



Associations between duck harvest, hunting wing ratios and measures of reproductive output in Northern Europe

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Abstract

Ducks are important game species, hunted in several countries throughout their annual cycle. We investigated whether the size of the annual duck harvest in Finland and Denmark reflected annual reproductive output in three common quarry duck species. Finland represents an important breeding area and Denmark important staging/wintering grounds for common teal (*Anas crecca*), Eurasian wigeon (*Mareca penelope*) and common goldeneye (*Bucephala clangula*). We assessed whether (i) annual duck harvest in these two countries correlated with variation in Finnish reproductive output or adult population size during 1990–2016 and (ii) variation in reproductive output of Finnish ducks was reflected in the juvenile ratios of birds harvested in Finland (2005–2007, 2014–2016) or Denmark (1990–2016). We hypothesised that variation in Finnish reproductive output would positively affect the size and juvenile ratio of the harvest, and that this effect would be stronger closer to the breeding grounds. Our data showed that the annual harvest of goldeneye in Finland was positively correlated with reproductive output, a desirable basis for applying sustainable management to this species. Teal and wigeon have much longer, more complex flyways, and their harvest did not mirror the annual production of young, although the wigeon harvest in Denmark increased with increasing juvenile ratio there. For these populations, we need to better define population units if we are to be able to assess harvest sustainability. We urgently need to monitor duck breeding success and harvest at larger spatial scales to support a comprehensive analysis of how well the harvest reflects reproductive output.

Keywords Sustainable harvest · *Anas crecca* · *Mareca penelope* · *Bucephala clangula* · Flyway · Wing samples

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Introduction

The size of duck populations vary naturally in response to environmental variation (Pöysä et al. 2016) and reproductive output (constrained by nest success and duckling survival), in addition to female survival, are prime vital rates that affect population growth rate (Hoekman et al. 2002; Coluccy et al. 2008). Ducks represent a group of popular quarry species, for which the harvest is a major contributory source of mortality (Cooch et al. 2014). Many natural populations that traditionally have been hunted for many generations have the capacity to generate a temporary major surplus in the balance of births over deaths, which represents a form of reproductive surplus that can be harvested, to a greater or lesser degree, without jeopardy to the long-term favourable status of the population. Because the size and nature of such a reproductive surplus varies in time and space due to environmental variation, harvesting can be

made to be sustainable if the annual yield is determined wisely based on the extent of the reproductive surplus (Hilborn et al. 1995; Sutherland 2001).

It has long been recognised in Europe that we do not know the degree to which our duck harvest is sustainable (Tamisier 1985; Guillemain et al. 2016), even though several international and national agreements and laws require sustainable and wise use of waterbirds (Elmberg et al. 2006; Madsen et al. 2015a, b). This has been the case because most common huntable duck species have shown increases in wintering population trends from the late 1940s until the late 1990s. As a result, there have been no strong arguments for regulating the European duck harvest in accordance with annual production (Hirschfeld and Heyd 2005; Kear 2005; Mooij 2005).

Currently, after extended periods of population growth, several numerous European duck species show a levelling off or decline in wintering numbers (e.g. Eurasian wigeon *Mareca penelope*, northern pintail *Anas acuta*, common pochard *Aythya ferina*; Nagy et al. 2015), creating management challenges for the future. The impact of hunting mortality on population trends remains unknown, as long as we have no systematically gathered national duck harvest data from throughout Europe. Some European countries have produced annual hunting bag estimates in recent years, but methods, reliability and frequency vary between species and countries (Guillemain et al. 2016). National long-term annual species harvest statistics and wing samples from hunters (to assess age ratios as an index of reproductive success) are collected systematically only in Denmark. These data have shown declining ratios of first year birds among many species, for example for Eurasian wigeon (hereafter wigeon) and common goldeneye (*Bucephala clangula*; hereafter goldeneye) (Christensen and Fox 2014; Fox and Christensen 2018), suggesting a decrease in reproductive output since 1982. In Finland, long-term breeding population monitoring since 1986 shows declining trends in the abundance of ducks (Pöysä et al. 2013; Lehtikoinen et al. 2016). Thus, there are indications that both breeding numbers and reproductive output are declining, which raises the question of what constitutes truly sustainable harvest levels.

Not all individuals in a population are equal concerning their effects on population dynamics. The harvest of juveniles is less detrimental for the population than the harvest of adults (Cooch et al. 2014). Previous research suggests that duck hunting tends to select for first year birds that are over-represented in the harvest relative to the population as a whole (e.g. Fox et al. 2015a, 2016). For wigeon at least, there is some evidence to suggest that the number of ducks shot per hunter/day locally is highly correlated with breeding success at the population level (Larsen 1997). These factors are important in the context of any potential management of the kill, since most duck species show much lower first year annual survival than adult birds (e.g. Blums et al. 1996; Gunnarsson et al. 2008;

Lawson et al. 2017). These young birds therefore likely contribute proportionally more to the potentially “harvestable surplus” than older individuals, so removal of individuals from this age class that would likely die later would have less impact on the long-term stability of the population than if adults were shot. Between year variation in the relative abundance of first year birds may therefore affect the size of hunting bags of specific species as well as affect the relative robustness of the population to accommodate the effects of a given harvest, without affecting the longer-term stability of population size.

We ask the question: how well do recent annual duck harvests follow annual reproductive output (measured by variation in the Finnish national duckling production index, i.e. the number of ducklings counted annually on national brood surveys) based on currently available data? To answer this, we tested whether (i) the size of the reported annual duck harvest in Finland and Denmark varied with reproductive output and (ii) the reproductive output of Finnish ducks correlated with the age ratios in Finnish and Danish harvest wing samples and whether the size of the annual harvest bag reflects the annual production of young. Finland represents important breeding and Denmark important staging/wintering areas for the common quarry species common teal (*Anas crecca*; hereafter teal), wigeon and goldeneye (BirdLife International 2004; Saurola et al. 2013), which might be suitable model species for developing duck management strategies in Europe (Holopainen et al. 2018).

We hypothesise that variation in reproductive output is reflected in the harvest, so we predict that juvenile wing ratio and harvest will be larger when reproductive output is high. We also expect that the juvenile wing ratio in the shot sample will better reflect that on the breeding grounds with decreasing distance to the nesting areas, because the nearer to ultimate wintering areas, the greater the mixing of ducks originating from different breeding provenances (Harradine and Clausager 1990). Furthermore, based on the geographical ranges of the species-specific flyways (Scott and Rose 1996), we expect that goldeneye, with its more restricted flyway, will show the clearest patterns, while teal with the longest and most complex flyway will be the most diffuse, with wigeon somewhere between the two.

Material and methods

Data

We used Finnish brood monitoring data for teal, wigeon and goldeneye from 1990 to 2016 to measure annual reproductive output in the boreal region of Finland. Brood surveys were carried out using the waterfowl point count method, a standard survey method used in waterfowl monitoring in Finland

(Koskimies and Pöysä 1991; Pöysä et al. 1993; see also Koskimies and Pöysä 1989). Voluntary hunters carried out brood surveys (started in 1989) at c. 200 sites from which the production of young per site could be estimated (i.e. not taking into account site-specific annual numbers of pairs, simply measuring the ultimate “output”). Under the Finnish brood monitoring system, one census is carried out each season, typically in late June or early July. The mortality of young is heavy especially during the first weeks from hatching (e.g. Paasivaara and Pöysä 2007 and references therein), and therefore, the timing of the brood census is critical. Large deviations from the average census date within an area would bias the production estimate. We controlled for this by constructing a model (using Gaussian errors) to generate expected geographical trends in census timing in each year; these trends were assumed as a function based on the interactions of year factor with longitude and latitude coordinates (in metres). The residuals of this model describe deviations from the expected trends. Then, we built a mixed model (based on Poisson errors) explaining fledgling numbers per site and year, i.e. our measure of “reproductive output”. Here, we incorporated a year factor and estimated date residuals as fixed variables and site ID as a random factor. In this model, annual coefficients (b_{year}) give production index vector: 0, $b_{2\text{nd}}$, $b_{3\text{rd}}$, ..., $b_{\text{last year}}$. These indices are logarithmic and hence the multiplicative form is $\exp(\text{index})$. The Poisson model was run separately for each species. We used the index of reproductive output as a proxy for the potential reproductive surplus, which we consider describes that part of production that remains after balancing the mortality that has taken place among the parental breeding population. To be able to determine whether harvest varies with annual reproductive output or adult population size, we used national duck pair surveys (started in 1986) as a reference for breeding population size. Pair surveys were undertaken using the same methods as brood surveys at c. 400 sites annually (see Pöysä et al. 2013; Lehikoinen et al. 2016) and provided an annual measure of adult population size (i.e. pair index).

In Finland, the timing and duration of the hunting season has remained reasonably unchanged throughout the study period. The duck hunting season starts on 20 August and lasted until the end of November (before 1993) and until the end of the year (since 1993). Daily bag limits do not exist (Väänänen and Malinen 2009). However, harvest levels dropped after the legislative ban on use of lead shot imposed in 1996 (Pöysä et al. 2013). We here used the Finnish harvest data from 1990 to 2016 (but note that the harvest survey period was changed in 1996, resulting in no harvest reporting in 1995). Harvest data are gathered from questionnaire surveys, and species identification in the harvest is based on the hunters’ own reporting. During 1990–2016, the average harvest was c. 137,000 teal and c. 84,500 goldeneye. The teal harvest includes small numbers of garganey (*Anas querquedula*); based

on wing samples from 2005 to 2007, it was estimated that only 500–1500 garganey are harvested per year (i.e. $\leq 1\%$ of the teal bag, Alhainen et al. 2010). There has only been a requirement to report numbers of shot wigeon since 2003; the average annual harvest during 2003–2016 was 41,500 birds. The annual harvest of the three species have been gradually decreasing since the 1990s (RKTL 2014, Appendix 1).

Finnish national wing sample surveys were carried out during two periods, 2005–2007 and 2014–2016. Hunters voluntarily submitted wings from shot birds, from which the species, age and sex were determined by professionals using standard protocols (see Alhainen et al. 2010; Pöysä and Väänänen 2018). In an attempt to confine this sample to Finnish breeding birds, we counted only those wings that were gathered in August and September, i.e. before the arrival of migrant birds of other breeding provenances east of Finland (note that a similar temporal filter was not possible to implement with regard to the harvest, because the bag questionnaire does not provide the date of shooting). The total number of wings submitted varied: in teal between 273 and 413 (average 334), wigeon 112–195 (135) and goldeneye 33–108 (65).

In Denmark, an average of c. 68,500 teal were shot annually during 1990–2016, compared to 46,000 wigeon and 13,000 goldeneye. During the study period, the hunting season duration has been subject to slight modification, but this is not believed to sufficiently affect the harvest bag size (see Sunde and Asferg 2014). Before 2011, the ratio of common duck species in the annual Danish harvest (reported as dabbling and diving ducks) was apportioned according to the species ratios in the wing samples, submitted voluntarily by hunters and analysed by professionals. Since 2011, hunters have reported species directly. However, to avoid compounding the effects of this change in method, here, we have analysed the species ratios with the same method throughout. We then corrected the numbers according to the countywide species-specific ratio of the bag (i.e. ratios counted at the country level might differ due to uneven geographical representation of species specific harvest rates).

We used Finnish duck ringing data and the resulting ring recovery dates of these originating from Denmark (Saurola et al. 2013) to determine the phenology of arrival of migrating ducks. Based on these results, we restricted teal and wigeon harvest data and age ratios from wings shot at the beginning of the hunting season (September and October only) and restricted goldeneye harvest data and wings shot in the late hunting season (December and January only). After applying these temporal filters, annual average numbers of submitted wings varied: 802–4929 (average 1996) for teal, 91–2225 (932) for wigeon and 121–366 (227) and for goldeneye. Accordingly, based on the wing ratios, we estimated that the harvest for the teal and wigeon (early season) were on average 55,800 and 30,600 respectively and for the goldeneye (late season) 7100 birds.

We recognise that during the prolonged duration of this study, there have been shifts in the wintering range of the goldeneye in response to climate change; Lehtikoinen et al. (2013) found that the wintering numbers of the species in the northern Baltic Sea have been increasing, although this does not seem to be the case for the two dabbling duck species (Dalby et al. 2013). Such distributional shifts may have affected the relative vulnerability of goldeneye to hunting with the time series presented, which in turn might have affected the harvest statistics, although we are not able to separate between these effects here.

Statistical analyses

We used linear regression to explain the relationships between reproductive output, juvenile ratio and harvest in teal, wigeon and goldeneye (Fig. 1). When attempting to explain the effect of annual reproductive output on the total harvest, we took into account the effect of adult birds by using the pair index as an explanatory variable. Using this approach, we can analyse whether the harvest varies as a result of reproductive output or adult population size. The former indicates the ideal situation, where harvest levels reflect annual production in the preceding summer, whereas the latter suggests that population density/size is the more dominant factor, where harvest varies more with the number of adult birds. To control for the temporal trends in most of the independent and depended variables, we took standardised residuals from all the variables to be able to separate the effects of common trends from the overall variance (i.e. the original values for each variable were replaced with standardised residuals from the regression models between the variables and year). To control for any effects of the lead ban implemented in 1996 on the size of the Finnish harvest, we introduced a temporal factor that divided the study period into that before the ban (1990–1995) and afterwards (1996–2015). We used R 3.4.0 (R Development Core Team 2017) to the testing and undertook data exploration following the protocol recommended by Zuur et al. (2010).

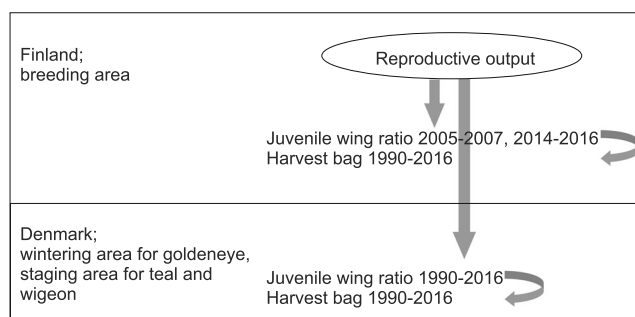


Fig. 1 The schematic framework for the study. The objective of the study is to attempt to explain annual variation in the Finnish and Danish harvest and juvenile ratios by the summer measures of reproductive output in Finland, as well as explain variation in total harvest by the juvenile ratio

Results

Variation in reproductive output of goldeneye explained variation in the size of the annual Finnish harvest (Table 1). Variation in Finnish teal pair index was a good explanatory variable for variation in the Danish harvest, while in goldeneye, there is some tendency to show a negative relationship between pair index and harvest (Table 2). We also note that in Finland, the annual harvest of all three species has been decreasing, while in Denmark only the bag of goldeneye shows a long-term significant decline during 1990–2016 (Appendices 1, 2).

The annual Finnish harvest did not vary with the juvenile ratio in the wing samples for any of the species (Table 3). Variation in annual Danish harvest of wigeon was positively related to the variation in the juvenile ratio (Table 4).

Variation in reproductive output of ducks did not explain the variation in juvenile ratio of Finnish wing samples, although there are some signs of that for goldeneye (Table 5). However, the effectiveness of this test is weakened by the small number of wing survey years ($N=6$) and the relatively few wings available for analysis. A significant negative trend for the teal was found using the wing survey data from Denmark (Table 6).

Discussion

We expected that harvest of all three species would, to some degree, reflect the variation in annual reproductive output, and

Table 1 Results from the species-specific linear regression models showing the effect of annual reproductive output and pair index on the species harvest in Finland 1990–2016 (excluding 1995) for teal and goldeneye, and 2003 onwards for wigeon. To control for long-term trends, we used the standardised residuals of all the continuous variables in the tests. The lead ammunition ban was incorporated as a piecewise two-level factor, representing the pre-ban years 1990–1994 (Intercept) and following the lead ban during 1996–2016. Significant P values (<0.05) are italicised

	Model	Estimate	SE	t value	P
Teal	(Intercept)	0.541	0.419	1.290	0.210
	Reproductive output	0.282	0.192	1.466	0.157
	Pair index	−0.241	0.189	−1.273	0.216
Wigeon	(Intercept)	−0.677	0.468	−1.446	0.162
	Reproductive output	−0.021	0.280	−0.075	0.942
	Pair index	0.117	0.250	0.466	0.651
Goldeneye	(Intercept)	−0.091	0.280	−0.326	0.750
	Reproductive output	0.674	0.403	1.673	0.109
	Pair index	0.372	0.179	2.085	<i>0.049</i>
	Lead ban	−0.004	0.213	−0.020	0.984
	Lead ban	−0.836	0.447	−1.871	0.075

Table 2 Results from the species-specific linear regression models showing the effect of annual reproductive output and pair index in Finland on the species harvest (early season for the teal and wigeon, late season for the goldeneye) in Denmark 1990–2016. To control for long-term trends, we used the standardised residuals of all the continuous variables in the tests. Significant *P* values (<0.05) are italicised

	Model	Estimate	SE	<i>t</i> value	<i>P</i>
Teal	Intercept	0.000	0.169	0.000	1.000
	Reproductive output	0.093	0.180	0.517	0.610
	Pair index	0.482	0.180	2.683	<i>0.013</i>
Wigeon	Intercept	0.000	0.190	0.000	1.000
	Reproductive output	-0.051	0.204	-0.251	0.804
	Pair index	-0.235	0.204	-1.152	0.261
Goldeneye	Intercept	0.000	0.178	0.000	1.000
	Reproductive output	-0.309	0.187	-1.651	0.112
	Pair index	-0.355	0.187	-1.896	0.070

that we would find better associations between reproductive output and harvest statistics closer to the breeding sites. The proportions of young birds shot in Finland should reflect better the Finnish annual breeding success, while by knowing when Finnish birds arrive in Denmark, we should find some correlations there as well. Based on our results, this seems not to be the case, which might suggest that the size of the harvest does not necessarily reflect reproductive output in these populations.

Variation in the harvest of goldeneye in Finland does seem to follow variation in Finnish reproductive output. Our results thus support the argument that goldeneye harvest in Finland is likely to be sustainable to some degree at current levels of production and exploitation, in the sense that bag size does not vary with numbers of pairs, but rather on variation in reproductive output. Whether the harvest rate is sustainable or not cannot be considered here, but with goldeneyes, the harvest appears to target young birds, as it ideally should. Furthermore, the goldeneye harvest in Finland might be growing with increasing juvenile ratio, but to verify this pattern, we

Table 3 Results from the species-specific linear regression models showing the effect of annual early season juvenile wing ratio on the species harvest in Finland 2005–2007 and 2014–2016. To control for long-term trends, we used the standardised residuals of the continuous variables in the tests

	Model	Estimate	SE	<i>t</i> value	<i>P</i>
Teal	Intercept	0.000	0.401	0.000	1.000
	Juvenile ratio	-0.188	0.491	-0.382	0.722
Wigeon	Intercept	0.000	0.406	0.000	1.000
	Juvenile ratio	-0.109	0.497	-0.219	0.837
Goldeneye	Intercept	0.000	0.400	0.000	1.000
	Juvenile ratio	-0.197	0.490	-0.401	0.709

Table 4 Results from the species-specific linear regression models showing the effect of annual juvenile wing ratio on the species harvest in Denmark 1990–2016 (early season for the teal and wigeon, late season for the goldeneye). To control for long-term trends, we used the standardised residuals of the continuous variables in the tests. Significant *P* values (<0.05) are italicised

	Model	Estimate	SE	<i>t</i> value	<i>P</i>
Teal	Intercept	0.000	0.186	0.000	1.000
	Juvenile ratio	-0.263	0.193	-1.364	0.185
Wigeon	Intercept	0.000	0.174	0.000	1.000
	Juvenile ratio	0.426	0.181	2.356	<i>0.027</i>
Goldeneye	Intercept	0.000	0.181	0.000	1.000
	Juvenile ratio	-0.339	0.188	-1.800	0.084

would need more wing sample years. However, this is not the case in Denmark, suggesting other factors may be involved, which might mask any such relationship there. For example, goldeneyes arriving to Denmark early and late within the hunting season likely originate from different breeding areas which may show differing demographic patterns. While most of the wings are harvested during the late season, it might be that wings collected at the early season represent local and more southern populations with differing breeding success, birds which also remain and will also be represented in the later harvest as well.

Against the predictions from our hypothesis, juvenile ratios among shot wigeon in Finland and Denmark were unrelated to measures of reproductive output in Finland. Of the three species considered here, only the harvest of wigeon seemed to increase with increasing juvenile ratio in Denmark. This implies a degree of sustainability in the current wigeon harvest within Denmark, although there seems to be no similar connection in Finland regarding this important quarry species. We note, however, that the low number of wing survey years in Finland makes our test unreliable. Our results from Denmark seem to support those results of Mitchell et al. (2008), who showed that favourable breeding conditions increased the proportion of young in the British and Danish harvest bags. On

Table 5 Results from the species-specific linear regression models showing the effect of annual reproductive output on the species early season juvenile wing ratio in Finland 2005–2007 and 2014–2016. To control for long-term trends, we used the standardised residuals of the temporal juvenile ratio and reproductive output in the tests

	Model	Estimate	SE	<i>t</i> value	<i>P</i>
Teal	Intercept	0.000	0.407	0.000	1.000
	Reproductive output	-0.081	0.498	-0.163	0.879
Wigeon	Intercept	0.000	0.387	0.000	1.000
	Reproductive output	-0.321	0.474	-0.677	0.535
Goldeneye	Intercept	0.000	0.269	0.000	1.000
	Reproductive output	0.752	0.330	2.278	0.085

Table 6 Results from the species-specific linear regression models showing the effect of annual reproductive output in Finland on the species juvenile wing ratio (early season for teal and wigeon, late season for goldeneye) in Denmark 1990–2016. To control for long-term trends, we used the standardised residuals of the juvenile ratio and reproductive output in the tests. Significant *P* values (<0.05) are italicised

	Model	Estimate	SE	<i>t</i> value	<i>p</i>
Teal	Intercept	0.000	0.173	0.000	1.000
	Reproductive output	-0.438	0.180	-2.439	<i>0.022</i>
Wigeon	Intercept	0.000	0.191	0.000	1.000
	Reproductive output	-0.109	0.199	-0.547	0.589
Goldeneye	Intercept	0.000	0.183	0.000	1.000
	Reproductive output	0.305	0.190	1.604	0.121

the other hand, Christensen and Fox (2014) and Pöysä and Väänänen (2018) found no correlation between favourable breeding conditions and the proportion of young among wing samples from Denmark and Finland, respectively.

It seems likely that our measures of Finnish wigeon reproductive output do not reflect those from larger areas of the breeding range. It has previously been demonstrated that trends in abundance among wintering aggregations may mask local changes in breeding distribution and abundance. For example, long-term declines in Finnish-breeding wigeon (Lehikoinen et al. 2016; Pöysä et al. 2017) contrast overall increases in wintering numbers in this flyway population until very recent years (Nagy et al. 2015; but see Fox et al. 2016), probably because Finnish wigeon are diluted by far greater numbers of largely Russian-breeding wigeon on the winter quarters. The result underlines the need for more systematic surveys on the breeding areas to be able to monitor the degree of annual variation in reproduction across different segments of the breeding areas. With our current levels of knowledge, it is difficult to argue whether wigeon harvest is sustainable or not, but it seems likely that there is a high level of mixing of different populations that dilute any possible patterns we could identify from our samples from restricted geographical areas.

The teal harvest in Finland did not vary with reproductive output. In contrast, in Denmark, the teal harvest increased with Finnish breeding pair abundance, so it is possible that breeding abundance correlates across large geographical areas, which could potentially lead to the good explanatory power of Finnish pair abundance to the Danish harvest, if harvest rates are following population dynamics. However, the juvenile wing ratio in the Danish harvest was negatively associated with Finnish reproductive output, possibly indicating differing demographic patterns. Other studies have suggested that population dynamics of the teal might differ between different parts of Europe. Devineau et al. (2010) concluded that at the current harvest rates, the European teal population required a source-sink-mechanism to maintain current levels of

population, because according to their model, based on high harvest rates in Western Europe, the teal population should crash rather than showing the stable/increasing trends at the population level as is the case now. At the flyway level, the annual harvest rate of the teal appears to be much higher in Europe than in North America, indeed, the survival of the species is also slightly lower in Europe (Devineau et al. 2010; Guillemain et al. 2010). To fill in the gaps in our knowledge, we would need more information about teal population dynamics and migration phenology.

Due to the rather similar plumage of different sex and age classes in autumn, it might be expected that duck hunting would be unselective, in the sense that the harvest should theoretically reflect the age and sex composition of the population as a whole. For wigeon, a species possible to identify to age and sex in the field, the young males are overrepresented in the wing samples, especially in the beginning of the hunting season (Fox et al. 2015a; Fox et al. 2016). Mitchell et al. (2008) found higher rates of young in wing samples from wigeon compared to field observations, suggesting that hunting affects age, but not sex ratios of wigeon in Britain and Denmark. Clausen et al. (2013) used only January data from Denmark and found no difference in age and sex ratios between wing samples and field observations suggesting temporal variation in age bias among hunted birds (as shown by Fox et al. 2016). Despite the problem, Fox et al. (2016) suggested that the ratio of young wigeon in the wing surveys gives an important reflection of the annual breeding success, but the bias must be considered in related studies (see also Pöysä and Väänänen 2018). Furthermore, recent analysis of the Danish wing samples shows that at the long-term sex ratio among harvested wigeon and teal wings has become more male biased (Fox and Christensen 2018). Both first-year and adult female rates have declined in these two species, while in goldeneye, the proportion of first-year female shows recent decline. Assuming that the sex ratios amongst shot wings are representative of those in the overall populations, these trends give considerable cause for concern and require closer investigation to determine the causes. As shown here, to be able to utilise the information from wing samples effectively, we need a better understanding of the population that is being shot, which contributes the harvested sample.

Despite declining Finnish duck breeding populations, the size of the current hunting harvest may not constitute the core cause of this trend, because both harvested and protected species are showing similar declines, with habitat quality seemingly the common denominator connecting the declining species (Pöysä et al. 2013). Lehikoinen et al. (2016) showed for several species breeding in a wide range of habitats that populations exhibited significantly negative long-term trends in eutrophic lakes but not in oligotrophic lakes, indicating problems in the breeding areas connected to particular trophic conditions in aquatic systems. Even though the current size of the

harvest may not be the main cause of population declines, over-zealous harvesting clearly will not contribute to restoring populations to former levels of abundance; there is therefore a clear need to adjust harvest levels according to reproduction success and ultimately overall population size to achieve sustainability. While there can be no certainty about the causalities, both duck numbers in general and the overall size of the harvest of all three species in Finland, as well as the goldeneye hunting bag in Denmark, have been decreasing. Even though annual harvest size may not vary in direct relation to annual reproductive output, similar long-term trends in harvest bag and population size may be in accordance with the long-term goals of sustainable management.

To be able to justify whether or not a given level of annual harvest from a population is sustainable, we need to not only monitor annual population size and reproductive output, but also harvest levels (Sutherland 2001; Madsen et al. 2015b). Historical harvest levels that probably have been sustainable, might not be necessarily sustainable under the current circumstances, which are driven more now, for instance, by wetland degradation and destruction and climate change (Fox et al. 2015b; Lehtikoinen et al. 2016; but see Gunnarsson et al. 2012). During the 1950s and 1960s, duck harvest rates were thought to be much higher than is currently the case, while survival rates did not seem to differ (Devineau et al. 2010).

Conclusions

As shown here, it is not easily possible to conclude whether or not our harvest in Northern Europe follows annual reproductive output or overall population size. Variation in reproductive output has been reflected in the harvest size only in the goldeneye in Finland. It might be that the harvest of goldeneye in Finland does follow the variation in reproductive output of Finnish birds, but for the other species, we cannot say whether this is the case.

There is a continuing lack of knowledge about duck breeding success and survival across their range. In addition, we still do not know how different populations distribute themselves from their respective breeding areas during winter, especially under the changing circumstances of current climate change (Guillemain et al. 2013; Lehtikoinen et al. 2013). As long as we lack knowledge of hunting harvest throughout the flyways, we also have little understanding of precisely how the nature and levels of harvest affect the population dynamics of our common duck species. Before we can be in a position to develop adaptive management frameworks for our common quarry duck species, it is essential that we derive improved understanding of their migration routes and phenology, as well as the size of the annual hunting bag and how it varies through the hunting period. We also need to better understand how their population dynamics from different parts of the flyway

contribute to overall population trends before we can make any assessment of how harvest pressure is distributed between the different breeding populations in addition to their age classes.

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