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ORIGINAL ARTICLE

Seasonal variation in the sex and age composition of the woodcock bag in Denmark

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Abstract The Eurasian woodcock is a highly valued game bird in Western Europe from which c. 2.7 million individuals are harvested annually from an estimated population of 20–26 million birds. The population size and status remains uncertain due to the cryptic behaviour and widespread and solitary occurrence of woodcock, on breeding and wintering areas, making reliable population surveys difficult. Hunting bag records provide age ratios amongst bagged birds, but sex ratios remain poorly known because of the sexually monomorphic nature of this species. We used DNA analysis to determine sex ratios amongst 327 shot woodcocks from two hunting seasons in Denmark (1 October–31 January, 2012/13 and 2013/14). Based on bag totals, age ratios and sex ratios, juvenile females constituted 37%, juvenile males 27%, adult females 16% and adult males 20% of the annual woodcock bag. The female bias was related to a significant deviation from parity in the sex ratio amongst juvenile birds in October, although no such deviation was found at other times or amongst adults. Compared to limited data from other European countries, our data suggest that autumn migration of woodcock involves an initial wave of juvenile females followed by juvenile males and adults, and perhaps that males stay further north in Europe than females during autumn and winter. This migratory pattern would suggest that postponing the opening of the hunting season could reduce the hunting bag on reproductively valuable females in this polygamous species.

Keywords Woodcock · *Scolopax rusticola* · Age ratio · Sex ratio · Hunting bag

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Introduction

The European wintering population of the Eurasian woodcock *Scolopax rusticola* (hereafter woodcock) originate from breeding areas throughout woodlands in western, central and northern boreal forest zones of Europe, European Russia and western Siberia (Hagemeijer and Blair 1997). The majority of the 20–26 million birds estimated for the whole population in this area (Nagy et al. 2015) winter in Western and Southern Europe with some movements into northern Africa (Birdlife International and NatureServe 2014). Some 3–4 million woodcock were estimated to have been harvested annually in Europe (Ferrand and Gossmann 2001), but more recent reports suggest 2.3 to 3.4 million (Lutz and Jensen 2005), excluding Russia, where the autumn hunting bag is estimated to be 50,000–60,000 (Blokhin et al. 2015). The majority of woodcock are shot in winter in France (c. 1.2 million), Spain (c. 35,000), UK (c. 125,000), Italy (105,000), Greece (c. 1 million) and Ireland (c. 125,000; Hirschfeld and Heyd 2005; Lutz and Jensen 2005; Ferrand et al. 2008) but hunting takes place throughout Europe during the autumn migration period. Traditional spring hunting has been closed in recent decades in most countries, but still takes place in Russia, amounting to approximately 166,000–213,000 individuals (Blokhin et al. 2015). It is claimed that the European population of woodcock is stable (Ferrand and Gossmann 2009), but reliable monitoring data of staging, wintering and breeding abundance are largely lacking. Breeding woodcock numbers are declining in Britain and Switzerland (Estoppey 2001; Mulhauser 2001; Heward et al. 2015) and there is evidence for low adult survival rates amongst woodcock wintering in France (Tavecchia et al. 2002; Duriez et al.

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2006, see also Aradis et al. 2008). Although assessments of population size and trends should be considered better than a 'best guess' and 'poor', respectively (as reported by Nagy et al. 2015), there is still an urgent need to understand how the current levels of hunting harvest affects the woodcock population in Europe if they are to conform to the concept of sustainability as required under the African-Eurasian Waterbird Agreement (AEWA) and the European Union Bird- and Habitat Directives (Madsen et al. 2015).

A major challenge facing woodcock research is the lack of distinctive sexual dimorphism making sex determination of live birds difficult using plumage and morphological characteristics (Clausager 1973; Cramp and Simmons 1983). During autumn/winter, first year birds can be reliably distinguished from older woodcock on plumage characteristics (Clausager 1973; CNB/OMPO 2002), but reliable sexing of woodcock requires genetic confirmation (see Fierke et al. 2010; Aradis et al. 2015) or inspection of internal organs, as overlap in morphological traits such as bill length, body mass and feather size preclude accurate live sex determination (Clausager 1973; Cramp and Simmons 1983). Consequently, sex ratios have rarely been determined in bird-ringing studies making comparisons of survival, dispersal and behaviour of males and females difficult, although dissection of hunted birds has provided limited data on annual sex ratios in national hunting bags (Clausager 1974; Hoodless 1994; Faragó et al. 2013; Boidot et al. 2015, http://www.beccacciaiditalia.it/web/attivita). The very few studies of sex ratios amongst shot birds in Europe and in the North American woodcock (*Scolopax minor*) have suggested that, males migrate earlier than females towards the breeding areas in spring (Glasgow 1958; Clausager 1974; Fokin and Blokhin 2000), probably reflecting the importance of being first to arrive on the best quality breeding territories (Sheldon 1967). Clausager (1974) showed that adult males in spring migrated first, followed by juvenile males, adult females and juvenile females. Clausager (1974) was not able to document marked temporal differences in the sex and age composition of the autumn and winter bag, although more juvenile females tended to be bagged early in the hunting season.

Spring hunting is known to disproportionately affect males (c. 80–95%; see Faragó and László 2013) due to male roding display activity when females remain cryptic, while autumn and winter woodcock hunting are less likely to select for one or other sex on the basis of behaviour. However, very little is known about the overall sex and age composition of European woodcock or how this varies in time or space. Furthermore, lamentably little is known about the age and sex composition within the hunted bag, although Clausager (1974) suggested there was a female juvenile bias in the Danish autumn hunting bag. This information gap needs to be addressed to improve our understanding of how any potential hunting related age/sex bias of the European woodcock might affect its population dynamics and form the basis for more appropriate and targeted management of woodcock hunting and the population.

In the present study, we use DNA analyses to determine the sex of woodcocks shot by hunters in Denmark during two seasons, 2012/13 and 2013/14, based on voluntarily submitted wings from the Danish Wing Survey. The aim was to estimate the seasonal variation and relative contribution of each sex and age class to the total hunting bag of woodcock shot throughout the hunting season (October–January). The results are discussed in relation to the present hunting pressure on woodcock in Western Europe, as well as the implications for management and sustainable exploitation of this natural resource.

Material and methods

We obtained annual numbers of woodcock shot in Denmark from the official Danish Hunting Bag Record, which have compiled mandatory bag reports submitted by individual hunters since 1941 (Strandgaard and Asferg 1980; Asferg 2015). To estimate the temporal age-specific occurrence of woodcock in the hunting bag, we used date-specific information from wings of hunter shot woodcocks retrieved by the Danish Wings Survey (Clausager 2004; Christensen 2016), which has classified submitted wings as first autumn/winter or older birds based on standard criteria using feather wear and moulting patterns (Clausager 1973; CNB/OMPO 2002) since 1985. Woodcock hunting in Denmark has been subject to several legislative changes in recent years. Most notably, spring hunting was banned in 1973; the autumn hunting period from 1 October to 31 December was extended to 15 January in 2004, and 31 January in 2011. To avoid biases resulting from variable season length, the present study only includes background data from the bag record and the Wing Survey from the hunting seasons 2011/12–2014/15. During this period, the average annual woodcock hunting bag was 33,393 (±3141 SE), while the Wing Survey comprised an average of 1256 (range 825–1580) woodcock wings annually, constituting 3.1 to 4.3% of the total annual bag.

The sex of shot woodcock was determined by DNA analyses of muscle tissue obtained from wing samples received through the Wing Survey in two hunting seasons, 2012/13 and 2013/14. A total of 349 birds was analysed, although 22 samples failed to provide DNA material, resulting in positive sex determination of 79 adults and 80 juvenile birds from the hunting season 2012/13 and 77 adults and 91 juvenile birds from 2013/14 (Table 1). The birds were selected from the central and western regions of mainland Denmark (Jutland) and were shot by 46 hunters at 51 different locations (20 locations in 2012/13 and 34 location in 2013/14; 12 locations in both seasons). In both hunting seasons, we aimed at analysing an evenly distributed number of 10 wings of both

Table 1 The temporal (half monthly) distribution of sexed adult and juvenile woodcock wings sampled from the two hunting seasons 2012/13 and 2013/14 in Denmark. The number of samples that failed to reveal a result is shown

			Oct 1	Oct 2	Nov 1	Nov 2	Dec 1	Dec 2	Jan 1	Jan 2	Sum
Adults	2012/13	Males	2	7	6	4	9	6	8	1	43
		Females	2	6	5	7	2	5	5	4	36
	2013/14	Males	2	9	7	7	4	7	3	3	42
		Females	3	4	5	6	4	3	5	5	35
	Failed		1			1	4	3		1	10
Juveniles	2012/13	Males	1	1	5	8	3	5	5	6	34
		Females	9	9	5	2	7	5	5	4	46
	2013/14	Males	6	2	4	6	4	6	5	4	37
		Females	8	13	6	2	5	4	8	8	54
	Failed				1	3	2	3	1	2	12

adults and juvenile birds per half-monthly period between 1 October and 31 January, although there was a deficit of adult wings early and late in both seasons (see Table 1). The majority of 299 sampled birds with a hunting method reference, was retrieved by hunters during battue hunting (14%) and with pointing dogs (80%) deviating slightly from the total Wing Survey reports (30% battue hunting and 60% pointing dog hunting, N = 2427). Extreme weather conditions were not considered to have affected the occurrence of woodcock or hunting opportunities for the species in Denmark during the period of study, 2011/12–2014/15, as all years were normal (relatively mild) years, and with extended periods of sub-zero temperatures first occurring in January and February.

DNA was extracted from the tissue samples using E.Z.N.A.® DNA/RNA Isolation Kit from Omega (www.omegabiotek.com) following the manufacture's protocol. After extraction, homologous sections of the chromo-helicase-DNA-binding (CHD) genes that are located on the Z- and W chromosome, were PCR amplified using primers P2 and P8 (Griffiths et al. 1998). The amplified sections incorporate introns which differ in length, specifying the W chromosome unique to females and Z chromosome which occurs in both females and males (ZW and ZZ respectively, Griffiths et al. 1998). After amplification, the products were cut overnight using restriction enzyme *HaeIII* for proper separation of the expected bands, as in some cases the size of two introns can be similar and difficult to separate on a normal 2% agarose gel (Griffiths and Tiwari 1996). The product was subsequently visualised on a 2% agarose gel where two bands of ~300 and 400 bp were observed for females and one band of ~300 bp for males.

The proportion of males amongst hunted woodcock was analysed from observation wise entries (Bernoulli binomials) in a generalised linear mixed model (GLMMs, GLIMMIX procedure in SAS 9.4) with a logit link function and a binomial error structure. Age class (juvenile or adult), date (1 Oct–31 Jan, entered as monthly categories in the a priori analyses and half-monthly intervals in post hoc investigations of the more detailed patterns of statistically significant variation between monthly time intervals) and hunting season (2012/13 vs. 2013/14) were tested as fixed effects and hunting location as random effects (controlling for any clumping in sex distribution between locations). Because information criteria based model estimates such as AICc are not comparable between models differing in pseudo-likelihoods (as is the case for GLMM with non-identity link functions and random effects) (Littell et al. 2006; Bolker et al. 2009; S.R. Lele, pers. communication), models were established on the basis of the change in deviance of nested models (log-likelihood ratio tests), differing in presence and absence of specific terms.

Seasonal and annual trends in sex composition were first modelled for each age class (juveniles and adults). To formally test whether date-specific sex ratios differed between age groups, we modelled sex ratios as a combined function of age and date. As a post hoc examination, age-specific sex ratios were also calculated for half-monthly intervals.

Results

Bag totals and age ratios

Separating the total woodcock bag of 33,393 birds into half-monthly periods based on the temporal distribution of Wing Survey data, the seasonal distribution of the bag showed a marked peak in the first half of November, although high numbers were persistent during the main migration period from late October through November (Table 2). In total, 74% of the annual bag was taken during 15 October–30 November. Through all half-monthly periods juvenile birds outnumbered adult birds, with highest proportions in October (c. 75–77%) and lowest in January (c. 55%) (Table 2). Overall, juveniles comprised 64% of the annual woodcock bag.

Table 2 Overview of the temporal distribution of data on hunted woodcock compiled in the Danish Wing Survey and Bag Record 2011/12–2014/15, age-specific male ratios (this study 2012/13–2013/14) and the estimated sex and age-specific bag sizes

Woodcock data 2011/12–2014/15		Oct1	Oct 2	Nov 1	Nov 2	Dec 1	Dec 2	Jan 1	Jan 2	Number	Percent
Number of Woodcock wings	*N*	75	498	1180	644	278	223	147	117	3162	
Average bag size	*N*	792	5259	12,462	6801	2936	2355	1552	1236	33,393	
Adults	%	0.5	4.0	13.9	8.4	3.3	2.6	1.6	1.7		36.0
Juveniles	%	1.8	11.8	23.4	11.9	5.5	4.5	3.1	2.0		64.0
Adults in the wing sample	%	22.6	25.3	37.3	41.4	38.1	37.0	33.5	44.8		
Juveniles in the wing sample	%	77.4	74.7	62.7	58.6	61.9	63.0	66.5	55.2		
Males amongst adults	%	44.4	61.5	56.5	45.8	68.4	61.9	52.4	30.8		
Males amongst juveniles	%	21.7	10.7	42.9	74.5	37.1	50.2	47.3	43.0		
Sex and age-specific bag sizes											
Ad male	*N*	81	819	2627	1291	765	539	272	170	6564	19.6
Ad female	*N*	99	512	2021	1525	353	332	248	383	5473	16.4
Juv male	*N*	133	419	3353	2969	674	745	488	293	9074	27.2
Juv female	*N*	480	3510	4460	1016	1144	739	544	389	12,282	36.8

Sex ratios in the woodcock bag

Of 171 juveniles and 156 adults, 71 and 85 were males (cf. Table 1), constituting a sex ratio of 40 and 54%, respectively, which were not significantly different from parity (GLMM estimate without covariates, 40%, 95% c.l. 30.4–50.4%, $p = 0.08$; 54%, 95% c.l. 46–63%, $p = 0.35$). The proportion of males was significantly lower amongst juveniles than amongst adults ($\chi_1^2 = 5.78$, $p = 0.017$).

Inspection of the covariance parameter estimates for sampling locations (random effects) did not suggest any dependence of sex distributions between sampling localities (all GLMM models, b/SE[b] ratios of covariance parameter ≤1).

Seasonally, there was statistically significant variation in sex ratio between months amongst juveniles, but not amongst adults (Table 3). The significant differential sex distribution amongst age and month classes observed in the combined dataset was due to males being underrepresented amongst juveniles in October (Table 3). Sex ratios did not deviate from parity amongst any age classes in other periods (Fig. 1a). There was no significant difference in the sex ratio between the two sampling seasons (Table 3).

Analysing data by half-monthly periods showed that the proportion of juvenile males in early and late October fell significantly below 50% (Fig. 1b), although a significant difference in sex ratios between age groups only occurred in the second half of October (Fig. 1b).

Sex and age-specific bag sizes

Combining the half-monthly seasonal distributions of age/sex ratios (Fig. 1b) with the distribution of the total annual reported bag size distributed between the same half-months (Table 2) revealed that juvenile females made up 37% of the total woodcock bag in Denmark, juvenile males 27%, while adults were bagged in comparable proportions, 20% males and 16% females (Table 2). Hence, over the entire hunting

Table 3 Statistical significances of variables or combination of variables on sex ratio variation in woodcock bagged by Danish hunters if tested in isolation or as partial effects to other variables entered under 'controlling for:'. The models account for random effects of sampling site

Age class	Variable	Controlling for:	Significance
Juveniles ($n = 171$)	Month	–	**
	Month	Year	**
	Year	–	****
	Year	Month	****
	Month*Year	Month + Year	****
	M+Y+M*Y	–	**
Adults ($n = 156$)	Month	–	****
	Month	Year	****
	Year	–	****
	Year	Month	****
	Month*Year	Month + Year	****
	M+Y+M*Y	–	****
All ($n = 327$)	Age	–	*
	Age	Month	*
	Month	–	*
	Month	Age	*
	Age*Month	Age + Month	*
	M+Y+M*Y	–	***
	Year	M+Y+M*Y	****

M month (Oct., Nov., Dec., Jan.), *Y* year (2012/13, 2013/14), *A* age class (juveniles, adults)

*$p < 0.05$; **$p < 0.01$; ***$p < 0.001$; ****$p \geq 0.05$

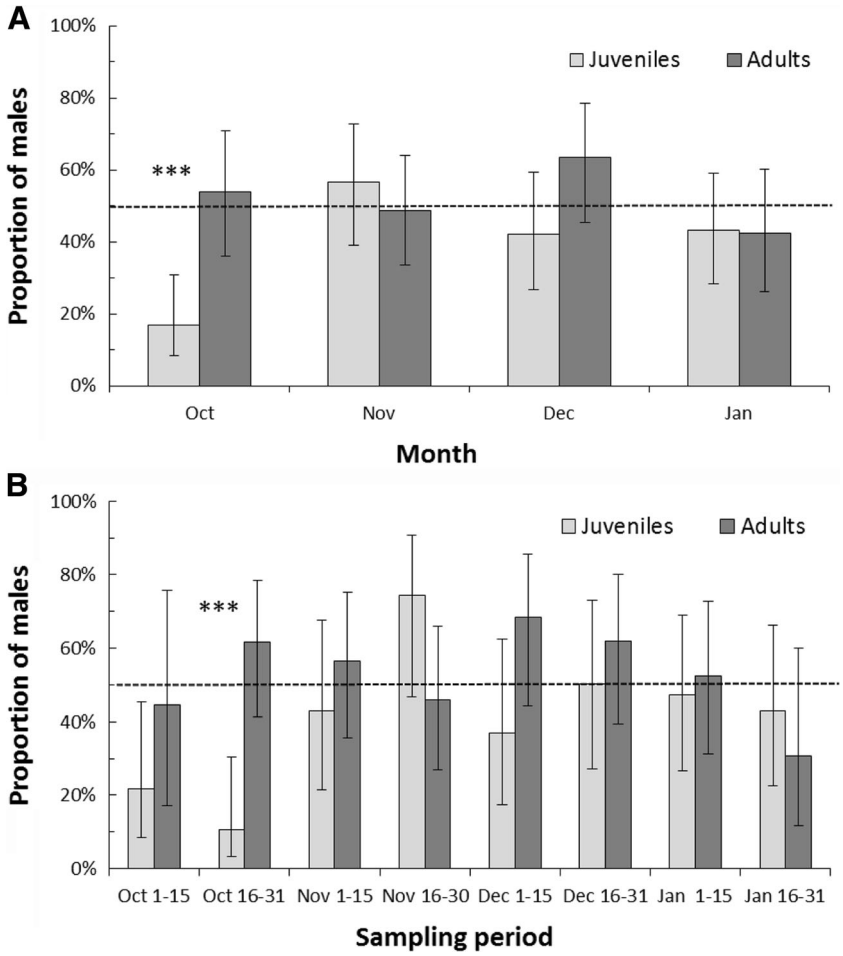

Fig. 1 Proportion of males (least square mean estimates from GLMMs with 95% c.l.) amongst juvenile and adult woodcock bagged by hunters in Denmark 2012/13 and 2013/14, divided on **a** monthly and **b** half-monthly intervals. *Horizontal dotted line* indicates an even (50:50) sex ratio. Statistical significance for differences in sex composition between age groups at individual time intervals, $*p < 0.05$, $**p < 0.01$, $***p < 0.001$

season, males comprised 55% of all adults and 43% of all juveniles and 47% of all bagged woodcocks.

The seasonal age and sex composition of the bag (Fig. 2) also revealed that adults showed single half-monthly peak periods while juvenile birds tended to be bagged over a more prolonged period covering 1 month. All age and sex classes peaked in early November, but juvenile females dominated the bag in late October and juvenile males in late November, showing a partial seasonal separation in occurrence.

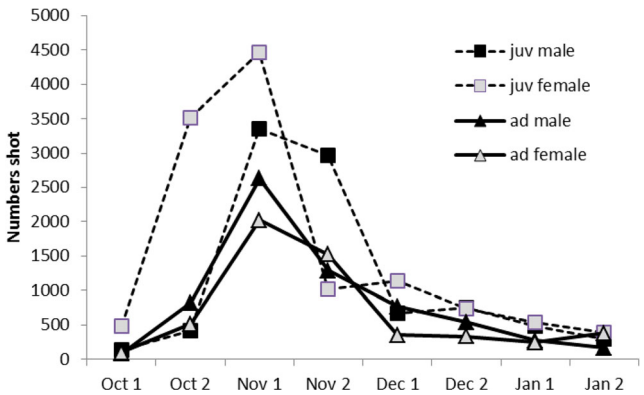

Fig. 2 Seasonal distribution of the total bag size of woodcock in Denmark 2011/12–2014/15, calculated separately for all sex and age classes at half-monthly intervals

Discussion

This investigation of the age and sex class composition of the woodcock hunting bag using DNA techniques revealed significantly higher proportions of juvenile females in the Danish woodcock bag, while the sex ratio of the adults did not differ significantly from parity. The difference resulted from high proportions of juvenile females shot in late October and early November, when woodcock are subject to a high level of hunting pressure. In Denmark, juvenile females most probably contribute disproportionately to the hunting bag, as it seems unlikely that the relative age and sex composition of the Danish hunting bag reflects that of the flyway population as a whole. Although the adult sex ratio does not deviate from parity in the Danish hunting bag, the high proportion of juvenile females gives some cause for concern given the uncertainties about the current population size and status of the woodcock in Europe.

Despite the availability of annual woodcock bag records from many countries, few report the sex ratio in the bag. In France, males constituted a relatively stable average of 38.7% (range 38.0–40.0) during 2004–2014, but no data were provided on relative age composition (Boidot et al. 2015 and annual reports in WSSG-Newsletter 2005–2014) suggesting bias for females. Portugal reported 46.7% males overall in 2009/10–2014/15, decreasing from an average of 48.5% (range 48.3–48.7) during 2009/10–2011/12 to 44.8% (range 44.0–45.9) during 2012/13–2014/15, although sample sizes were small (Rodrigues et al. 2015 and annual reports in WSSG-Newsletter 2010–2014). Based on data from 2009 to 2014, the proportion of males amongst juveniles was 49.1% (range 37.4–54.5%, $N = 422$) compared to 44.5% amongst adults (range 38.5–53.8%, $N = 305$; Portuguese National Association of Woodcock Hunters and University of Porto, annual reports accessed from http://www.galinhola.pt/?pagina=ancg), but neither juvenile nor adult sex ratio deviated significantly from parity (χ_{juv}^2, $p = 0.14$; χ_{ad}^2, $p = 0.59$). In Britain, Hoodless (1994) reported a female bias amongst adults and an equal sex ratio amongst juveniles on a very small number of birds. We are not aware of other data presenting age-specific sex composition of woodcock bags from other European countries. In North America, the overall sex ratio in the bag of American woodcock has been reported as 45.1% males, which was mainly due to a difference amongst adult birds (38.7% males) compared to juveniles (50.8% males) (Sheldon 1967). Several other American studies confirm the overall deficit of males in the woodcock hunting bag (41.2–46.2% males), but none separated sex ratios into age classes (Mendall and Aldous 1943; Greeley 1953; Blankenship 1957; Glasgow 1958). Most recently (2013–2015), the sex ratio of adults in North America averaged 42.7% males (range 35.6–50.0%, Cooper and Rau 2014 and 2015, Seamans and Rau 2016), suggesting a stable long term male deficit in the adult segment of the shot sample. These reports give no data on juvenile sex ratios.

The uneven sex ratio in the woodcock observed in the Danish bag could be (1) the result of underlying differential age and sex ratios in the population as a whole or (2) the result of differential susceptibility of one or more age and sex classes in time and space to hunting mortality. Unfortunately, there is little hard evidence to preferentially support one or other of these hypotheses at present, although we attempt to review this below, acknowledging that our data are restricted to two seasons.

Hypothesis 1 suggests that the female bias in the woodcock bag in Europe and North America is caused by an underlying overall greater proportion of females in these populations. If we assume that there is no differential susceptibility of either sex to hunting, the skewed ratio in the hunting bag could result from higher male mortality associated with their earlier arrival to the breeding grounds, where males risk being caught in unfavourable weather conditions and from a potentially higher predation rate (including spring hunting), due to the conspicuous roding flights (Sheldon 1967, Kalchreuter 1975). Significant deviation from parity in the sex ratio at hatching is extremely unusual in birds (Clutton-Brock 1986), so we predict a 50:50 sex ratio in first year birds. As greater male mortality only affects the sex ratio after the first year, (i) no differences in the sex ratio is expected amongst first year birds, at any time during the hunting season and along the flyway and (ii) a higher proportion of females is expected in the adult bag. Consequently, from this differential vulnerability of females to hunting mortality, it would be expected that (iii) the skewness towards adult females in the hunting bags would decrease with increasing distance down the autumn flyway as adult females are removed in greater numbers during the course of the season. While there is support from North America and Portugal for (i), this is not supported by data from Denmark in the present study. Similarly, while data from North America and Portugal supports (ii), the Danish data suggest parity in the bag of adult woodcock. The proportion of females in the adult bag in Portugal is actually far higher (65.5%) than those in Denmark (45.5%), which fails to support prediction (iii). In addition, it is well recognised that hunters do not harvest birds of different age and sex classes at random, often shooting a higher frequency of juvenile birds than in the population as a whole (e.g. Madsen 2010, Fox et al. 2016). For these reasons, we can find little support for hypothesis 1.

Hypothesis 2 suggests that it is differential exposure of juvenile female woodcocks to hunting mortality that explain the observed patterns. It is fair to assume that females, and especially juveniles, unencumbered by the needs of territorial defence, depart the breeding areas in autumn earlier and arrive to breeding areas in spring later than males, exposing themselves to prolonged periods of hunting susceptibility during the non-breeding season compared to males (Fadat 1989). In contrast, we would predict that males of all ages generally would tend to remain as high up along the flyway corridor in autumn and winter as their fitness would permit, to be closest to breeding territories the following spring. The tendency for the adult male ratio to be higher in the Danish hunting bag compared to those in the French and Portuguese bags supports this assertion. The autumn flight contains a very high preponderance of juveniles, indicating a large wave of juveniles arriving in October/November. This wave comprises an initial group of females (October/early November) which are followed by juvenile males (in November) as reflected in the hunting bag. These patterns are confirmed in the present analysis and by earlier Danish studies during 1969–1971 (Clausager 1974) and by a generally earlier autumn arrival of females to France further down the flyway (Fadat 1989). The French woodcock hunting season starts early, with 23% of the hunting bag taken in September/October (estimated

from the annual 'Hunting index of abundance'; Boidot et al. 2015) when juvenile females are especially likely to be arriving. This could explain the observed major contribution of females to the overall hunting bag. However, bias in sex ratios in the hunting bag could also arise from differential susceptibility to hunting. In Denmark, significantly more juvenile woodcock were shot by hunters using pointer dogs (61%) compared to other methods of hunting (52%, Christensen and Asferg 2013). Although the proportion of woodcock hunted by pointers fell from 70% in October/early November to 50–60% for the rest of the hunting season (i.e. coinciding with the change in sex ratio amongst juveniles), there was no corresponding change in the sex ratio amongst shot adults as would have been expected if males and females have a different vulnerability to hunting for behavioural or physiological reasons.

It is highly likely that there are interactions between the effects of hunting and the underlying age and sex composition of the Eurasian woodcock population throughout autumn and winter. As juvenile woodcock comprise 60–70% of the kill reported in national hunting bags their removal most probably affects the underlying age and sex composition of the population. Likewise, an uneven removal of juvenile females, as seen in Denmark, is likely to contribute to the availability of age and sex classes later in the season further down the flyway, indicating some interaction between hunting and population structure and migration.

As woodcock are considered successively polygamous (Cramp and Simmons 1983, Ziel et al. 2010), the female population size is the reproductively limiting factor, and excessive harvest of females will have direct consequences for population development. The present study provides some evidence that the early arrival of juvenile females may result in their overrepresentation in the hunting bag. This gives some cause for concern, since the size of their annual hunting bag compared to that of juvenile males suggests reduced recruitment due to hunting mortality, which is considered additive to natural mortality (Duriez et al. 2005).

The apparently stable population of 20–26 million birds (Nagy et al. 2015) and a least concern classification on the IUCN red list (Birdlife International 2014) implies that current levels of hunting in Europe may be considered sustainable, with no need for adjustment. However, given the recent declines in several western European countries, if future studies prove that the woodcock no longer qualifies as having favourable conservation status, the development of a European management plan for the population is required to justify future hunting in any form (cf. Lutz and Jensen 2005). This would ideally sit within an adaptive harvest management (AHM) framework, where the effectiveness of different harvest schemes is assessed in relation to agreed management targets, as has been done for the Svalbard Pink-footed Goose (Madsen and Williams 2012). Given the results presented here, one potential manipulative management tool aimed at enhancing survival of first year female woodcock would be to postpone the opening of the woodcock hunting season to 1 November in Denmark specifically, but potentially throughout the European wintering area. Whereas sex and age differentiated hunting management is widely applied to large quarry species such as ungulates (Fryxell et al. 2014), such practices are generally uncommon amongst bird species, although they have been successfully applied to target species showing conspicuous plumage differences (e.g. male and female Common Eider *Somateria mollissima* Christensen and Hounisen 2014). For monomorphic species such as the woodcock, field age and sex identification is impossible even under optimal conditions. Hence, such geographical or temporal mediated actions may be the only possible management proscriptions on a flyway scale that can deliver demographic benefits and help restore the population to favourable conservation status.

Ringing data and stable isotope analyses of feathers show that woodcock wintering in Spain and France pass through Denmark to breeding areas in central eastern Europe, the Baltic and western European Russia (Bønløkke et al. 2006, Ferrand and Gossmann 2009, Guzmán et al. 2011, Hobson et al. 2013a, b; Hoodless et al. 2013). More recent data, based on satellite telemetry, suggest that Spanish wintering woodcock breed further east in Russia than birds wintering in France, confirming leap-frog migration (Arizaga et al. 2015) as proposed by Ferrand and Gossmann (2001). To what extent males and females, adults and juveniles differ in their adoption of such a strategy is unknown. Similarly, it is unclear to what extent migration patterns differ in years of more extreme weather conditions, compared to those observed during normal (mild) seasons as recorded in the present study period. Far more sex- and age-specific data on the temporal and spatial patterns of migration of woodcock, of the kind presently generated in France (Argos programme, Gossmann et al. 2015), is required to document such potential differences, to improve our understanding of woodcock migration strategies, and to assess how hunting on a European scale affects population development of this highly valued game bird.

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