Productivity estimation in waterfowl using a non-invasive method

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Abstract

The response of a waterfowl population to a harvest pressure depends on its capacity to renew. The recruitment, i.e. the number of young adults reproducing for the first time, is a key indicator to describe the renewal of a population, and therefore an essential tool in population management. The productivity, i.e. the number of recruits produced per breeder, is even more informative because it is independent of the breeding population size and allows comparisons over time and between species. The proportion of young adults in a waterfowl population, which is a main step in estimating productivity, is often estimated from game-hunting samples. However, this proportion is not accessible in years without harvest, or with a low harvest rate. Moreover, the age-structure in the harvest samples, commonly called hunting bag, does not necessarily reflect the underlying age-structure of the population. It is often skewed towards juveniles and can lead to an overestimation of the productivity. In waterfowl, adult males usually display brighter colours than immatures and females. This dichromatism can be characterized and monitored from count surveys, a non-invasive method. Such information can be used to infer the proportion of young adults, and consequently the productivity. In using two populations of ruddy duck, *Oxyura oxyura*, this study develops a Bayesian method to estimate the productivity from count data. The results are compared to productivity estimates from samples and are discussed by testing their consistency with the population growth rates. The results suggest that the counting method is a versatile tool to estimate the productivity if the species is monitored during the appropriate time period.

1 Introduction

1.1 Definitions

One defines the productivity of a breeding population as the average number of recruits produced per each breeder (Johnson et al. 1987). If one considers a species reaching the sexual maturity as early as its first year, all individuals are mature at the reproduction season. The productivity is thus the ratio of the number of young adults at the reproduction season in year t, i.e. the recruits, to the number of all individuals at the reproduction season in the previous year, $t-1$.

The population size in year t is equal to the number of breeders that survived over year $t-1$ plus the juveniles 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 productivity and the adult survival rate.

The productivity parameter is complex because it is composed of two sub-parameters: the reproduction succes, which is the product of the nesting and the hatching success, and the juvenile survival.

The use of productivity in population management

The management of an exploited population generally aims at...

Many studies focus on the monitoring of the reproduction success of waterfowl species is not sufficient to manage properly a population to estimate population growth rate changes (Dzus and Clark 1998). Productivity defined as recruit per breeder is better, but nesting and hatching success are keys to understand the reasons of productivity variability.

The variability of the productivity

A waterfowl species that is released in a favourable habitat will naturally expand (Malthus 1872). The growth of such a population can be explained by its productivity parameter that is higher than its 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. This competition commonly induces a lower reproduction success or/and a higher youth mortality. The productivity then decreases because it is dampened by density-dependent effects. For an endemic species evolving in stable environmental conditions, the productivity and the adult mortality rate are balanced, which explains the stabilization of the number of individuals.

Hunting waterfowl induces adult and juvenile mortality (ref). Paradoxically, this juvenile mortality does not always induce a decrease of productivity (ref). Indeed, one expects that a population with a high adult mortality rate combined to a low productivity would rapidly extinct. However, hunting waterfowl has a long history, and most of these species have persisted over time. The reason is that harvest pressure reduces the competition for space and food. The density-dependent effects affecting the productivity in case of high population density are dampened by the harvest mortality. The exploitation of a population thus increases adult mortality, but also productivity. A balance between these two parameters can be reached if the population is exploited to a constant and moderate harvest rate. The size of a newly exploited population in stable environmental conditions should thus reach a new equilibrium, which is expected to be lower than the size without exploitation.

Productivity is thus a varying parameter that reaches its highest values when no density-dependent effects occurs. Exploring the gradient of productivity, and defining the maximum productivity to predict the response of a population to different harvest rates is a challenge in population management.

What part of the productivity gradient should we know for population management?

What is the ideal biological model to explore the gradient of the productivity?

Hunting waterfowl has a long history, and few species have observed long-term moratorium, so few opportunities to explore the response of the productivity to a gradient of pressure. Alien species colonizing new territories and then heavily controled are a good model to overcome density-dependent effects and explore the gradient productivity. These species are often introduced during unvoluntary release events. Since its presence might impact the balance of the colonized ecosytem, it happens that managers take control measures to restrict the growth of these populations or to eradicate them.

In Europe, a population following its maximum growth rate is a perfect study model

What are the limitations of the sampling method to estimate the productivity?

- We cannot explore the productivity when there is no harvest, however, it is crucial to explore what happens when there is no harvest in a scenario where we suggest a moratorium to let the population recover.
- Biais because hunting like any predation action is selective. Often towards the weakest individuals. So overstimation of productivity, and potentially maximum sustainable harvest rate overestimated and consequently depletion of the managed population.

For hunted duck species in North America, the mortality rate on first-year immatures compared to adults is higher by a factor ranging from 1.4 to 2 (.

Why counting data is a potential tool to estimate the productivity?

Long time series, easy access, no need of samples. Can only provide subestimation of productivity because if some male recruits have already their male colours, they are considered as adult and not a recruit.

What is the methodology of this study?

Nichols -> il faut compter de la façon dont on demande

idée: estimer l'age moyen de la pop grâce la vulnerabilité et le sexe ratio chez les adultes

breeding/reproduction success good but not enough because variable survival of juveniles

Introduction:

productivity often defined as Jt/At but more realistic to defined as Jt/At-1

2 Materials & methods

2.1 The studied species

The ruddy duck is a species introduced in the United Kingdom in the 50's. The first reproduction was observed in the 60's. The population rapidely grew until reaching about 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 few individuals from the United Kingdom. This population set up around a single wintering spot, the Grand Lieu Lake. Since this species is considered as a major threat to the white-headed duck because of the risk of hybridization (AEWA report), a European plan of eradication has been concluded (EU report). Control measures were taken in both countries from 1999 in the UK and 2004 in France.

2.2 Dichromatism characterization

Figure 1: Typical ruddy duck flock observation 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

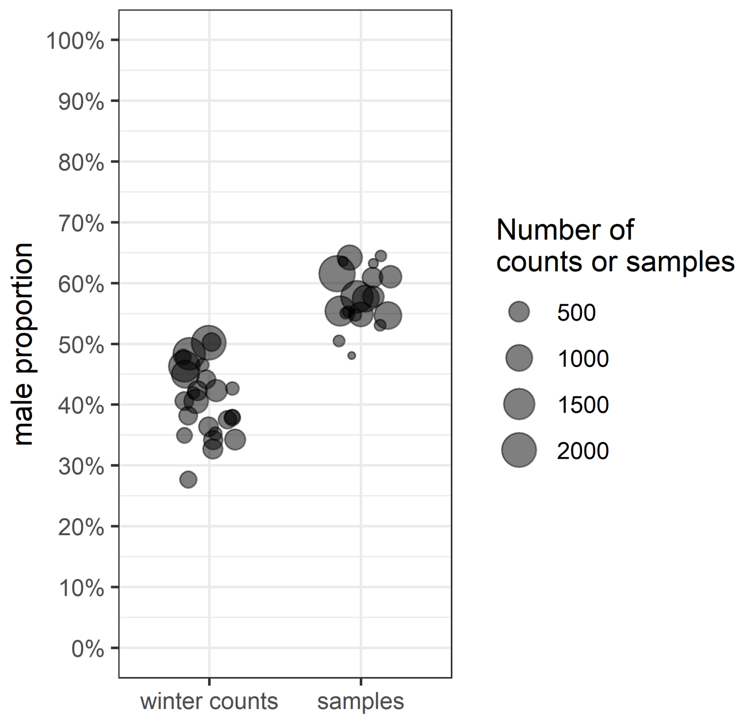

Figure 2: Apparent male proportion in winter counts vs male proportion in adult samples; for the first category, one point corresponds to the proportion of male-like plumage in a population counted in winter; for the second category, the male proportion is estimated from the adult ruddy ducks sampled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

Pictures of male juvenile in winter Pictures of male in winter

2.3 Data time series

The French and the UK wintering populations have been monitored since the presence of the first individuals was validated.

$PR_{i,t}$ estimation by the counting method

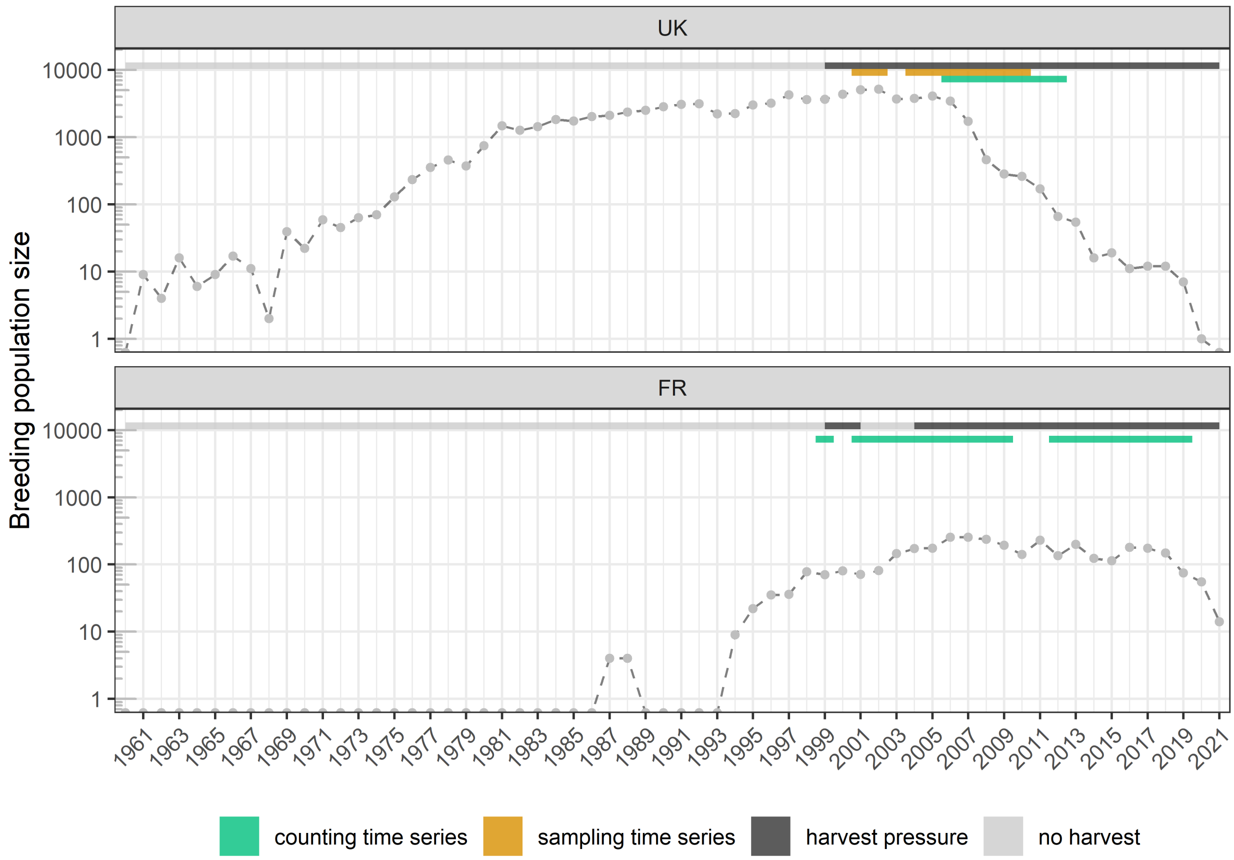

Figure 3: Evolution of the size of the two Ruddy duck populations in light of the data time series; on restricted time periods with available data, population growth rates can be estimated (slopes in red for the UK and in blue for France)

2.4 Model

Name	Class	Description
SM	Data	Total number of adult males sampled
SF	Data	Total number of adult females sampled
PM	Parameter	Proportion of males in the adult part of population at its equilibrium
$S_{i,t}$	Data	Number of individuals sampled in population i in year t
$SJ_{i,t}$	Data	Number of juveniles sampled in population i in year t
$CM_{i,t}$	Data	Cumulated number of type-male individuals counted in population i in year t
$C_{i,t}$	Data	Cumulated number of individuals counted in population i in year t
$Cmax_{i,t}$	Data	Maximum number of individuals counted in population i in year t
$PR_{i,t}$	Parameter	Proportion of recruits in population i in year t
$R_{i,t}$	Parameter	Number of recruits in population i in year t
$P_{i,t}$	Parameter	Number of recruits in population i in year t per breeder in year $t-1$
$N0_j$	Parameter	Intercept of the regression model, the j index refers to a restricted time period for a single population
SD_j	Parameter	Standard deviation of the regression model, the j index refers to a restricted time period for a single population

Name	Class	Description
λ_j	Parameter	Population growth rate (in $year^{-1}$), the j index refers to a restricted time period for a single population
S_j	Parameter	Adult survival rate (in $year^{-1}$), the j index refers to a restricted time period for a single population

The proportion of males in the adult part of a population at its equilibrium is inferred from the samples.

Indeed, the available French samples were insufficient to get Since the . Age in samples to 2003 to 2020 for the United Kingdom and

$$PM \sim \mathsf{Beta}(SM, SF) \tag{1}$$

$PR_{i,t}$ estimation by the counting method

$$CM_{i,t} \sim \mathsf{Binom}(PM.(1 - PR_{i,t}), C_{i,t}) \tag{2}$$

$PR_{i,t}$ estimation by the sampling method

$$SJ_{i,t} \sim \mathsf{Binom}(PR_{i,t}, S_{i,t}) \tag{3}$$

From $PR_{i,t}$ estimates, $R_{i,t}$ and $P_{i,t}$ are expressed as:

$$R_{i,t} = PR_{i,t}.Cmax_{i,t} \tag{4}$$

$$P_{i,t} = \frac{PR_{i,t}.Cmax_{i,t}}{Cmax_{i,t-1}} \tag{5}$$

The index j refers to a single population i and a restricted time period for t. The evolution of the population size can be related to the time to infer the population growth rate. It is a linear regression on the logarithm scale:

$$log(Cmax_{i,t}) \sim \mathsf{Norm}(N0_j + log(\lambda_j).t, SD_j) \tag{6}$$

$$S_j = \lambda_j - \overline{P_{i,t}} \tag{7}$$

2.5 Result validation using survival analysis

The adult survival is commonly assessed by capture mark recapture and published in the literature. Since the survival can also be estimated from both the counting and the sampling methods, the consistency of the two approaches is discussed by comparing the survival estimates with the literature values.

Name	Description
N_t	Number of breeders in year t
D_t	Number of breeders removed in year t
R_t	Number of recruits in year t
S_t	Adult survival rate, i.e. proportion of breeder in year $t-1$ still alive in year t

Name	Description
P_t	Number of recruits in year t produced per breeder in year $t-1$

The proportion of males in the adult part of a population at its equilibrium is inferred from the samples.

Indeed, the available French samples were insufficient to get Since the . Age in samples to 2003 to 2020 for the United Kingdom and

$$\begin{aligned}
N_t &= N_{t-1} - D_{t-1} + R_t && (8)\\
N_t &= N_{t-1} - (1 - S_t).N_{t-1} + P_t.N_{t-1}\\
N_t &= S_t.N_{t-1} + P_t.N_{t-1}\\
\frac{N_t}{N_{t-1}} &= S_t + P_t\\
\lambda_t &= S_t + P_t && (9)
\end{aligned}$$

develop the counting method :

2 ways to check the method :

sampling method? Ok but few data as poorly harvested

realistic survival? if > 1, estimated productivity is too low to support the maximum growth rate in the range of similar species in litterature -> satisfying

blabla

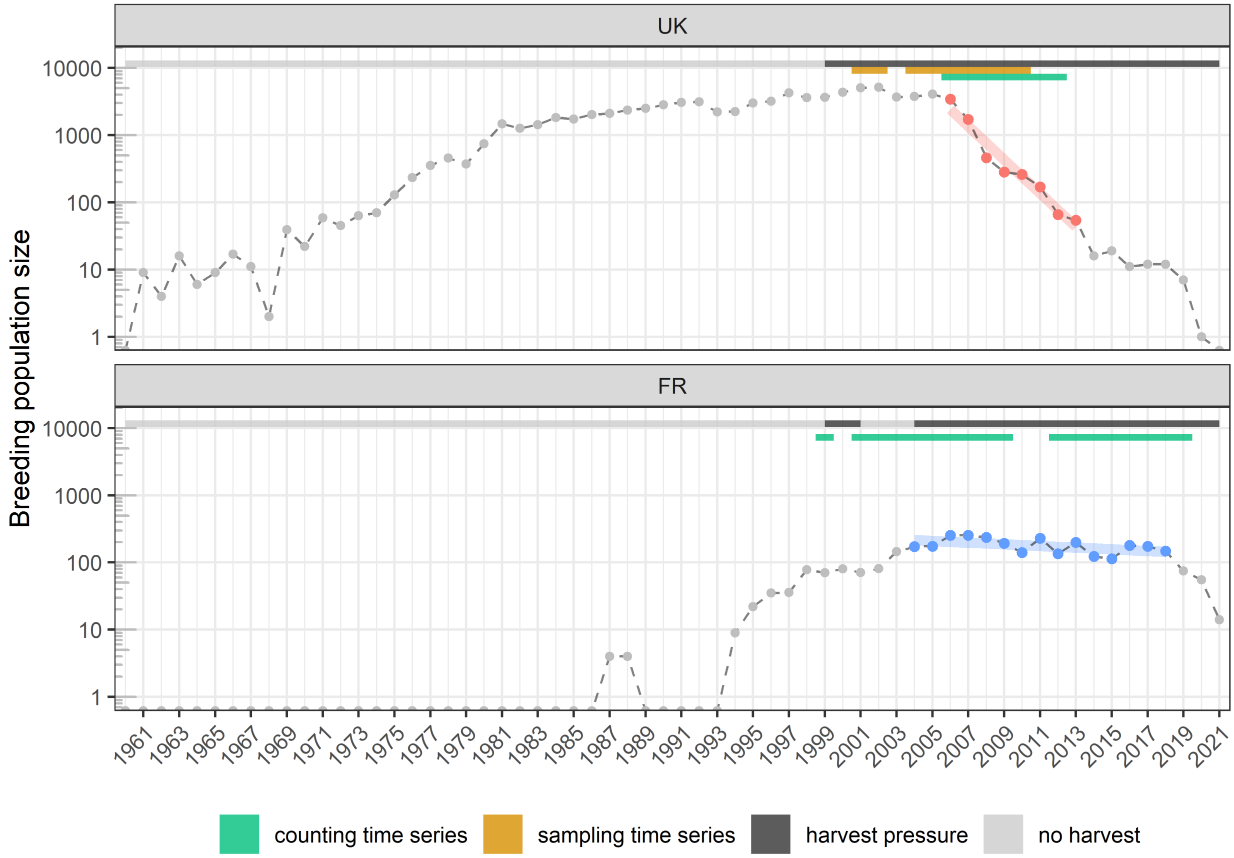

Figure 4: Evolution of the size of the two Ruddy duck populations in light of the harvest pressure; on time periods without harvest, population growth rates can be estimated (slopes in red for the UK and in blue for France)

2.6 Result validation by comparison to maximum productivity

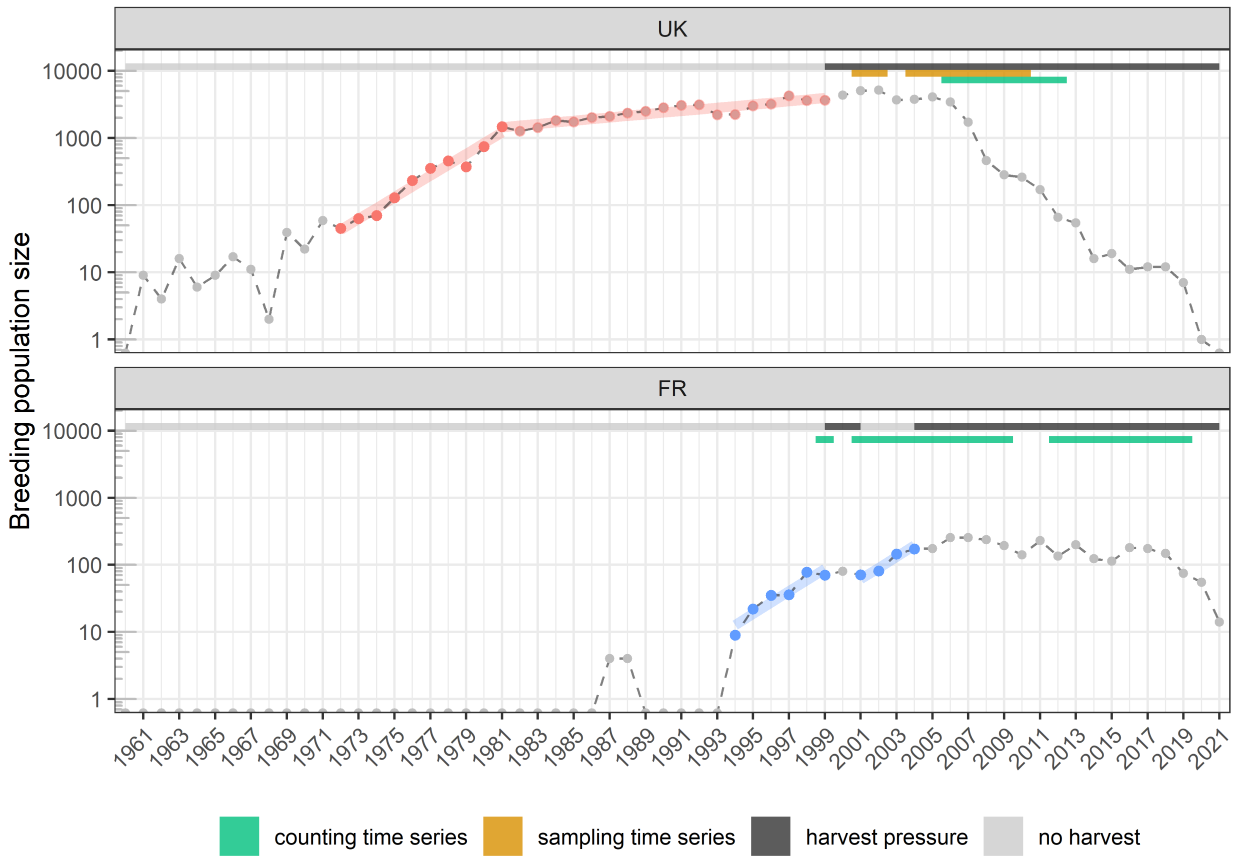

Figure 5: Evolution of the size of the two Ruddy duck populations in light of the harvest pressure; on time periods without harvest, population growth rates can be estimated (slopes in red for the UK and in blue for France)

3 Results

3.1 Productivity variability

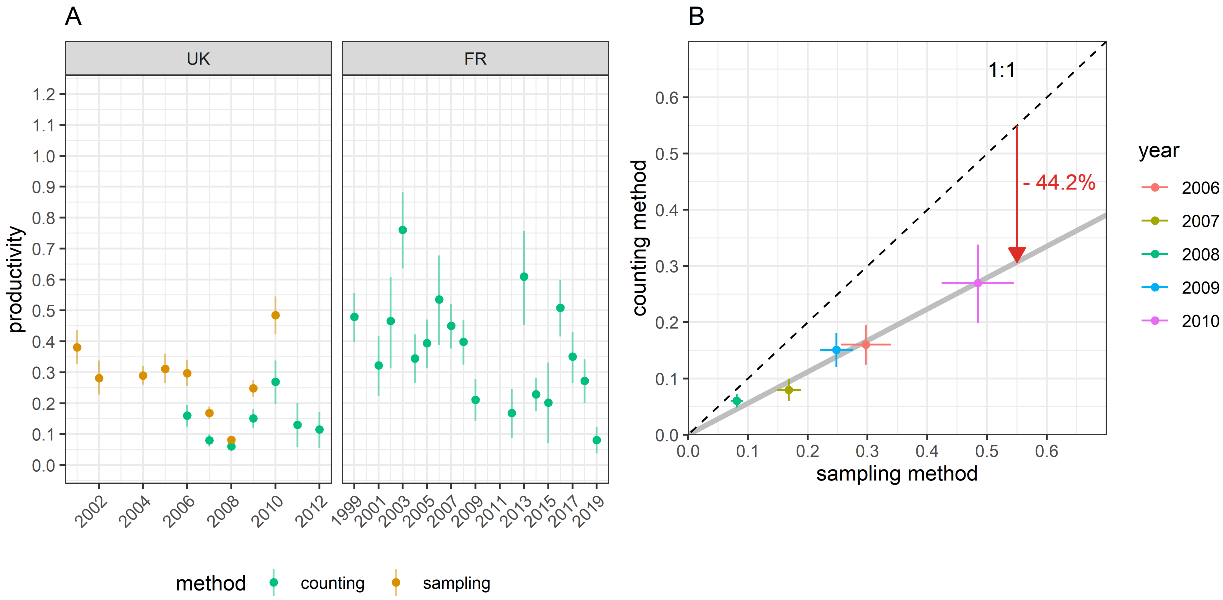

Figure 6: (A) Estimates of productivity, i.e. average number of recruits produced per breeder; (B) Comparison of the productivity values between the two estimation methods; bars define the 95% confidence intervals

3.2 Result validation using survival analysis

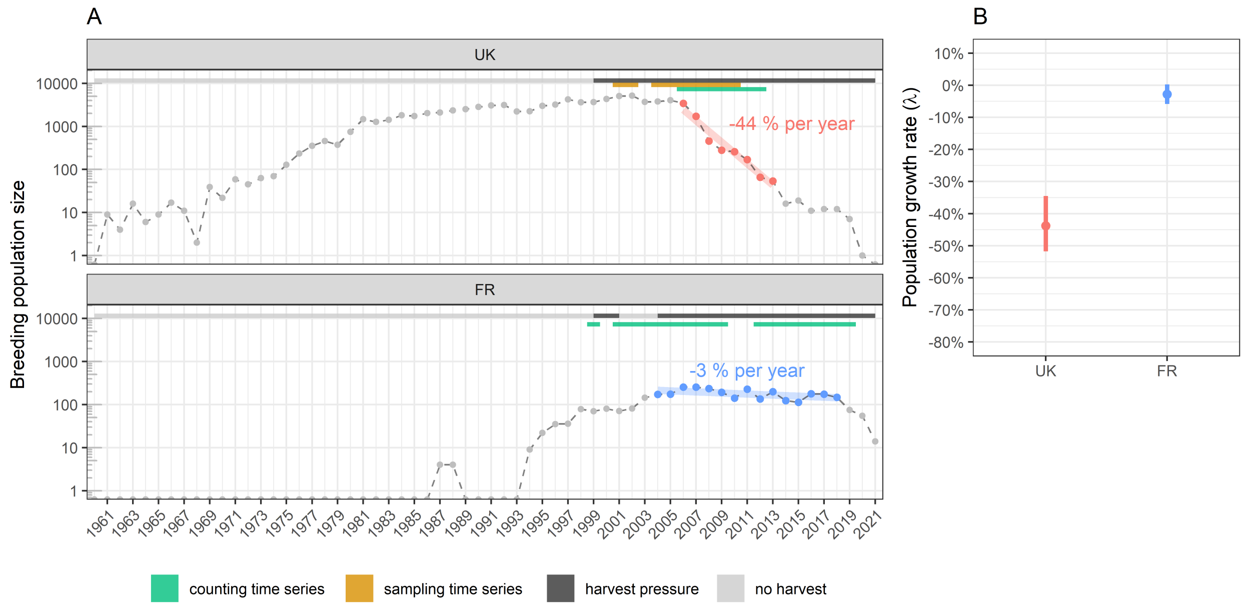

Figure 7: (A) Estimates of the population growth rate on time intervals with data availability. This aims at producing survival estimates to discuss the reliability of the methods to estimate productivity; (B) Growth rate estimates; bars define the 95% confidence intervals

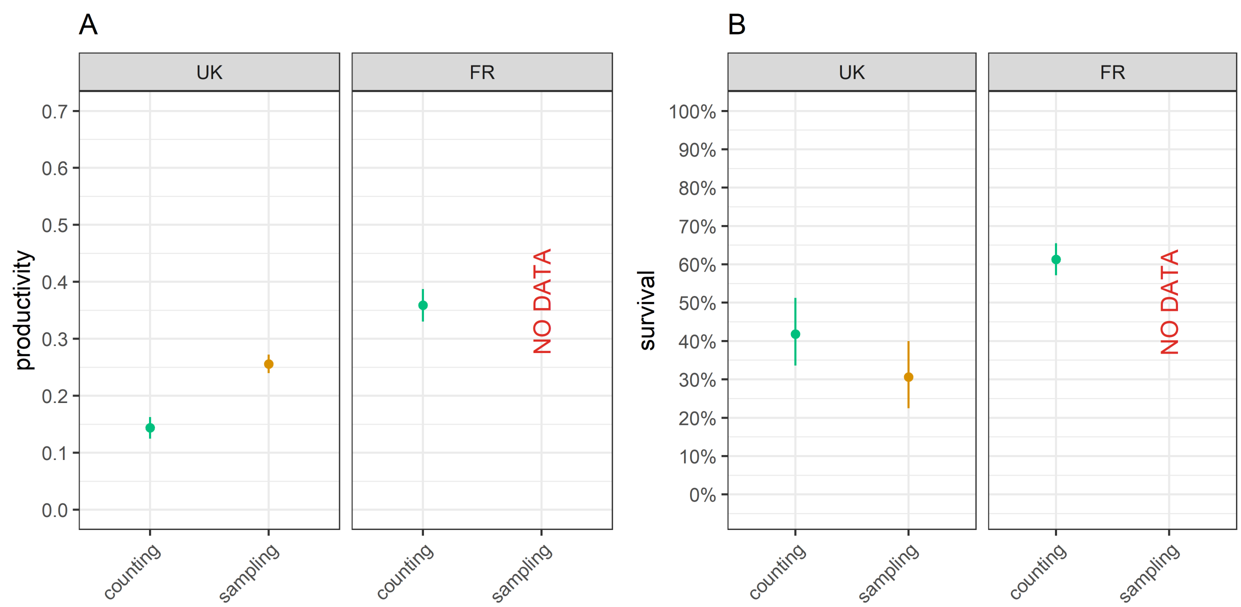

Figure 8: (A) Average productivity estimates on the time intervals defined for survival analysis; (B) Average survival estimates deduced from growth rate and productivity estimates on the time intervals; bars define the 95% confidence intervals

3.3 Result validation by comparison to maximum productivity

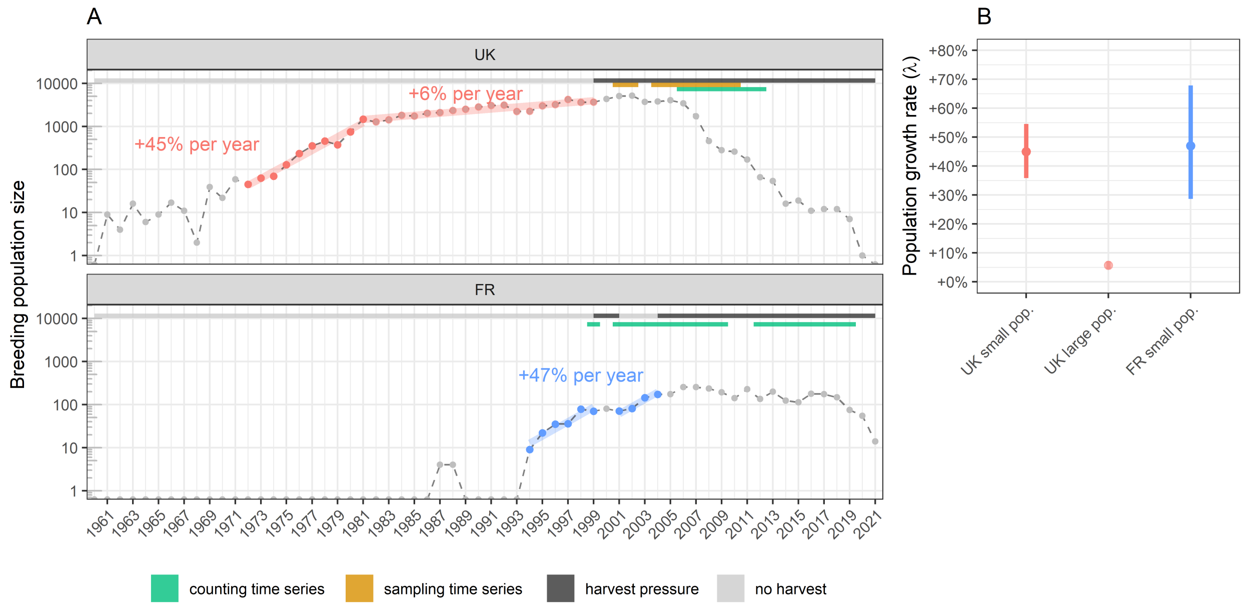

Figure 9: (A) Estimates of the population growth rate without harvest; two estimates were produced for the UK population because the growth rate dropped significantly when its size reached more than 1000 individuals; (B) Growth rate estimates; bars define the 95% confidence intervals

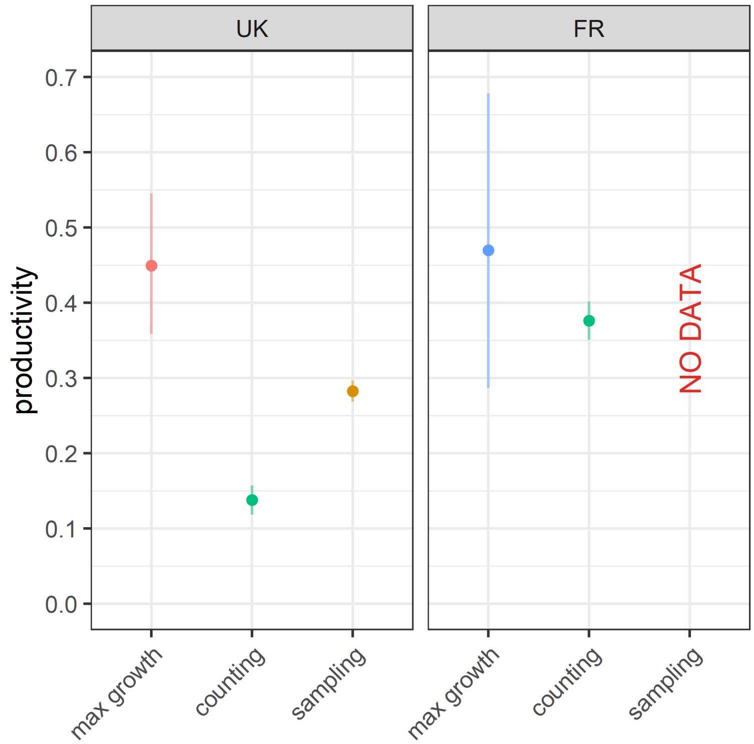

Figure 10: Comparison between a proxy of maximum productivity and the average productivity estimated following *counting* and *sampling* methods; the proxy is estimated during the maximum growth periods by combining the growth rate to the hypothesis of a 100% adult survival (*max growth*); this hypothesis implies that the true maximum of productivity is likely higher; bars define the 95% confidence intervals

4 Discussion

Productivité: Stabilité grosse pop, variabilité petite pop.

Productivity: drop from 2009

blabla

Nichols -> il faut compter de la façon dont on demande

Aknowledgements

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Supplement 1

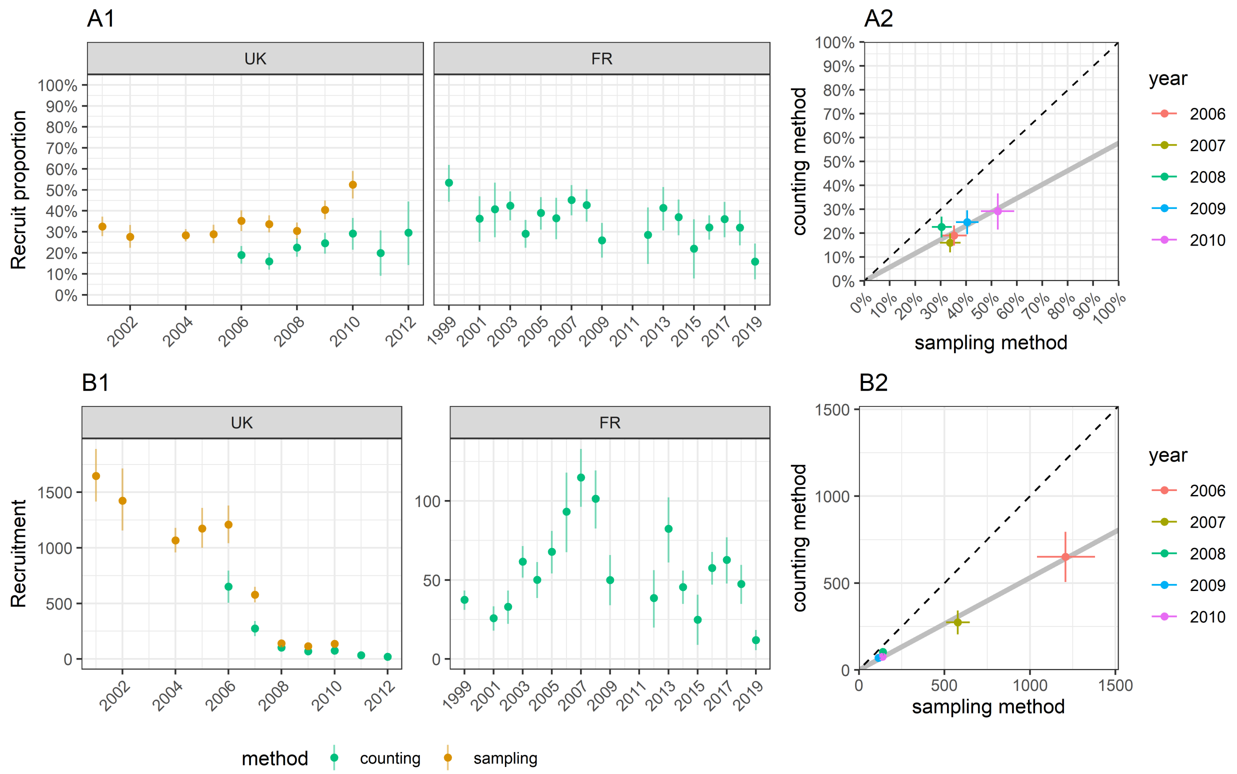

Figure 11: (A1) Estimates of the number of recruits, i.e. the young adults reproducing for their first time; (B1) estimates of the proportion of recruits in the population at the reproduction period; (A2) & (B2) comparison of the values between the two estimation methods; bars define the 95% confidence intervals