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

**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 Ducks, 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 - juvenile – duck

**Introduction**

Assessing population growth-rate is a key step towards a better understanding of factors underlying the dynamics of natural populations (see Niel and Lebreton 2005 etc). It is also, crucial for measuring the efficacy of management actions eventually undertaken to help population recovery, control or eradication (réfs). Among the approaches available to managers for reaching these goals, those relying on the monitoring of the numbers of individuals (counts) are by far the most popular (Rintala et al. 2022). In many instances, these methods even allow investigating environmental factors underlying changes in population size and hence to implement some mitigating actions (Réfs sur climate change and etc). 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’s growth rate is affected by change survival rather than to variations in reproductive parameters or productivity (). To assess the relative sensitivity of population growth-rate to factors affecting survival or reproductive parameters, demographers most often resort on the monitoring of individuals by capture-mark-recapture (CMR, see 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. Estimating the number of young produced in addition to alive adults in counts, may allow estimating adult survival and recruitment rate and hence to assess which of adult survival and productivity has the most influence on population growth-rate. Unfortunately, this only possible in a limited number of species in which broodless females/pairs and those with young display the same detectability. Alternatively, assessing the sex and age structure in hunting bags has been used to infer the role of decreasing reproductive success in population declines in a number of games species including ducks and geese (Fox et al 2018). However, this approach is not suited for protected/endangered species. Here we exemplify how, in dimorphic species, delayed maturity of males can be used as a proxy for estimating productivity/recruitment and adult survival by differentiating males and females in repeated (winter) counts. We use 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 occur in late autumn-early winter (November-December). This mean that the apparent proportion of male 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 young into the populations and hence to the reproductive success and the recruitment rates. We used the increasing proportions of male as a proxy of productivity/recruitment to assess the impact of two different eradication strategies deployed in Great Britained and France respectively.

**Materials & methods**

The ruddy duck is a stiff-tailed duck native from the Americas. From seven individuals initially acclimated in the Slimbridge Wetland Centre in the Great Britain in the 40’s (Gutiérrez-Expósito et al., 2020), a feral population began to establish with the first observed reproductive attempts in the wild in the 60s. This feral population rapidly grew and spread to the entire country to reach more than 5000 individuals in the early 2000s. By the end of the 80s, a feral population began to establish also on the continent (France), supposedly owing to the arrival of individuals born in Great Britain (GB). Contrary to what was observed in the GB, the French Ruddy duck population did not spread much, with the vast majority of observations and breeding attempts clustering in Western France (Mayenne and Loire-Atlantique regions). In France, during winter, almost none Ruddy duck is observed outside the lake of Grand Lieu (47.09°N, 1.67°W), which is thus the exclusive wintering site and greatly facilitates the monitoring of this population.

The feral European population of Ruddy duck is considered as a major threat to the endangered native White-headed duck population of the South-Western Mediterranean because of hybridisation risks and thus an elevated potential for genetic pollution and eventually genetic assimilation of the latter by the former (Muñoz-Fuentes et al., 2007). In order to mitigate the risks of genetic pollution of the White-headed duck by Ruddy ducks a European plan of eradication of Ruddy ducks has been adopted by the European Commission. As result, eradication measures were taken both in France and Great Britain in the late 90s (Gutiérrez-Expósito et al., 2020).

The release non-native species in the wild (including Ruddy ducks) is forbidden in countries of the EU, and the status of White-headed duck populations is highly unfavourable. The use of capture-mark-recapture to monitor populations of these species was thus in possible, as a result the effectiveness of the eradication of Ruddy ducks and management actions intended to favour the recovery of White-headed ducks were essentially checked through censuses. Censuses, however, did not allow assessing the relative effects or variations in survival and reproductive success/recruitment on population growth-rate, which is a key towards a proper understanding of the efficacy of management actions (see introduction).

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 late autumn/winter, see figure 1). Thus, by monitoring the seasonal evolution of sex-ratio it is possible to assess the proportion of young into populations, which, combined with reliable counts and under some reasonable assumptions (e.g., even sex-ratio at birth, comparable mortality rates between females and males among juveniles, unchanging adult sex-ratio over he monitoring period…) allow estimating both recruitment (a proxy of breeding success) and annual adult survival.

We monitored the demography of Ruddy duck populations in both Great-Britain and France thanks to exhaustive counts on the wintering grounds during the period between December 1 and January 31. In addition to these exhaustive counts, censuses that distinguished female- from male-like individuals were performed from late-autumn and late-winter (late November – 31 early March) from 2007 to 2012 in UK, and in 1999, 2000-2009, 2012-2019 in France. During all of these years the eradication effort (number of individuals culled), under control of the authorities in both countries, was also scrupulously recorded.

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**Results**

Time series derived from these counts show that the two populations display comparable growth (Figure 2.3). They grew freely in both countries until 1999. Although shooting was initiated in 1999 in both countries, both populations begun declining only after much higher control efforts had been achieved in 2005 and 2018 respectively (figure 3). This history underlines that both populations observed a large spectrum of harvest effort, from no pressure to very high pressure. For sake of interpretation, we ascribed the time-period 2001-2004 to the *no harvest* category in France because the harvest pressure was negligible hand hence had no effect on the population growth.

Also, covering contrasted populations dynamics corresponding to different levels of harvesting pressure (Figure 2.3). In France, data before 2004 correspond to a period of steady 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 2.3). 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.

Estimating recruitment rate from the evolution of apparent sex-ratio in winter

(Figure 2.3)