Sex ratios in some common British wintering ducks

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Scientists and wildfowlers in Europe and North America have long been intrigued by the unevenness in the proportion of males and females in wintering flocks of ducks. In almost all cases where a disparity exists it is males that predominate.

In a massive analysis of ringed birds, Bellrose *et al.* (1961) found that a sex ratio bias within North America varied geographically, with a preponderance of males further north. This was confirmed by a broad-based field count survey in the late 1970s (Alexander 1983). Similar disparities have been noticed in Europe (Lebret 1950; Nilsson 1970; Campredon 1983; Van Impe 1984) and Perdeck and Clason (1983) confirmed that female ducks migrate further than males to winter in more southerly areas (alloheimy).

There are several interesting questions that arise from this pattern:

a) Why do females fly further than males?

b) Do flocks dominated by females exist and if so where are they?

c) What is the population sex ratio?

d) If the population ratio is unbalanced, why is this so?

The usual explanation for differential migration invokes a cold stress theory: females are smaller than males and therefore more susceptible to cold. While this may be true for some species, cold sensitivity is better used to account for the northernmost limit of wintering ranges (LeFebvre & Raveling 1967) and does not satisfactorily explain alloheimy in European ducks (Perdeck & Clason 1983). There is evidence which supports intraspecific competition as a factor influencing sexual bias within flocks and wintering ranges (Alexander & Hair 1979; Nichols & Haramis 1980; Hepp & Hair 1984).

In the winter of 1983–4 we carried out a pilot study, chiefly in Britain, to find out whether or not the sex ratios of the populations under study were biased and, if so, to what extent; whether or not the latitudinal relationship found in North America existed here; and if there was any evidence to support current explanations for sex ratio bias.

Methods

The pilot project concentrated on four common species. Wigeon *Anas penelope* and Pochard *Aythya ferina* are almost wholly migratory and both were previously known to show marked sex ratio bias in winter. Mallard *Anas platyrhynchos* and Tufted Duck *Aythya fuligula* breed in Britain in large numbers and are only partially migratory.

We collected data from wintering flocks throughout Britain in conjunction with the National Wildfowl Counts. Because of the difficulty in determining sex in the field early in autumn, data were collected each month from October to March. Participating observers, selected geographically, were sent forms for completion. Questionnaires were also sent to observers overseas, through the International Wildfowl Census network, to coincide with the count date in January 1984.

Observers were asked to give the number of the particular species at the site, the size of the flock sampled, the number sexed, the number of females, the part of the flock sampled and the activity of the sexed birds, as well as date and time of day.

Data from the wing surveys organised by the British Association for Shooting and Conservation (BASC) (formerly the Wildfowlers' Association of Great Britain and Ireland) were examined as well as information from the literature.

Results

Response to the survey in Britain

Forms were sent to 103 observers in 79 counties, ensuring good geographic cover from Cornwall to Shetland and West Wales to East Anglia. Of these, data were returned by 70 observers (68%) from 52 (66%) of the counties. Data were finally received from a total of 184 sites, whose distribution is shown in Fig. 1. Although the sites are obviously clumped, few large portions of the country are unrepresented.

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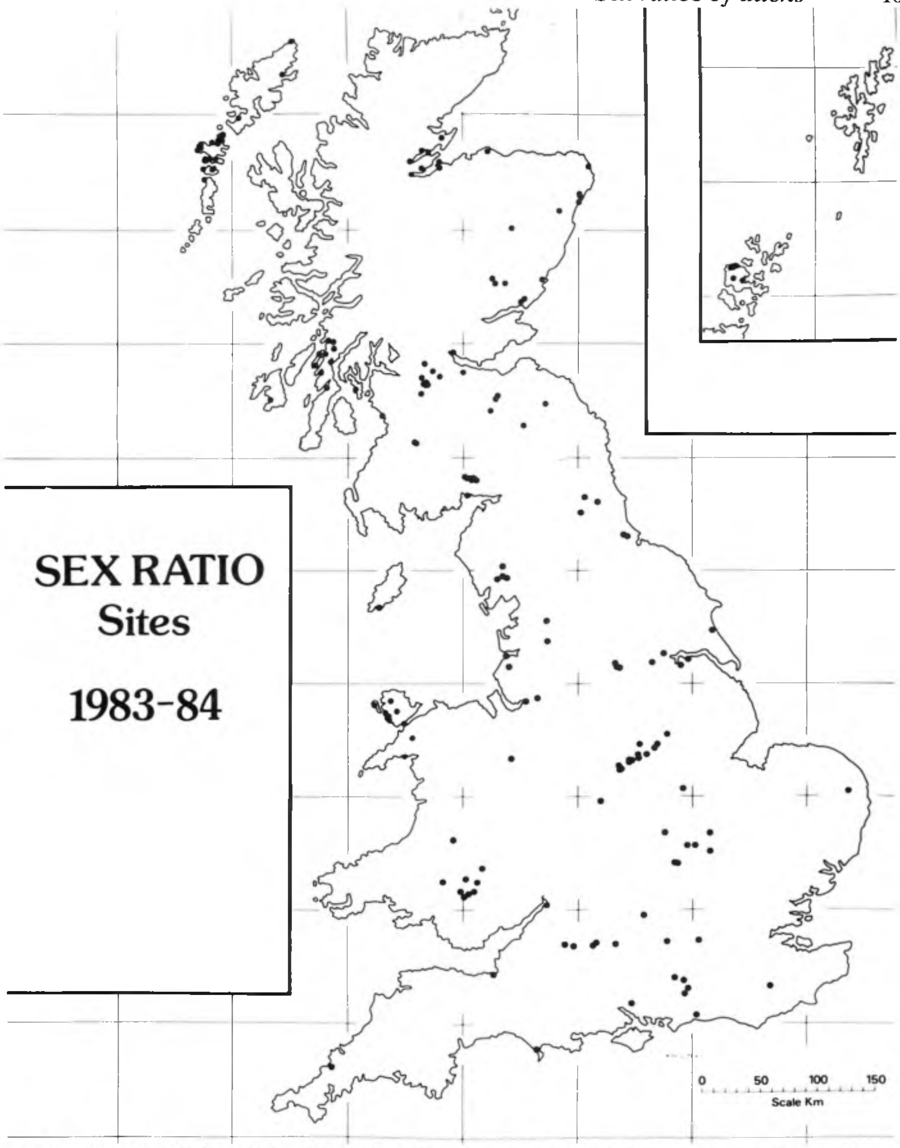

Figure 1. The distribution of the 184 sites in Britain from which sex ratio data were collected in 1983–4.

The number of sites providing data for the individual species, the sample sizes, and overall sex ratio are given in Table 1. There is a clear preponderance of males in all the species, with Pochard showing the greatest disparity. Samples at the same site over several months may include some ducks more than once. In addition to the four target species, lesser amounts of data for Teal *Anas crecca,* Shoveler *A. clypeata* and Scaup *A. marina* are also shown in Table 1, but will not be considered further here.

Table 1. Number of sites and sample sizes for individual species in the sex ratio survey. The sample includes several months for some sites.

Species	Sites	Sample	% Females	M/100F
Mallard	115	38681	44.4	125
Wigeon	117	34317	42.2	137
Pochard	114	24173	29.5	239
Tufted Duck	114	21471	41.3	142
Teal	8	991	46.5	115
Shoveler	4	136	39.0	157
Scaup	2	516	45.9	118

Total sites covered: 184

Seasonal variation in sex ratio

Most sex ratio information was collected at the time of the wildfowl count towards the middle of each month. The monthly pattern of sex ratios is shown in Table 2. When adequate samples are available there is little seasonal variation in Mallard or Wigeon. If samples are small or collected from few sites seasonal variation may be due to other factors. However, many young male Wigeon are difficult to distinguish from females until December, so early season ratios probably underestimate males. The large proportion of male Pochard in October probably reflects the fact that some moult migrants (mostly males) still remain and the same is likely to be true for the Tufted Duck. Sexing of the latter species is difficult until December, which accounts for the apparently low November ratio. In most of the following analyses the October and November data for Tufted Duck and Wigeon are excluded because of the sexing difficulties. There is no significant variation in sex ratio for any of the four species from December to March (Chi-Squared). The "wintering" ratios for the four species are: Mallard 120, Wigeon 140, Pochard 236, and Tufted Duck 149 males per 100 females.

Geographical variation

The data were grouped by degrees of latitude and longitude. The longitude relationships showed no significant trends for any species, partly because, owing to the shape of the island, longitude and latitude are not independent. For example, all the areas east of Greenwich are in southern Britain, while the far westerly areas are in the Outer Hebrides. The relationship with latitude is shown in Figure 2. Only for Pochard is the correlation consistent but it is startlingly clear for that species (Spearman rank correlation: $r_s = 0.95$, $P < 0.01$). Thus south of 51° (the southernmost 4 sites in Fig. 1) there were 150 male Pochard for every 100 females ($n = 2382$) whereas north of 58° (Orkney) there were 840 males per 100 females ($n = 983$).

The effect of habitat

All sites were classified into one of five types according to habitat, which were examined separately. The sex ratio between habitats for each species were significantly different, as shown in Table 3. In Mallard, a higher than expected proportion of males was found on natural lakes and gravel pits (Chi-Squared = 26.63, $P < 0.001$, df = 4), while for Wigeon natural lakes had low and estuaries high male to female ratio (Chi-Squared = 34.91, $P < 0.001$, df = 4). Wigeon are traditionally a coastal species and, apart from one notable exception (the Ouse Washes, East Anglia), most of the

Table 2. The monthly variation in sex ratio in the sample from 1983–84, for the four target species.

Month	Mallard		Wigeon		Pochard		Tufted Duck	
	M/100F	n	M/100F	n	M/100F	n	M/100F	n
October	170	976	140	995	348	886	269	236
November	132	14443	130	10450	235	6348	128	7919
December	125	8614	165	4376	267	5328	161	3451
January	117	6181	128	3700	206	3869	159	2712
February	114	5522	138	8981	239	4598	145	3550
March	120	2465	132	5778	223	3030	157	2678
April	–	–	–	–	–	–	86	783

Table 3. The sex ratio (males per 100 females) of the four species on each of five habitat types.

Habitat	Mallard		Wigeon		Pochard		Tufted	
	M/100F	n	M/100F	n	M/100F	n	M/100F	n
Natural lakes	129.1	12718	123.8	3758	275.2	9211	144.0	5350
Reservoirs	118.0	13426	136.9	12001	194.6	4729	162.5	4677
Gravel pits	130.3	6167	136.2	2152	212.9	7147	142.7	4410
Rivers/marshes	119.9	2309	130.5	800	339.7	1684	127.4	630
Estuary/coast	123.1	2929	142.8	7353	241.5	881	165.9	343

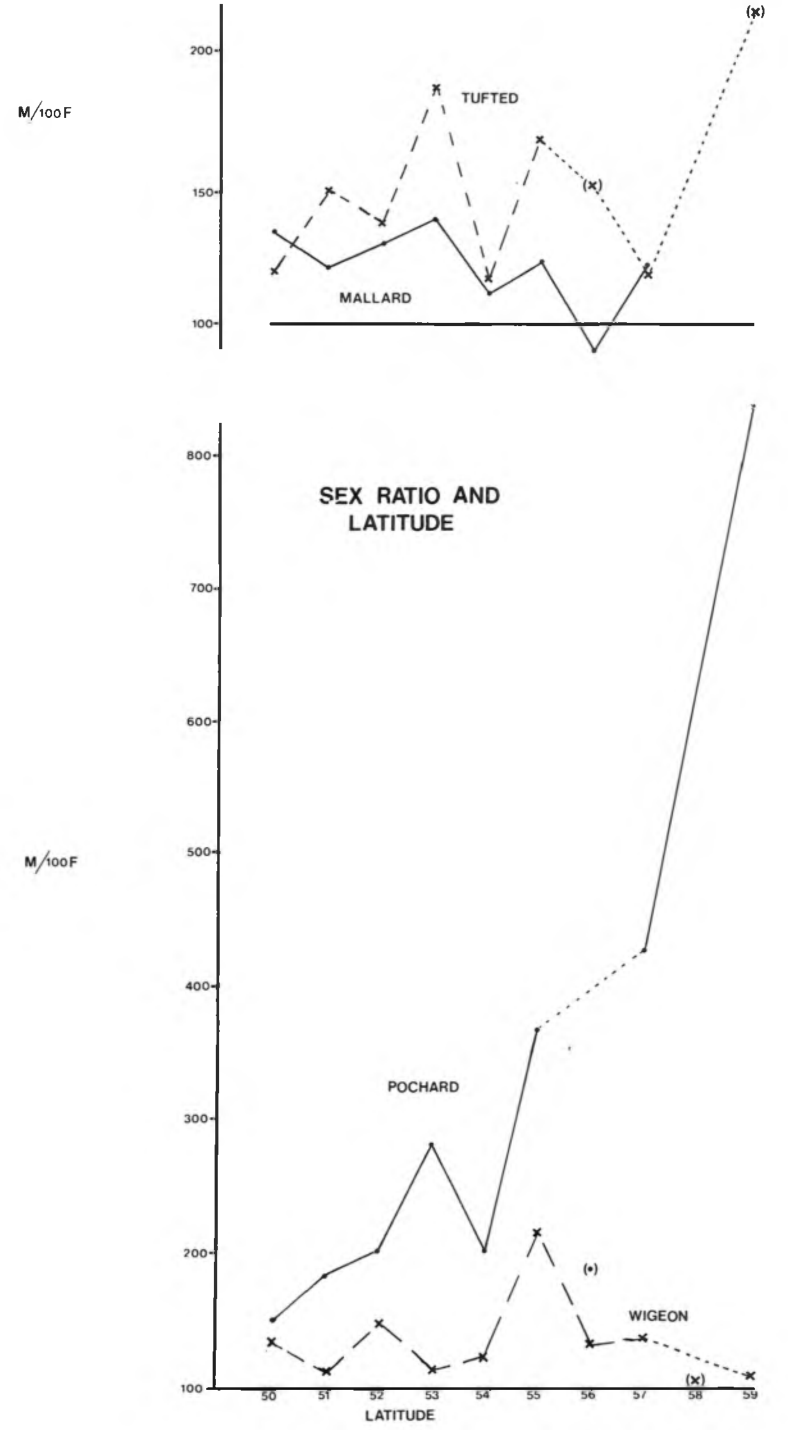

Figure 2. The relationship between sex ratios and latitude (in degree blocks) for the four principal species studied.

large concentrations are found on estuaries. High ratios in Pochard were on natural lakes and rivers and marshes (Chi-Squared = 129.77, $P < 0.001$, df = 4). The Pochard is primarily a vegetarian diving duck, and mature standing waters and floodland are probably the most favoured sites for this species. Interestingly, the marked deviation from the trend for this species at 56°N in Fig. 1 occurs where all sites counted were reservoirs with flocks of less than 50 birds (see effect of flock size below). The highest proportion of male Tufted Ducks was on reservoirs and gravel pits (Chi-Squared = 47.76, $P < 0.001$, df = 4). These habitats are the most important for this species and the increase in their availability in recent decades has been responsible for more than doubling of numbers in Britain since 1960 (Owen *et al.* 1986).

If there were inter-gender competition, and if males dominated females we would expect males to predominate on preferred habitats. The habitat effect is consistent with this hypothesis for three species though not clear for the Mallard.

Size of concentration

Individuals of different sexes might be prone to gather or to avoid flocks of different sizes especially if bird density and competition varied with bird numbers. The results of an analysis by flock size are shown in Table 4.

There are significant differences in ratios for different flock sizes in all species except for the Mallard (Chi-Squared). The Mallard just fails to show significance but there is a positive trend in the proportion of males with increasing flock size. If the data are divided roughly in half, the proportion of males is higher in large (more than 250) than in small (less than 250) flocks (Chi-Squared $P < 0.05$).

In all species except the Tufted Duck, the trend is clearly for the ratio of males to females to increase with flock size. For that species, however, the largest flock size has the smallest ratio. Again the Pochard shows the most marked tendency, with flocks of over 100 accounting for most variation; over 500 there are more than 3 males per female whereas in gatherings of under 50 the ratio is less than 2:1.

Sex ratios in the shooting bag

The BASC production survey from wing samples sent in by shooters has been going on since the mid-1960s (Boyd *et al.* 1975; Harradine 1981). The main aim is to provide information about age ratios in the shooting bag, but all wings are also classified according to sex. The species in which we are interested pose no particular problems as far as sex determination is concerned. Early data were extracted from the WAGBI/BASC annual reports, and BASC have kindly supplied data from their 1983–4 survey (Harradine & Macfarlane 1984, and unpublished). The results of this survey and of the long-term sample of duck wings is compared with our data in Table 5.

Although shooting is thought to be selective for males over females, agreement between the sex ratio in the population and in the bag is surprisingly good for Wigeon and Mallard where the shot samples are large. This means that sex ratios from the BASC wing surveys give a good indication of the ratio in the population at large, at least in the more common species.

Information on sex ratios of both shot birds and field samples in the same localities in 1983–4 were obtained. However, samples from The Fleet, Dorset, were unfortunately not large. On the Ribble Estuary, where 652

Table 4. The sex ratio of four duck species in relation to the number of individuals in the flock sampled.

Flock size	Mallard		Wigeon		Pochard		Tufted	
	M/100F	n	M/100F	n	M/100F	n	M/100F	n
up to 20	117.7	2194	128.2	582	177.0	1967	146.2	1226
21–50	120.9	3945	133.1	2044	195.5	3389	134.3	2484
51–100	119.5	6676	150.0	2973	228.2	4604	163.4	3183
101–250	128.0	8121	140.8	6660	267.5	5980	161.8	4634
251–500	128.9	9964	135.3	4208	227.1	4543	124.5	1922
501–1000	127.7	7504	132.6	4056	365.6	2786	–	–
1000+	134.7	277	153.1	2349	277.4	1404	–	–

shot Wigeon were examined, the ratio in the bag (172M/100F) was significantly higher than that in a sample of 729 visually sexed on the estuary (129M/100F); the significance of this is unclear in view of the national picture.

Sex ratios elsewhere in Europe

The appeal for data from international counters yielded information from only five countries. The results, shown in Table 6, are consistent with the pattern found in Britain, with more southerly areas (or in the case of Ireland more westerly) at the end of the migration route holding a smaller proportion of males. Those samples showing a high proportion of females are very small and must be treated with caution.

The effect of cold sensitivity

As an aside to the main analysis we examined the effect of cold stress as a factor determining the segregation of sexes within species. The Lowest Critical Temperature (LCT) was determined for each sex for each of the target species using data from ringing stations in Scotland and England. The LCT is the lowest environmental temperature at which a thermoregulatory animal can maintain its basal metabolic rate whilst resting. At ambient temperatures below the LCT the animal must raise its metabolic rate in order to generate heat energy to compensate for heat lost to the environment and maintain its core temperature. As such LCT is a good indicator of an animal's ability to withstand cold. The LCT was calculated using the Aschoff-Pohl equation, $TLC = T_b - (4.73 * Wt^{0.274})$, where $T_b = 40°C$ for non-passerine birds and Wt = weight of the bird in grams. The results of our calculations are shown in Table 7.

Table 7. The mean Lowest Critical Temperatures (LCT), mean weights and sample sizes for both sexes of the target species.

Species and sex	Sample size	Mean weight (gms)	Mean LCT (°C)
Male Mallard	2146	1184.00	7.12
Female Mallard	3701	1022.80	8.41
Male Wigeon	85	694.81	11.62
Female Wigeon	58	652.88	12.10
Male Pochard	81	839.32	10.41
Female Pochard	62	839.32	10.46
Male Tufted Duck	160	700.20	11.52
Female Tufted Duck	62	657.1	12.01

Table 5. The sex ratios of ducks shot by wildfowlers in 1983–4 and in the long term, 1965–80. Data from Duck Production Reports published by WAGBI/BASC, and from Harradine and Macfarlane (1984).

	Mallard		Wigeon		Pochard		Tufted	
	M/100F	n	M/100F	n	M/100F	n	M/100F	n
Shot 1965–80	116.8	18965	140.4	15434	171.0	244	131.5	271
Shot 1983–84	118.4	1114	143.1	496	267.0	66	113.0	50
Our survey	125.4	38681	139.6	22872	238.6	24173	149.2	13174

Table 6. Sex ratios of ducks from other European countries in January 1984.

Country	Mallard		Wigeon		Pochard		Tufted	
	M/100F	n	M/100F	n	M/100F	n	M/100F	n
Sweden	135.5	4627	154.0	89	532.1	335	127.8	3258
Belgium	128.6	1909	181.9	3115	–	–	125.1	1875
Ireland*	–	–	102.3	1078	143.0	51	132.0	165
S. France	161.8	1558	163.7	828	145.9	1972	77.0	78
Cyprus	99.0	137	97.0	63	138.0	19	85.0	24

* February/early March observations

All of the four species showed a significant difference between the LCT of males and females (t-test) but for Wigeon and Pochard the difference was less than 1°C and for Tufted Duck and Mallard less than 2°C.

Discussion

We have confirmed, using a relatively large sample of ducks sexed in the field, that all four species under scrutiny had a preponderance of males, Pochard to the most extreme extent. The results are consistent with field counts and ringing recovery studies made in North America and Europe. Analysis of ringing recoveries has shown that males of most ducks leave the breeding areas soon after their mates have begun to incubate their eggs and start the journey to the wintering ground. Females rearing young lag behind them but by mid-winter have over-flown males to locations, on average, further south (Perdeck & Clason 1983).

Much has been made of the increased cold sensitivity of females to explain differential migration with many authors citing data from the extremely harsh winters of 1947 and 1961 (Lebret 1950; Johnsgard & Buss 1956; Campbell 1977; Nichols & Haramis 1980; Sayler & Afton 1981). Whilst the effect of severe cold on duck populations is not questioned, the role of cold sensitivity in explaining differential migraton of the sexes in average winters has not been tested thoroughly enough to justify being quoted as the sole or even primary reason for the pattern. Birkebal *et al.* (1966) investigated the differences in heat loss between adult males and immature females (the largest and smallest classes) for two subspecies of Canada Goose *Branta canadensis parvipes* and *B. c. maxima*. Heat loss differences within and between these two subspecies were significant but LeFebvre and Raveling (1967) came to the conclusion "that many *maxima* populations winter farther south (cf. Hanson 1965) than the interaction of cold stress and heat balance would dictate". Wigeon and Tufted Duck are smaller than Pochard so any effect of cold stress should be more marked in the former two species, yet they do not show as clearly the latitudinal trend seen in Pochard (Fig. 2).

Nichols and Haramis (1980) suggested that latitudinal segregation in Canvasbacks *Aythya valisneria* was due to competition between the sexes. They found that females were often in small flocks on small, confined bodies of water whilst males frequented larger, more open lakes. The dominance of males over females and habitat preferences have also been described for Goldeneye *Bucephala clangula* (Sayler & Afton 1981) and Mallard (Heitmeyer & Vohs 1984). Hepp and Hair (1984) suggested that late-pairing species (such as Pochard) should show greater differentiation between sexes in winter than early-pairing species (such as Mallard) since females of the former remain subordinate for a longer period and so would be excluded from preferred feeding sites, particularly during times of limited resources. Our data, in terms of both flock size effect and the preponderance of males on preferred habitats, are in accordance with an inter-gender competition hypothesis as a primary explanation for the differential migration of the sexes.

What of the population sex ratio? We had hoped for more data from international counts which would have made it possible to answer this question. For Mallard, where there is no consistent geographical trend, there appears to be between 120 and 150 males per 100 females (40–45% females) in all parts of the range. For Wigeon, even in southern France, males predominate but the ratio is almost unity in Ireland. Sex and age ratios are available for Wigeon from the whole of the range of the north-west European breeding population in continental Europe and north Africa for 1981–2 (Campredon 1983). Although the latitudinal trend was confirmed males were prevalent in nearly all areas, including Morocco. Campredon estimated that the continental sex ratio was 134 males per 100 females (42.7% females). Adding our data from Britain and Ireland amends this figure only slightly to 132 males per 100 females (43.1% females). Interestingly, the proportion of young males (distinguishable from adult males in the field) in the flocks decreases towards the north in Campredon's study. A similar relationship between age ratio and latitude has also been noticed in Goldeneye (Sayler & Afton 1981) and is probably due to competition between age classes of a similar nature to that which we postulate between the sexes.

A substantial proportion of European Pochard winter in Spain and North Africa

(Atkinson-Willes 1976; Ruger *et al.* 1986) for which countries we have no data for 1983–4. However, to balance the preponderance of males in northern flocks the southern groups would need to have an excessively high proportion of females. The results from southern France and Cyprus (Table 6) suggest that this is unlikely and that there is a substantial excess of males in the population. The Tufted Duck is predominantly found in north and central Europe. Published data from Switzerland indicate that midwinter flocks there have 60% males (Pedroli 1981). Our results from northwest Europe lead us to believe that there is a preponderance of males throughout the range with a ratio probably exceeding 130 males per 100 females. A marked increase in the proportion of males in large flocks in Sweden (Nilsson 1970) supports the inter-sexual competition hypothesis.

It seems, therefore, that males outnumber females in the populations of the four species examined. There is no evidence of disparity at hatching. Indeed, Swennen *et al.* (1979) recorded equal sex ratios at hatching during a three-year study of the Common Eider *Somateria mollissima* and found no difference related to sex between the weights of ducklings at hatching. However, they did find that in some years female ducklings are more prone to some fatal diseases. It has been suggested that casualties from predation of females on the nest are a possible cause of unbalanced sex ratios in some species (Sowls 1955), but losses are generally too small to produce the major imbalance seen in wintering flocks. Canvasback and Pochard nest over water and would be expected to show less vulnerability to on-nest predation, yet their populations show a sex ratio more highly weighted in favour of males than those of the ground-nesting dabbling ducks.

If inter-sexual competition is the major cause of differential migration of the sexes in duck populations, this could bring with it a difference in mortality rates. The longer the migratory journey, the greater the energy demand and the likelihood of death through starvation in unfavourable conditions. The exposure to hunting can also be a potent factor, particularly in Europe, where the southerly parts of the range of most species is subject to longer open seasons and to more intensive hunting pressures than more northerly and westerly areas (Tamisier 1985). It is also possible that if wintering habitat is limiting, exclusion of the less dominant sex from favourable feeding areas could lead to direct mortality through starvation.

If the capacity of the wintering grounds determines the size of the breeding populations, and there is some evidence for a density-dependent control of overwinter loss in the Mallard (Hill 1982), and in the Canvasback (Alexander & Taylor, in press), production of young must be depressed by the unbalanced sex ratio. In North America there are attempts to redress this balance by allotting differing numbers of hunting "points" to the sexes such that a hunter reaches his daily points limit when he shoots a smaller number of females than males. There have also been suggestions that in certain circumstances there should be male-only shoots as well as a harvesting scheme weighted in favour of females (Alexander & Taylor, in press). In Europe, control of hunting is not as sophisticated as in North America, and the evidence that unbalanced sex ratios affect duck numbers less strong. More research is needed into the sex ratios in whole populations and into the mechanisms of inter-sexual competition before we can decide whether sexual imbalance has a significant effect on the size and productivity of duck populations in Europe.

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Summary

A preliminary survey of the sex ratios of Mallard *Anas platyrhynchos,* Wigeon *A. penelope,* Pochard *Aythya ferina* and Tufted Duck *A. fuligula* by field counts was made in the winter of 1983–4. Data were collected from 184 sites with a good geographical spread in Britain.

There was no significant variation in the sex ratio for any species in any month from December to March. Only Pochard showed significant trend with latitude, but the effect was substantial. South of 51°N there were 150 male Pochard per 100 females, compared with 840 north of 58°N.

There were significant variations among

habitat types and size of flocks, and in both cases the variation was consistent with the hypothesis that there is competition between the sexes for favoured sites.

The sex ratio in the shooting bag, as shown by national wing surveys, was similar to that in the field, so that there is no significant differential vulnerability between males and females.

Data from the remainder of the wintering range indicate that the populations of each of the four species has a surplus of males. The estimates were 120–150 males per 100 females for Mallard, 132M/100F for Wigeon, 150–250M/100F for Pochard and in excess of 130M/100F for Tufted Duck.

We support the hypothesis that inter-sexual competition rather than cold stress is the main factor leading to differential migration of the sexes. Females travel further and probably suffer greater mortality as a result. Inter-sexual competition is probably also responsible for increasing female mortality directly, through starvation caused by exclusion from wintering habitat.

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