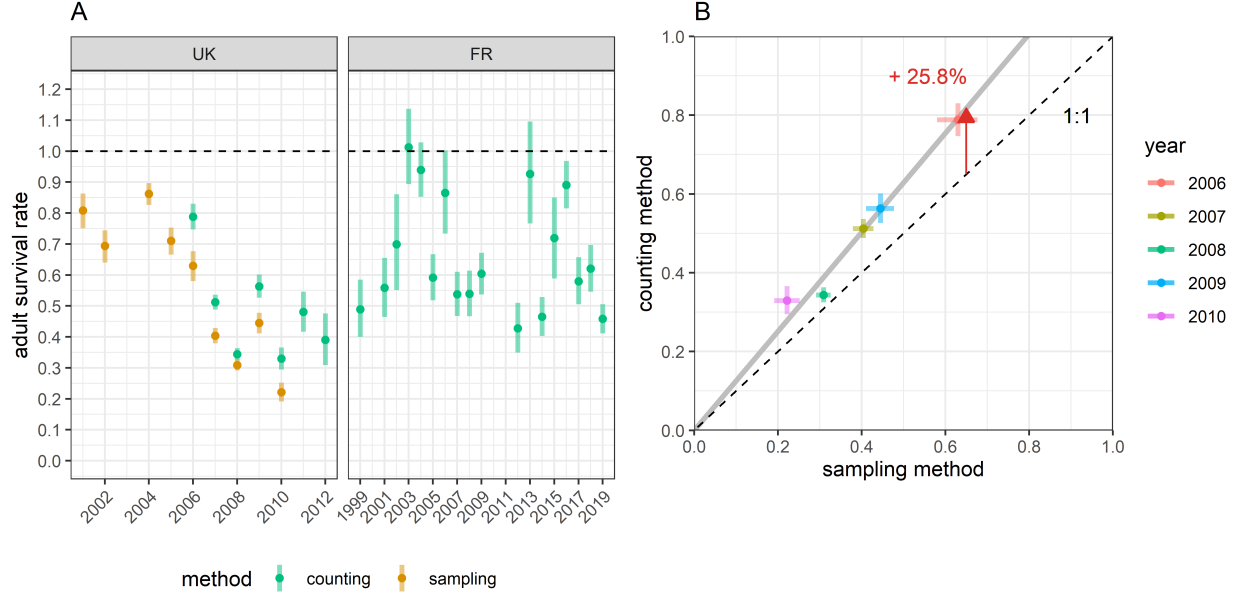


Figure 6: (A) Estimates of adult survival rate using population growth rates; (B) Comparison of the survival rate values between the two estimation methods; bars define the 95% confidence intervals

3.3 Comparison to maximum recruitment rate

Maximum population growth rates are similar for the two populations, 1.45 [1.36; 1.55] and 1.47 [1.29; 1.68] for UK and France respectively, which corresponds to an increase of about 45% per year (Figure 7). After reaching a certain size (~ 1000 individuals), the UK population growth rate falls to 1.06 [1.04; 1.07], which corresponds to an increase of 6% per year, even though no harvest pressure was applied on it.

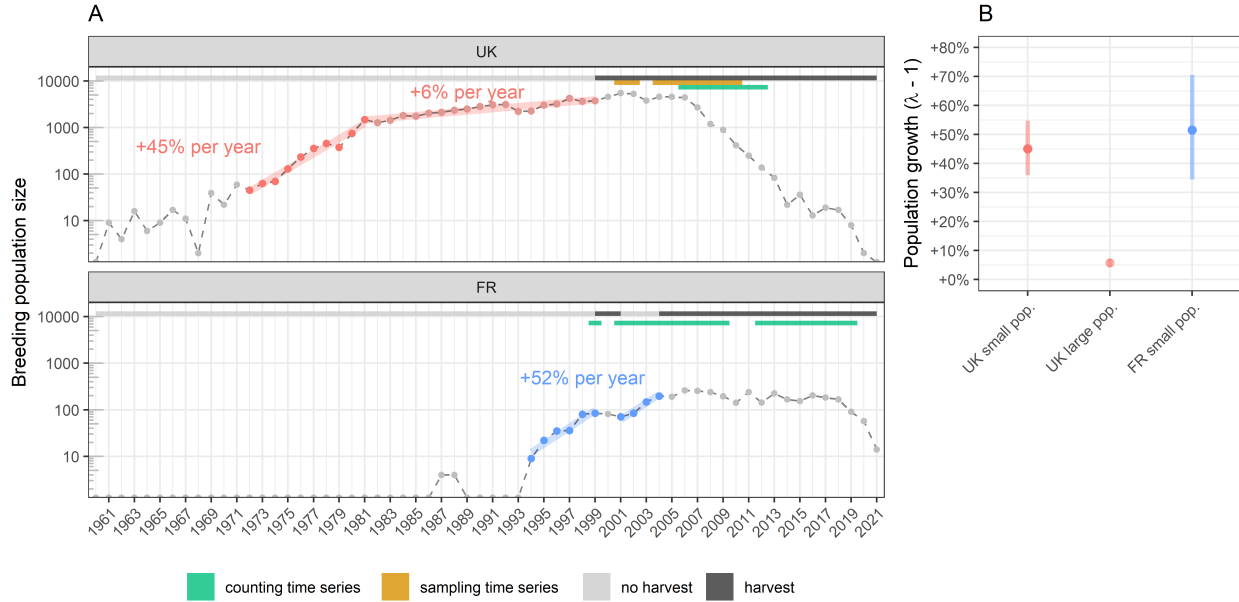


Figure 7: (A) Estimates of the maximum population growth without harvest ($\lambda - 1$); two estimates were produced for the UK population because the growth rate dropped significantly when its size reached more than 1000 individuals; (B) Growth rate estimates; bars define the 95% confidence intervals

311 Upon the conservative assumption of a maximum adult survival uniformly distributed over 0.70 to 0.90,
 312 the maximum recruitment rate reaches 0.65 [0.51; 0.75] and 0.66 [0.45; 0.90] recruits per breeder for UK
 313 and France respectively (Figure 8). When there is no harvest, the estimated average recruitment rate of
 314 the French population is in the range of the proxy of the maximum recruitment rate, 0.51 [0.46; 0.57]
 315 recruits per breeder. When there is harvest, the average recruitment rates are 0.14 [0.12; 0.16] and 0.33
 316 [0.31; 0.36] recruits per breeder for the UK and France respectively. Both values are significantly lower than
 317 the maximum recruitment rate, and it is noticeable that the average recruitment rate is lower for the UK
 318 population, which is in depletion over the count time series, than for the French population, which of the
 319 dynamic is mostly stable over the monitored period.

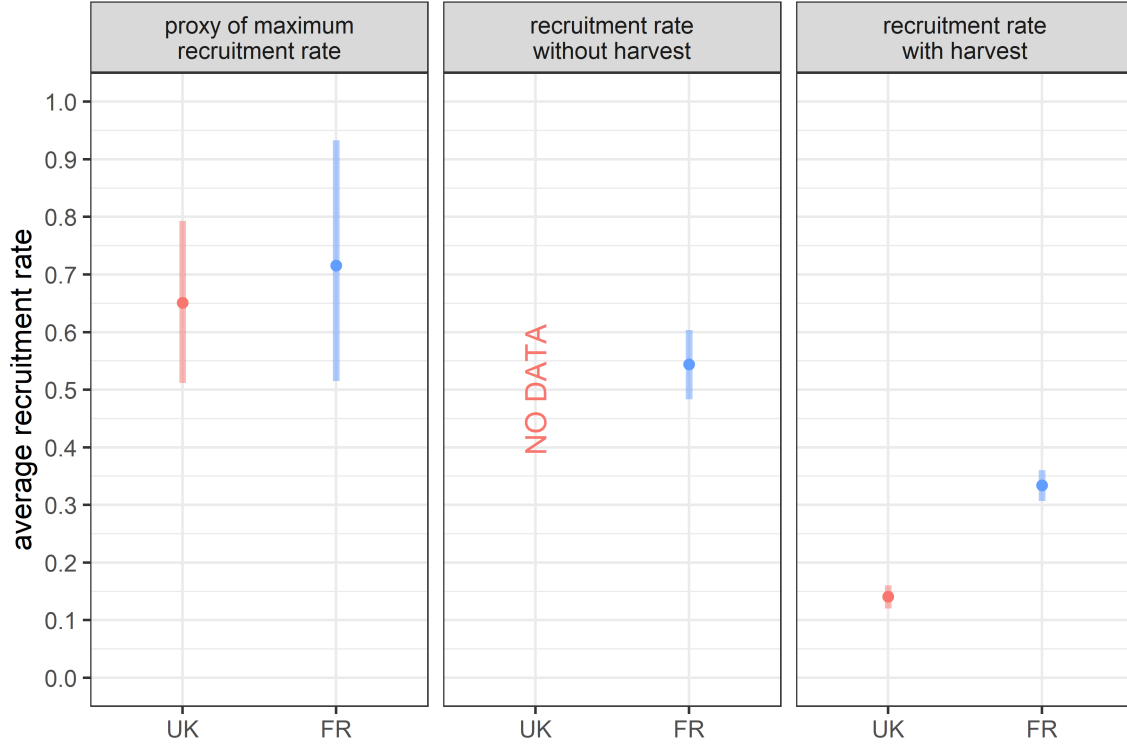


Figure 8: Comparison between proxies of maximum recruitment rate and average recruitment rates estimated with and without harvest (*counting* method only); proxies are estimated by using the maximum growth rates; bars define the 95% confidence intervals

4 Discussion

Count data in waterfowl that differentiate adult males from other individuals are successfully used in this study to infer estimations of recruitment rates. Since this parameter usually explains mostly the population growth in waterfowl (e.g. Arnold, 2018), the non-invasive method introduced in this study might be considered as a candidate tool to monitor at low cost waterfowl populations. In the following section, one checks the accuracy of the method from indicators that were developed for this purpose. From the outputs on the two populations of ruddy duck, one discusses about the effects of the harvest on the recruitment rate and its implications on waterfowl management.

4.1 Accuracy of the counting method

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

Assuming that the sample data provide a good picture of the interannual variability of the recruitment rate, the good correlation with the outputs of the counting method demonstrates the ability of this method to

track the recruitment rate variability. This result is quite robust because the correlation is obvious with only a five-year time series. The assumption of a constant adult sex ratio over time is then acceptable because a significant change in adult sex ratio among years would have biased the evolution of the recruitment rate. Since this ratio integrates many age-cohorts, the temporal autocorrelation is structurally strong. Significant variations can then occur only every multiple years, especially if the species is long-living. Consequently, it is not necessary to monitor and update the adult sex ratio on a yearly base. The adult sex ratio found here on a restricted time period is in line with the ruddy duck in its native area (0.62 in Bellrose, 1980) and with other duck species (Wood et al., 2021). The robustness of the correlation between the two methods might be overrated because two successive population size values are parts of the recruitment rate, which mechanically scale the outputs. It explains why the correlation on the immature proportion, the other component of the recruitment rate, is a bit more noisy than for the recruitment rate (Figure 9A). The uncertainty around the estimates is similar for the two methods even though the counting method is more indirect to infer on the recruitment rate, which is satisfying.

The counting method always provides recruitment rates significantly lower than the sampling method by a factor close to two, a result that is in line with the hypothesis that the harvest is generally selective towards immature individuals in waterfowl because they are more vulnerable than adults to hunters (Bellrose, 1980; A. D. Fox et al., 2014). For hunted duck species in North America, the harvest-induced mortality on first-year immatures compared to adults is higher by a factor ranging from 1.3 to 2.6 (Bellrose, 1980). This is a robust result because the approach used to control ruddy ducks differ strongly from usual hunting practices and is *a priori* less selective. It is especially clear in the UK, for which control operations occurred in winter using long-range rifles that prevents the bird from escaping from the threat. The assumption on the accuracy of the counting method is then not excluded from the consistency of this result.

Annual adult survival rates deduced from observed population growth rates and recruitment rate estimates are on average in line with the literature on species of similar weight (Buxton et al., 2004; Krementz et al., 1997; Nichols et al., 1997), which reflects that there is no apparent scaling issue. The assumption that male-like individuals corresponds only to adult males is then acceptable. This result supports that the counting method is poorly biased if it is. However, some adult survival rate values are outside the range of expected values even if they never significantly exceed the maximum possible value of one. A likely reason to these extreme values is a corruption of the closed population assumption on some years. Indeed, if there is an arrival from another ruddy duck population, the true recruitment cannot explain by itself the apparent population growth and indirectly leads to an overestimation of the adult survival.

Proxies of maximum recruitment rate are very close for the two populations. This strengthens that the ruddy duck species reached its intrinsic biological reproduction limit, at least given the environmental conditions of the western Palearctic. The consistency of this intermediate result suggests that the population size estimation is quite good for both populations and demonstrates that their evolution is well tracked even with a few individuals. The average recruitment rates estimated from the counting method, with and without harvest, are never higher to the proxies of maximum recruitment rate for both populations. The assumption on the accuracy of the counting method is then again not excluded from the consistency of this result.

Overall, even if the true values of recruitment rates are not known to test the accuracy of the counting method, a beam of arguments support that the method is not heavily biased. This consists in a big difference with the sampling method as demonstrated in A. D. Fox et al. (2014), even when one considers a age structure picture that is limited to the end of the hunting season to limit the bias (A. Fox et al., 2016).

4.2 Influence of harvest on the recruitment rate

Only the French population was monitored over a period covering years without and with harvest. The harvest pressure, that is defined into a binary variable (no harvest / harvest), affects on average negatively both the recruitment rate and the adult survival for this population, as expected. If it explains only 4.6% of the variance of the adult survival, this value raises to 19.3% for the recruitment rate of the French population. The harvest pressure applied in France is thus a factor that likely induces a strong juvenile mortality that

impacts the recruitment rate, but a negligible mortality on the adults. This conclusion is obviously opposed to the hypothesis that the heterogeneity in immature individuals would dampen the effect of the harvest pressure on the resulting recruitment rate. Two points can however explain this apparent discrepancy. Since the management targeted the eradication of this ruddy duck population, the harvest on immatures might be simply far higher than what the population could compensate and finally affects the recruitment rate. Also, the population started to be controlled when it was still growing at a high rate, so immature individuals were not suffering from density-dependent effects and were consequently sensitive to any additional mortality sources, like the new harvest pressure for instance. The low impact of the harvest on adult survival compared to the recruitment rate might be due to the timing of the management strategy adopted in France. Since the culling efficiency is poor on the wintering spot, most of control operations occurred in summer just after the reproduction, when the proportion of immature birds is the largest.

The UK population depleted from 2005, which also corresponds to a significant increase of the harvest effort. Even if only a few data from the sampling method are available before and after this year, it seems that the recruitment rate is not affected by this increase of harvest, but was already in the lower range of the recruitment rate of the French population when it was exploited. On the other hand, the adult survival dropped significantly from 2005. This differs strongly from the response of the French population to the harvest. Unlike in France, a significant part of the control operations in UK occurred in winter, which could explain this difference. Indeed, winter corresponds to the season just before the reproduction period, when the proportion of immatures in the population is the lowest, the juvenile survival being far lower than adults (e.g. Arnold, 2018). The adult survival seems then mostly affected by the harvest pressure applied in winter.

The different responses to the harvest pressure of the two ruddy duck populations demonstrate that it is necessary to account for the time window over which the harvest occurs to produce proper predictions. Controlling a waterfowl population is then not only a question about how big should be the harvest effort, but also mostly when this effort should focus within a year to be efficient. These first insights suggest that further investigation on this topic would be valuable to calibrate the response of the population to different harvest regimes.

4.3 Implication in waterfowl management

Age ratio, or indifferently recruit proportion, is commonly used to describe the renewal capacity of a waterfowl population and to track the evolution of its productivity (Bellrose, 1980; Robertson, 2008; Rodway et al., 2015; C. M. Smith et al., 2001; Zimmerman et al., 2010). The recruitment rate is however a better indicator than the age ratio, the latter having only the advantage to be more directly accessible. Indeed, the age ratio/recruit proportion does not account for the dynamics of the population and reflects the population productivity only if the population growth is steady. For instance, for a breeding population of 100 individuals reaching the next year 100 individuals and then 60 individuals the second year, a 1:1 age ratio, or a 50% recruit proportion, for both years reflects actually a strong decrease of the recruitment rate, respectively 0.5 recruits per breeder and 0.3 recruits per breeder. This demonstrates that the age ratio/recruit proportion suffers from caveats that can be misleading for a manager. According to Blums & Clark (2004), the recruitment for diving ducks is not related to the fecundity, but depends mostly on the juvenile survival, the other component of the recruitment that is mostly driven by the weather conditions. Studies on other birds also conclude of the poor correlation between fecundity and recruitment (e.g. Murray, 2000). Fecundity alone does not provide all knowledge that is required for a manager to understand the dynamics of a population.

Adult survival and recruitment rate equally influence the growth rate variability of the studied ruddy duck populations, but the relative variability of the adult survival is more than three times smaller than the recruitment rate. This observation is in line with the demographic buffering, or canalization hypothesis, on the adult survival parameter (Gaillard & Yoccoz, 2003; Lenzi et al., 2021). Arnold (2018) even demonstrates that the recruitment rate can be the most influencing factor on the population growth in some waterfowl species. Population management in waterfowl cannot neglect a careful monitoring of the recruitment rate, even if this parameter might be more difficult to track compared to the adult survival. A drop in the recruitment rate points out that a population renewal is affected but does show the causation. It is however

a signal that intermediate life stages before recruitment must be investigated to provide a diagnostic on the changes of the environment conditions that have affected the recruitment rate.

Immatures are more prone to die naturally than adults and are submitted to density dependent processes, which explains why the recruitment rate is the most sensitive parameter to density dependent effect (Koons et al., 2014). The evolution of the UK population size seems to show first signs of density dependence from 1000 individuals, but the process was obviously not big enough to fully curb the population growth. Since there is a strong correlation between the number of birds observed and the number of sites occupied by the birds, this inflexion may be simply due to a limited number of new favourable sites to be colonized. Such density dependent process implies that culling mostly immatures could have only a limited effect on the population dynamics if the harvest pressure remains moderate. Considering that the harvest effort occurring in winter impacted mostly the adult survival and led to the strong depletion of the UK ruddy duck population, harvesting early in the season should be favoured if the objective is to maximize the catch in preserving the resources. If the goal is to eradicate a population, a strong effort should be done especially in the late season just before the reproduction, as done in the UK. These hypotheses still requires to be tested thanks to a population model linking the harvest rate to state variables describing the population. Such tool is valuable to assess precisely the impact of the harvest pressure and to test hypotheses on the functioning of the harvest mortality (Plard et al., 2019).

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

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A Supplement

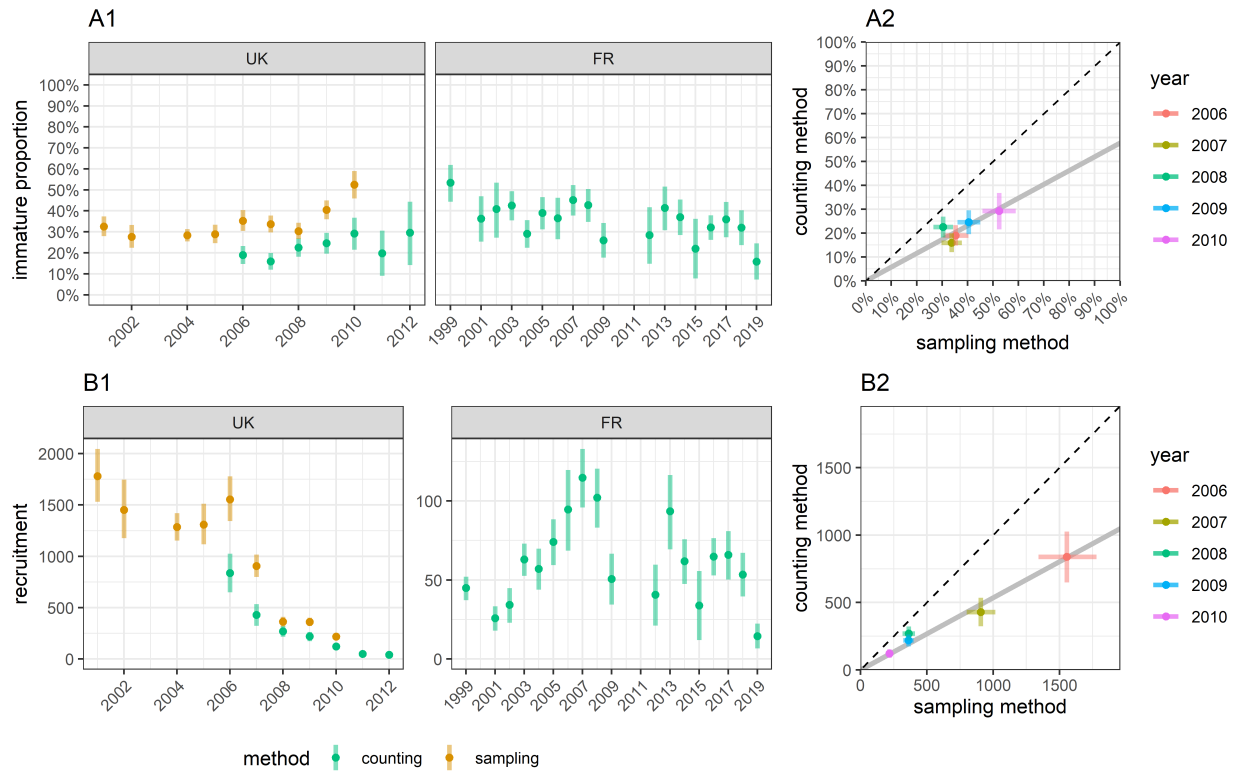


Figure 9: (A1) Estimates of the proportion of the immature individuals in the wintering population; (B1) estimates of the number of recruits, i.e. the young adults reproducing for their first time; (A2) & (B2) comparison of the values between the two estimation methods; bars define the 95% confidence intervals