



RESEARCH ARTICLE

## Demographic heterogeneity among individuals can explain the discrepancy between capture–mark–recapture and waterfowl count results

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Received February 14, 2014; Accepted February 17, 2014; Published May 7, 2014

### ABSTRACT

Demographic heterogeneity has long been considered within wildlife populations, but only the modern development of capture–mark–recapture methods allows this to be easily tested and quantified. It is now possible to rapidly assess whether the modeling of heterogeneous populations, in which categories of individuals differ in survival rate, performs better than traditional approaches, in which all individuals are considered equivalent within a sex and age class. Using long-term banding data for 4,703 adult female Green-winged Teal (*Anas crecca*) from the Camargue, southern France, we show that a heterogeneous model outperformed a homogeneous model. Individuals from the high survival category had a ~60% annual survival rate, whereas birds in the second category had a survival rate reduced by a factor of 0.76–0.80, depending on the model (i.e. <50%). We could not demonstrate that individuals within the high survival category were larger or heavier. The link between survival rate and potential differences in individual morphometrics or individual behavioral strategies thus remains to be established. Previous studies in which a Green-winged Teal population was modeled as homogeneous suggested it should decline (population growth rate <1), which we also found when using demographic parameters obtained from a homogeneous model. This finding contradicts waterfowl surveys that show a long-term population increase in this flyway. Modeling the population as heterogeneous led to growth rates of 1.03–1.05 (a 3–5% annual increase), numbers consistent with the growth rate inferred from duck counts and that also partly explain how species such as Green-winged Teal can increase in numbers despite large hunting harvest, sustaining harvest to some extent.

**Keywords:** *Anas crecca*, Green-winged Teal, demographic heterogeneity, population growth rate, survival rate

### La heterogeneidad demográfica entre individuos puede explicar la discrepancia entre los resultados de captura–marcado–recaptura y conteos de aves acuáticas

### RESUMEN

Hace tiempo se ha considerado la heterogeneidad demográfica en las poblaciones de animales silvestres, pero solo mediante el desarrollo moderno de los métodos de captura–marcado–recaptura ha sido posible poner a prueba y cuantificar dicha heterogeneidad fácilmente. Ahora es posible determinar rápidamente si el modelamiento de poblaciones heterogéneas, en el que las categorías de individuos tienen tasas de supervivencia diferentes, se desempeña mejor que las aproximaciones tradicionales en las que todos los individuos de una clase de sexo y edad se consideran equivalentes. Usando datos de anillamiento de largo plazo para 4,703 hembras adultas de *Anas crecca* de Camargue, sur de Francia, demostramos que un modelo heterogéneo sí se desempeña mejor que un modelo homogéneo. Los individuos de la categoría de mayor supervivencia tuvieron una tasa anual de supervivencia cercana al 60%, mientras que los de la segunda categoría tuvieron tasas de supervivencia reducidas por un factor de 0.76 a 0.80 dependiendo del modelo (i.e. por debajo del 50%). No pudimos demostrar que los individuos de la categoría de alta supervivencia fuesen más grandes o tuviesen mayor masa. Por esto, el vínculo entre la tasa de supervivencia y las diferencias potenciales en la morfometría de los individuos o en las estrategias individuales de comportamiento aún tiene que ser establecido. Un estudio previo en el que una población de *A. crecca* fue modelada como homogénea sugirió que la población debería mostrar una disminución (tasa de crecimiento poblacional < 1), lo que también fue encontrado en este estudio cuando usamos los parámetros demográficos obtenidos de un modelo homogéneo. Este resultado contradice los censos de aves acuáticas, que muestran un incremento a largo plazo en la población en este corredor de vuelo migratorio. Modelar la población como heterogénea arrojó tasas de crecimiento de 1.03 a 1.05 (un

incremento anual de entre 3% y 5%). Estas tasas concuerdan con la tasa de crecimiento inferida a partir de conteos y también puede explicar en parte cómo especies como *A. crecca* pueden aumentar en número a pesar de sufrir de fuertes extracciones por cacería, lo que sostiene la extracción hasta cierto punto.

**Palabras clave:** *Anas crecca*, heterogeneidad demográfica, tasa de crecimiento poblacional, tasa de supervivencia

## INTRODUCTION

Heterogeneity among individuals is a keystone of evolution theory because differences between individuals allow natural selection to take place and evolution to occur (review in Bergeron et al. 2011). While this may seem obvious, most population studies have considered average values of demographic parameters at the population level or, at best, for each sex and age class, and thus have failed to account for individual heterogeneity.

The question of modeling inter-individual heterogeneity in demographic rates has been addressed in recent studies, the results of which demonstrate the value of this approach for better understanding population dynamics (Robert et al. 2002, Gimenez and Choquet 2010, Plard et al. 2012, Cam et al. 2013). From a conservation perspective, population heterogeneity has, for example, been especially useful in studying extinction risks in small populations (Kendall and Fox 2002, Robert et al. 2003). The development of analytical software has allowed testing whether capture–mark–recapture (CMR) models that consider multiple classes of individuals better fit the data than those that consider a population to be homogeneous (Pledger et al. 2003, Pradel 2009). These models do not require that individuals be assigned a priori to one or the other category (as would be the case with sex, for example). One only needs to specify how many categories to consider for a given parameter (e.g., survival rate), and both the assignment of individuals to the categories and the estimator of the demographic parameter for each category (hence the difference between categories) can be computed, together with their statistical significance.

Ducks of a population should not be considered identical because individual behavioral strategies could lead to differences in measures such as body condition (Heitmeyer et al. 1993, Guillemain et al. 2002). For instance, divergent strategies of habitat use in winter between resident birds and vagrants were observed in ducks (Pradel et al. 1997, Guillemain et al. 2007). It was hypothesized that winter resident birds would have a greater survival rate than vagrants, which move continuously between regions and are hence less familiar with their environment and associated risks (Guillemain et al. 2010a); however, with only behavioral and bird census data, this could not be easily tested.

Traditional CMR models that consider populations as homogeneous have provided paradoxical results, suggesting, for example, that the Western European teal

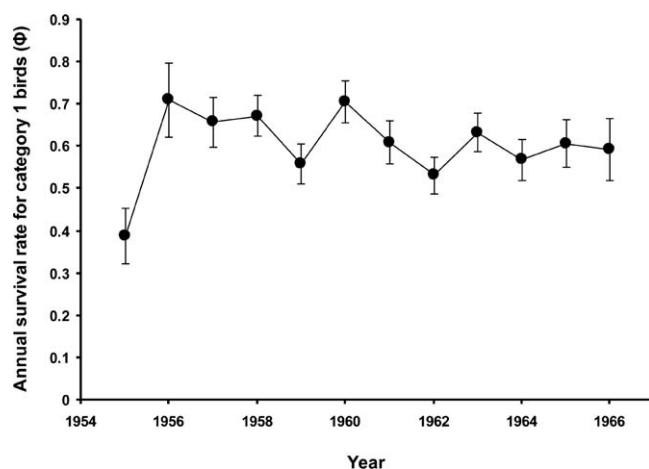
population growth rate should be  $<1$  ( $\lambda = 0.968$ ; i.e. a 3.2% annual decrease on average; Devineau 2007). On the contrary, the International Waterbird Censuses have shown that these teal numbers have been clearly increasing over the last 4 decades, both in France (e.g., Fouque et al. 2009 reporting a 3.95% annual increase on average) and in Western Europe as a whole (Wetlands International 2013 reporting a 2.62% increase for northwestern Europe over 1974–2005 and a 6.45% increase over 1996–2005).

The first aim of our study was to determine if teal wintering populations should be considered heterogeneous in terms of survival rates. Based on a large dataset of teal banded in winter in Camargue, southern France, we tested if a CMR approach considering 2 categories of individuals with different survival rates provides a better fit to the data than the traditional approach where all individuals are considered to have the same survival rate. We then tested whether there were differences in terms of relative size and relative body mass between the birds of each survival rate category. Based on the results of the CMR modeling, the second goal of this study was to reevaluate the population growth rate when accounting for heterogeneity in the population model.

## METHODS

### Field Procedures

Teal were captured and banded at Tour du Valat, Camargue, southern France (43.5°N, 04.67°E) from January 1952 to February 1978. The majority of the banding occurred in the 1950s and 1960s (figure 1 in Guillemain et al. 2005a), and the analysis was restricted to birds banded from 1955 to 1967. A season was considered the yearly interval between August and July (e.g., any banding, live recaptures, or dead recoveries that occurred between August 1, 1955, and July 31, 1956, took place during the 1955 season). In practice, most captures occurred during the autumn and winter period (i.e. August to March), and data from the few birds banded during spring or early summer were discarded. Standard baited traps hidden in vegetation were used, as described by Bub (1991). Upon capture, all birds were weighed to the nearest gram, had their wing chords measured to the nearest millimeter with a ruler, and were fitted with a metal band bearing an individual code. Many of these birds were subsequently recaptured alive, which always occurred at the same site (other duck banding sites were few in Europe in those years, and no other important site existed in France). In



**FIGURE 1.** Annual survival rate ( $\phi$ ) per year for teal of category 1 (i.e. those with a greater survival rate ringed in Camargue, France, between seasons 1955 and 1967). Estimates from model 1. Vertical bars show standard errors.

addition, band recoveries of dead birds were provided (mostly by hunters) throughout Europe (Guillemain et al. 2005b).

### Model Structure

One common problem of duck banding datasets in Europe is that capture operations mostly occur in winter, when bird density is higher and the number of captures potentially greater. This was the case in our study, which means banding occurred during the hunting season (August to March in those years). Birds banded early in the season were therefore exposed to hunting for a longer period than birds banded later in the year (see discussion about this problem specifically for teal in Gitay et al. 1990). To deal with this issue, one approach we considered was to split the year into several shorter periods of a few months. This option would have likely over-complicated the analysis, however (Devineau 2007, Tavecchia et al. 2001), and it was eventually rejected. Instead, we opted to pool all recoveries from the year of banding with those of the following year. A year or season was here considered to span from August 1, year  $n$ , to July 31, year  $n + 1$ . We considered only the birds banded between August 1 and March 31, which is the period of greatest Teal presence in the area.

Recoveries could occur anytime in the year. This approach prevents detailed analysis of intra-annual recoveries and movement between sites. The estimation of juvenile demographic rates also becomes more difficult; it is not known whether birds ringed as juveniles were recovered again as juveniles in their first year or as adults in their second year. To control for this, data for juveniles that were recovered during the first or second year post-

capture were discarded, juveniles recaptured alive during the second year or later were considered to have been banded as adults on the day of recapture, and any data from previous encounters were discarded. As a result, estimating demographic rates was limited to birds aged as adults when first captured, or birds recaptured as adults if initially banded as juveniles. This approach should not bias annual adult survival rate estimates and heterogeneity in this parameter, which was the aim of this study.

Because we were ultimately interested in the computation of the population growth rate, the analysis was restricted to females. After the removal of data that did not meet the above criteria, the dataset comprised the encounter histories of 4,703 adult female teal ringed in Camargue between seasons 1955 and 1967.

Individual encounter histories started with the first capture and marking in Camargue (event coded 1) and continued with subsequent live recaptures (events also coded 1) or dead recovery (event coded 2). Because we were mostly interested in survival rate (rather than potential movement between wintering areas, for example), when live recaptures and dead recovery occurred during the same year, only the recovery was considered.

The joint analysis of recoveries and recapture data allows, under certain circumstances, survival and fidelity to be estimated separately (Burnham 1993), but this is not possible when emigration out of the study area is random. Because goodness-of-fit tests did not provide any evidence that the hypothesis of random temporary emigration should be rejected, we retained the classical parameterization of CMR models. We used multi-event modeling (Pradel 2005) with program E-SURGE (Choquet et al. 2009a) to estimate annual survival ( $\phi$ , the probability that an individual alive in a given year is still alive 1 year later), encounter ( $p$ , the probability that an individual is recaptured alive in a given year), and dead recovery ( $D$ , the probability of recovering a ring conditional on death of the individual) probabilities.

We considered the population to be composed of 2 categories of individuals potentially differing in survival and encounter rates (for simplicity, we did not consider more than 2 categories). Individuals composing category 1 would have survival rates higher (if different) than those of category 2. This was achieved by multiplying this high survival by a coefficient of heterogeneity ( $0 \leq \alpha \leq 1$ ) estimated from the data to obtain survival of individuals in the second category (see Cresspin et al. 2008 for the same approach applied to heterogeneity in catchability). The 2 categories could then be considered as the “good” (high survival rate) category 1 and the “poor” (lower survival rate) category 2.

Whether or not the 95% confidence interval of  $\alpha$  approached the value of 1 provided a test of the population's heterogeneity in terms of survival. A value

of 1 is strictly analogous to fitting a model of homogeneity. Encounter rate was also considered to potentially differ between the 2 categories ( $p_c$ ). The probability  $\pi$  for newly marked birds to be assigned to category 1 was also estimated.

All parameters could either vary across years (i.e.  $\phi_t, \alpha_t, p_{ct}, D_t, \pi_t$ ), or be constant (i.e.  $\phi, \alpha, p_c, D, \pi$ ). Combinations where survival was constant in category 1 but time-dependent in category 2 (i.e.  $\phi, \alpha_t$ ) were not considered because they do not make much biological sense; all other combinations, 24 possible models, were tested. Model selection was assessed using the Akaike Information Criterion corrected for small sample size (AICc; Burnham and Anderson 2002).

We assessed the fit of the fully time-dependent heterogeneity model ( $\phi_t, \alpha_t, p_{ct}, D_t, \pi_t$ ) in 2 steps (see Rivalan et al. 2005 for a previous application of this procedure). First, using program U-CARE (Choquet et al. 2009b), we calculated the goodness-of-fit statistic of the fully time dependent model without heterogeneity ( $\phi_t, p_{ct}, D_t$ ). We then calculated the likelihood ratio test statistic between the 2 models. This statistic represents the part of the lack of fit in the model without heterogeneity that is explained by the model with heterogeneity. Accordingly, we assessed the fit of the heterogeneity model ( $\phi_t, \alpha_t, p_{ct}, D_t, \pi_t$ ) by discounting the likelihood ratio test statistic from the goodness-of-fit test statistic of the model without heterogeneity ( $\phi_t, p_{ct}, D_t$ ). Because the fit was satisfactory (see Results) we did not have to correct the results for over-dispersion, and the model selection was based on AICc.

### Individual Features Leading To a Heterogeneous Population

For the best model, E-SURGE provides the probability  $\pi$  that individuals with a given capture–recapture history type are assigned to category 1 (i.e. high survival rate). To determine whether this probability was associated with individual morphometric features, we first modeled it as a linear regression of these morphometric covariates (wing length and body mass). The relationship may not be that simple and linear, however, so we also compared mean wing length and mean body mass between individuals from the 2 categories. Because we only had an assignment probability associated with some potential error, we first compared mean wing length and mean body mass between individuals most likely to be better survivors ( $\pi > 0.75$ ) and those most likely to be poorer survivors ( $\pi < 0.25$ ) using a simple comparison of means, then repeated the same test with a 50% threshold. Note that body mass and wing length were both standardized prior to comparison.

### Population Trend

Using the survival estimates of the best models completed by other demographic parameters from the literature, we estimated the expected annual growth rate for our study population. Considering an immediate post-breeding situation, we estimated the probability of a female surviving until the next breeding season. We used Devineau's (2007) 41.2% annual survival rate for juveniles and our estimates for adults in category 1 (high survival) or category 2 (low survival). We used the Blums et al. (1996) 70% estimate of breeding propensity for 1-year-old females and considered that 100% of adult females attempt breeding each year.

Bengtson (1972) observed that only 7.1% of teal females skip reproduction each year, a percentage that includes both first-year and adult females, suggesting that virtually all adults attempt breeding each year. The present analysis was repeated using a more conservative estimate of 90% of adult females attempting to breed annually, which led to similar results (not shown), although with lower population growth rates. Each breeding female was assumed to produce 2.53 fledged juveniles per year (mean of minimum and maximum published estimates for teal; 1.36 in Elmberg et al. 2003 and 3.7 in Bengtson 1972). Because the sex-ratio is generally even at fledging for dabbling ducks (Bellrose et al. 1961), each breeding female would then produce 1.265 fledged female per breeding attempt.

At the beginning of the modeling exercise, 500 adult and 500 juvenile birds were considered and initially assigned to each of the 2 survival categories following the mean value of  $\pi$  provided by the model. Similar tests were also performed in which the initial population was strongly skewed toward first-year birds (75% juveniles at time step 1) or, conversely, toward adults (75% of the initial population). In both cases this could affect population size during the first time steps because adult females are considered to be more productive than first-year females, but after a few years the results were always similar (not shown). We tested 3 scenarios: (1) survival category is fully heritable (i.e. females of category 1 only produce young females of category 1); (2) category is not heritable (i.e. females produce juveniles in both categories 1 and 2, according to the mean value of  $\pi$  in the population), and (3) a homogeneous population (i.e. adult females all have an annual survival rate corresponding with the mean of the estimates in category 1 and category 2 of the heterogeneous populations from the other 2 scenarios).

Population size and composition were then computed over 50 years, which corresponds with the temporal scale of duck count datasets (1960s to present). We also computed the mean population growth rate  $\lambda$  over the 50 years for each scenario. [Estimates and mean values are given  $\pm$  SE throughout the results section].



**TABLE 1.** Model selection results using Akaike's Information Criterion corrected for small sample size (AICc) and multi-event capture-mark-recapture modeling of annual probabilities of survival for individuals of category 1 ( $\phi$ ), correction factor to survival for category 2 ( $\alpha$ ), encounter ( $p$ ), recovery ( $D$ ), and assignment of newly banded birds to category 1 ( $\pi$ ). Each parameter was tested as time-dependent (t subscript) or constant over years (.). All combinations were tested except those with  $\phi_t$  (see text for more details). Encounter rate was modeled as different between the 2 categories of individuals (i.e. noted  $p_c$ ). The 2 models used to compute the goodness-of-fit statistic for the fully time-dependent heterogeneous model (model 10, fully time-dependent heterogeneous model; and model 11, fully time-dependent homogeneous model) are also presented.

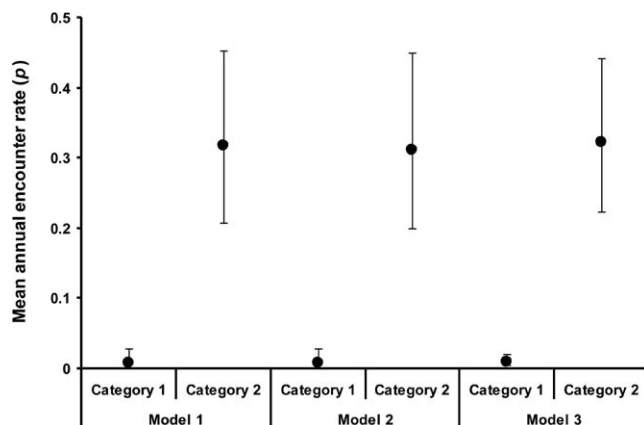
Model number	Model structure	$K^a$	Deviance	AICc	$\Delta AICc$
1	$\phi_t \alpha. p_c. D. \pi_t$	28	6,444.629	6,500.929	0.000
2	$\phi. \alpha. p_c. D_t \pi_t$	28	6,445.161	6,501.461	0.532
3	$\phi. \alpha. p_c. D. \pi_t$	17	6,467.909	6,502.022	1.093
4	$\phi. \alpha. p_{ct} D. \pi.$	39	6,426.471	6,505.048	4.119
5	$\phi_t \alpha. p_c. D_t \pi_t$	39	6,426.737	6,505.315	4.386
6	$\phi_t \alpha_t p_{ct} D. \pi.$	50	6,408.796	6,509.742	8.814
7	$\phi_t \alpha. p_{ct} D_t \pi_t$	61	6,386.825	6,510.232	9.303
8	$\phi_t \alpha_t p_c. D. \pi_t$	38	6,435.296	6,511.845	10.916
9	$\phi_t \alpha_t p_{ct} D. \pi_t$	60	6,391.769	6,513.130	12.201
10	$\phi_t \alpha_t p_{ct} D_t \pi_t$	70	6,381.734	6,523.586	22.657
11	$\phi_t p_{ct} D_t$	35	6,488.550	6,559.017	58.088

<sup>a</sup> Number of separately estimable parameters

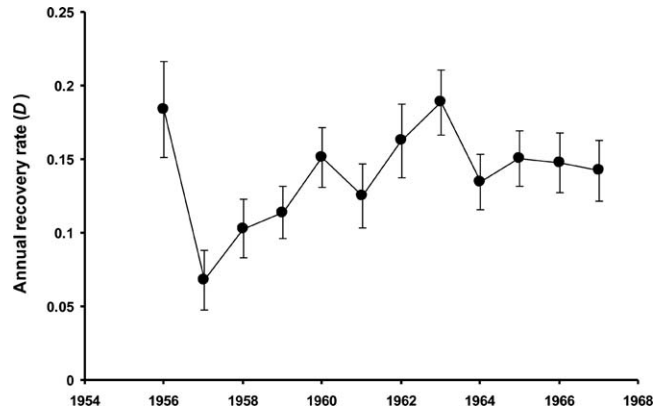
## RESULTS

### Demographic Rates

The goodness-of-fit statistic for the fully time-dependent homogeneous model was  $X^2_{87} = 155.09$ , and the likelihood ratio statistic corresponding to heterogeneity was  $X^2_{35} = 106.82$ . Hence, the goodness-of-fit statistic for the fully



**FIGURE 2.** Mean annual encounter rates ( $p$ ) for the 2 categories of teal (category 1: high survival rate; category 2: lower survival rate) ringed in Camargue, France, between seasons 1955 and 1967. Estimates from the 3 best models. Vertical bars show 95% confidence intervals.



**FIGURE 3.** Annual recovery rate ( $D$ ) of teal ringed in Camargue, France, between seasons 1955 and 1967. Estimates from model 2. Vertical bars show standard errors.

time-dependent heterogeneous model was not significant at the 5% level ( $X^2_{52} = 48.27$ ,  $P = 0.62$ ), which validated the use of this model for comparison.

The 9 best-AICc models plus the 2 models used for the goodness of fit (Table 1) show that models 1, 2, and 3 were equally supported by the data ( $\Delta AICc \leq 2$ ). Model 1 suggested that the survival rate of birds in category 1 was time-dependent. One season (winter 1955–1956) was particularly different, with an annual survival rate of  $0.38 \pm 0.07$  as opposed to a mean of  $0.62 \pm 0.02$  ( $n = 11$ ) during the other years (Figure 1). Models 2 and 3 both suggested a constant annual survival rate for category 1 birds of  $0.60 \pm 0.02$ , which was very similar to the mean of annual values in model 8.

For all 3 best models, the heterogeneity factor  $\alpha$  was modeled as a constant parameter. The value of  $\alpha$  in these models ranged from  $0.76 \pm 0.06$  in model 1 to  $0.80 \pm 0.06$  in model 3, with the value 1 always strongly rejected (increase in AICc if setting  $\alpha = 1$ : 17.23 for model 1, 7.87 for model 2, and 6.32 for model 3); therefore, all models supported the hypothesis that considering 2 categories of individuals with high and low survival provided a better fit than a homogeneous model, with birds in category 2 having a mean survival rate that was only 76–80% that of individuals in category 1.

Encounter rate  $p$  was considered constant over time in all 3 best models and was consistently much smaller for category 1 ( $p_1 = 0.008$ – $0.009$ ) than for category 2 ( $p_2 = 0.311$ – $0.323$ ). The associated 95% CI did not overlap between the 2 categories, indicating a significant difference between the 2 types of individuals (Figure 2).

Recovery rate was both constant and similar in models 1 and 3 ( $D = 0.14 \pm 0.01$  in both cases), whereas in model 2 it was time dependent, mostly caused by a drop of the value during the 1957–1958 season (Figure 3).



**FIGURE 4.** Annual probability of assignment to category 1 individuals ( $\pi$ ) (i.e. those with a greater survival rate) of teal ringed in Camargue, France, between 1955 and 1967. The thick line shows the estimates from model 1, the dotted line from model 3, and the thin line from model 2. Annual estimates significantly increase over years in all 3 cases (see text). To ease reading, standard errors are not shown.

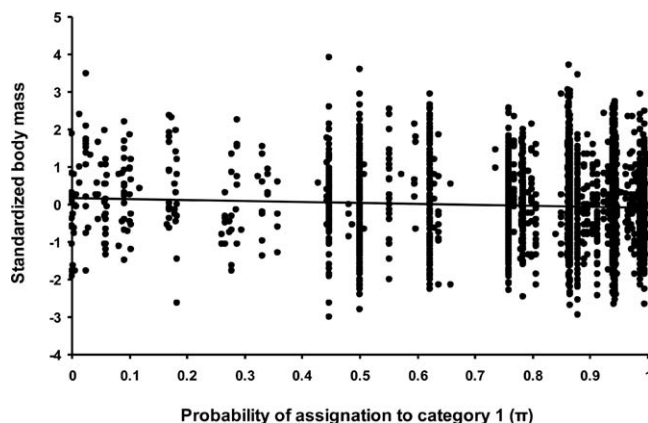
Finally, the 3 best models suggested that the probability  $\pi$  of newly banded birds being assigned to category 1 was time-dependent, and they yielded similar estimates. In all cases there was a drop in the value of  $\pi$  during the 1956–1957 season and a general trend toward an increase in this rate over years (Spearman correlations ranging from  $r_s = 0.73$ ,  $P < 0.5$  for estimates from model 2 to  $r_s = 0.79$ ,  $P < 0.05$  for estimates from model 1; Figure 4).

### Individual Features Leading to a Heterogeneous Population

From model 1 we obtained the probability of being assigned to category 1 (high survival individuals), depending on individual encounter histories. The 4,703 females showed 140 different possible encounter histories. Testing the relationship between this probability and individual morphometric covariates yielded inconsistent results.

There was no significant relationship between the probability of belonging to category 1 and standardized wing length (linear regression,  $r^2 = 0.0005$ ,  $P = 0.11$ ). Comparing the mean standardized wing length between birds with  $\pi$  below or over 0.5 indicated a significant difference ( $-0.160 \pm 0.030$ ,  $n = 891$  vs.  $0.105 \pm 0.016$ ,  $n = 3,812$ , respectively; t-test:  $t = -7.15$ ,  $P < 0.001$ ), indicating that birds in the low survival group tended to have shorter wings. When tested between birds with  $<25\%$  or  $>75\%$  probability of belonging to category 1, however, the difference was no longer statistically significant ( $0.206 \pm 0.080$ ,  $n = 125$  vs.  $0.087 \pm 0.018$ ,  $n = 3,422$ , respectively; t-test:  $t = 1.27$ ,  $P = 0.20$ ).

The results were opposite when considering standardized individual body mass. First, body mass significantly decreased with increasing probability of belonging to



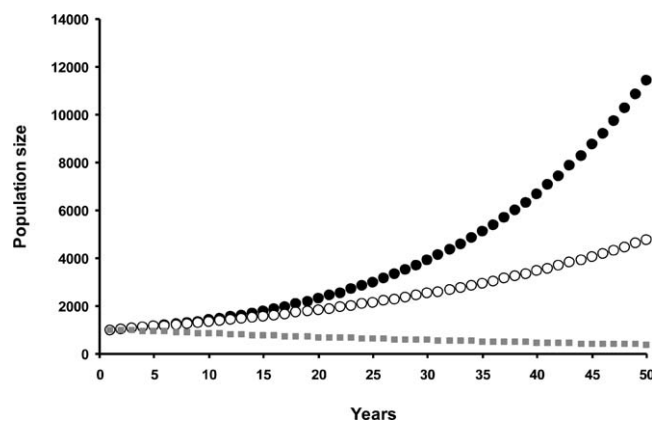
**FIGURE 5.** Standardized individual teal body mass plotted against the probability for each individual to be assigned to category 1 ( $\pi$ ) (i.e. higher survival rate). The linear regression was statistically significant ( $y = -0.264x + 0.185$ ,  $r^2 = 0.003$ ,  $P = 0.0001$ ).

category 1, although a small part of the variance was explained ( $r^2 = 0.003$ ,  $P < 0.001$ ; Figure 5); however, there was no significant difference in mean standardized body mass between birds with a probability of belonging to category 1 under or over 50% ( $-0.003 \pm 0.034$ ,  $n = 891$  vs.  $-0.028 \pm 0.016$ ,  $n = 3,812$ , respectively; t-test:  $t = 0.67$ ,  $P = 0.50$ ). Conversely, the difference was significant when comparing birds with a probability of belonging to category 1  $<25\%$  or  $>75\%$  ( $0.281 \pm 0.097$ ,  $n = 125$  vs.  $-0.038 \pm 0.016$ ,  $n = 3,422$ , respectively; t-test:  $t = 3.65$ ,  $P < 0.001$ ). We thus found no consistent evidence to support the hypothesis that the probability of belonging to the high survival category is associated with specific wing length or body mass when compared with birds of lower survival.

### Population Trend

On average over the years, model 1 suggested that 80.6% of birds were assigned to category 1 and had a mean annual survival rate of 60.3%. The survival rate of the 19.4% birds in category 2 was reduced to 76.4% of those in category 1 (i.e. survived from year to year by 46.1%). Both scenarios 1 and 2 (assignment to category 1 is heritable vs. not heritable) predicted that the population should increase. Mean population growth rate over 50 years was  $\lambda = 1.05$  under scenario 1, and  $\lambda = 1.03$  under scenario 2 (Figure 6). Scenario 1 not only yielded a more rapid rate of population growth, but also gradually translated into the percentage of the population in category 1 increasing from 80.6% to 99.99%, which was obvious under this simple scenario. By contrast, in scenario 2 this percentage only increased from 80.6 to 82.55%.

When the population was modeled as homogeneous (scenario 3) with the survival rate intermediate between those of categories 1 and 2 (i.e. 53.2%), the population was



**FIGURE 6.** Trends in the number of teal in a heterogeneous population depending on whether belonging to the high survival category is fully heritable (i.e. category 1 female produce category 1 offspring; black dots) or not heritable (i.e. females of both categories 1 and 2 produce the same percentage of offspring of the 2 categories; the percentage of each generation in categories 1 and 2 remain constant; white circles), and in a homogeneous population (i.e. intermediate adult survival rate; gray squares).

predicted to decline ( $\lambda = 0.98$ ; Figure 6) over the 50-year period.

## DISCUSSION

Modeling a heterogeneous population clearly outperformed homogeneous models in fitting the teal banding data from Camargue. That duck populations could be composed of relatively different categories of individuals is not a new idea; Heitmeyer et al. (1993) highlighted that hunter-killed Mallards (*Anas platyrhynchos*) may be a specific category of birds in terms of general behavior and habitat use, which potentially translates into differences in body condition and demographic rates. Fedynich (1987) and Baldassarre et al. (1988) suggested that 2 categories of wintering Green-winged Teal coexisted in the southern high plains of Texas, one that remains within the same winter quarter throughout the season and another that is more mobile and has greater winter dispersal rates. Similar variety in habitat use strategies was hypothesized for Common Teal in Europe. Such hypothetical differences were invoked to explain variation in body condition indices among individuals, which were supposed to translate into differences in survival rates (Guillemain et al. 2002, 2007). To our knowledge, the present study is the first to quantify such differences in survival rates within a wild dabbling duck population.

We could not demonstrate a relationship between the probability of belonging to a high or low survival category and individual bird morphometrics. This was unexpected because body mass and/or body condition are often used

as a proxy for individual fitness, including survival, in bird demographic studies (e.g., Johnson et al. 1992). Furthermore, it was the actual observation of contrasted body masses that suggested the duck populations in the studies mentioned above could be heterogeneous (Heitmeyer et al. 1993, Guillemain et al. 2002, 2007). A clear link between local residency, body mass, and individual survival could not be demonstrated here. Conversely, individuals with a greater survival rate (category 1) also had a lower live encounter rate (i.e. were less likely to be recaptured at the local banding site), which may indicate that high survival teal were more likely to be transient than teal with lower survival rates, contradicting our initial prediction. This result, however, may be biased by trap-shyness processes and differential energy requirements between high- and low-survival birds. Because traps were baited with rice (*Oryza sativa*), we cannot exclude the possibility that the birds in poorer physiological condition (with consequently lower survival rates) were more likely to come repeatedly to the baited area. The links between habitat use strategies, morphometrics, and survival rates in Teal deserves further study.

The annual survival rates we obtained for the category 1 and 2 birds, ~60% and 47%, respectively, are consistent with estimates for adult Green-winged Teal in the most recent studies: 54.5% in Devineau et al. (2010), 66% in Lake et al. (2006), 51% in Chu et al. (1995), and 41–58% in Gitay et al. (1990). The drop in annual survival for the 1955–1956 season can be easily explained by the harshness of that February, which experienced one of the worst cold spells to hit southern France during the second half of the 20th century (see also Impeken 1965).

Recovery rate was fairly constant in models 1 and 3 but was lower during the 1957–1958 season after model 2. We do not have a biological explanation for this, and it may simply be an artifact of leakage between variables after forcing survival rates to be time-independent in this model while actual survival likely differed during the 1955–1956 season, as previously explained.

The probability of assignment to the high survival category was high and increased from ~50% to 98% over the study period, possibly consistent with a gradual improvement of the environmental conditions for these birds during winter (see also Guillemain et al. 2010b). It could also indicate that belonging to the high survival category was heritable to some extent.

Considering a homogeneous population with a survival rate being the mean over the 2 categories (scenario 3) suggested that the population should decrease over years. This is similar to findings by Devineau (2007) while modeling a homogeneous population and was expected given that the 2 studies used the same source of data. Devineau (2007) used more years (i.e. also years with few



birds captured), however, and split annual survival rates into seasonal estimates.

The period considered here (1955–1967) was just before the European waterbird censuses were initiated (January 1967; Hémery et al. 1979); however, a population growth rate  $<1$  is not consistent with the definite population increases recorded for teal in France during the late 1960s and the 1970s (Hémery et al. 1979). Conversely, modeling a heterogeneous population did suggest a positive population dynamic; the 3–5% increase (with scenario 2 or 1) is more in accordance with the long-term growth of the European populations observed from continuing annual counts (Wetlands International 2013). Modeling a heterogeneous population may provide the solution to the long-held paradox in teal—that banding data were suggesting a decrease in numbers while duck counts in the geographic area were showing the opposite (Devineau 2007).

A striking feature of Green-winged Teal is their general positive population trends, despite a large hunting harvest. Throughout the European Union, the estimated annual harvest is 1,042,000 individuals from an estimated total population size of  $\sim 3,000,000$  birds (Mooij 2005). Similarly, an estimated 1,950,000 Green-winged Teal were harvested during the 2011–2012 season in North America (Raftovich et al. 2012), while the pre-breeding population in spring 2011 was estimated to be 2,900,000 individuals and increasing over the long term (Zimpfer et al. 2011).

Several specific features of the Green-winged Teal may contribute to this apparent ability to compensate for harvest mortality at the population level. First, the populations may be geographically heterogeneous, with sub-populations from some parts of the geographic range having a greater average survival rate gradually repopulating areas of greater mortality throughout the season (Devineau et al. 2010). The rapid turnover of individuals observed within winter quarters is consistent with this hypothesis (Pradel et al. 1997, Caizergues et al. 2011). Second, the short generation time of teal (due to relatively low annual survival rates and annual breeding attempts often starting at 1 year of age) means the 2 species are likely to have a relatively high maximum annual population growth rate (i.e. a greater potential to be harvested while still showing positive population dynamics).

Niel and Lebreton (2005) demonstrated a link function with near constant parameters (“demographic invariants”) between the generation time and maximum population growth rates in birds. Demographic heterogeneity within the population as demonstrated here also likely contributes to this ability to sustain harvest; differences in survival rates among individuals should translate into contrasted reproductive values (i.e. contribution to population dynamics), so that harvesting individuals of high survival category 1 or low survival category 2 does not have the

same impact. If hunting is differentially distributed over the 2 categories of birds, and more likely targeted at birds from category 2, then harvest has a more limited effect on population dynamics than if the same number of individuals was harvested from high-quality, category 1 birds (Lindberg et al. 2013).

The idea that there should be heterogeneity or individual “frailty” within populations is not novel (e.g., Vaupel et al. 1979) and has gained interest over recent years (Robert et al. 2002, Gimenez and Choquet 2010, Plard et al. 2012, Cam et al. 2013). Waterfowl are still managed in North America using harvest models in which populations are considered homogeneous, although potential geographic heterogeneity is considered in demographic rates (e.g., Fleming and Howell 2013, specifically for teal). Recent advances in statistical modeling now make it possible to assess the long-claimed existence of demographic heterogeneity within wildlife populations. In particular, this approach may affect the predicted magnitude of the impact of harvest in such models, which may be overestimated by the current approach that does not take demographic heterogeneity into consideration. This advancement opens new perspectives to link CMR modeling, census schemes, and harvest data within a unified approach, which should be beneficial in the context of wildlife management and policy, especially for exploited species.

## ACKNOWLEDGMENTS

We are most grateful to Luc Hoffmann, Hubert Kowalski, Heinz Hafner, Alan Johnson, and the other people who ringed teal at Tour du Valat for more than 25 years. We thank Jane Austin, Chris Nicolai, and an anonymous referee for their comments on an earlier version of the manuscript, and David Simpson for improving the text. We would also like to thank Marc Lutz, Paul Isenmann, and the Centre de Recherche sur la Biologie des Populations d'Oiseaux (Muséum National d'Histoire Naturelle, Paris) for their help while computerizing the teal database, and the MAVA Foundation for financial support.

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