Changes in the sex ratio of the Common Pochard *Aythya ferina* in Europe and North Africa

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Abstract

Assessments of the sex ratio among Common Pochard *Aythya ferina* flocks were undertaken in countries across Europe and into North Africa in January 2016, for comparison with results from surveys carried out over the same area in January 1989 and January 1990. The mean (± 95% CI) proportions of males in the population were estimated as 0.617 (0.614–0.620) in 1989–1990 and 0.707 (0.705–0.710) in 2016; this difference between surveys was found to be highly significant. Whilst male bias increased with latitude in both surveys, this relationship was weaker in 2016 as the increases in male bias between 1989–1990 and 2016 were greater in countries further south. Given that the sex ratio of Pochard broods is approximately 1:1 at hatching, the strong male bias observed among adult birds is indicative of lower survival of females compared with males. The results of this study suggest that factors adversely affecting female survival rate (relative to that of males) may partly explain the decline in overall Common Pochard abundance. Given the widespread and ongoing decline of this species throughout most of Europe and North Africa, further information on possible demographic drivers of change is urgently required.

Key words: *Aythya ferina,* Common Pochard, demography, population ecology, sex ratio, species decline.

With an estimated *c.* 600,000 birds in the Central Europe, Black Sea and Mediterranean population and *c.* 250,000 birds in the Northeast/Northwest Europe population, the Common Pochard *Aythya ferina* (hereafter Pochard) is a common and widespread species across Europe and North Africa (Wetlands International 2017). Following steady declines in winter abundance indices since the 1990s (Nagy *et al.* 2014), however, and also a 30–49% decline in breeding abundance over three generations (BirdLife International 2015), its conservation status was up-listed from Least Concern (LC) to Vulnerable (VU) on the European and global IUCN Red Lists in

2015. Given the widespread and ongoing decline of Pochard throughout most of Europe and North Africa, information highlighting possible demographic drivers of the changes in population size therefore is urgently required.

Sex ratio data can potentially provide useful information on the differential survival rates of the sexes (Donald 2007). As such, sex ratio data can potentially be used to infer the demographic causes of declines in population size amongst avian species. In a review of sex ratios of adult birds, Donald (2007) found that increasing male bias is a common feature of threatened populations, and noted that such changes in the sex ratio may reflect differing mortality risks posed to the different sexes. For instance, studies in New Zealand of the Kaka *Nestor meridionalis septentrionalis*, which is included as Endangered (EN) on the IUCN Red List, found that mainland populations exposed to introduced predators have sex ratios that are highly male-biased, whereas populations on predator-free islands have balanced sex ratios (Greene & Fraser 1998). Although there are relatively few cases where the mechanism for higher female mortality has been confirmed, in some migratory species the longer migrations undertaken by the smaller sex (usually female) may put them at greater risk (review in Donald 2007). Moreover, for waterfowl (including Pochard) where the female undertakes most or all of the incubation, nesting females are known to be sensitive to predation during the breeding season (Sargeant *et al.* 1984; Baldassarre & Bolen 1994; Blums *et al.* 1996). These factors can lead to a skew towards males among adults, which may be particularly evident among breeding birds. It therefore seems that changes in the variables that influence sex ratios can translate into population-level effects, such as declining numbers, and that information on any change in the sex ratio for a species can provide a valuable insight into its population processes (Donald 2007).

Any assessment of changes in sex ratio must, however, account for potential differential spatial patterns in the distributions of males and females. Many duck populations wintering in the northern hemisphere exhibit geographical gradients in sex ratio, with greater proportions of males wintering further north (Bellrose *et al.* 1961; Perdeck & Clason 1983; Owen & Dix 1986). In the case of the Pochard, Owen & Dix (1986) found that the sex ratio among flocks of the species at sites in the United Kingdom during winter 1983/84 was highly correlated with latitude, with a greater male bias in more northerly areas. At a larger spatial scale, analysis of sex ratio data recorded for Pochard across Europe and into North Africa during surveys made in January 1989 and January 1990 similarly found a latitudinal effect, with a higher proportion of males recorded at higher latitudes (Carbone & Owen 1995).

In the study presented here we assess the sex ratios among Pochard wintering across Europe and into North Africa in January 2016, for comparison with those from the 1989–1990 survey over the same area (reported by Carbone & Owen 1995), and consider the results in light of the population decline recorded between the two surveys. Given the observed decline in the number of Pochard recorded over the past 20 years, and the increasing male bias found in declining populations of other species, we hypothesised that the male bias in the Pochard population would be greater in the more recent survey.

Methods

Sex ratio survey

National coordinators of the annual International Waterbird Census (IWC), which has been organised by Wetlands International (previously the International Waterfowl and Wetlands Research Bureau; IWRB) each year since 1967, were asked to organise sex ratio determinations of Pochard to be undertaken by their network of volunteer counters during the mid-January IWC in 2016. Bird-watchers were also invited to submit data collected outside of the IWC counts and the project was heavily promoted on social media, using the Twitter hashtag #Pochard to encourage interest among the bird-watching community.

Observers were asked to record for each site visited the total flock size, the number of birds for which sex was determined, the number of males and the number of females, location name, latitude and habitat. Data were submitted online via the Duck Specialist Group website (http://www.ducksg.org/projects/compoch/), or via various online recording portals used by waterbird counters and birdwatchers, including BirdTrack and Observation.org. In order to ensure that the results were comparable with those of the 1989–1990 survey (*i.e.* Carbone & Owen 1995), only data collected during a 16-day period (9–24 January 2016) were used in the analysis, with 45.5% (n = 834 flocks; 106,288 individual birds) of the sex ratio samples collected on the 2016 IWC focal dates (16–17 January).

For some surveys, sex could not be determined for all individuals within the flock, in which case the sex ratio in the sample was assigned to the full flock to yield weighted estimates of the total numbers of males and females, after Carbone & Owen (1995). Following the approach of earlier studies (*e.g.* Sheldon 1998; Hardy 2002; Donald 2007), sex ratio was expressed as the proportion of males within the sample, calculated as:

$$\text{Sex ratio} = n_m/(n_m + n_f),$$

where n_m and n_f refer to the total numbers of males and females, respectively. This formula allowed the sex ratio to be calculated for any sample of birds, including for an individual country or the total population. Whilst data for individual flocks were not reported in Carbone & Owen (1995), data on the numbers of males and females were presented for each country, which allowed comparison with our 2016 data. Countries for which data were not available for either the 1989–1990 or 2016 surveys were not included in the analysis. Because of the strong relationship between male bias and latitude, standardising the surveyed area to a consistent set of countries was necessary to permit comparison of the 1989–1990 and 2016 survey results. In total, data from 13 countries were available from both the 1989–1990 and 2016 surveys: Algeria, Britain, Denmark, France, Germany, Greece, Hungary, Italy, the Netherlands, Republic of Ireland, Romania, Spain and Switzerland. For the 1989–1990 and 2016 surveys, we calculated the sex ratio for each country based on the total numbers of males and females in that country, whilst the population sex ratio was based on the total numbers of males and females in all 13 countries.

To verify that the coverage achieved by the 1989–1990 and 2016 surveys were comparable, we estimated the proportion of the total population of Europe and North Africa that were within the countries included in the surveys, based on the mean IWC counts over the four years leading up to the survey years (*i.e.* in January 1985–1988 and January 2012–2015). The IWC mean count data showed that these 13 countries included in both surveys accounted for 0.724 and 0.729 of the total numbers of Pochard in 1985–1988 and 2012–2015, respectively, suggesting that the 1989–1990 and 2016 surveys were based on almost identical proportions of the total populations.

Statistical analyses

All statistical analyses were carried out using R version 3.3.0 (R Development Core Team 2016), with statistically significant results attributed where $P < 0.05$; all P values were adjusted using Holm-Bonferroni corrections to account for multiple comparisons (Holm 1979). First, to assess whether the sex ratio of: (i) each country, and (ii) the total population, differed significantly between the two surveys, we used a 2-sample binomial test for equality of proportions to assess whether the proportion of males in the 1989–1990 survey differed significantly from the proportion of males recorded in 2016 (Crawley 2005). Second, for each survey we used a two-tailed binomial test to assess the significance of the deviation of the total numbers of males and females for: (i) each country, and (ii) the total population, from a 1:1 ratio. In both cases, the binomial tests allowed 95% confidence intervals to be estimated for the proportion of males in the sample, based on the approach of Clopper & Pearson (1934).

For the country-level weighted sex ratio data for both surveys, we used linear models with Gaussian error structures to assess the relationships between the sex ratio (expressed as the proportion of males) and: (i) survey year, (ii) central latitude for each country, and (iii) the interaction between year and latitude. The inclusion of survey year, and its interaction with latitude, allowed us to test whether the proportion of males differed between years, and whether the magnitude of any difference was consistent over the range of latitudes surveyed. Following inspections of the model residuals, to meet the assumptions of the linear modelling approach we square-root transformed the response variable (sex ratio) (Zuur *et al.* 2010).

Results

The mean (± 95% CI) proportion of males in the population was estimated as 0.617 (0.614–0.620) in 1989–1990, and 0.707 (0.705–0.710) in 2016 (Table 1); a 2-sample binomial test for equality of proportions indicated that this 0.09 difference in the sex ratio was highly significant ($\chi^2_1 = 1893.58$,

Table 1. A comparison of the weighted sex ratios (proportion of males) for each country included in the current study and the earlier 1989–1990 survey of Carbone and Owen (1995), as well as for the total populations. The sample sizes (*n*) represent the total numbers of individuals counted in each country. All *P* values were adjusted using Holm-Bonferroni corrections for multiple comparisons.

Country	Latitude (decimal degrees)	1989–90 survey					2016 survey					Comparison between surveys		
		Sex ratio (prop. males)	Lower 95% CI	Upper 95% CI	Binomial test *P* value	*n*	Sex ratio (prop. males)	Lower 95% CI	Upper 95% CI	Binomial test *P* value	*n*	Change in prop. males	Test for equal proportions χ^2	*P* value
Algeria	28.00	0.112	0.092	0.136	<0.001	836	0.458	0.314	0.608	1.000	48	0.346	44.65	<0.001
Britain	53.83	0.716	0.708	0.723	<0.001	14,722	0.713	0.705	0.721	<0.001	12,413	–0.002	0.13	1.000
Denmark	56.00	0.713	0.697	0.729	<0.001	3,153	0.699	0.675	0.723	<0.001	1,397	–0.014	0.84	1.000
France	47.00	0.625	0.618	0.631	<0.001	22,351	0.700	0.677	0.723	<0.001	1,609	0.076	36.54	<0.001
Germany	51.00	0.654	0.641	0.666	<0.001	5,654	0.723	0.717	0.729	<0.001	20,722	0.069	102.14	<0.001
Greece	39.00	0.476	0.470	0.482	<0.001	25,702	0.566	0.554	0.577	<0.001	7,735	0.089	189.99	<0.001
Hungary	47.00	0.858	0.797	0.906	<0.001	176	0.617	0.582	0.650	<0.001	811	–0.241	36.47	<0.001
Italy	43.00	0.616	0.590	0.642	<0.001	1,409	0.685	0.678	0.693	<0.001	15,569	0.069	28.29	<0.001
Netherlands	52.32	0.653	0.643	0.662	<0.001	9,971	0.739	0.732	0.747	<0.001	12,949	0.086	200.52	<0.001
Republic of Ireland	53.00	0.750	0.717	0.782	<0.001	705	0.747	0.688	0.803	<0.001	231	–0.003	0.00	1.000
Romania	46.00	0.754	0.747	0.762	<0.001	13,310	0.666	0.640	0.691	<0.001	1,361	–0.089	50.93	<0.001
Spain	40.00	0.522	0.507	0.538	0.029	4,285	0.682	0.671	0.693	<0.001	7,016	0.160	287.00	<0.001
Switzerland	46.83	0.676	0.637	0.714	<0.001	591	0.747	0.741	0.752	<0.001	24,527	0.071	14.47	0.002
Total	–	**0.617**	**0.614**	**0.620**	**<0.001**	**102,865**	**0.707**	**0.705**	**0.710**	**<0.001**	**106,388**	**0.090**	**1893.58**	**<0.001**

P < 0.001). The numbers of males were significantly higher than expected for a 1:1 ratio for every country in the 1989–1990 survey except Algeria and Greece (which had significant female biases), and for every country in the 2016 survey except Algeria (which had no significant bias) (Table 1). Of the 13 countries compared between 1989–1990 and 2016, eight showed significantly greater male bias in 2016, whilst two showed significantly reduced male bias (Table 1; Fig. 1). However, these two countries, Hungary and Romania, contributed relatively few birds (811 and 1,361, respectively) to the total sample, and hence did not counteract the overall pattern of greater male bias in 2016 that was observed for the total population.

We found significant positive effects of both latitude and year on the proportions of males in each country ($F_{3,22}$ = 18.65, P <0.001, R^2_{adj} = 67.9%; Table 2; Fig. 2). Furthermore, we found evidence of a significant, negative interaction between latitude and year, such that the increases in male bias in 2016 were greater for countries

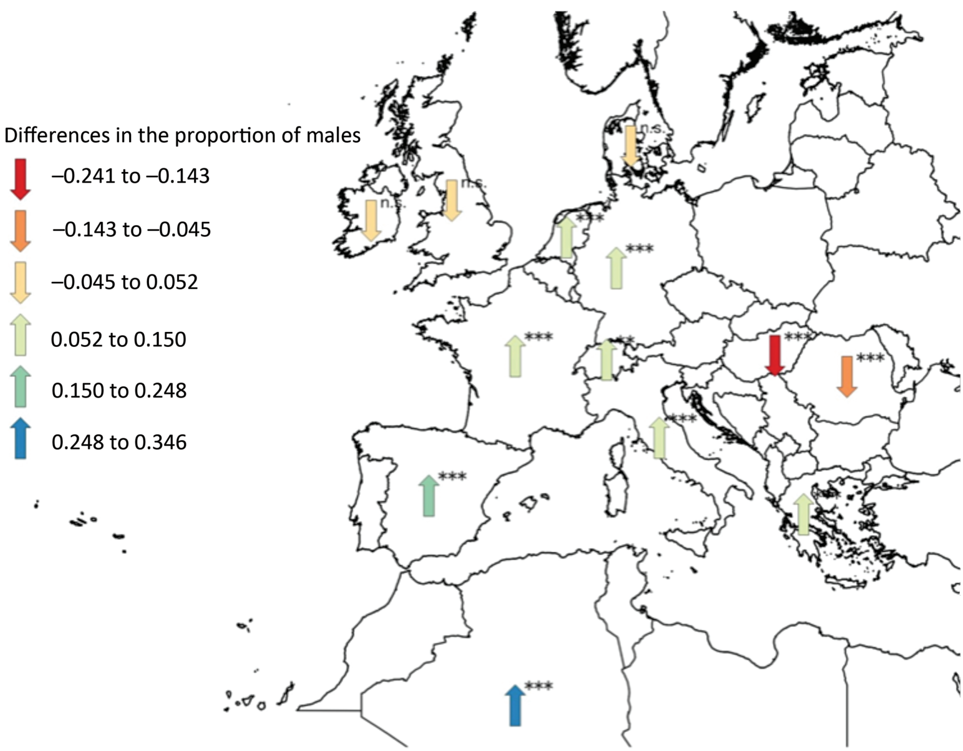

Figure 1. The size and direction of the difference in male bias in the sex ratio (expressed as the proportion of males) between the 2016 and 1989–1990 surveys. Positive values indicate a greater male bias in 2016 compared with 1989–1990. The statistical significance of the difference is indicated for each country (see Table 1): *** = P <0.001, ** = P <0.01, n.s. = P > 0.05.

Table 2. The mean (± s.e.) estimates and significance of the effect sizes of the parameters in our linear model on square-root-transformed sex ratio (proportion of males) in the 13 countries surveyed in both 1989–1990 and 2016. All *P* values were adjusted using Holm-Bonferroni corrections for multiple comparisons and are statistically significant.

Parameter	Estimate	s.e.	*t* value	*P* value
Intercept	–38.3006	11.6570	–3.29	0.029
Latitude	0.7781	0.2483	3.13	0.034
Year	0.0193	0.0058	3.31	0.029
Latitude * Year	–0.0004	0.0001	–3.09	0.034

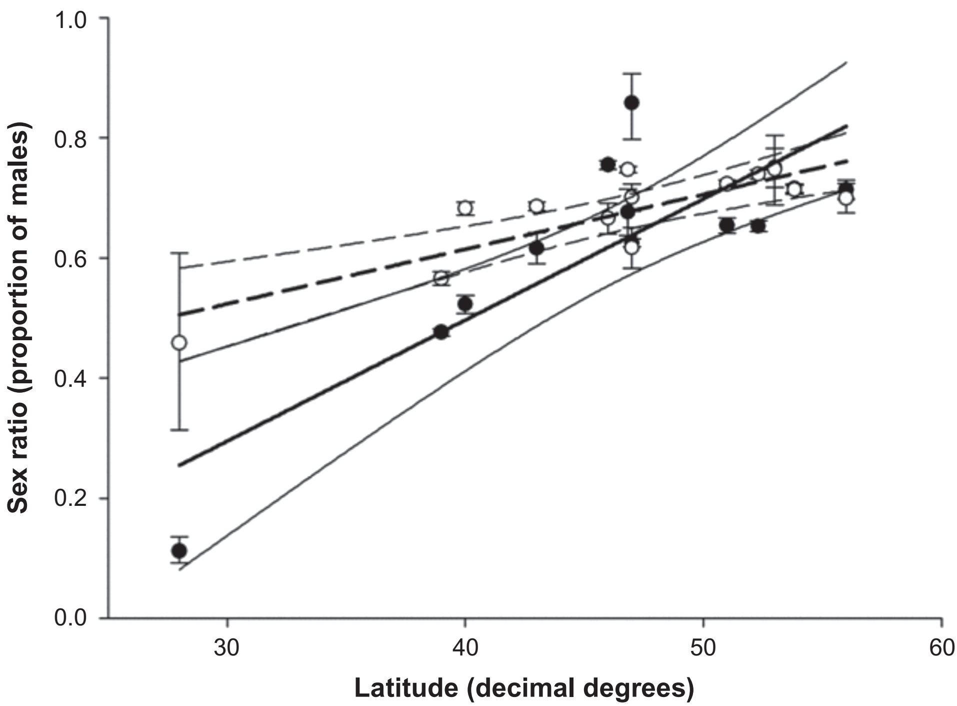

Figure 2. The mean (± 95% CI) effect of latitude on Pochard sex ratio, based on the 1989–1990 (solid circles and lines) and 2016 (open circles and dashed lines) surveys.

at lower latitudes, albeit sample sizes for Algeria in 2016 were low (Table 2; Fig. 2).

Discussion

The 2016 survey found, as expected, that Pochard sex ratios continue to show a strong male bias, as previously described by Owen & Dix (1986) and Carbone & Owen (1995), with a relatively greater proportion of females wintering in countries in the south of the range. We also found evidence that this latitudinal effect on sex ratio was weaker in 2016 than in 1989–1990, however, with lower latitude countries showing the greatest increases in male bias. Males are typically dominant over females in this species, and therefore are able to occupy more favourable wintering areas that are closer to the breeding grounds, resulting in the sub-dominant females moving further afield (Choudhury & Black 1991). The greater capacity of males to withstand cold temperatures has also been proposed as an explanation for the tendency observed in small-bodied birds, including ducks, for a higher proportion of males to winter at higher latitudes (Ketterson & Nolan 1976; Nichols & Haramis 1980; Owen & Dix 1986; Carbone & Owen 1995; Evans & Day 2001). For example, Owen & Dix (1986) calculated that the lower critical temperature for Pochard (representing the minimum air temperature at which an animal can maintain its basal metabolic rate whilst resting without incurring additional thermoregulatory costs) was 7.1°C for males but 8.4°C for females.

The analyses also indicated that the male bias for all Pochard surveyed across Europe and North Africa was significantly greater in 2016 (0.71 males in all birds surveyed) than in 1989–1990 (0.62 males). The two surveys covered the same 13 countries and an almost identical proportion of the population, suggesting that the observed change in sex ratio represents a real change in population structure, rather than being an artefact of the sampling process. Given that we had data only for two survey periods, it was not possible to determine whether the difference in sex ratios formed part of a trend of increased male bias over time. The change in the proportion of males recorded in each of the different countries, and the continued relationship between sex ratio and latitude, does however reinforce the view that there was a greater proportion of males in the population in 2016. Countries at lower latitudes were more likely to show an increased male bias in the sex ratio in 2016 compared with 1989–1990, whereas more northerly countries typically showed little or no change. For instance, we found no difference in the proportion of males reported in Denmark between study periods, which concurs with Christensen & Fox (2014) who similarly found no significant trend in the sex ratio of Pochard wintering in Denmark between 1982 and 2010 on analysing hunter-shot wing samples. Nonetheless, that age checks for Pochard in low-latitude countries such as Algeria, Greece, Italy and Spain, and also across the whole study area, all showed stronger male bias in 2016 may have consequences for Pochard population dynamics and for the success of any conservation measures. For example, Donald (2007) noted that increasingly male-biased sex ratios can lead to lower *per capita* productivity where intense male competition hinders female reproduction. Given the current skew, productivity in Pochard is likely to be limited not by males but by the number of adult breeding females, as found in other duck populations (*e.g.* Hoekman *et al.* 2002).

Given that the sex ratio of Pochard broods is approximately 1:1 at hatching (Blums & Mednis 1996), the male bias observed among full-grown birds suggests a lower survival of females compared with males. Moreover, the declining population size together with the greater male bias recorded in 2016 indicates that female survival rates may have decreased more sharply than those of males. Theoretically male survival rates could have increased more than those for females, but given the overall population trend this is unlikely. The observed change in the sex ratio could alternatively have resulted from a shift in winter distribution, resulting in a lower proportion of all females being counted during the IWC, but this seems also unlikely for two key reasons: (1) the proportion of the total numbers that were included in the two sex ratio surveys were almost identical, and (2) where shifts in duck distribution have been found in Europe they have typically been to the north and east, which given the positive relationship between the proportion of males and latitude should have resulted in more females and fewer males being counted in 2016, which was not the case. Shifts in winter distribution, generally northeast towards breeding areas, have been demonstrated for a wide range of species, including some diving ducks, in recent decades (Lehikoinen *et al.* 2013). For Pochard, declines in wintering numbers in the west of the range have tended to be greater than the overall population trend (*e.g.* 65% decline between winters 1988/89 and 2013/14 in the UK, Hayhow *et al.* 2017; *c.* 60% during 2004–2013 in the Netherlands, Hornman *et al.* 2015) and increases have been observed further east (*e.g.* wintering numbers have increased in Sweden, Nilsson 2008). However, our finding that the 13 countries included in both sex ratio surveys held a consistent proportion of 0.72–0.73 of the total number of Pochard counted by the IWC suggests that any redistribution of birds from the westernmost countries was largely within the area covered by this survey and thus did not affect the overall sex ratio assessment.

There are several potential direct and indirect factors which may explain the apparent relative decrease in female survival. The two most likely are changes in levels of: (i) direct and indirect hunting mortality, and (ii) predation. Pochard is a widely huntable species, being legal quarry in at least 26 countries throughout Europe (Powolny & Czajkowski, in press). Waterbird hunting pressure within Europe is widely recognised as being greatest in southern Europe (Mateo 2009) where the largest proportion of female Pochard overwinter, a view supported by a recent compilation of hunting bag estimates for 17 European countries by Powolny & Czajkowski (in press). In addition, Pochard are huntable from 1 August in several east European countries, which could cause additional selective hunting mortality on breeding females and naïve juveniles prior to their departure to winter quarters, with most males having already migrated away by the beginning of August (Fox *et al.* 2016). Spatial differences in hunting pressure may also influence female survival indirectly through mortality on the birds ingesting spent lead gunshot. The prevalence of lead gunshot ingestion by waterbirds varies considerably among European countries but tends to be higher in southern Europe (Mateo 2009). Furthermore, two recent studies have demonstrated a relatively high susceptibility of Pochard to lead ingestion, both within the UK (Green & Pain 2016) and across Europe (Andreotti *et al.* in press). Whilst the latter did not investigate sex differences in Pochard mortality attributable to lead poisoning, the authors estimated that it accounts for the death of 56,511 Pochard in Europe each year (Andreotti *et al.* in press). Given the apparent elevated risk to female Pochard from direct and indirect hunting related mortality, greater hunting pressure in southern Europe therefore could be an important factor in the apparent decrease in the proportion of females in the population.

Increased female mortality from predation is another possible reason underlying the shift in the sex ratios between surveys, with a recent review of the decline in Pochard numbers suggesting that predation by a range of species (including non-native mammals), could be a major threat to breeding Pochard populations (Fox *et al.* 2016). Female Pochard spend more time on the breeding grounds, incubating eggs and raising ducklings, than do males, leading to an increased level of predation, particularly during the incubation period. Devineau *et al.* (2010) reported that for Green-winged Teal *Anas crecca* lower female survival rates compared with males were apparent during the breeding season, likely resulting from greater predation of females, but not during winter. Such nest predation is often by non-native mammal species, such as Racoon Dog *Nyctereutes procyonoides* and, particularly, American Mink *Mustela vison* (*e.g.* Blums *et al.* 1996). Although data on the population trends of invasive non-native mammals are scarce, it is widely recognised that they are increasing, especially Raccoon Dog which now occurs in 21 countries in Europe (Genovesi *et al.* 2009).

The causes of the changes in sex ratio in time and space remain unknown and further research to estimate and compare male and female survival rates (*e.g.* using a capture-mark-resight approach; White & Burnham 1999) would provide valuable demographic information needed to help understand these changes. Such an analysis of marked birds would allow spatial and temporal patterns in survival to be assessed, and potential drivers of survival rates to be examined (*e.g.* Wood *et al.* in press). Furthermore, such an approach can identify whether changes in survival are limited to particular age classes, sexes, or regions, all of which are currently unknown for Pochard. Previous research has estimated survival rates for female Pochard breeding in Latvia (*e.g.* Blums *et al.* 1996, 2002), but we currently lack comparable survival estimates for males. Collecting information on hunting bag sizes, and other sources of hunting mortality, could permit assessment of the relative impact on male *versus* female Pochard. It would also be advantageous to initiate routine collection of sex ratio data as part of standard waterbird surveys, such as the IWC. Such data would help to provide a better understanding of the patterns of inter-annual variation in sex ratios, and thus differentiate between long-term trends and fluctuations between years. Annual data collection is ongoing in some European countries, but currently too few to describe population-scale trends. Surveys of duck wings from hunted birds can also provide a valuable additional source of data for assessing trends in the sex and age composition of the population (Christensen & Fox 2014).

Overall, we currently lack the knowledge to explain the demographic causes and underlying drivers of the observed decrease in the proportion of female Pochard wintering in Europe and North Africa. Nevertheless, our findings suggest that female survival in relation to that of males is now lower than during the late 1980s, and that aspects of the life-cycle more strongly pertinent to females are likely to be contributing to the observed decline in overall population size. Better monitoring and analyses of demographic information will help to elucidate the situation and to facilitate the further development of targeted conservation and management actions for this declining duck species.

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