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When survival matters: is decreasing survival underlying the decline of common pochard in western Europe?

Benjamin Folliot, Guillaume Souchay, Jocelyn Champagnon, Matthieu Guillemain, Maurice Durham, Richard Hearn, Josef Hofer, Jacques Laesser, Christophe Sorin and Alain Caizergues

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In western Europe, common pochard populations have experienced a sharp decline over the last two decades, together with an increasing proportion of males. Both of these changes were suggested to result from decreasing survival of nesting females (i.e. survival of adult females) owing to increasing predation pressure. To test this hypothesis, we used capture-mark-recapture/recovery data of common pochard ringed during autumn–winter (October–February) in three countries of western Europe (Switzerland, United Kingdom and France). We found no evidence for decreasing survival of individuals ringed in the United Kingdom or in Switzerland over the long term (1977–2011). In France, adult males and juvenile females experienced significant decreasing survival over a shorter interval (2004–2017). Overall, females displayed lower survival than males, although this was only weakly supported by the French dataset. In contrast, only sex differences and no age differences in survival rates were recorded in the UK and Switzerland (females 0.67 ± 0.03 and 0.69 ± 0.03 ; males: 0.81 ± 0.01 and 0.75 ± 0.01 , respectively), while both age and sex differences were recorded for France (adult females 0.62 ± 0.07 , adult males 0.66 ± 0.07 , juvenile females 0.49 ± 0.08 , juvenile males 0.54 ± 0.08). Therefore, decreasing survival of adult females was unlikely the underlying cause of the decline of common pochard populations in western Europe. Using an age-structured two-sex matrix population model, we show that when adult males experience higher survival than adult females (as it is the case for common pochards), decreasing survival of nests and/or juveniles can trigger decreasing population size and increasing proportions of males at the same time.

Keywords: CMR, multistate models, recoveries, sex ratio, survival, waterfowl

The long-term sustainability of exploited wildlife populations relies on appropriate management policies (Lebreton 2005). Informed conservation of a species requires understanding the dynamics and drivers of population vital rates and harvest (Johnson et al. 1992, Williams et al. 2002).

The common pochard *Aythya ferina* (hereafter pochard) is a diving duck hunted throughout most of the Western Palearctic. Three Western Palearctic flyways/populations

were initially recognized: the Northwestern European flyway, the Central European flyway and the Southwestern Asian flyway (Scott and Rose 1996, Fig. 1). Since the mid-1990s, pochards have undergone sharp declines in western and central Europe, as indicated by the analysis of trends at the level of the two former European flyways (mean annual rates of change of -5.97% and -2.16% , respectively for the Northwestern and Central European flyways, Nagy et al. 2014, BirdLife International 2015). Such negative trends have caused the species to be up-listed from Least Concern (LC) to Vulnerable (VU) on the European and global IUCN Red Lists in 2015 (BirdLife International 2015). Recent evidence gathered using both genetic markers and ring recoveries clearly demonstrates high connectivity among these

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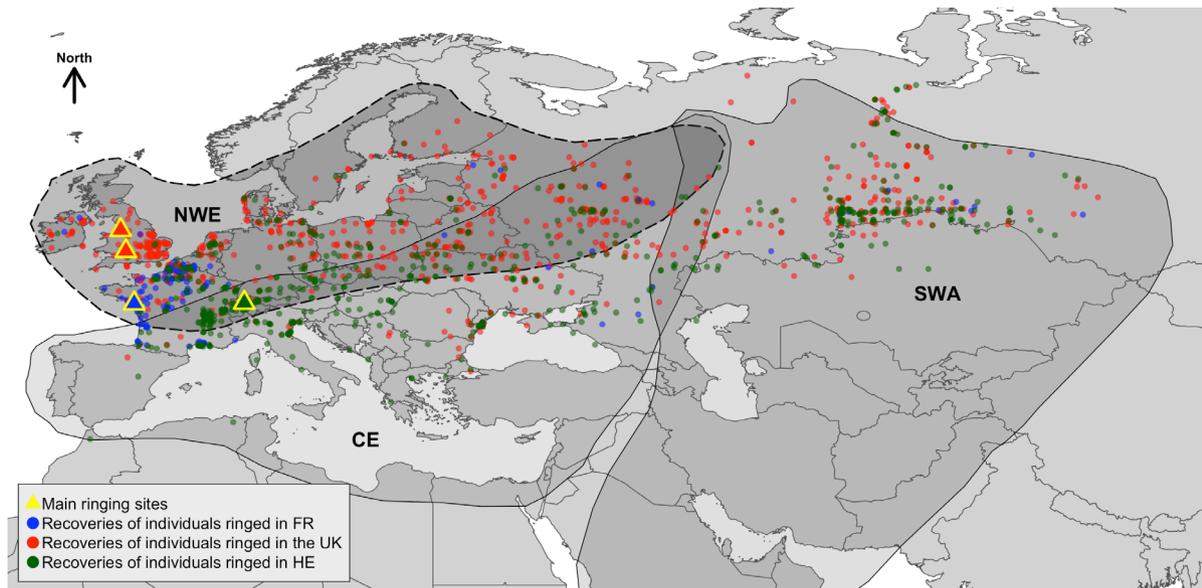


Figure 1. Ringing sites (yellow triangles) and recoveries of pochards caught in western Europe, 1976–2017 (FR: France, CH: Switzerland and UK: United Kingdom). The spatial distributions of recoveries (Folliot et al. 2018) challenges the traditional putative flyways (NWE: northwest Europe; CE: central Europe, Black Sea and Mediterranean; SWA: southwest Asia; see Scott and Rose 1996).

traditional flyways, and general negative trends in numbers (Liu et al. 2011, Folliot et al. 2018). We here used the term ‘western Europe’ to refer to pochards dwelling in the ‘former’ Northwestern European flyway including the overlapping zone with the ‘former’ Central European flyway.

In western Europe, the vulnerable status of pochard has prompted a range of studies about its demographic traits including survival probabilities (Gourlay-Larour et al. 2014), seasonal patterns of movements, individual turnover during winter (Keller et al. 2009, Gourlay-Larour et al. 2012, 2013, 2014, Caizergues et al. 2016, Folliot et al. 2018), as well as nesting success (Folliot et al. 2017). A recent review of the potential causes of the decrease of populations in western Europe indicated possible decline of both adult female survival and breeding success in former strongholds of the species, owing to increasing predation pressure during nesting (Fox et al. 2016). This hypothesis is supported by the assessment of changes in sex-ratio over the past 20 years in western Europe, suggesting increasing proportions of males in the wintering populations (Brides et al. 2017).

Owing to a relatively heavy body-mass (700–1100 g for females), and long life-expectancy (adult survival > 60%, Blums et al. 2002, Fransson et al. 2010, Gourlay-Larour et al. 2014), the pochard should belong to the category of species whose demography is typically driven by changes in adult survival rather than by changes in recruitment (Stearns 1976, Gaillard et al. 2016). Indeed, in lesser scaup *Aythya affinis*, a close relative species to the pochard displaying similar bio-demographic traits, both reduced fecundity and improvement in adult survival rates respectively explained the persistent decline (1983–2006), and subsequent recovery (since 2006) of populations in North America (Arnold et al. 2016, Koons et al. 2017). Therefore, adult survival should actually be one of the most important driving factors of demographic rates in species like pochard, meaning that a decline in adult survival could underlie the current population decline in this species.

The aims of the present study were to assess whether pochards ringed in western Europe experienced a decrease in survival probability, and whether or not this decrease has been affecting females (especially adults) more than males. Indeed, while global declines in survival could account for the observed population decline, a greater decrease in survival rates of females than that of males could in addition explain the observed recent increase in sex-ratio bias towards males (Brides et al. 2017). To achieve these goals, we gathered currently available (i.e. digitized) recapture/recovery dataset collected over the long-term in sites/countries of western Europe representative of likely variable hunting pressure situations. This study therefore includes analyses of both capture–dead recovery and capture–recapture data of individuals ringed in the United Kingdom (two main ringing sites, lower hunting pressure), Switzerland (one main ringing site, lower hunting pressure) and France (one ringing site, higher hunting pressure) over the past 41 years (for hunting bag data in Europe, Hirschfeld and Attard 2017, Hirschfeld et al. 2019).

Material and methods

From the Euring databank (du Feu et al. 2016) and the ringing datasets for each country with complete information (including fitted rings that were not recovered), we compiled data for pochards ringed during the wintering season in France (hereafter ‘FR’), Switzerland (‘CH’) and the United Kingdom (‘UK’) (Supplementary material Appendix 1). We discarded from the analyses any data for which the age or sex of individuals at ringing was not documented (less than 1% of the dataset). In contrast to some other duck species, neither the determination of sex nor that of age is an issue for the pochard (Mouronval 2016). During winter, all individuals can therefore be easily assigned to two categories: juvenile (aged ≤ 9 months) versus adults (aged ≥ 18–19 months).

The CH and UK datasets included 35 years of ringing and dead recoveries (1977–2011), from a number of different ringing sites (two main ringing sites in the UK and one site in CH; Fig. 1). The FR dataset spanned 14 years (2004–2017) and originated from a single ringing site (the lake of Grand-lieu, northwest France, Fig. 1). These three datasets covered periods of the steepest declines of pochard numbers in western Europe (1999–2002 and 2008–2015, Folliot et al. 2018) and were likely representative of a range of situations regularly encountered by pochards in western Europe. Indeed while the UK and CH datasets probably better reflect the ‘average’ conditions of many sites/countries of northwestern Europe characterized by low to moderate hunting pressure, Grand-lieu (FR) would be more representative of situations encountered in wetlands such as the Camargue (southern France) and Guadalquivir deltas (southern Spain), where hunting pressure is presumably higher (Hirschfeld and Attard 2017, Hirschfeld et al. 2019). Unfortunately, Grand-lieu is the only dataset currently available for pochards potentially exposed to a higher hunting pressure and covering periods of both decline and stability of the species in western Europe. In addition to physical recaptures and dead recoveries, the dataset from Grand-lieu also included visual ‘recaptures’ of individuals fitted with nasal saddles bearing an alphanumeric code (Rodrigues et al. 2001). Previous studies have shown that the presence of nasal saddle did not negatively affect survival (Hořák 2002, Regehr and Rodway 2003). More importantly, survival estimates of nasal saddled individuals derived from a CMR analysis of movement patterns were within the range or higher than values previously estimated for this species using regular metal rings only (respectively 0.66 against 0.65 for nasal saddled adults, Gourlay-Larour et al. 2013 and ringed only adult females, Blums et al. 1996). Soiling and loss can become a problem with the ‘ageing’ of the nasal saddle. A crude estimate indicates that the mark is kept by all individuals and can be read without particular difficulty for at least three years, and a majority of individuals (~80%) still wear a perfectly readable mark for five years (Caizergues unpubl.). Nevertheless, to mitigate this potential problem, we allowed capture probability to decrease after three years of marking. Finally, some individuals caught in France also wore a reward ring (Henny and Burnham 1976, Zimmerman et al. 2009, Souchay et al. 2014), as part of an ongoing study aiming to assess hunting mortality (see below). Therefore, compared to CH and UK datasets, the FR dataset included live recaptures and potentially provided higher recovery rates (due to rewards rings) thereby greatly enhancing the potential to detect any effect (e.g. time, sex) on survival probabilities. Because it included recaptures in addition to ring recoveries and spanned a different period than the CH and UK datasets, the FR dataset was analysed separately. There were no differences in the range of recoveries from each ringing location (Fig. 1). While the bulk of direct ring recoveries was from western Europe, a substantial proportion of indirect recoveries spanned over the three putative flyways (Fig. 1, see also Folliot et al. 2018). We performed all analyses using conventional, capture–mark–recapture/recovery models as described in Lebreton et al. (2009).

Dead-recoveries of the individuals ringed in Switzerland and the United Kingdom

Only dead recoveries were available for the individuals ringed in CH and the UK. To minimize heterogeneity due to large differences in the duration of exposure to hunting between individuals ringed at the beginning or at the end of the hunting season (hunting and ringing occurred over the same period of the year), we retained only those individuals ringed during the peak of the wintering season (1 December–29 February). Our analysis is based on a total of 17 198 individuals ringed between 1977 and 2011, with an average of 287 ± 122 and 204 ± 273 (\pm SD) ringed per year in CH and the UK, respectively (Supplementary material Appendix), yielding a total of 1466 dead recoveries. We discarded recoveries not caused by hunting (less than 6% of the total number of recoveries) in order to minimize possible biases due to the strong uncertainty about the exact date of death for most of these individuals and to reduce heterogeneity in ring reporting rates when diverse sources of recoveries are considered. We considered two age classes in our analyses: juveniles for individuals ringed during the winter following their hatching year (hereafter ‘JUV’) and adults for those ringed during subsequent winters (hereafter ‘AD’) (see above for the definitions of these age classes).

We used a multistate framework with an $\{S-r\}$ parametrization (Seber 1971, Gauthier and Lebreton 2008) to assess annual survival probability (i.e. the probability for an individual to survive between year t and year $t+1$) and recovery probability (the probability of recovering a ring conditional on death of the animal, see Gauthier and Lebreton 2008).

We used four variables to explain variations in survival: the place/country of ringing (hereafter ‘CountryRing’, i.e. CH versus UK), the sex of the individual (hereafter ‘Sex’), the year as factor or quantitative variable, and the age at the time of ringing (hereafter ‘Age’, adults/AD versus juveniles/JUV, with juveniles having potentially different survival rates than adults during the first year after ringing). Regarding potential temporal variation, due to scant sample sizes in some years, we also tested a 3-year period effect (hereafter ‘PooledYears’) rather than a typical year effect. Pooling data into three-year periods allowed us to better assess temporal variations in survival and recovery probabilities without assuming that each year was unique or that annual variation followed a strictly linear trend over the entire time series. Nevertheless, based on the AIC approach, we assessed which level of temporal variation (one year versus three years pooled) was the most relevant at each step for our analyses. PooledYears was always selected preferentially to Year after the model results.

Four variables were tested to explain potential variation in recovery probabilities: PooledYears, Sex, Age and a variable ‘time since marking’ or ‘TSM’ distinguishing direct (recoveries from the season of ringing) from indirect recoveries (recoveries occurring in subsequent years).

Regarding GOF tests for dead recovery models, given that each individual only contributes a single observation to the likelihoods (i.e. it dies and is recovered or it is not recovered), there is no potential for overdispersion (Lebreton 2001) and individual heterogeneity in recovery probabilities has

negligible consequences on survival estimates (White et al. 2013). Moreover, because individuals are only encountered a single time (at most) following their death, there can be no trap dependence, and because dead recoveries can be obtained from throughout the species range, there are no concerns about transience either. We therefore used AIC to compare models for dead recovery data.

Recaptures-recoveries of individuals ringed on Grand-lieu (FR)

In addition to dead-recoveries, the dataset of the individuals ringed on the lake of Grand-lieu included physical and visual recaptures (of individuals fitted with a nasal saddle). To minimize heterogeneity, only individuals caught during winter (from 1 October to 31 December) and recaptures performed between 1 October and 31 December each year were taken into account. We physically recaptured individuals using barrier traps (i.e. a submerged cage with an opening on the side where the diving duck inadvertently enters when feeding) baited with wheat (Haramis et al. 1982) at the ringing site, whereas visual recaptures included data from camera traps placed in front of barrier traps as well as observations by birdwatchers from anywhere in Europe. Recoveries include data from individuals shot anytime during the regular hunting season (from 1 September to 31 January). A total of 2391 individuals were ringed from 2004 to 2017, with an average of 171 ± 106 (\pm SD) individuals per year (Supplementary material Appendix). Moreover, the dataset included 760 recaptures (mostly visual) and 403 dead-recoveries throughout the species' distribution range. Since the 2012–2013 hunting season, 173 randomly selected individuals were fitted with a 70-euro reward ring at lake Grand-lieu, as part of an ongoing project aimed at estimating harvest rate (Guillemain et al. unpubl.). These individuals represented 7.2% of the total number of individuals considered in the present analysis and 28.6% of those ringed since 2012. Because reward rings usually display higher recovery probability (Nichols et al. 1991), the presence of the reward ring on the recovery rate was taken into account in the analyses by considering two categories of individuals with or without a reward ring. We also took into account that the behaviour of hunters could have changed since the onset of the reward study (from 2012 onward) and, as a result, that the reporting rate could have increased since that time, by introducing a temporal variable with two categories (before 2012 and after 2012).

We derived estimates of annual survival and of recapture and recovery probabilities from conventional multistate models using a similar approach as described above, with the difference that they included recapture probability (Gauthier and Lebreton 2008). Five potential underlying factors of recapture probability were tested: the age of the individuals at ringing 'Age', their sex 'Sex', the time elapsed since marking 'TSM', the year effect 'Year' and the possible wear, soiling or loss of the nasal saddle (see above), which could prevent resighting after three years (hereafter 'Lost-Tag'). Concerning recovery probabilities, five variables were tested: the year effect 'Year', the presence/absence of a reward ring (hereafter 'Reward'), two periods of ringing (before and after 2012, hereafter 'RewardPeriod'), the sex of the

individual 'Sex' and the Time since marking 'TSM'. Selection of the survival model was performed using the best models for both recapture and recovery (Doherty et al. 2012).

Before running the analyses, we tested the goodness-of-fit of our multistate models taking into account Sex and Age, using U-CARE (ver. 2.3.4, Choquet et al. 2009a). Whenever needed, a variance inflation factor \hat{c} was applied to correct the variance of estimates and adjust model selection using QAIC (Burnham and Anderson 2002, Choquet et al. 2009b).

Model selection and linear effects of time

Both the capture-recoveries of the CH and UK data and capture–recapture–recoveries of Grand-lieu (FR) were fitted using E-SURGE software (ver. 2.1.4, Choquet et al. 2009b) using the parametrizations presented in Supplementary material Appendix 2. Model selection followed a multi-step downward approach. This approach consists in assessing all the effects/factors of interest (starting with the most complex model including, as far as possible, all biologically meaningful effects and their interactions), for each parameter of interest separately, beginning with dead recovery and ending with survival (Doherty et al. 2012). Model simplification is based on the minimum AIC model as a starting point for the next step (Burnham and Anderson 2002, Lebreton et al. 2009). For the French dataset, the modelling approach was like that of Gauthier and Lebreton (2008), whereby recapture models were first assessed, followed by models for recovery probabilities and then models for survival probabilities. As recommended by Lebreton and Pradel (2002), we used the 'multiple random' option to fit the same model 10 times from different initial values to avoid local minima (Choquet and Nogue 2011). All resulting probability estimates are expressed with their mean \pm standard error (SE).

In addition, to test for the hypothesis of a decline in survival over the study period, we also tested a linear trend of survival for each class of individuals (male/female, adult/juvenile) separately, using analyses of deviance (ANODEV, Skalski 1996, Grosbois et al. 2008, Lebreton et al. 2012). We accounted for possible differences in survival between sites (UK versus CH) by allowing the intercepts to vary between sites. We therefore implicitly assumed that if a decrease in survival occurred it had been affecting individuals ringed in CH and the UK to the same extent. Finally, because we aimed at testing expected decreases (rather than changes) in survival, we used one-tailed instead of two-tailed *t* tests. We provided ANODEV statistics as well as average slope of the trend together with their 95% confidence interval.

Results

Dead-recovery models for individuals ringed in CH and the UK (1977–2011)

The model retained for the analyses of capture-recovery of individuals ringed in CH and the UK included an interaction between sex (Sex), the country of ringing (Country-Ring), time (PooledYears) and type of recovery (direct versus indirect, TSM) on the annual recovery probability, as well

as the effects of country of ringing, sex and the interaction between these two variables on annual survival (Table 1).

Overall, individuals ringed in CH displayed higher direct recovery probabilities than those ringed in the UK (CH females = 0.107 ± 0.012 , males = 0.144 ± 0.004 , with point estimates being slightly higher in the UK [stats]). In contrast, indirect recovery probabilities did not display any marked difference between countries (CH females = 0.050 ± 0.004 , males = 0.087 ± 0.004 , with point estimates being slightly higher in the UK [stats]). Males had both higher direct and indirect recovery probabilities than females whatever the country of ringing. Finally, whatever the country or sex, recovery probabilities significantly declined over time as measured with three years pooled.

Males displayed higher survival probabilities than females in both countries (Fig. 2), although the between-sex difference in survival was more pronounced in CH than the UK (CH females = 0.67 ± 0.03 , males = 0.81 ± 0.01 ; UK females = 0.69 ± 0.03 , males = 0.75 ± 0.01). Over the 1977–2011 period, there was no evidence for any decrease in survival probabilities over time whatever the sex or country. Moreover, we detected no difference of survival before and after the population decline in western Europe, i.e. before and after 1996 (Folliot et al. 2018). More importantly,

regardless of the age class (AD versus JUV) or sex considered, we detected no linear decrease in survival probability over time (time used as a quantitative variable), except perhaps for adult males (ANODEV analysis, see Table 2). In all these cases, the slope of the trend was weak and 95% CI largely overlapped with 0 (Table 2).

Recapture–recoveries of the individuals ringed on Grand-lieu lake (FR, 2004–2017)

Goodness of fit tests (for transience and trap-dependence) did not detect any significant lack of fit, except for trap-dependence (i.e. trap-happiness) in adult females and juvenile males and females (Supplementary material Appendix 3). Based on GOF tests, an over-dispersion coefficient of $\hat{c} = \chi^2/df = 234.9/218 = 1.08$ was taken into account in the analyses below and model selection thus relied on QAIC.

Three of the five best models for recapture probability included an effect of Sex (Table 3). Concerning recovery probabilities, three models were within two units of QAIC, of which two included the type of recovery (direct versus indirect, TSM), time (Year) and the presence of a reward ring (Reward) (Table 3). Finally, the best model for survival probability included the effect of age (JUV versus AD),

Table 1. Summary table of the best models for capture–mark–recovery data of common pochards ringed during winter (December–February) in Switzerland and the United Kingdom from 1977 to 2011. Models in bold are the 'best' models according to Δ AIC. TSM=time elapsed since marking (direct versus indirect recoveries), PooledYears=time effect tested for 'bouts' of three years pooled, Age (juveniles versus older individuals), CountryRing (Switzerland versus United Kingdom).

	Models	k	Deviance	AIC	Δ AIC	
Recovery	TSM × [Sex + CountryRing + PooledYears]	60	15898.9	16018.9	0.0	
	Sex + CountryRing + PooledYears	46	15948.1	16040.1	21.2	
	TSM + Sex + CountryRing + PooledYears	47	15947.2	16041.2	22.3	
	Sex + PooledYears	45	15951.4	16041.4	22.5	
	TSM + Sex + PooledYears	46	15950.9	16042.9	24.0	
	Sex + CountryRing	33	16005.8	16071.8	52.9	
	TSM + Sex + CountryRing	34	16005.5	16073.5	54.7	
	Sex	32	16011.7	16075.7	56.8	
	PooledYears	44	16018.9	16106.9	88.0	
	CountryRing + PooledYears	45	16017.4	16107.4	88.5	
	TSM + CountryRing	33	16064.2	16130.2	111.3	
	Year	70	15990.6	16130.6	111.7	
	CountryRing	32	16071.5	16135.5	116.6	
	Survival	CountryRing × Sex	34	15945.7	16013.7	0.0
		CountryRing + Sex	33	15951.0	16017.0	3.4
Age + CountryRing + Sex		34	15949.6	16017.6	4.0	
Age × CountryRing + Sex + PooledYears		60	15900.2	16020.2	6.5	
Age × CountryRing + Sex		36	15948.8	16020.8	7.2	
Sex		32	15961.7	16025.7	12.0	
Age + Sex		33	15959.9	16025.9	12.2	
PooledYears + CountryRing + Sex		46	15933.9	16025.9	12.3	
Age × Sex		34	15959.9	16027.9	14.2	
Age × PooledYears.Sex		82	15863.9	16027.9	14.2	
Age + CountryRing + PooledYears + Sex		47	15934.3	16028.3	14.6	
PooledYears + Sex		45	15939.2	16029.2	15.5	
Age + Sex + PooledYears		46	15940.1	16032.1	18.4	
CountryRing		32	15969.8	16033.8	20.1	
Age + CountryRing		33	15968.6	16034.6	21.0	
CountryRing × Sex × PooledYears		84	15866.8	16034.8	21.1	
Age		32	15982.0	16046.0	32.4	
PooledYears		44	15963.5	16051.5	37.8	
Year		70	15936.9	16076.9	63.3	

K is the number of estimated parameters, AIC is the Akaike information criteria, Δ AIC represents the difference in AIC between the current model and the model with lowest AIC value.

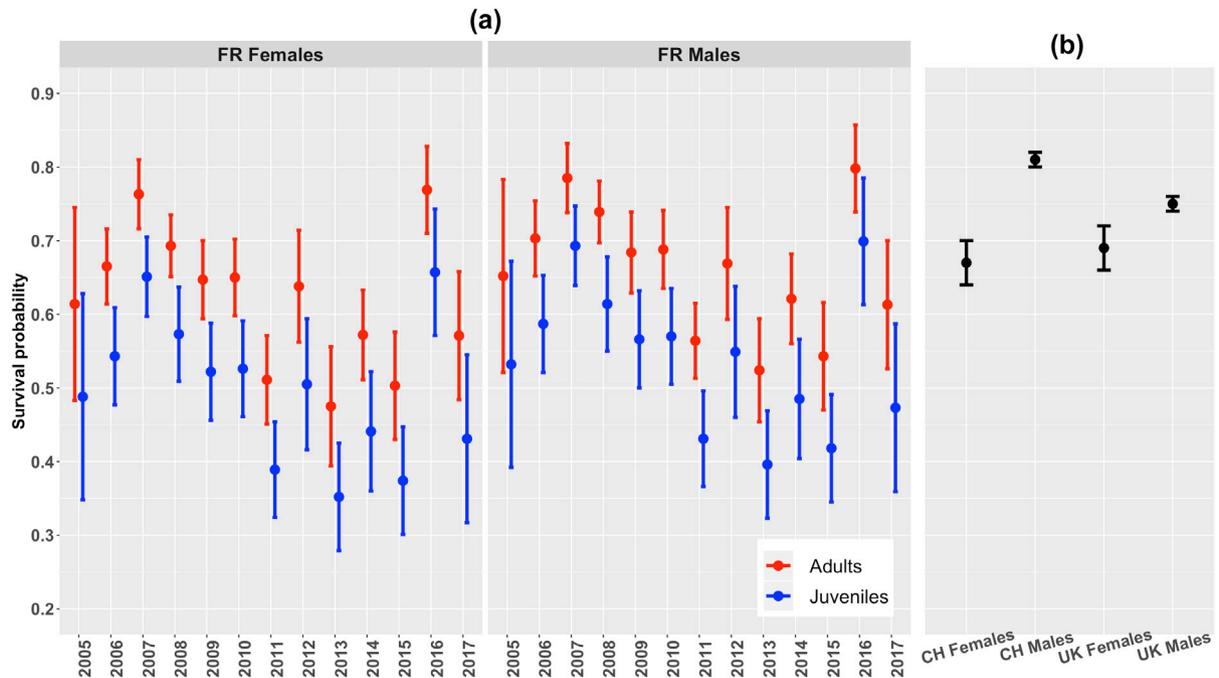


Figure 2. (a) Temporal variations in survival probabilities \pm SE derived from the model $S - \text{Age} + \text{Year}$, of capture–recaptures/recoveries of pochard ringed in Autumn–early winter (October–December) on Grand-lieu lake (France), 2004–2017. A significant decrease in survival probabilities (represented by the black dashed-line) was observed over the study period. It was apparently due especially to a decrease in survival towards the end of the study period (2013–2015). (b) Survival probabilities \pm SE derived from the model $S - \text{Sex} \times \text{Country} \times \text{Ring}$, of capture–recoveries of pochards ringed in winter (December–February) in Switzerland and the United Kingdom between 1977 and 2011.

time (Year) and sex (Table 3). Juveniles and females displayed lower survival probabilities than adults and males, respectively (juvenile females 0.49 ± 0.08 , range over the study period [0.35–0.65]; juvenile males 0.54 ± 0.08 , range [0.39–0.70]; adult females 0.62 ± 0.07 range [0.48–0.76] and adult males 0.66 ± 0.07 , range [0.52–0.80], all the yearly estimates shown in Table 4). However, the effect of sex was only weakly supported by our analysis, because the difference in QAIC compared to the second-best model, which did not include ‘Sex’, was only 1.2.

Although statistically different, live recapture probabilities of females and males were very close, that is, 0.091 (± 0.009) and 0.102 (± 0.012), respectively. As expected, both females and males displayed higher direct than indirect dead recovery probabilities of 0.185 (± 0.015) and 0.153 (± 0.013) respectively, with values much higher than those reported for the individuals ringed in CH and the UK. However, even though the effect of age was not retained in

the top models for recoveries, because all juvenile recoveries are by definition ‘direct recoveries’, one cannot exclude that higher direct recoveries were at least in part due to the higher vulnerability of juveniles towards hunting.

Individuals ringed as juveniles (JUV) displayed lower survival probabilities (during the first year following ringing) than those ringed as adults (AD) (juveniles 0.53 ± 0.08 versus adults 0.64 ± 0.06 , see also Fig. 2). Finally, the ANODEV showed that adult males and juvenile females experienced a linear decrease in survival over the study period, whereas over the same period the survival rates of adult females and juvenile males remained stable (Table 2).

Discussion

This study is the first investigation of survival probabilities of both male and female pochards over several decades in

Table 2. Analysis of deviance (ANODEV) assessing a linear decrease of survival by age and sex for common pochards ringed in Switzerland (CH)/United Kingdom (UK) and France (FR). For the CH/UK dataset, possible differences in survival between sites were accounted for by allowing the intercepts to differ between sites. Slope [95% CI] means the average slope with a 95% confidence interval. Significant p-values are shown in bold.

Dataset	Group	F	R ²	p-value	One-tailed p	Slope [95% CI]
CH/UK	Juvenile females	0.43	0.013	0.519	0.260	+0.145 [−0.410; +0.700]
	Adult females	1.51	0.040	0.226	0.113	+0.052 [−0.208; +0.313]
	Juveniles males	1.40	0.041	0.245	0.123	−0.510 [−0.937; +0.083]
	Adult males	3.98	0.095	0.053	0.027	−0.038 [−0.194; +0.118]
FR	Juvenile females	18.83	0.611	0.001	< 0.001	−0.696 [−1.086; −0.306]
	Adult females	0.35	0.029	0.562	0.281	−0.053 [−0.331; +0.226]
	Juveniles males	1.31	0.099	0.274	0.137	−0.274 [−0.639; +0.090]
	Adult males	5.51	0.315	0.037	0.018	−0.363 [−0.592; −0.133]

Table 3. Summary table of capture–mark–recaptures/recoveries models for common pochards ringed during autumn/early winter (October–December) on Grand-lieu lake (France) between 2004 and 2017. Models in bold are the ‘best’ models according to Δ QAIC. TSM=time elapsed since marking (direct versus indirect recoveries), Age (juveniles versus older individuals), LostTag (time parameterisation taking into account the possible wear, soiling or loss of the nasal saddle after three years) and Reward for the presence/absence of a reward ring.

Parameter	Models	k	Deviance	QAIC	Δ QAIC
Recapture	Sex	61	5735.7	5432.9	0.0
	TSM	61	5736.2	5433.3	0.5
	LostTag	61	5737.2	5434.2	1.4
	TSM+Sex	62	5735.8	5434.9	2.1
	LostTag+Sex	62	5735.9	5435.0	2.2
	Year	73	5716.5	5439.0	6.2
	Sex+Year	74	5715.6	5440.2	7.3
	TSM+Year	74	5716.1	5440.7	7.9
	TSM \times Year	86	5705.5	5454.9	22.0
	Constant	60	5917.7	5599.4	166.5
Recovery	TSM + Reward + Year	48	5745.5	5415.9	0.0
	TSM + Sex + Reward + Year	49	5744.9	5417.4	1.4
	Sex + Reward + Year	48	5747.7	5418.0	2.0
	Reward + Year	47	5751.2	5419.2	3.3
	TSM + Year	47	5754.3	5422.0	6.1
	Year	46	5758.4	5423.8	7.9
	TSM + Sex + Year	48	5754.2	5424.0	8.0
	Sex + Year	47	5756.6	5424.2	8.3
	Reward + RewardedPeriod	35	5800.1	5440.4	24.5
Survival	Age + Sex + Year	34	5755.4	5397.1	0.0
	Age + Year	33	5758.9	5398.3	1.2
	Year + Sex	33	5763.9	5403.0	5.9
	Year	32	5768.6	5405.3	8.3
	Age \times Year	46	5749.3	5415.4	18.3
	Age + Sex	21	5809.0	5420.7	23.7
	Sex \times Year	46	5753.9	5419.7	22.6
	Age	20	5812.3	5421.7	24.6
	Sex	20	5817.3	5426.4	29.3
	Age \times Sex \times Year	74	5719.3	5443.6	46.5

K is the number of estimated parameters, QAIC is the Akaike information criteria for overdispersed count data, Δ QAIC represents the difference in QAIC between the current model and the model with lowest QAIC value.

western Europe. It provides updated survival data for females, that could be the cornerstone of future models of adaptive harvesting of this species in Europe, and gives useful insights into the understanding of the causes of the decline in numbers (Folliot et al. 2018). Based on extensive datasets collected over large spatial scales, covering a wide array of environmental conditions and anthropic pressures (including hunting pressure) potentially experienced by pochards, we could not gather evidence for decreasing survival of adult females. Our results, therefore, do not support that decreasing survival of adult females (due to increasing predation pressure during the nesting period) is the underlying cause of the decline of pochard in western Europe (Fox et al. 2016, Brides et al. 2017). When evidenced (Grand-lieu lake, France), the temporal variations in adult female survival did not display any particular trend over years. One may argue that the limited numbers of recoveries may have impaired the detection of temporal changes in survival for the datasets of CH and UK. However, the estimates of adult female survival ringed in these areas were higher than those reported in Europe before the population decline (adult females = 0.59 at Engure lake in Latvia, Blums et al. 1996 versus 0.67 ± 0.03 and 0.69 ± 0.03 in CH and the UK in the present study, respectively), even if this comparison has to be done cautiously (use of joint live–dead encounter model in the present study that measures ‘true survival probability’ versus live-encounter model that measures ‘apparent survival’

in Blums et al. 1996, see White and Burnham 1999). Moreover, we did not detect any decrease in adult female’s survival in France (average survival of adult female 0.63 ± 0.02), even though the analyses benefited for greatly enhanced testing power thanks to the availability of live recaptures and resighting data (both temporal variations of survival and linear trend were detected for adult males and juvenile females in this dataset). Altogether, our data also confirm that diving ducks tend to be in the upper part of the range of survival probabilities observed in ducks (Krementz et al. 1987).

Survival probabilities and the excess of males on wintering sites

Females displayed significantly lower survival probabilities than males, with differences that varied from 2.7% to 7.9 percentage points in the UK and Switzerland, respectively. Such between-sex differences in survival probabilities are common in ducks (Bellrose and Kortright 1976, Arnold et al. 2016). They have been suggested to result from the higher vulnerability of females to predation during the breeding season (Krementz et al. 1987, Batt et al. 1992, Arnold et al. 2012). Whether the between-sex differences in survival observed in our study are of such amplitude to explain the excess of males into the wintering population remains to be properly assessed (using Leslie–Usher matrix modelling for example, Caswell 1980, Ramula et al. 2018). Nevertheless, here we

Table 4. Survival probabilities (mean \pm SE) by age, sex and year derived from capture to recaptures/recoveries of pochard ringed on Grand-lieu lake (France) between 2004 and 2017.

Year	Juveniles		Adults	
	Females	Males	Females	Males
2005	0.48 \pm 0.14	0.53 \pm 0.14	0.61 \pm 0.13	0.65 \pm 0.13
2006	0.54 \pm 0.07	0.58 \pm 0.07	0.66 \pm 0.06	0.70 \pm 0.06
2007	0.65 \pm 0.06	0.69 \pm 0.05	0.76 \pm 0.04	0.79 \pm 0.04
2008	0.58 \pm 0.06	0.62 \pm 0.06	0.69 \pm 0.05	0.73 \pm 0.05
2009	0.52 \pm 0.06	0.57 \pm 0.06	0.65 \pm 0.05	0.69 \pm 0.05
2010	0.52 \pm 0.06	0.57 \pm 0.06	0.65 \pm 0.05	0.69 \pm 0.05
2011	0.38 \pm 0.06	0.43 \pm 0.06	0.51 \pm 0.06	0.55 \pm 0.06
2012	0.50 \pm 0.09	0.55 \pm 0.09	0.63 \pm 0.08	0.67 \pm 0.07
2013	0.35 \pm 0.07	0.39 \pm 0.08	0.48 \pm 0.07	0.52 \pm 0.07
2014	0.44 \pm 0.07	0.49 \pm 0.07	0.57 \pm 0.07	0.62 \pm 0.06
2015	0.37 \pm 0.07	0.42 \pm 0.07	0.50 \pm 0.06	0.55 \pm 0.06
2016	0.65 \pm 0.09	0.70 \pm 0.08	0.76 \pm 0.07	0.80 \pm 0.06
2017	0.44 \pm 0.09	0.48 \pm 0.09	0.57 \pm 0.09	0.61 \pm 0.09

urge once again that because the between-sex differences in survival rates remained stable over the study period at all locations, the hypothesis that increasing male bias in western Europe would simply result from an increase in female mortality relative to male (Brides et al. 2017) is not supported by our analyses.

Between-sites differences and hunting pressure

Overall, we observed significant differences in estimates and patterns of recoveries and survival probabilities between sites/areas (Fig. 2). Although individuals ringed in Switzerland (CH) and the United Kingdom (UK) showed quite comparable survival and indirect recovery probabilities, direct recovery rates were direct recovery rates in CH were almost three times higher than those in the UK. Therefore, because survival rates were similar in the two countries, we can hypothesize either: 1) that hunting pressure was similar between these areas and that the differences in direct recovery rates were due to differences in reporting rates (the return of rings to the ringing centers by hunters), or 2) that the differences in recovery rates reflected different hunting pressures, but a phenomenon of compensation of hunting mortality occurred (increasing survival of non-hunted individuals or among-individual heterogeneity in survival, Sedinger and Herzog 2012).

We could not gather reliable data about hunting pressure over the whole study period. However, according to recently estimated hunting bags, the hunting pressure would be higher in FR than in both UK and CH (Guillemain et al. 2016, Hirschfeld and Attard 2017). Indeed, although the lake of Grand-lieu itself is a strictly protected area, hunting pressure can reach high levels in its direct vicinity (300–800 pochard would be killed each year out of 3000–5000 counted at the peak of the wintering season; Reeber 2016). In France, the hunting bag during the 2013–2014 season was ca 25 000 individuals out of 65 000 counted in January (Guillemain et al. 2016). The hunting pressure is much lower in the United Kingdom and almost null in Switzerland, with an annual bag for the 2013–2014 hunting season estimated around 2500 (Hearn, unpubl. of the British Association for Shooting and Conservation) and 91 pochards respectively,

out of wintering numbers of ca 25 000 and 35 000 individuals, respectively (Guillemain et al. 2016, Hirschfeld and Attard 2017). Lower direct recovery rates in the UK than CH may therefore reflect lower reporting rates, whereas the higher direct recovery rates and lower survival recorded for individuals ringed in FR likely reflect higher hunting pressure. In support of this hypothesis, survival rates of adult Tufted ducks were found to be lower for individuals ringed on Grand-lieu (males and females combined = 0.57 \pm 0.05) than for those ringed over the same years just 200 km away in Mayenne (western France) (females only = 0.77 \pm 0.04; Caizergues et al. unpublished data). There was no evidence for any change in direct recovery rates of pochards over the study period on Grand-lieu. On this premise, one can probably rule out that increasing hunting pressure was likely the cause of the recent decline of survival of individuals ringed in the area.

Age and survival

Being naïve, juveniles would be more vulnerable to hunting mortality and predation than older individuals. In support of this hypothesis, numerous studies have shown that juveniles display significantly lower survival probabilities and greater recovery rates than older birds (in their second year of life or older, Johnson et al. 1992, Blums et al. 1996, Péron et al. 2012, Gourlay-Larour et al. 2014, Arnold et al. 2016). Nevertheless, in this study, no differences in survival probabilities were detected between juveniles and adults, except for individuals ringed on Grand-lieu (juveniles = 0.51 \pm 0.04, adults = 0.63 \pm 0.02). However, our inability to detect any between-age difference in survival in CH and the UK may be an artefact of including in the analyses only birds ringed towards the end of the hunting season (December–February), hence after the period when most between-age differences in survival often occur (Guillemain et al. 2013). Alternatively, the difference in survival rates between juveniles and adults could be more pronounced under higher hunting pressure (FR), owing to greater susceptibility of juveniles to this source of mortality (Krementz et al. 1987, Christensen 2001). In other words, differences in survival between juveniles and adults could decrease in areas with lower hunting pressure, as well as after 1 December, which is the date when the newly marked individuals were considered in the analyses in Switzerland and United Kingdom. In France, where juveniles were found to display lower survival rates than adults, the date when the newly marked individuals were considered in the analyses was earlier, i.e. 1 October. There were therefore more opportunities for any age differences to become apparent in the French than in the Swiss or the British datasets.

Anatids display a wide range of demographic strategies; with the blue-winged teal *Spatula discors* and the tundra swan *Cygnus c. columbianus* being respectively the fastest and slowest species in this taxonomic group (generation times close to 2 and 11 respectively, Koons et al. 2014). However, even the ‘fastest’ duck species is more sensitive to variations in adult survival than to variations in reproductive success. With such values of survival as those estimated in our study, the pochard would be no exception to this rule. In practice, key components of fitness, such as adult survival in ducks,

are ‘buffered’ by natural selection (i.e. with dampened variations over the years), whereas parameters of lesser importance such as juvenile survival (Stearns and Kawecki 1994, Morris and Doak 2004, Koons et al. 2016) and fecundity (nest success) usually display larger annual variations of up to 90% (Folliot et al. 2017). Therefore, when they occur, changes in population size of species displaying quite high adult survival, like the pochard, are usually driven by variations in recruitment parameters like juvenile survival or nest success (Koons et al. 2016, reviewed by Koons et al. 2014). In view of the high adult survival probabilities assessed in this study, the explanation for the decline of pochards in western Europe could be more likely to be explained by a decrease of juvenile survival and/or or nesting success.

Refining our ‘starting’ hypothesis

Several hypotheses have been expressed to explain the declining numbers of pochards and the changes in sex ratio recorded in Europe over the last decades (Fox et al. 2016). Few factors however have the potential to explain both patterns simultaneously. Among them, one can for example mention range shifts related to global warming, that may affect the spatial distribution of sexes over the wintering grounds (Lehikoinen et al. 2013, Elmberg et al. 2014), or alteration of primary sex-ratio due, for example, to embryos’ exposure to endocrine disruptors (Carere et al. 2010). However, these two hypotheses both predict decreasing proportions of males. Indeed, the pochard is a typical partial migrant in western Europe, with females moving farther south than males during the wintering season (Brides et al. 2017). Thus, a range shift towards the north-east would likely trigger an increase in the proportions of females in many countries of western Europe. Moreover, even though they may affect fecundity (and therefore productivity), endocrine disruptors seem to induce feminization of males rather than masculinization of females (von Engelhardt et al. 2004, Bouland et al. 2012), hence leading to an increase in the number of females rather than the opposite.

Most authors more or less explicitly assumed that changes in sex ratio could only result from sex-specific changes in vital rates (alteration of primary sex-ratio or sex-specific variations in survival at various stages of the life cycle, Lehikoinen et al. 2008, Fox et al. 2016, Brides et al. 2017, but see Ramula et al. 2018). Using an age-structured two-sex matrix population model implemented in the ‘popbio’ package in R (Stubben and Milligan 2007, <www.r-project.org>, Fig. 3), we explored some conditions that could explain simultaneous

increasing proportions of males and decreasing overall numbers without resorting to sex-specific changes in vital rates. We show that when adult male survival is higher than female adult survival (like in CH and the UK for pochards), reducing juvenile recruitment (by decreasing either nest success or juvenile survival) is sufficient to explain observed population changes in pochards (Supplementary material Appendix 4), without the need for any change in adult survival in any sex. For example, by decreasing either juvenile survival S_j (or nest success, NS_j and NS_a) by 50%, (initial values: $S_j=0.20$; $NS_j=0.03$, $NS_a=0.53$), while the other parameters were held constant (adult survival, males=0.81, females=0.69, Clutch-size adult females 9.2 juvenile females 8.3, primary sex ratio=0.50), we triggered both an increase in the proportion of males (from 60.1 to 74%), and a sharp decline in asymptotic population growth rate (λ) from 1.07 to 0.89. According to this simulation, therefore, there was no need to resort to sex-specific changes in vital rates for explaining the patterns observed for pochards in western Europe. Because adult female pochards exhibit lower survival than adult males, like in many ducks species, decreasing recruitment rate (through lower reproductive success and/or juvenile survival) affecting both sexes in the same manner could simultaneously explain the increasing proportion of males and declining overall numbers. Such a process has the advantage of being both biologically credible and parsimonious at the same time. Finally, it should be noticed that increasing the proportion of males at hatching from 50% to 60% (a very unlikely situation in natural conditions) triggered an increase in the proportions of breeding males from 60.1 to 72%, but the asymptotic population growth rate remained superior to 1 ($\lambda=1.01$). Therefore, although an increasing proportion of males at hatching may have a strong impact on the proportion of males into the breeding population it has only a moderate impact on population growth rate and hence is unlikely the underlying cause of the decline of pochards.

Conclusions

According to this study, one can rule out that a decreasing survival of adult females is the underlying cause of the decline of pochard in western Europe from 2000s onwards. More importantly, our results emphasize, that even if we do not need to invoke sex-specific changes in vital parameters for explaining variations in sex ratio and/or population size, monitoring both sexes is a prerequisite towards a better understanding of the underlying causes and patterns of

$$\begin{bmatrix} N_{Fj} \\ N_{Fa} \\ N_{Mj} \\ N_{Ma} \end{bmatrix}_{t+1} = \begin{bmatrix} F_{Fj} \times S_j & F_{Fa} \times S_j & \dots & \dots \\ S_{Fa} & S_{Fa} & \dots & \dots \\ F_{Fj} \times S_j & F_{Fa} \times S_j & \dots & \dots \\ \dots & \dots & S_{Ma} & S_{Ma} \end{bmatrix}_t \times \begin{bmatrix} N_{Fj} \\ N_{Fa} \\ N_{Mj} \\ N_{Ma} \end{bmatrix}_t$$

Figure 3. Age-structured two-sex matrix population model of a hypothetical common pochard population. Values of parameters are derived from the present study: survival of adult males $S_{Ma}=0.81$, survival of adult females, $S_{Fa}=0.69$, from Folliot et al. (2017): clutch-size: adult females 9.2, juvenile females 8.3, nest survival: adult females=0.53, juvenile females=0.30 and from Folliot et al. (2018): juvenile survival $S_j=0.20$. The proportion of males at hatching (SR) was set at 0.5. In the matrix, F_{Fj} =clutch-size of juvenile females \times nest survival of juvenile females \times SR (for males) or $(1 - SR)$ (for females) and F_{Fa} =clutch-size of adult females \times nest survival of adult females \times SR (for males) or $(1 - SR)$ (for females) (see Supplementary material Appendix 4 for details about the implementation of the model).

population changes. The pattern observed in pochards does not tightly mirror that of Lesser scaup, which after having experienced a sharp decline since the 1980s, recovered thanks to improvement in adult female survival (Koons et al. 2017). It looks much like that of the common eider *Somateria mollissima*, whose increasing proportion of males originate from differences in survival of prime breeders too (i.e. lower survival of females, Ramula et al. 2018). However, unlike Ramula et al. (2018), we emphasize that increasing proportions of males recently observed in common pochard in western Europe 1) were possible because adult males displayed higher survival than adult females, but, 2) originated from lowered reproductive success and/or juvenile survival (since survival patterns of adults did no changes over very long periods). Currently, in the absence of reliable data, it is not possible to firmly conclude about the prime role of decreasing nest versus juvenile survival in the decline of pochard populations of western Europe (Fox et al. 2016). Here, we document stable survival for adult females during the period of steepest pochard decline in western Europe in three countries with different hunting pressure. This suggests, therefore, either that increasing predation of females during the breeding season (Fox et al. 2016, Brides et al. 2017) is not the underlying factor of pochard decline (for example if nests were destroyed but incubating females were not predated), or that increasing predation occurred but the resulting higher mortality of females was compensated by increased survival 'outside' the nesting season. Therefore, rather than focusing on factors acting solely during the nesting season (e.g. increased predation pressure on nests and/or incubating females), one should also consider underlying factors that could affect both sexes simultaneously, during brooding or outside the breeding season. For example, alteration of brooding habitats in former strongholds of the species (including the newly identified breeding grounds in the river Orb watershed, see Folliot et al. 2018) should be seriously investigated.

Finally, survival parameters estimated in our study could serve as a basis for more complex models (e.g. integrated population models and/or life table response experiments) to be implemented as part of increasing adaptive management schemes for waterfowl in Europe (Madsen et al. 2017). Such research should help disentangling the effect of hunting and natural mortality on population trends in the future, via various population modelling exercises (Nichols et al. 2007, Arnold et al. 2018, Zhao et al. 2019).

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Supplementary material (available online as Appendix wlb-00682 at <www.wildlifebiology.org/appendix/wlb-00682>). Appendix 1–4.