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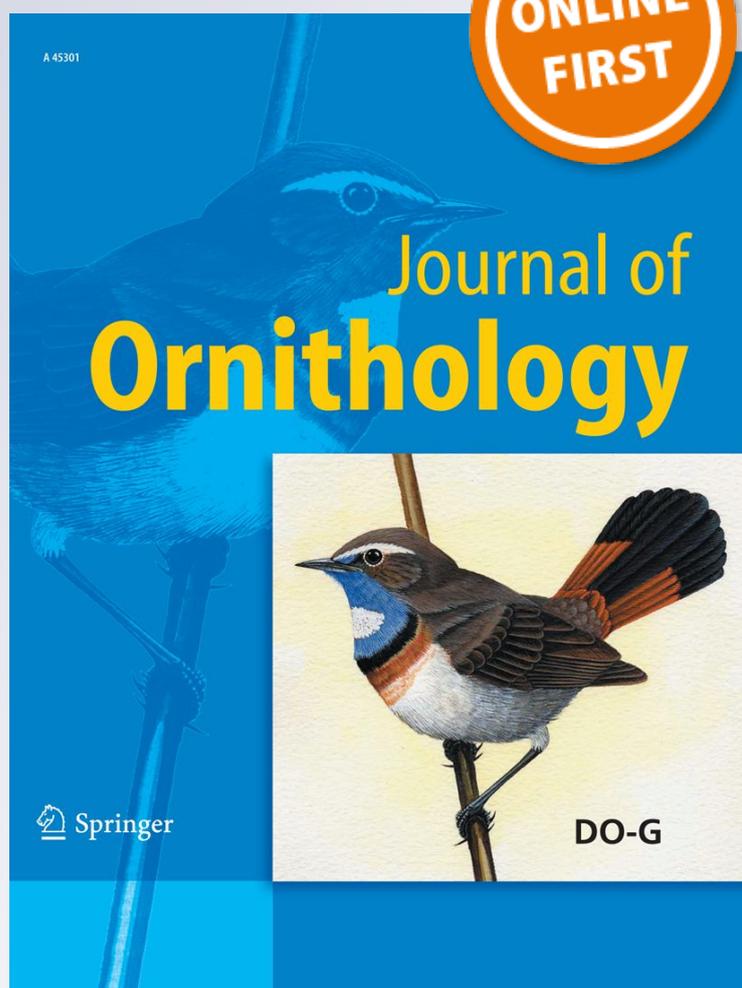
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Autumn survival inferred from wing age ratios: Wigeon juvenile survival half that of adults at best?

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Abstract Measures of first-year autumn mortality rates are important parameters for understanding population dynamics, but have been hitherto unavailable for dabbling ducks in Europe, because most ducks are ringed in winter. We used the temporal change in the proportion of juveniles in wing samples from hunters in Finland, Denmark and UK, together with adult survival estimates from the literature, to estimate juvenile autumn survival in Wigeon *Anas penelope*. Wing samples from Finland and Denmark were collected during the late breeding (August–September) and migration (October–December) periods. The proportion of juveniles decreased from 80 % (females) and 74 % (males) in Finland to 63 and 45 % in Denmark, respectively. Combining the changes in the proportion of juveniles in the wing sample with adult Wigeon 3-month survival rates inferred from a Bayesian meta-analysis (89 % in males and 88 % in females), estimated autumn juvenile survival

probability was 29 % for females and 22 % for males. The results show that autumn mortality is far higher in juvenile Wigeon than amongst adults, consistent with previous results in Teal *Anas crecca*, and may reflect a wider pattern in dabbling ducks. Such low survival rates are especially important in Wigeon given observed long-term declines in breeding productivity in this population.

Keywords Wing examination · Hunting bag · Age ratio · Survival · Autumn

Zusammenfassung

Ab schätzung der herbstlichen Überlebensrate aus dem Alter von Flügeln: Pfeifenten Jugendsterblichkeit gerade maximal die Hälfte der der Altvögel?

Die Mortalitätsrate von Erstjährigen zwischen Flügge werden und Winter ist ein wichtiger Parameter in der

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Populationsdynamik von Schwimmenten. Weil Enten in Europa hauptsächlich im Winter beringt werden, existieren Angaben zu Überlebensraten nur für Altersklassen ab dem ersten Winter, also erst nach der Mortalität im Herbst. Wir bestimmten den Anteil an erstjährigen Pfeifenten *Anas penelope* in Flügelsammlungen von Jägern aus Finnland und Dänemark zwischen August und Dezember. Aus der Abnahme dieses Anteils zwischen Finnland und Dänemark und aus einer Meta-Analyse von Literaturangaben zu Überlebensraten von Adulten schätzten wir die 3-monatige Überlebensrate der Erstjährigen im Herbst. Der Anteil Erstjähriger sank von 80 % (Weibchen) und 74 % (Männchen) in den Monaten August und September in Finnland auf 63 % und 45 % in den Monaten Oktober und November in Dänemark. Die 3-monatige Überlebenswahrscheinlichkeiten waren 89 % für adulte Männchen und 88 % für adulte Weibchen. Die Kombination der Überlebenswahrscheinlichkeit für Adulte und der Abnahme des Anteils Erstjähriger über die Zeit ergab, dass nur 29 % der erstjährigen Weibchen und 22 % der erstjährigen Männchen die drei Herbstmonate überleben. Das Resultat zeigt, dass die Sterblichkeit im Herbst bei Erstjährigen sehr viel höher liegt als bei adulten Pfeifenten und dass diese Zeit ein Flaschenhals in der Lebensgeschichte der Pfeifente ist. Ähnliches wurde bereits für die Krickente *Anas crecca* gezeigt und ist auch für weitere Schwimmentenarten zu erwarten. Die tiefe Überlebensrate von Erstjährigen bei der Pfeifente bedeutet, dass die europaweit beobachtete langzeitliche Abnahme des Bruterfolgs ernst genommen werden muss.

Introduction

Juvenile mortality during the first months after fledging is an important driver of population dynamics in most dabbling duck species, where the production of young is among the vital rates that influence population growth rate the most (e.g. Hoekman et al. 2002; Coluccy et al. 2008). Naïve juveniles are supposedly more exposed to threats than adults (e.g. hunting, disease and predation loss during migration; Hickey 1952; Parker 1991; Owen and Black 1991; Newton 2008). However, information on juvenile autumn survival is generally unavailable for ducks in Western Europe, where ringing has mostly occurred during the winter (Owen and Black 1990; Mitchell 2002; Hofer et al. 2010, see however Gunnarsson et al. 2008). An indirect method combining known adult survival rate (inferred from winter ringing–recovery data) and the rate of decrease in the age-ratio over time, assessed from hunting bags, has recently overcome this problem. This has allowed estimation of autumn (August–November) survival in first-

year Teal *Anas crecca*, which suggested that only 14.7 % of these birds survived from the breeding grounds in Finland to the winter quarters in western France (Guillemain et al. 2010).

This paper estimates autumn survival rates of juvenile Wigeon *Anas penelope*, a popular game species throughout the north-western European flyway (Harradine 1985; Larsen 1997; Hirschfeld and Heyd 2005) showing signs of declines in reproductive success since the 1980s (Mitchell et al. 2008; H. Pöysä, unpublished data). Fewer and fewer juveniles have been produced in recent decades, making it crucial to understand patterns in their survival rates.

We estimated the annual proportion of juveniles throughout the autumn by examining wings in hunting bags, expecting a gradual decrease in the proportion of young as time progresses and the birds move towards their wintering grounds. From this rate of decrease in the proportion of juveniles in the hunting bag, survival rate of first-year birds can be inferred if adult survival rate is known. We here used a Bayesian meta-analysis to obtain sex-specific adult survival estimates. From these rates and the change in age-ratios over time in the Finnish and Danish wing samples, an estimate for juvenile autumn survival was obtained. The information from the literature (on adult survival) and from the wing sample data (on age ratio) was combined using Bayesian methods, which allows propagation of uncertainties of the two estimates (adult survival and age-ratio) into uncertainty of the resulting juvenile autumn survival estimates.

Methods

Wing data from hunting bags

A total of 20,485 Wigeon wings were provided on a voluntary basis by hunters from Finland, Denmark and the United Kingdom from the 1996–1997 to 2008–2009 hunting seasons (Table 1). A “season” hereafter refers to the annual hunting period, extending from August (September in Denmark) to the following January (December in Finland) inclusive, the season being defined by the August of that year (i.e. 2002 for the August 2002–January 2003 hunting season). Because the number of wings from Finland was relatively limited, the analysis was carried out combining all data at the national scale rather than distinguishing regional samples.

New wing feathers are generally produced by Wigeon only at birth (first-year birds), during breeding (adult females) or at specific moulting areas (adult males; Cramp and Simmons 1977; Ginn and Melville 2007; see, however, Rodrigues et al. 1997). The age of an individual can

Table 1 Annual proportions of male and female juvenile Wigeon *Anas penelope* wings within the samples supplied by hunters in each country along the flyway; sample sizes (i.e. number of wings examined in each category) shown in parentheses

Seasons	Finland		Denmark		UK	
	Females	Males	Females	Males	Females	Males
1996					0.53 (785)	0.33 (1,235)
1997					0.65 (509)	0.44 (786)
1998					0.63 (478)	0.45 (576)
1999					0.59 (228)	0.43 (313)
2000					0.58 (346)	0.39 (396)
2001					0.60 (213)	0.51 (274)
2002			0.66 (365)	0.59 (390)		
2003			0.67 (900)	0.56 (1,246)		
2004			0.77 (1,514)	0.66 (1,881)		
2005	0.86 (120)	0.72 (93)	0.67 (655)	0.51 (916)		
2006	0.71 (91)	0.77 (40)	0.57 (473)	0.38 (916)		
2007	0.83 (86)	0.74 (42)	0.64 (1,013)	0.47 (1,539)		
2008			0.61 (790)	0.49 (1,279)		
Mean value	0.80 (297)	0.74 (175)	0.66 (5,710)	0.52 (8,164)	0.60 (2,559)	0.42 (3,580)

therefore be determined with confidence throughout the year from examination of wing feathers, since there is no gradual moult along the flyway. Age-ratios in the hunting bag may not directly reflect the true age-ratio in the wild population, since the probability of being shot by hunters differs between age classes (Mitchell et al. 2008). Our approach is thus based on relative changes in the proportion of first year birds in the hunting bag along the flyway, assuming that the difference between population and hunting bag age-ratios remains constant (see below).

Survival of first-year birds was estimated based on differences in age-ratios between the Finnish and Danish data. Data were limited to the years 2005–2007 during which samples of wings were simultaneously available from both countries. Great Britain data existed only from earlier years, so that they could not be directly included in the analyses. These are nonetheless presented here to show the consistent trend of decreasing age-ratio along the flyway. The Danish dataset contained 5,512 wings, of which 859 were from September, 2,520 from October, 1,401 from November, 678 from December and 54 from January. The proportion of juvenile males in September was lower than during the other months (Fig. 1), because of an overrepresentation of adult males due to their moult migration (Mitchell et al. 2008). The proportions of juveniles in January varied greatly between years due to low sample size. We therefore omitted data obtained in September and January from the Danish dataset. The average collection date for the Finnish wing data was 30 August and, after the selection process above, 3 November for the Danish data. This translates into an average time difference of 2.1 months between the two datasets.

Differential migration of the age classes has been documented in Wigeon, at least amongst males: adult males of

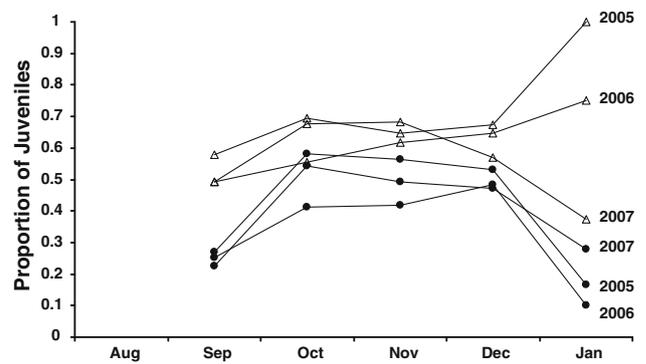


Fig. 1 Monthly proportions of female (open triangles) and male (filled circles) juvenile Wigeon *Anas penelope* wings within the hunter supplied samples received in Denmark during the 3 years 2005–2007

this species generally winter further north than females and juveniles of both sexes on average (e.g. Campredon 1983). Differential migration may potentially confound the estimation of juvenile survival if of sufficient magnitude, as it may lead to unequal distribution of first-year birds along the flyway, resulting in a greater proportion of juveniles at the southern end of the range. However, the present data originate from the autumn (i.e. early in the season) and from Denmark, which is relatively upstream within the flyway. Unpublished data from France suggest that the proportion of juveniles in that country did not differ markedly ($\leq 5\%$ when there was a difference) from the proportion in Denmark. Seemingly, differential migration is much less pronounced in our dataset than reported for the early 1980s (Campredon 1983). For this reason, we assumed that differential migration was negligible, contributing only a weak positive bias to juvenile survival estimates.

Table 2 Adult survival estimates for Eurasian *Anas penelope* and American Wigeon *A. americana* from the literature that were used to estimate juvenile autumn survival

Species	Location	Source	Sex	Year(s)	Method	Yearly survival estimate	Uncertainty measure	Type of uncertainty measure	Standard error
<i>Anas americana</i>	Gray Lodge Wildlife Area, California, USA	Rienecker (1976)	M	1953–1967	Jolly–Seber model	0.6604	0.6333–0.6875	90 % CI	0.0187
<i>Anas americana</i>	Gray Lodge Wildlife Area, California, USA	Rienecker (1976)	F	1953–1967	Jolly–Seber model	0.5824	0.5229–0.6418	90 % CI	0.0362
<i>Anas americana</i>	Imperial valley, California, USA	Rienecker (1976)	M	1951–1961	Jolly–Seber model	0.6300	0.5971–0.6628	90 % CI	0.0200
<i>Anas americana</i>	Imperial valley, California, USA	Rienecker (1976)	F	1951–1961	Jolly–Seber model	0.5892	0.4851–0.6933	90 % CI	0.0633
<i>Anas americana</i>	Imperial valley, California, USA	Rienecker (1976)	M	1963–1969	Jolly–Seber model	0.6262	0.5915–0.6609	90 % CI	0.0211
<i>Anas americana</i>	Imperial valley, California, USA	Rienecker (1976)	F	1963–1969	Jolly–Seber model	0.6668	0.5683–0.7653	90 % CI	0.0599
<i>Anas penelope</i>	Finland	Grenquist (1965)	?	?	Ring recovery, but method not clear	0.57	$n = 32$	Sample size	0.1107
<i>Anas penelope</i>	Abberton Reservoir, Essex, UK	Wainwright (1966)	?	1949–1966	Ring recoveries Bellrose and Chase (1950)	0.57	$n = 306$	Sample size	0.0314
<i>Anas americana</i>	St. Denis Nat. Wildlife area, Saskatchewan, Canada	Arnold and Clark (1996)	?	1982–1993	Resightings of nasal marks, Jolly–Seber model	0.635	0.103	Standard error	0.103

For each estimate, important characteristics of the study are given (species, location, sex, years when the study was conducted). The adult survival estimates are given together with the uncertainty measures reported in each study. The last column gives the standard errors that we obtained from the reported uncertainty measures and that we used in the meta-analysis

Meta-analysis model for adult survival

Estimates of adult Wigeon survival rates based on ringing in western Europe are few and derive from relatively old studies (Table 2), since when analytical methods have improved. Wigeon survival rate may also have changed over time owing to changes in habitat (Owen and Williams 1976; Guillemain et al. 2002). To partially overcome this problem, we complemented existing Eurasian Wigeon data with more recent adult survival rate estimates for the closely-related American Wigeon *Anas americana* (Rienecker 1976; Arnold and Clark 1996; Table 2).

To combine information about adult survival from the different studies in the literature, we used normal distributions to describe the available information about adult and juvenile survival probabilities. The 95 % confidence intervals of these survival probabilities lay all within the interval 0.4–0.8 (Table 2). Within this range, the distribution of the mean survival probabilities can, for the purpose of our analyses, be satisfactorily approximated by a normal distribution. The different measures of uncertainty provided by the authors were all transformed to standard errors (Table 2). For 90 % confidence intervals, a normal distribution was derived with given mean and 5 and 95 % quantiles, and its standard deviation used as standard error. If only sample size was given, the inverse binomial test was used to obtain a 68 % confidence interval that corresponded approximately to the mean \pm 1 standard deviation in a normal distribution. This standard deviation was then used as the standard error for the survival estimate. We used a hierarchical model approach to combine adult survival estimates from the different studies for males and females as described in Gelman et al. (2004). The published estimates for annual adult survival of males and females in study i , respectively $\widehat{s}_{m,i}$, $\widehat{s}_{f,i}$, were assumed to be a realisation from a normal distribution with a study-specific mean survival probability, $\theta_{m,i}$, $\theta_{f,i}$, and a standard deviation corresponding to the standard error reported in the study or obtained from other uncertainty measures that were reported in the study (Table 2) $\widehat{\sigma}_{m,i}$, $\widehat{\sigma}_{f,i}$:

$$\widehat{s}_{m,i} \sim \text{Norm}\left(\theta_{m,i}, \widehat{\sigma}_{m,i}^2\right)$$

$$\widehat{s}_{f,i} \sim \text{Norm}\left(\theta_{f,i}, \widehat{\sigma}_{f,i}^2\right)$$

The study-specific mean survival probability per sex was assumed to be normally distributed around the sex-specific survival probabilities:

$$\theta_{m,i} \sim \text{Norm}\left(\theta_m, \sigma_m^2\right)$$

$$\theta_{f,i} \sim \text{Norm}\left(\theta_f, \sigma_f^2\right)$$

To also include the information from the studies presenting survival probabilities for the two sexes combined, \widehat{s}_i , a further hierarchical normal model was constructed. We assumed that the survival probability reported by these studies was the average of the two sex-specific survival probabilities:

$$\widehat{s}_i \sim \text{Norm}\left(\theta_i, \widehat{\sigma}_i^2\right)$$

$$\theta_i \sim \text{Norm}\left(\theta, \sigma^2\right), \text{ with } \theta = \frac{\theta_m + \theta_f}{2}, \text{ and } \sigma^2 = \frac{1}{4}\left(\sigma_m^2 + \sigma_f^2\right)$$

Flat prior distributions for the means and standard deviations of the sex-specific survival probabilities were used: $p(\theta_m) = p(\theta_f) = \text{Norm}(0, 1000)$ and $p(1/\sigma_m) = p(1/\sigma_f) = \text{Gamma}(0.01, 0.01)$. The model was fitted to the data from the literature by Markov Chains Monte Carlo (MCMC) simulations in WinBUGS (Lunn et al. 2000) using the R-interface R2WinBUGS (Sturtz et al. 2005). Two Markov chains of length 10,000 were simulated. The first 2,000 simulations were discarded as burn-in, and from the remaining chain every 5th simulation was used to describe the posterior distribution of survival and associated standard error estimates. Convergence was checked using the R-hat value (Brooks and Gelman 1998), and was below 1.01 in all cases. The combined annual survival estimates were $\widehat{\theta}_m = 0.627$ (SE = 0.065) for males and $\widehat{\theta}_f = 0.595$ (SE = 0.066) for females. This corresponds to 3-monthly survival probabilities of 0.887 (SE = 0.026) for males and 0.876 (SE = 0.029) for females.

Age-ratio model and the derivation of juvenile survival

Juvenile survival can be inferred from the rate of change in the proportion of juveniles in hunting bags over the considered time period given known adult survival rate. Juvenile survival would be equal to that of adults if the age-ratio remains constant along the flyway. A trend in age-ratio, assuming constant adult survival, thus enables the estimation of a relative juvenile autumn survival rate.

Four independent binomial models were used to estimate the proportions of juveniles in Finland (*SF*) and Denmark (*DK*) for both sexes (f and m), $p_{\text{sex,country}}$, from the observed numbers of juvenile wings contributed per year y , $n_{\text{juv,sex,country},y}$, and the annual total number of wings, $n_{\text{total,sex,country},y}$. The estimated proportion of juveniles per sex and country, $p_{\text{sex,country}}$, represents the mean across the 3 years.

$$n_{\text{juv,sex,country},y} \sim \text{Binom}\left(p_{\text{sex,country}}, n_{\text{total,sex,country},y}\right)$$

Annual adult survival estimates obtained from the meta-analysis model were transformed to 2.1-monthly estimates

(the time-lag between mean wing collection dates in Finland and Denmark) by expressing annual adult survival estimates to the power 2.1/12. The 2.1-monthly adult survival rates, $S_{ad,f}^T$ and $S_{ad,m}^T$, where $T = 2.1$, were combined with the estimated age-ratio in the two countries to obtain the juvenile survival probabilities for both sexes, $S_{juv,f}^T$ and $S_{juv,m}^T$, using the formula:

$$S_{juv,sex}^T = \frac{S_{ad,sex}^T (1 - p_{sex,SF}) p_{sex,DK}}{(1 - p_{sex,DK}) p_{sex,SF}},$$

where sex = males or females, DK = Denmark, and SF = Finland.

Uncertainty measures for the estimated juvenile survival probabilities were obtained by calculating the juvenile survival probability for all MCMC simulations from the posterior distributions of the model parameters. This resulted in a sample of values that together described the posterior distribution of the juvenile survival probability. We used the mean as estimate and report the 2.5 and 97.5 % quantiles of these distributions as lower and upper limits of the 95 % credible interval.

Flat prior distributions were used for the proportion of juveniles $p(p_{sex,SF}) = p(p_{sex,DK}) = \text{Unif}(0,1)$. For annual adult survival probabilities, the results from the meta-analysis that combined the information from the different publications were included as informative prior distributions: $p(S_{ad,m}) = \text{Norm}(0.627, 0.065^2)$ and $p(S_{ad,f}) = \text{Norm}(0.595, 0.066^2)$. The model was fitted to the data from the 3 years (2005–2007) using the same methods as for the meta-analysis of adult survival (i.e. Bayesian methods in WinBUGS, see above). Model fit was assessed by comparing the observed and predicted numbers of juveniles of each sex in the hunting bag of each country in each year. The 2.1-month juvenile survival estimates for the two sexes were then transformed to 3-month survival probabilities to ease comparison with the earlier Teal results (Guillemain et al. 2010).

Results

The proportion of juveniles in the wing samples was lower in Denmark (where Wigeon were mostly shot in October or early November) than in Finland (where they were mostly shot in late August and September), both amongst males and females (Table 1). The proportions of juveniles in the British data were even lower than the Danish ones, but are only presented here to show the consistency of this trend along the flyway. The numbers of juveniles in the Danish hunting bag predicted by the model coincided well with the observed values (graph not shown).

Estimated average proportions of juveniles were 0.735 (SE = 0.033) and 0.802 (SE = 0.023) for males and females respectively in Finland, and 0.507 (SE = 0.010) and 0.650 (SE = 0.011) in Denmark (2.1 months later). From the decrease in the proportions of juveniles over time and knowledge about adult survival from the literature (meta-analysis), we obtained estimated juvenile 3-month (autumn) survival probabilities of 22 % (CI: 0.13–0.35) for males and 29 % (CI: 0.18–0.44) for females.

Discussion

The proportion of juveniles in the Wigeon hunting bag declined with time along the flyway, from Finland to Denmark. The British ratios were lower than the Danish ratios, as predicted because the UK lies further down the flyway from Finland and Denmark.

This trend in age-ratios along the flyway cannot reflect gradual changes in wing plumage over the season, as wing feathers are almost exclusively produced on the northern breeding or moulting sites, i.e. prior to autumn migration (e.g. Ginn and Melville 2007). We assumed that differential migration of the age classes did not affect the present analysis (see “Methods”). We cannot exclude a negative bias in the juvenile survival estimate if the juveniles gradually learnt to avoid hunters. However, we consider such an effect as unlikely or at least negligible because Wigeon forage in groups of mixed age classes and sex, so that hunter avoidance behaviour should be group-specific rather than age-specific, even if hunting mortality is apparently higher in juveniles on average.

The present modelling exercise suggests juvenile Wigeon survival in autumn is 0.29 in females and 0.22 in males. Such 3-month survival rates are twice those of the estimates derived for Teal (13.9–15.4 %; Guillemain et al. 2010). It is unlikely that such results simply reflect a differential ability of observers to discriminate juveniles from adults in Wigeon compared to Teal, with more juvenile Wigeon being incorrectly assigned as adults: Wigeon age classes are far easier to discriminate based on wing plumage than are Teal (Rousselot and Trolliet 1991). The difference between the juvenile survival rates in the two species is actually consistent with established allometric relationships that suggest survival increases with body size among Anatidae (Krementz et al. 1997). The Wigeon values are also consistent with the 0.72 mortality rate computed from the few Wigeon summer ringing data from Finland, although these are old and based on few individuals (Grenquist 1965). With regard to current Wigeon population dynamics and the development of conservation policy, the present results suggest, as for the Teal, that the population is probably maintained through high annual

breeding output. The size of the northwest European population (based on mid-winter inventories) was considered to be stable until very recently (Delany and Scott 2006). Although many Wigeon wintering in Denmark and the United Kingdom originate from Russia as well as Fennoscandia (Scott and Rose 1996), the steady decline in Wigeon breeding success index in Finland (H. Pöysä, unpublished data) and in the proportions of young in the wing surveys in the UK and in Denmark recently (Mitchell et al. 2008; Christensen, unpublished data) suggest that productivity rates may be declining, which should be regarded with some concern. In Finland, the number of individuals fledged per pair has declined more than the densities of breeding pairs, but the causes of declines in productivity have not been determined, nor is it clear whether such declines are evident amongst the large Russian element of the breeding population.

Female juvenile survival in autumn appeared somewhat higher than in males, in contrast to most studied species (e.g. Mallard *Anas platyrhynchos*: Nichols et al. 1987; Gunnarsson et al. 2008; American Wigeon: Rienecker 1976; Eurasian Teal: Devineau et al. 2010). Although it is not possible to test at present, one hypothesis to explain this could be that juvenile males are simply more mobile than females (see Guillemain et al. 2005 for the same pattern in Teal). This could expose males to all forms of mortality, including hunting, to a greater extent than females.

As in the case of Teal, juvenile Wigeon survival in autumn is a fraction (ca. 25 % in males, 33 % in females) of adult survival during the same period. The computation of juvenile survival here was based on adult autumn survival, assuming constant adult survival rate over the year. However, it is unlikely that we overestimated adult autumn survival rate, although hunting certainly increases mortality during autumn. Adult mortality is expected to be high also during winter (harsh climate) and summer (predation of females on nests). At any rate, the most important result of the present study is the relative survival rate of juveniles compared to adults, rather than the absolute value of survival rate obtained for juveniles.

Consistent differences between adult and juvenile survival rates in two duck species with differing diets (mostly granivore for Teal, herbivore for Wigeon) and nesting habits (wetland breeder in the former species, more upland nester in the latter; Cramp and Simmons 1977) suggest this may be a widespread feature of dabbling ducks. Such differences are likely common amongst the Anatidae in general. For example, in Barnacle Geese *Branta leucopsis*, a species with high parental investment in brood care and family cohesion, autumn survival between Svalbard breeding areas and arrival on the winter quarters was 95.5 % amongst adults and 65.1 % amongst goslings

ringed at age 3–5 weeks (Owen and Black 1989). First autumn survival rates should be taken into consideration in future population dynamics models for duck species generally, which have tended to use adult survival rates as a proxy for juvenile values. A juvenile survival rate half that of adults may be a conservative model for such future population modelling, especially considering temporal changes in both annual survival and reproductive success.

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