Temporal changes in the sex ratio of the Common Pochard *Aythya ferina* compared to four other duck species at Martin Mere, Lancashire, UK

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Abstract

Duck populations tend to have male-biased adult sex ratios (ASRs). Changes in ASR reflect species demographic rates; increasingly male-biased populations are at risk of decline when the bias results from falling female survival. European and North African Common Pochard *Aythya ferina* numbers have declined since the 1990s and show increasing male bias, based on samples from two discrete points in time. However, lack of sex ratio (SR) data for common duck species inhibits assessing the pattern of change in the intervening period. Here, we describe changes in annual SR during winters 1991/92–2005/06 for five duck species (Common Pochard, Gadwall *Mareca strepera*, Northern Pintail *Anas acuta*, Northern Shoveler *Spatula clypeata* and Tufted Duck *Aythya fuligula*) at Martin Mere, Lancashire, UK. Pochard, Pintail, Tufted Duck and Shoveler showed significantly male-biased SRs, with the male bias increasing in Pochard and Shoveler, exhibiting a weak decrease in Pintail, and with no significant trend recorded for Tufted Duck or Gadwall. The increasing male-biased Pochard SR at Martin Mere contrasts with the stable trend for Britain, suggesting that site trends may not reflect those at the national level. The results provided insight into limitations of local datasets and the potential usefulness of widespread SR data. Given potential associations between changes in SR with demographic rates and population trends, regular collection of SR data is recommended for wildfowl as part of routine long-term monitoring of these species.

Key words: adult sex ratio, demography, long-term monitoring, population ecology, species decline.

One third of all species are threatened with extinction globally (IUCN 2017) confirming the importance of monitoring species' abundance. Long-term monitoring data on numbers, population structure and demographic rates improves our understanding of the biological reasons for population trends (Nichols 1991; Thomas & Martin 1996) by determining responses to both anthropogenic and natural variables in the environment (Nichols & Williams 2006; Lindenmayer & Likens 2009). For instance, adult sex ratios (ASRs) can provide useful information on population structure and potential differences in survival rates of males and females (Donald 2007) to infer demographic or ecological causes of changes in population size (Bellrose *et al.* 1961; Lehikoinen *et al.* 2008; Brides *et al.* 2017; Ramula *et al.* 2018). This provides a scientific basis for the implementation of research and management focused on threatened species (Hagan 1992; Thomas & Martin 1996).

The Common Pochard *Aythya ferina* (hereafter Pochard) was recently reclassified as Vulnerable in the International Union for the Conservation of Nature's Red List (IUCN 2018). An increasingly male dominated ASR may reflect decreases in female survival, and contribute to the species' decline (Owen & Dix 1986; Carbone & Owen 1995; Donald 2007; Brides *et al.* 2017). Male sex ratio (SR) bias increased from 0.617 in winter 1989/90 to 0.707 in winter 2015/16 across the winter range in Europe and North Africa, with the most pronounced increases in more southerly countries (Brides *et al.* 2017). Evidence suggests no sex disparity at hatching (Blums & Medinis 1996), implying differential survival of the sexes (Clutton-Brock 1986; Donald 2007). The association between changes in SR and declines in Pochard numbers across Europe has been attributed *inter alia* to increased predation on the feeding grounds, because only the females incubate and rear the young (Fox *et al.* 2016).

For most sites and species, we lack time-series data on SR to provide greater resolution of changes in SR in relation to population change. The samples of Pochard SR come from two discrete points 26 years apart, and the situation is similar for other ducks, including sea ducks (but see Lehikoinen *et al.* 2008; Christensen & Fox 2014; Fox & Christensen 2018). Interpretation of results from periodic surveys would benefit from a better understanding of the spatial and temporal (*i.e.* inter-annual) variation in the SRs of the species involved. In the case of the Pochard, although Brides *et al.* (2017) found an overall change in SR across Europe and North Africa, there was no significant change for Britain, where the proportion of males wintering in the country was estimated as 0.705 in 1983/84 (Owen & Dix 1986), 0.716 in 1989/90 (Carbone & Owen 1995) and 0.713 in 2015/16 (Brides *et al.* 2017). There has been a steady decline in Pochard numbers wintering in the country since the 1990s (Cabot 2009), and its wintering range in Britain and Ireland shrank by 21% between 1981/1984–2007/2011, including a 76% reduction in Ireland (BTO 2018). More frequent sampling of SR in Britain would help determine the degree of annual variation in SR, to confirm if there has genuinely been a lack of change over time.

There is also a lack of systematically-recorded SR data for other duck species, to provide comparisons with the changes in the declining Pochard population. Whilst the need for ASR data is long established (*e.g.* Leopold 1933; Bellrose *et al.* 1961; Owen & Dix 1986), there is limited long-term monitoring of sex ratios for most duck species across Europe. Changes in ASR based on Danish hunting data have been assessed for some duck species (Christensen & Fox 2014; Fox & Christensen 2018), and for Baltic Common Eider *Somateria mollissima* (Lehikoinen *et al.* 2008), but much of Europe remains data deficient.

This study analyses annual changes in Pochard SR at one site in northwest England in the winters of 1991/92 until 2005/06, to compare with the national trend of Brides *et al.* (2017). For comparison, SR data were gathered for four other duck species wintering at this site: Tufted Duck *Aythya fuligula*; Northern Pintail *Anas acuta* (hereafter Pintail); Gadwall *Mareca strepera*; and Northern Shoveler *Spatula clypeata* (hereafter Shoveler), all of which show increasing flyway numbers over the same period (Wetlands International 2018).

Methods

Field observations

Numbers of Pochard, Tufted Duck, Pintail, Gadwall and Shoveler were recorded during weekly counts across the Wildfowl & Wetlands Trust (WWT) Martin Mere reserve

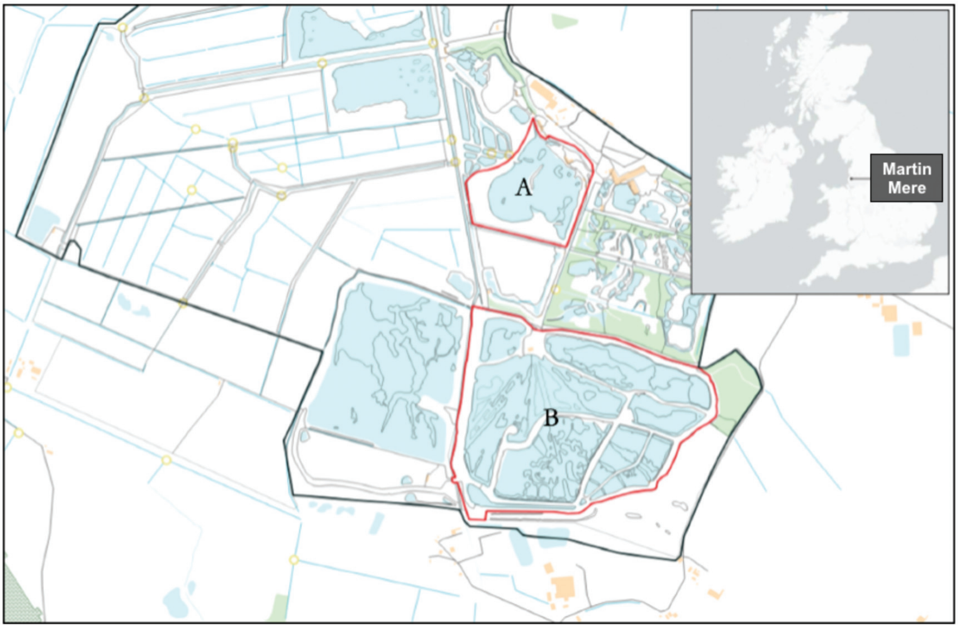

Figure 1. Study site at Martin Mere, Lancashire, UK. Areas surveyed are marked in red. A = the Mere; B = the Reedbed.

(53.62°N, 2.87°W; Fig. 1), a site of international importance for overwintering waterbirds (JNCC 2018). Sex-ratio data were collected for birds observed on the main lake – "The Mere" (Fig. 1) – at least weekly during winter (November–March inclusive), from November 1991 to March 2006, when the birds' plumage made it easy for trained observers to distinguish between the sexes. Ducks almost exclusively used The Mere until late 2004, when they started to take advantage of deeper water provided by a new Reedbed (Fig. 1), thereafter included in the surveys. Data were collected mainly between 11:00–14:00 h, when the birds were most settled and relatively inactive, to improve count accuracy. Sex ratios were determined by sexing every individual present in each of the count areas using two click counters, one in each hand for each sex, with total counts derived from the sum of males and females.

Statistical analysis

Statistical analysis was carried out using RStudio version 1.1423 (RStudio Team 2015). For each species, the sex ratio for each winter was calculated from the peak count from the refuge data (*i.e.* SR was calculated from data collected on the date on which the maximum count was recorded for each species; Fig 2). Following the formula in previous studies (Hardy 2002; Donald 2007; Brides *et al.* 2017) sex ratio was calculated thus:

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

Where n_m and n_f are the number of males and females respectively. For each species, a two-tailed binomial test was used to assess the significance of the deviation of the mean numbers of males and females over the study period from a 1:1 ratio. Statistically significant results were inferred in all cases where $P < 0.05$. Furthermore, the binomial tests permitted 95% confidence intervals to be estimated for the mean SR, based on the approach of Clopper & Pearson (1934).

Species-specific linear models with Gaussian error structures were used to examine temporal trends in SR for each of the five focal duck species. Initial exploration of linear model residuals using the nlme package (Pinheiro *et al.* 2017) showed no evidence of statistically significant temporal autocorrelation over successive years for any of the five species ($P > 0.05$ for all time lags); therefore, no autocorrelation structure was included in subsequent models.

For each species, three temporal models of annual SR values were tested: (i) a linear trend, (ii) a quadratic trend, and (iii) the null model (*i.e.* no temporal trend). All SR data were square root transformed to meet the assumptions of the linear modelling approach. For each of these models the second order Akaike Information Criterion (AIC_c) was calculated using the MuMIn package (Barton 2012) and used to select the model that represented the best fit to the data for each species. The model with the lowest AIC_c was deemed the best-supported model for that species, whilst any model with a ΔAIC_c value of ≤ 2.0 was judged to have considerable support in the data (Burnham *et al.* 2011). Three further metrics were used as indicators of the relative support for each model in the data to allow more detailed comparisons between the three models. These were: (i) the ratio of

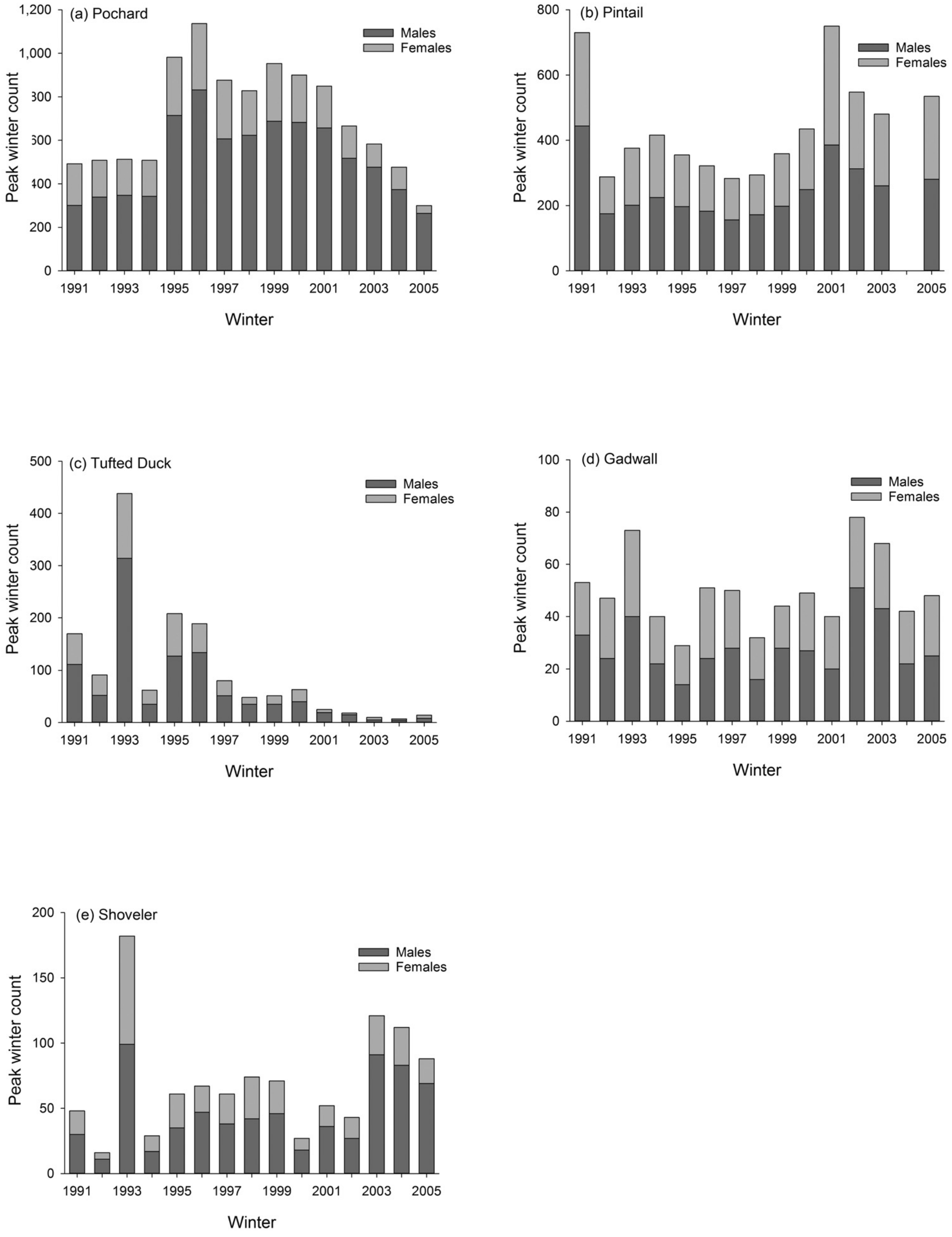

Figure 2. The annual winter peak counts recorded for each species, showing the numbers of males and females observed.

ΔAIC_c values for each model relative to the whole set of candidate models (the "Akaike weight" w_i), (ii) the probability of a given model being the best-fitting model compared with the best-supported model shown by AIC_c (termed the "relative likelihood"), and (iii) how many times less likely a model was to be the best-fitting model compared with the best-supported model shown by AIC_c (termed the "evidence ratio") (Burnham *et al.* 2011). Finally, the adjusted R-squared (R^2_{adj}) value for each model was used to assess the proportion of the variance in the temporal trend in SR explained by that model (Mac Nally *et al.* 2018).

To test whether the timing of the annual peak count had become progressively earlier or later over time, which could have confounded any trend in SR, three temporal models of the timings of the annual peak count were tested: (i) a linear trend, (ii) a quadratic trend, and (iii) the null model (*i.e.* no temporal trend). The timing of the peak count was the number of days after 1st November (*i.e.* the start of the study period) that the peak count was recorded. Model selection was carried out using the same approach as used for the SR models.

Results

The mean SR values over the 1991/92–2005/06 study period were found to be significantly male-biased for Pochard, Pintail, Tufted Duck and Shoveler, but not for Gadwall (Table 1; Fig. 3).

For the Pochard, a comparison of the three temporal models indicated that a model comprised of a positive linear effect of winter on SR had the lowest AIC_c value, followed by the quadratic model. The difference between these values was 3.8, indicating substantially more support in the data for the linear trend compared to either the quadratic model or the null model (Table 2; Fig. 3). There was no evidence that the timing of the peak Pochard count at Martin Mere had shown either a linear or

Table 1. A summary of the mean (± 95% CI) sex ration (SR) over the 1991–2005 study period. The significance of the deviation from parity for each species was assessed using a binomial test. *n* = sum of the mean annual numbers of males and females over the study period.

Species	**Mean SR**	**95% CIs**	***n***	***P* value**
Pochard	0.734	0.701–0.767	705	<0.001
Pintail	0.558	0.510–0.605	441	0.017
Tufted Duck	0.667	0.565–0.758	99	0.001
Gadwall	0.560	0.413–0.700	50	0.480
Shoveler	0.657	0.534–0.767	70	0.012

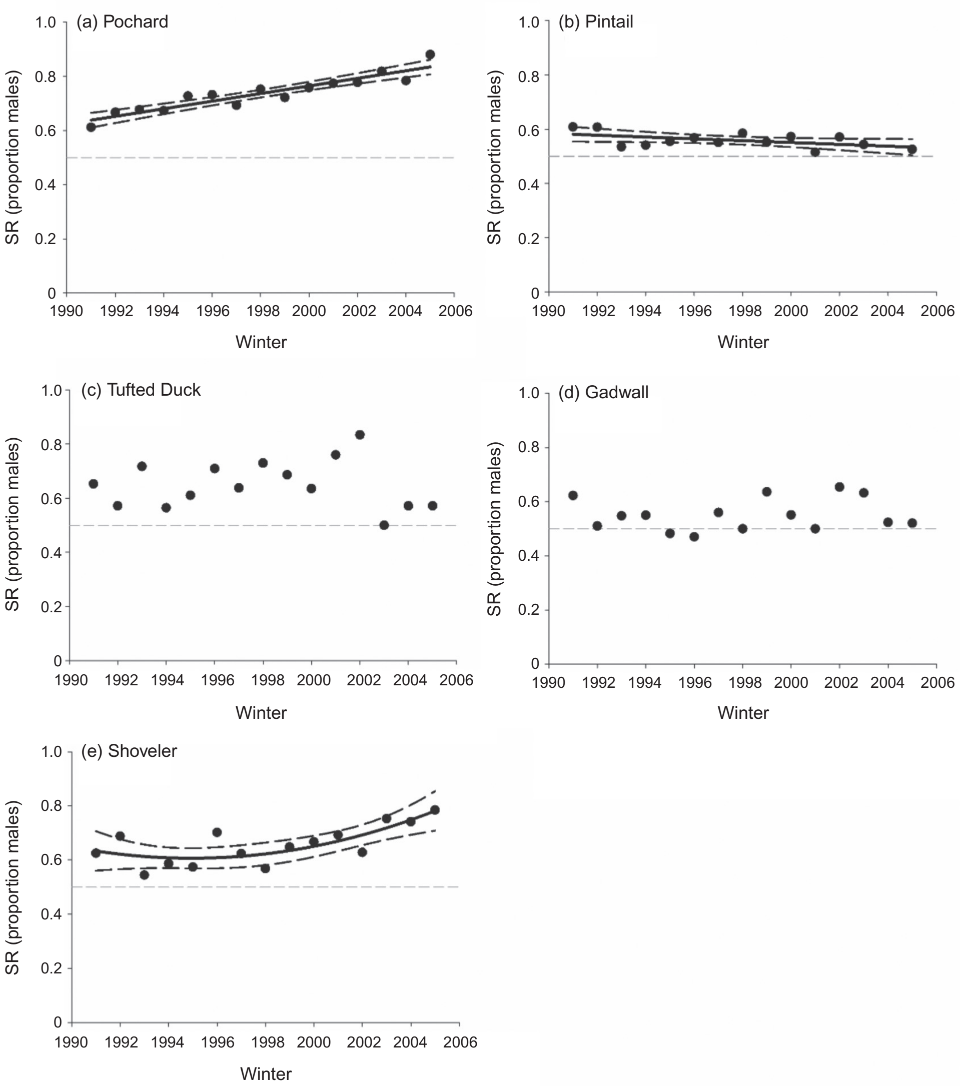

Figure 3. The annual sex ratio (SR) value for each species with the mean (± 95% CI) trend for the best-supported model plotted (where the null model was the best fit no trend has been plotted). The grey dashed line indicates a hypothetical sex ratio of 0.5.

non-linear trend over the study period (Table 3, Fig. 4).

For the Pintail, the linear trend model had the lowest AIC_c value, the ΔAIC_c of the null model was < 1.1, indicating comparable support between these two models (Table 2). Furthermore, examination of evidence ratio values indicated that the null model was only 1.68 times less likely to be the "true" best-supported model compared with the linear

Table 2. A summary of the support and explanatory power of the three models of temporal change in sex ratio for each species. The best-supported model for each species is indicated in bold. *k* refers to the number of fitted fixed effect parameters in each candidate model.

Species	Model	*k*	AIC_c	ΔAIC_c	Relative likelihood	Akaike weights	Evidence ratio	Adjusted R^2
Pochard	**Linear**	**2**	**–8.98**	**0.00**	**1.00**	**0.87**	**1.00**	**0.860**
Pochard	Quadratic	3	–5.18	3.80	0.15	0.13	6.69	0.848
Pochard	Null	1	18.42	27.40	0.00	0.00	890236.11	0.000
Pintail	**Linear**	**2**	**–4.1**	**0.00**	**1.00**	**0.57**	**1.00**	**0.206**
Pintail	Null	1	–3.1	1.03	0.60	0.34	1.68	0.000
Pintail	Quadratic	3	–0.3	3.88	0.14	0.08	6.97	0.143
Tufted Duck	**Null**	**1**	**28.7**	**0.00**	**1.00**	**0.74**	**1.00**	**0.000**
Tufted Duck	Linear	2	31.8	3.13	0.21	0.16	4.78	0.731
Tufted Duck	Quadratic	3	32.6	3.92	0.14	0.10	7.10	0.050
Gadwall	**Null**	**1**	**18.7**	**0.00**	**1.00**	**0.79**	**1.00**	**0.000**
Gadwall	Linear	2	21.6	2.92	0.23	0.18	4.31	0.000
Gadwall	Quadratic	3	25.2	6.44	0.04	0.03	24.98	0.000
Shoveler	**Quadratic**	**3**	**15.8**	**0.00**	**1.00**	**0.91**	**1.00**	**0.518**
Shoveler	Linear	2	21.6	5.79	0.06	0.05	18.10	0.380
Shoveler	Null	1	22.1	6.26	0.04	0.04	22.90	0.000

Table 3. A summary of the support and explanatory power of the three models of temporal change in the timing of the peak count at Martin Mere for each species. The best-supported model for each species is indicated in bold. *k* refers to the number of fitted fixed effect parameters in each candidate model.

Species	Model	*k*	AIC$_c$	ΔAIC$_c$	Relative likelihood	Akaike weights	Evidence ratio	Adjusted R^2
Pochard	**Null**	**1**	**135.06**	**0.00**	**1.00**	**0.73**	**1.00**	**0.000**
Pochard	Linear	2	137.34	2.28	0.32	0.23	3.12	0.000
Pochard	Quadratic	3	141.03	5.96	0.05	0.04	19.71	0.000
Pintail	**Linear**	**2**	**141.3**	**0.00**	**1.00**	**0.62**	**1.00**	**0.230**
Pintail	Null	1	142.8	1.46	0.48	0.30	2.08	0.000
Pintail	Quadratic	3	145.3	3.97	0.14	0.08	7.30	0.149
Tufted Duck	**Null**	**1**	**141.5**	**0.00**	**1.00**	**0.58**	**1.00**	**0.000**
Tufted Duck	Linear	2	143.2	1.80	0.41	0.24	2.46	0.020
Tufted Duck	Quadratic	3	143.8	2.39	0.30	0.18	3.30	0.142
Gadwall	**Null**	**1**	**147.0**	**0.00**	**1.00**	**0.72**	**1.00**	**0.000**
Gadwall	Linear	2	149.1	2.16	0.34	0.24	2.95	0.000
Gadwall	Quadratic	3	152.9	5.97	0.05	0.04	19.77	0.000
Shoveler	**Quadratic**	**3**	**147.7**	**0.00**	**1.00**	**0.86**	**1.00**	**0.702**
Shoveler	Linear	2	151.4	3.71	0.16	0.14	6.39	0.550
Shoveler	Null	1	161.2	13.47	0.00	0.00	839.96	0.000

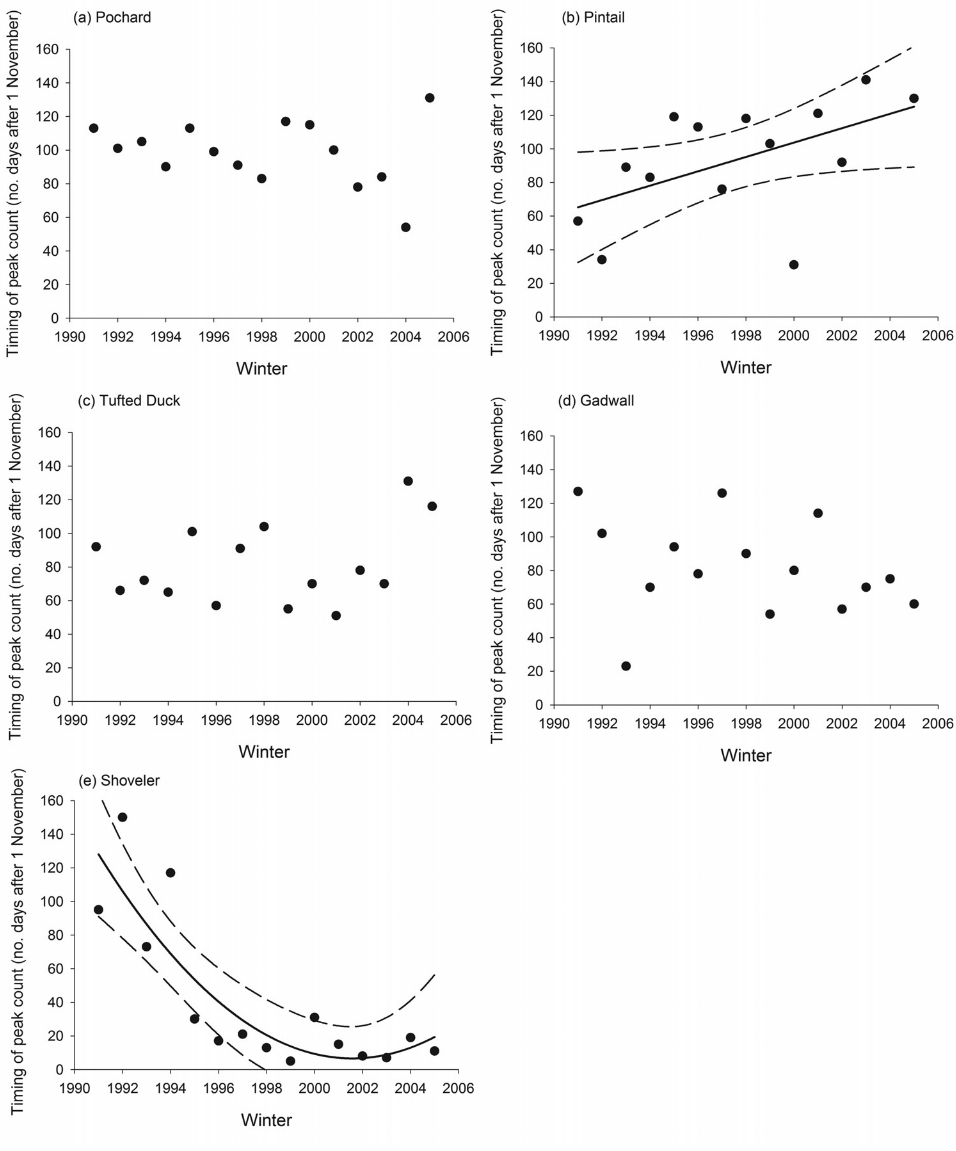

Figure 4. The timing of the annual peak count for each species with the mean (± 95 % CI) trend for the best-supported model plotted (where the null model was the best fit no trend has been plotted).

trend model (Table 2). The R^2_{adj} suggested that any decrease in male bias over time was weak (Fig. 3). There was some evidence that the peak count for Pintail occurred progressively later over the study period, as the linear trend model of peak Pintail count timings had the lowest AIC_c (Table 3, Fig. 4). However, the null model (*i.e.* no temporal trend) also received substantial support in the data with an associated $\mathrm{AIC_c}$ value only 1.46 greater than that of the linear trend model (Table 3).

For Tufted Duck, the null model had the lowest $\mathrm{AIC_c}$ value thus offering the best fit, followed by the linear model (Table 2; Fig. 3). The difference between these values was 3.1. The timings of the peak Tufted Duck counts did not vary consistently over time (Table 3, Fig. 4).

For Gadwall, the null model had the lowest $\mathrm{AIC_c}$ value thus offering the best fit, followed by the linear model (Table 2; Fig. 3). The difference between these values was 2.9. The Akaike weight of the null model was considerably higher than the values for the linear and quadratic models, respectively (Table 2). Peak counts of Gadwall did not show any consistent temporal trend (Table 3, Fig. 4).

For Shoveler, the quadratic model had the lowest $\mathrm{AIC_c}$ value thus offering the best fit, followed by the linear model (Table 2). The difference between these values was 5.8, indicating considerably greater support for the quadratic model and a non-linear change in SR over time; Shoveler SR was relatively stable between winters 1991/92 and 1998/99, before undergoing a sustained increase in male bias from 1998/99 onward (Fig. 3). The difference between the $\mathrm{AIC_c}$ values of quadratic model and the null model $\mathrm{AIC_c}$ values was 6.3. The greatest support in the data was found for a non-linear trend in the timings of the peak Shoveler count at Martin Mere (Table 3); peak counts occurred progressively earlier until around 1996/97, where after the timings remained relatively consistent (Fig. 4).

Discussion

Despite the fact that inter-annual variability and long-term trends in ASR data contributes valuable information on changes in demographic rates, we lack ASR data for most wildfowl. Although we could not differentiate first winter SR from ASR here, this is one of the few studies to present continuous time-series data on changes in overall SR in Pochard, a species of growing conservation concern (Fox *et al.* 2016). Changes in annual SRs provide greater temporal resolution than comparisons between two separate points in time (*e.g.* Brides *et al.* 2017), although these data originate from just one site, which would benefit from more data from a broader geographic range.

The steady increase in male bias among Pochard at Martin Mere differed from the national trend of no significant change in Britain between 1989/1990 and 2016 (Brides *et al.* 2017), so single site SR assessments clearly do not reflect national trends, for which there could be several explanations. Martin Mere is designated a Special Protection Area under the EC Birds Directive (JNCC 2018), and habitat management may affect the SR in birds' use of the site, but the pattern could also result from regional ecological effects or to its position along the flyway.

Shoveler and Gadwall were amongst the least abundant species at Martin Mere and showed a greater degree of inter-annual variability in SRs, while Tufted Duck abundance showed great inter-annual variability, reflected in large inter-annual variability in SR. These results suggest possible explanations for analogous patterns in duck SR over time and the necessity of frequent sampling to determine representative trends. In contrast, the more numerous Pochard showed steady year-on-year increases in male bias, indicating that a comparison of two discrete time-points could be sufficient to identify the long-term trend. Whether such inter-annual differences in peak counts reflect between-year differences in survival rates and productivity or between-year differences in habitat use or winter distribution is unclear (Arnold & Clark 1996; Blums *et al.* 1996).

The small difference between the Pintail linear model and the null model, combined with a low adjusted R^2_{adj} indicates a weak (potentially local) trend.

The trends in Pochard, Tufted Duck and Gadwall SR were not confounded by changes in the timing of the peak count, unlike those of Pintail and Shoveler (Table 3, Fig. 4). As a result, their SR patterns need to be interpreted cautiously, as they may reflect an effect of count timing rather than an underlying biological effect. The analysis perhaps highlights the limitations of this data set. Because, unlike for Pochard (Brides *et al.* 2017), no range-wide SR assessments have been made for Pintail or Shoveler, it is impossible to determine whether the trends documented at Martin Mere are localised or reflect a larger-scale trend.

The increasing Pochard male bias since 1983 is associated with a period of numerical decline (Owen & Dix 1986; Brides *et al.* 2017). The hypothesis that the increased proportion of males results from lower female survival has been attributed to several factors. Choudhury and Black (1991) found that male Pochard outcompeted females at feeding sites, suggesting that where food is limited females may lose out and thus move to sub-optimal feeding areas, potentially increasing female mortality. Whilst these findings support intersexual competition as a factor (Hepp & Hair 1984; Carbone & Owen 1986), local support for this hypothesis necessitates an assessment of food availability per individual at Martin Mere with an understanding of how this might have changed locally over time. Dredging of The Mere in summer 1990 and the subsequent build-up of silt, as well as construction of the reed bed pools in 2004 during this study, may have changed habitat quality and food availability to contribute to changes in SR at Martin Mere, not manifest at the national scale. Alternatively, changes in habitat quality across the region have potentially increased competition at sites such as Martin Mere. Further research is needed in this area.

Males of five species of dabbling ducks leave the breeding grounds whilst females incubate eggs and rear young based on ringing data (Perdeck & Clason 1983). Theory suggests that females arriving at optimal feeding sites near the breeding grounds already occupied by males would be forced to migrate further down the flyway, a hypothesis supported by latitudinal trends in Pochard SR (Carbone & Owen 1995; Brides *et al.* 2017). Incubating female Pochard (compared to males) are thought to be exposed to increased levels of predation from a number of species (Fox *et al.* 2016). Moreover, hunting pressure and exposure to lead shot is greater in southern Europe, where a higher proportion of females overwinter (Mateo 2009; Green & Pain 2016; Andreotti *et al.* 2018). While these factors potentially affect population SR, they can only contribute to changes at the local scale.

Overwintering ducks at Martin Mere originate from different breeding provenance, for example, Pintail ringed at Martin Mere have been recovered in Iceland and Russia. Contrasting conditions encountered along separate migration routes contribute differentially to variation between their SRs, and as a result influence species abundance and SR at Martin Mere. Annual SR data collection at multiple sites would allow the detection of non-linear trends, such as this study found for Shoveler. Requesting SR data collection through existing national and international networks of counters proved highly effective for Pochard (Brides *et al.* 2017) and could be utilised to collect annual SR data on a range of species, potentially to become a standard element of international wildfowl counts. As Leopald (1933; 165–166) argued: "*All measurements of either game populations or game productivity are enhanced in their significance and value if the sex and age as well as the number of individuals be determined.*"

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References

Alexander, W.C. 1983. Differential sex distributions of wintering diving ducks (Aythyini) in North America. *American Birds* 37: 26–29.

Andreotti, A., Guberti, V., Nardelli, R., Pirrello, S., Serra, L., Volponi, S. & Green, R.E. 2018. Economic assessment of wild bird mortality induced by the use of lead gunshot in European wetlands. *Science of the Total Environment* 610: 1505–1513.

Arnold, T.W. & Clark, R.G. 1996. Survival and philopatry of female dabbling ducks in southcentral Saskatchewan. *Journal of Wildlife Management* 60: 560–568.

Barton, K. 2012. *MuMIn: Model Selection and Model Averaging Based on Information Criteria*. R package version 1.13.4. Available at https://CRAN.R-project.org/package=MuMIn (last accessed 31 July 2018).

Bellrose, F.C., Scott, T.G., Hawkins, A.S. & Low, J.B. 1961. Sex ratios and age ratios in North American ducks. *Illinois Natural History Survey Bulletin* 27: Article 6.

Blums, P. & Mednis, A. 1996. Secondary sex ratio in Anatinae. *Auk* 113: 505–511.

Blums, P., Mednis, A., Bauga, I., Nichols, J.D. & Hines, J.E. 1996. Age-specific survival and philopatry in three species of European ducks: a long-term study. *Condor* 98: 61–74.

Brides, K., Wood, K.A., Hearn, R.D. & Fijen, T.P. 2017. Changes in the sex ratio of the Common Pochard *Aythya ferina* in Europe and North Africa. *Wildfowl* 67: 100–112

British Trust for Ornithology (BTO). 2018. Species focus: Pochard. Available at https://www.bto.org/about-birds/species-focus/pochard (last accessed 10 April 2018).

Burnham, K.P., Anderson, D.R. & Huyvaert, K.P. 2011. AIC model selection and multimodel inference in behavioral ecology: some background, observations, and comparisons. *Behavioral Ecology and Sociobiology* 65: 23–35.

Cabot, D. 2009. *Wildfowl*. Collins New Naturalist Library, Book No. 110. HarperCollins, London, UK.

Carbone, C. & Owen, M. 1995. Differential migration of the sexes of Pochard *Aythya ferina*: results from a European survey. *Wildfowl* 46: 99–108.

Choudhury, S. & Black, J.M. 1991. Testing the behavioural dominance and dispersal hypothesis in Pochard. *Ornis Scandinavia* 22: 155–159.

Christensen, T.K. & Fox, A.D. 2014. Changes in age and sex ratios amongst samples of hunter-shot wings from common duck species in Denmark 1982–2010. *European Journal of Wildlife Research* 60: 303–312.

Clopper, C.J. & Pearson, E.S. 1934. The use of confidence or fiducial limits illustrated in the case of the binomial. *Biometrika* 26: 404–413.

Clutton Brock, T.H. 1986. Sex ratio variation in birds. *Ibis* 128: 317–329.

Donald, P.F. 2007. Adult sex ratios in wild bird populations. *Ibis* 149: 671–692.

Fox, A.D., Caizergues, A., Banik, M.V., Devos, K., Dvorak, M., Ellermaa, M., Folliot, B., Green, A.J., Grüneberg, C., Guillemain, M., Håland, A., Hornman, M., Keller, V., Koshelev, A.I., Kostiushyn, V.A., Kozulin, A., Ławicki, Ł., Luigujõe, L., Müller, C., Musil, P., Musilová, Z., Nilsson, L., Mischenko, A., Pöysä, H., Ščiban, M., Sjeničić, J., Stīpniece, A., Švažas, S. & Wahl, J. 2016. Recent changes in the abundance of Common Pochard *Aythya ferina* breeding in Europe. *Wildfowl* 66: 22–40.

Fox, A.D. & Christensen, T.K. 2018. Could falling female sex ratios among first-winter northwest European duck populations contribute to skewed adult sex ratios and overall population declines? *Ibis* online early doi:10.1111/ibi.12649.

Green, R.E. & Pain D.J. 2016. Possible effects of ingested lead gunshot on populations of ducks wintering in the UK. *Ibis* 158: 699–710

Hagan, J.M. 1992. Conservation biology when there is no crisis – yet. *Conservation Biology* 6: 465–476.

Hardy, I.C.W. (ed.) 2002. *Sex Ratios: Concepts and Research Methods*. Cambridge University Press, Cambridge, UK.

Hepp, G.R. & Hair, J.D. 1984. Dominance in wintering waterfowl (Anatini): Effects on distribution of sexes. *Condor* 86: 251–257.

International Union for Conservation of Nature (IUCN). 2017. Summary statistics Available at: www.iucnredlist.org/about/summary-statistics (last accessed 10 April 2018).

International Union for Conservation of Nature (IUCN). 2018. The IUCN Red List of threatened species Available at: www.iucnredlist.org (last accessed on 10 April 2018).

Joint Nature Conservation Committee (JNCC). 2018. Special Protection Area (SPA) Review site accounts: Martin Mere. Available at: http://jncc.defra.gov.uk/page-1985 (last accessed on 3 May 2018).

Lehikoinen, A., Christensen, T.K., Öst, M., Kilpi, M., Saurola, P. & Vattulainen, A. 2008. Large-scale change in the sex ratio of a declining eider *Somateria mollissima* population. *Wildlife Biology* 14: 288–301.

Leopold, A. 1933. *Game Management*. Charles Scribner's Sons, New York, USA.

Lindenmayer, D.B. & Likens, G.E. 2009. Adaptive monitoring: a new paradigm for long-term research and monitoring. *Trends in Ecology & Evolution* 24: 482–486.

Mac Nally, R., Duncan, R.P., Thomson, J.R. & Yen, J.D. 2018. Model selection using information criteria, but is the "best" model any good? *Journal of Applied Ecology* 55: 1441–1444.

Nichols, J.D. 1991. Extensive monitoring programmes viewed as long term population studies: the case of North American waterfowl. *Ibis* 133 (Supplement No. 1): 89–98.

Nichols, J.D. & Williams, B.K. 2006. Monitoring for conservation. *Trends in Ecology & Evolution* 21: 668–673.

Owen, M. & Dix, M. 1986. Sex ratios in some common British wintering ducks. *Wildfowl* 37*:* 104–112.

Perdeck, A.C. & Clason, C. 1983. Sexual differences in migration and winter quarters of ducks ringed in the Netherlands. *Wildfowl* 34: 137–143.

Pinheiro, J., Bates, D., DebRoy, S., Sarkar, D. & R Core Team. 2017. *nlme: Linear and Nonlinear Mixed Effects Models*. R package version 3.1-131. Accessible at https://CRAN.R-project.org/package=nlme (last accessed 31 July 2018)

Ramula, S., Öst, M., Lindén, A., Karell, P. & Kilpi, M. 2018. Increased male bias in eider ducks can be explained by sex-specific survival of prime-age breeders. *PLoS One* 13: e0195415.

RStudio Team. 2015. *RStudio: Integrated Development for R*. RStudio, Inc. Boston, MA, USA.

Thomas, L. & Martin, K. 1996. The importance of analysis method for breeding bird survey population trend estimates. *Conservation Biology* 10: 479–490.

Wetlands International. 2018. *Waterbird Population Estimates*. Available at wpe.wetlands.org (last accessed 10 April 2018).

Photograph: Pochard and Tufted Duck at Martin Mere, Lancashire, UK, by James Lees/WWT.