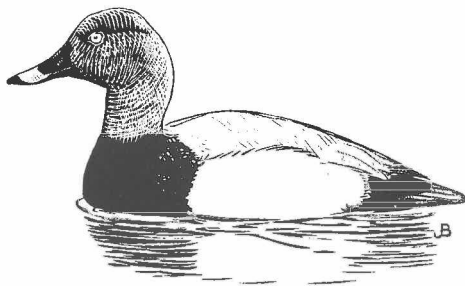


Differential migration of the sexes of Pochard *Aythya ferina*: results from a European survey



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The number of male Pochard per 100 females varied from 300 at 57° North to 75° at 37° North throughout its European and North African range. Sex ratio bias related to long term mean January temperatures was also found, but as temperature is correlated with latitude, these results cannot be used to reject any of three hypotheses (cold tolerance, breeding advantage and intersexual competition) put forward to explain differential migration. However, studies of breeding biology and habitat use of duck species offer greater support for the intersexual competition hypothesis.

This survey indicated that the sex ratio in this species is male biased, and suggested that the overall sex ratio lies between 140 and 230 males per 100 females. As sex ratios are near unity at hatching, females must suffer significantly higher mortality at some stage during development or adulthood. It has been suggested that adult female mortality may be particularly high during autumn migration and the winter season (Owen & Dix 1986) and that this is likely to be responsible for the disparity. There may also be an effect of higher hunting pressure at the southern end of the range where females winter predominantly.

Keywords: Pochard, Migration, Sex Ratio, Intersexual Competition

Several duck species exhibit differential migration, whereby females settle further south on the winter grounds after the autumn migration, as in Wigeon *Anas penelope* (Campredon 1983), Pochard *Aythya ferina* and Tufted Duck *Aythya fuligula* in Europe (Salomonsen 1968). In North America, differential migration has been identified in Canvasback *Aythya valisineria* (Nichols & Haramis 1980, Alexander 1983), Ringed-necked Duck *A. collaris*, Redhead *A. americana* (Alexander 1983) and Common Merganser *Mergus merganser* (Anderson & Timkin 1972). In both Europe and North America, these trends have been found in Goldeneye *Bucephala clangula* (Nilsson 1969, Saylor & Afton 1981) and Pintail *Anas acuta* (Lebret 1950, Alford & Bolen 1977, Perdeck & Clason 1983).

In a survey of several duck species in the United Kingdom, Owen & Dix (1986) found that sex ratios in the Pochard were highly correlated with latitude. Males predominated in the north, with

over 800 males/100 females at 59° and only 150 males/100 females at 50°. The Pochard's winter range extends across northwest Europe and the Black Sea/Mediterranean regions, and as far south as northern Africa. The main aim of this survey was to determine whether the patterns in sex ratios identified by Owen & Dix (see also Salomonson 1968) occurred throughout the rest of the Pochard's winter range and to use these results to estimate the population sex ratio. We also examine these results in the light of three hypotheses commonly proposed to explain differential migration.

Methods

The survey was conducted during the winters of 1988-89 and 1989-90 with the help of the International Waterfowl and Wetlands Research Bureau and The Wildfowl and Wetlands Trust. Regional organisers arranged for counts to be

made at sites of national importance for Pochard using their networks of volunteer observers. The dates of the survey (10-25 January) were set to coincide with the International Waterfowl Census and the majority of the counts were obtained during this period. Observers were asked to estimate the total number of Pochard at a site, the size of individual flocks being sampled and to attempt to obtain a relatively unbiased sample of the flock sex ratios.

The location of each site was estimated to the nearest degree of latitude and longitude. Linear regression, polynomial regression and analysis of co-variance were used to analyse trends in the sex ratio. Occasionally (especially in large flocks) the counters would not count the whole flock, but would make an approximation of the total number and sexed only part of the flock. In these cases, the sample sex ratio was applied to the whole flock, which provided weighted estimates of sex ratio. This method gives greater weight to larger flocks, but does not take into account the percentage of the flock sampled. Unweighted averages were obtained from the mean of all counts for a particular category. Both weighted and unweighted average sex ratios are presented in the analysis.

Sex ratios were compared with long-term mean January air temperatures measured before the survey period (WMO 1970). Each count site was assigned to a temperature category

ranging from -5.0°C to 12.5°C in 2.5°C intervals, and the sex ratio estimates were then grouped according to temperature. An unweighted mean sex ratio was thus derived for each temperature category. The relationship between mean sex ratio and temperature was tested using linear regression.

Results

Response to the Survey

Of the 56 regional organisers contacted, 36 (64%) collected data for the survey. The distribution of the counts covers a broad area of the Pochard's winter range (**Figure 1**). In all, 843 counts were made in 17 countries. The response from Greece, France, The Netherlands and Turkey was especially good. Mean estimates of males/100 females, average flock size and total number of birds counted for each country are listed in **Table 1**.

Approximately 75% of the counts were obtained from small flocks with fewer than 100 birds. The mean flock size was 152.6 ± 23.3 ($n=843$). Of these, an average 98.5 ± 12.3 ($n=843$) (64.5%) were actually counted and sexed. The unweighted overall average sex ratio was 231.8 males/100 females ± 9.0 , ($n=746$). The weighted average was 143.6 males/100 females, based on an estimated total of 72,056 males and 50,161 females (see below).

Table 1. Total number of Pochard counted, average sex ratio and flock size (\pm standard error) summarised by country. ¹Values represent weighted averages (see text for details). ²Data collected in the winter of 1988-1989. ³Data collected in the winter of 1989-1990.

	<i>n</i>	M/100F ¹	Av. Flock Size
Denmark	3,153	248.8	131.4 (63.2)
England	14,722	251.5	88.7 (14)
Ireland ²	705	300.6	100.7 (40.4)
Netherlands	9,971	188	84.1 (15.7)
Germany	5,654	188.8	134.6 (50.2)
France	22,351	166.5	95.9 (24.3)
Switzerland ²	591	208.7	53.7 (9.6)
Hungary ³	176	604	19.6 (6.6)
Romania ³	13,310	307.3	578.7 (396.1)
Portugal ²	220	124.5	44 (32.5)
Spain	4,285	109.4	69 (16.2)
Italy ²	1,409	160.4	704.5 (93.5)
Greece	25,702	90.9	285.3 (71.4)
Turkey ²	18,181	102.9	1136.3 (859.5)
Algeria ²	836	12.6	209 (76)
Tunisia ²	3,651	108.7	304.2 (157.1)

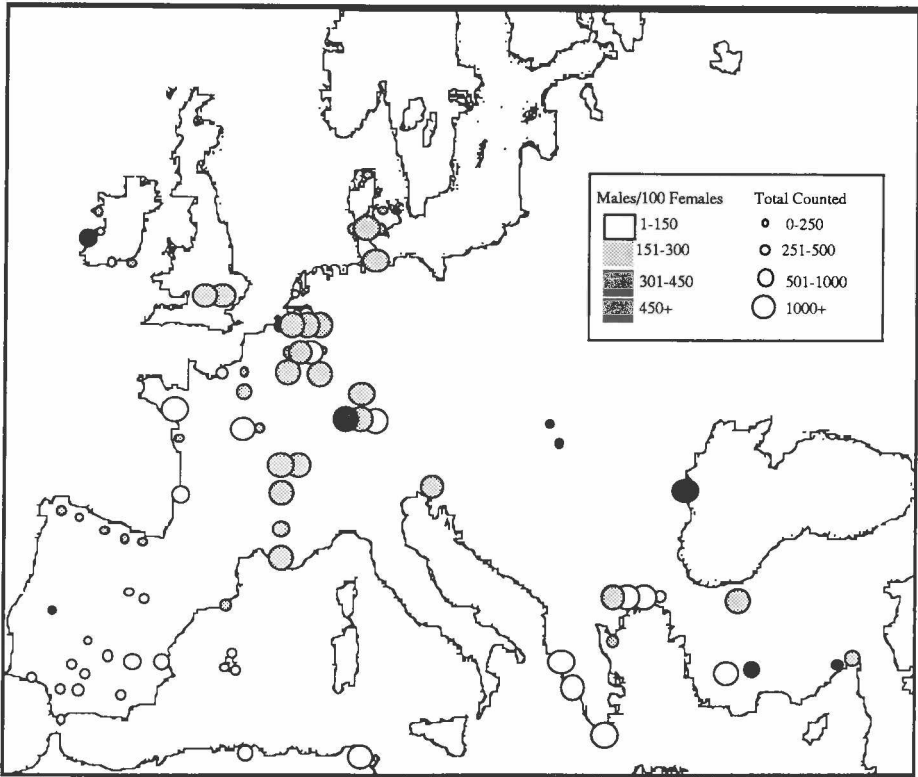


Figure 1. The locations, sex ratio (mean male/100 female) and sample size of the counts of Pochard for the survey. Data summarised by categories, shading represents sex ratio, size represents sample size (values given in box).

Geographic Variation in Sex Ratio

Sex ratio was strongly correlated with latitude, with approximately 300 males/100 females at 57°N, declining to approximately 75 males/100 females at 37°N (**Figure 2**). The data from 1988-89 and 1989-90 were analysed separately using an analysis of co-variance. In both years of the survey, sex ratio (males/100 females) was significantly correlated with latitude (linear regression: 1988-89; $r^2=0.56$, $P<0.003$, 1989-90; $r^2=0.20$, $P<0.04$). As there is no significant interaction between year, sex ratio and latitude ($P=0.6$), the data were combined and showed a highly significant correlation ($r^2=0.54$, $P=0.0001$, **Figure 2**). The relationship between sex ratio and longitude, however, was not significant ($r^2=0.05$, $P=0.18$).

The data were grouped into four geographical regions (northwest,

northeast, southwest, southeast) of approximately equal area in order to understand better the trends identified in the survey. The number of flocks counted, average flock size, weighted sex ratios and total number counted are presented for each region in **Table 2**. The weighted mean number of males/100 females in the northwest and northeast regions were 206.9 and 456.5 respectively, while in the southwest and southeast regions the means were 131.5 and 123.3, respectively. Very few counts, however, were made in the northeast region.

On average, flocks sampled in northern regions were smaller. Average flock size in the northwest and northeast was 82.6 and 19.9 respectively, compared with 153.3 and 420.9 in the southwest and southeast regions. In the north, 44,226 birds were sampled in total, compared with 80,691 in the south.

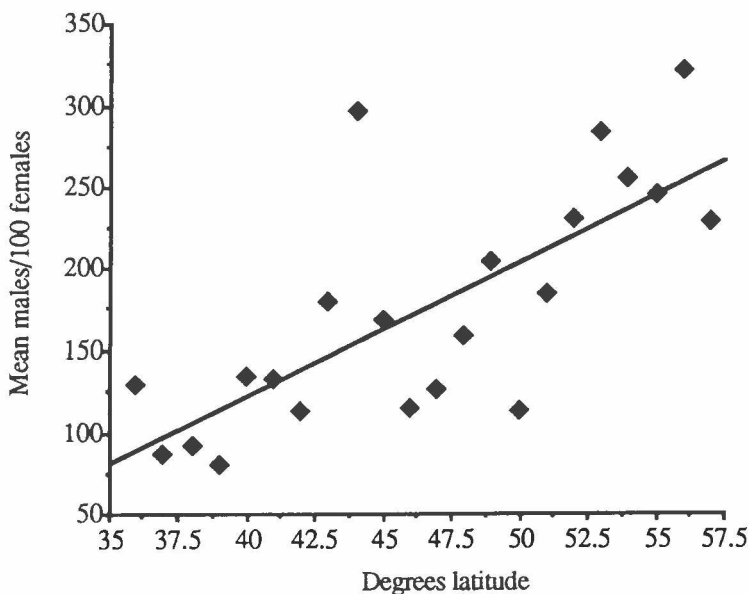


Figure 2. The linear regression of sex ratio (males/100 females) of Pochard against degrees latitude. $Y=8.2x-205.7$; $r^2=0.54$; $P=0.0001$. Data obtained from the winters of 1988-1989 and 1989-1990. Data grouped by longitude to obtain a weighted average for each latitudinal degree.

Table 2. Number of flocks of Pochard counted, average flock size (\pm standard error), weighted average sex ratio (see text for details) and total number counted, summarised by region. Regions include area from: ¹47° to 56° North, and 10° West to 12° East. ²47° to 56° North, and 13° to 35° East. ³36° to 46° North, and 10° West to 12° East. ⁴36° to 46° North, and 13° to 35° East.

	Count	Mean Flock	(M/100F)	n
northwest ³	536	82.6 (8.6)	206.9	43,970
northeast ⁴	13	19.7 (6.2)	456.5	256
southwest ⁵	143	153.3 (38.9)	131.5	21,926
southeast ⁶	143	420.9 (122)	123.3	58,765

The relationship between flock size and sex ratio was analysed by the four geographical regions. This relationship was significantly positively correlated in the northern regions (linear regression: northwest, $r^2=0.08$, $P<0.0002$, $n=536$; northeast, $r^2=0.51$, $P<0.05$, $n=13$), but was not in the southern regions (southwest, $r^2=0.001$, $P=0.69$, $n=143$ southeast, $r^2=0.004$, $P=0.82$, $n=143$).

Sex ratio and temperature

The average sex ratio was significantly correlated with temperature (linear regression: $r^2=0.62$, $P=0.02$, **Figure 3**). However, temperature was also negatively correlated with latitude

(polynomial regression: $r^2=0.82$, $P=0.0001$; x , $P=0.012$, x^2 , $P=0.018$, x^3 , $P=0.025$, **Figure 4**).

Discussion

Geographic distribution

In this survey, a strong relationship was found between sex ratio (males/100 females) and latitude with roughly three times as many males as females in the northern sites, declining to about unity in southern sites. Sex ratios were also correlated with long-term average January air temperature, and temperature was correlated with latitude.

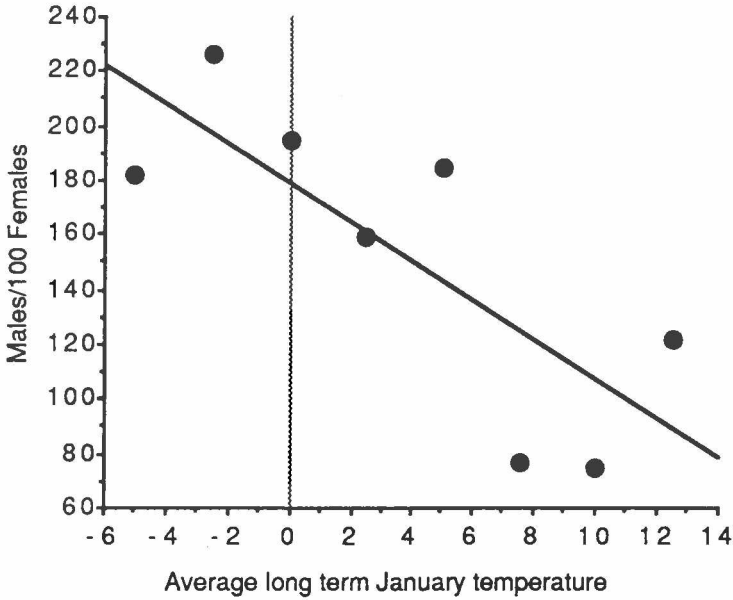


Figure 3. Linear regression of sex ratio (males/100 females) of Pochard against 30 year mean January air temperature ($^{\circ}\text{C}$). $Y = -7.19x + 179.6$; $r^2 = 0.62$; $P = 0.02$. Data grouped by temperature category to obtain a weighted average.

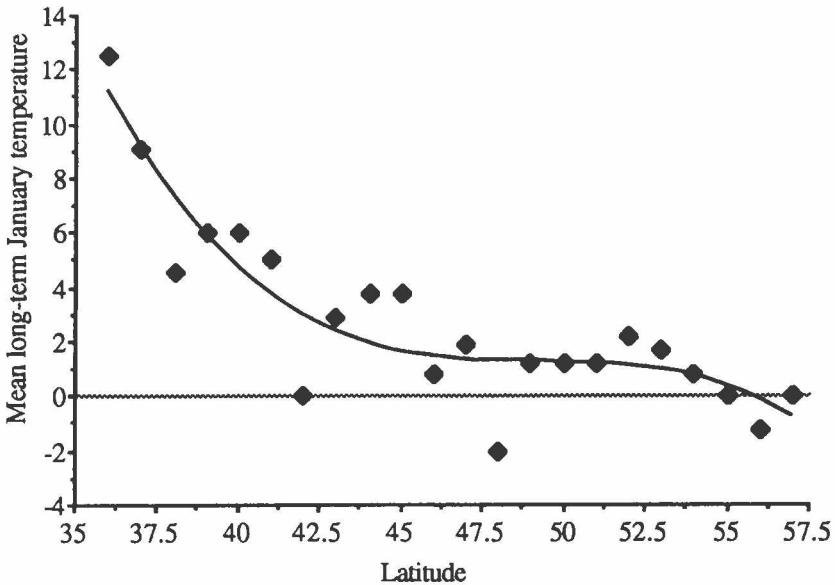


Figure 4. 3rd order polynomial regression of 30 year mean January air temperature (at the location of the counts) against latitude (see text for details). $Y = 449.6 - 30.3x + 0.62x^2 - 0.004x^3$; $r^2 = 0.82$. Data grouped by longitude to obtain an average for each latitudinal degree.

Review of hypotheses

Three hypotheses have been used frequently to explain differential migration in migratory birds (for reviews on other bird species see Myers 1981 and Arnold 1991). Each of these are discussed in light of the results of this survey and are summarised briefly below.

i) Cold tolerance (body size) hypotheses: given sex differences in body size, the smaller sex will tend to have a relatively higher metabolic rate and lower fat reserves (Calder 1974). This leads to sex difference in tolerance to cold climates. The smaller sex, therefore, is predicted to migrate further south to increase over-winter survival.

ii) Breeding advantage (arrival time) hypothesis: one sex (usually males) experiences greater benefits from arriving earlier on the breeding grounds (because e.g. due to competition for breeding territories). This sex stays further north in order to arrive earlier.

iii) Intersexual competition (dominance) hypotheses: one sex is dominant and chooses the nearest suitable overwintering area and the subordinate sex is displaced further south by competitive exclusion.

Cold Tolerance

Winter temperatures have been found to influence the mass movements of wildfowl species (Cramp & Simmons 1977, Nilsson 1984). It seems likely that the migratory route of the Pochard follows a temperature gradient, in a generally northeast-southwest direction, from the low temperature regions of the northeast Europe and north western Asia, to warm coastal regions of the Mediterranean (Monval & Pirot 1989). This notion is supported by the correlation found between sex ratio and average January temperature. However, temperature is also correlated with latitude or distance along the migratory route. It is difficult, therefore, to use these results to refute the predictions of the other two hypotheses mentioned.

A number of studies on the effect of temperature on wildfowl movements, support the cold tolerance hypothesis. Bauer & Glutz von Blotzheim (1969)

suggested that female Pochard react more strongly to cold temperatures than males. Alford & Bolen (1977) found that the proportion of female Pintails decreased as temperature decreased, and suggested that during these periods females migrate further south. Saylor & Afton (1981) found that both male and female Goldeneyes increased the percentage of time spent feeding during cold periods; however, females increased their feeding time 7-9% more than males. Campbell (1977) found that female Goldeneyes predominated in bays which were sheltered from the wind. However, other factors, such as habitat differences or intersexual competition, which may have influenced the distribution of females, were not monitored. Duncan & Marquiss (1993), on the other hand, also working in Scotland, argued that the preponderance of male Goldeneyes at lower elevations was due to competitive exclusion of females from favourable feeding sites. Anderson & Timkin (1972) found that body weight of Red-breasted Mergansers *Mergus merganser* increased with latitude and suggested that larger individuals remained further north because of greater tolerance to cold. However, these individuals may have increased their fat reserves in response to the cold.

Contrary to the studies mentioned above, Perdeck & Clason (1983) found that for Pintail, Wigeon and Teal *Anas crecca*, differences between the sexes in winter distribution are not increased in cold winters and concluded that it is unlikely that differences between the sexes are due to reaction to temperature. However, their analysis was very broad and general and may not have been able to detect this. Alexander (1983) suggested that studies which have identified sex differences in response to climate were made in unusually cold years. He argued that sex differences in body mass are not great enough to account for substantial differences in tolerance. Owen & Dix (1986) estimated the lowest critical temperature (LCT) that males and females of several common duck species could withstand without adjusting their metabolism. The differences between male and female body mass ranged from 0-14.0%,

equating to a maximum difference in LCT of 1.3°C which was unlikely to affect the distribution of the sexes substantially. Furthermore, the Mallard *Anas platyrhynchos* which had the greatest sex difference in body mass, also had the least segregated distribution geographically, whilst in Pochard there was little or no difference in body mass between the sexes, this species had a highly segregated distribution. These results provide strong evidence against the cold tolerance hypothesis.

Breeding advantage

The breeding advantage hypothesis assumes that one sex settles further north in order to arrive earlier on the breeding grounds. However, in many duck species, both sexes arrive on the breeding grounds simultaneously (Lebrecht 1950, Weller 1965, Anderson *et al.* 1988). For example, the Goldeneye (Nilsson 1969), and Canvasback (Johnsgard & Buss 1956) both exhibit differential migration, but pair before migrating to the breeding grounds. Although Pochard males arrive earlier on the breeding grounds (Cramp & Simmons 1977), they are not territorial or site faithful, and so there appear to be no obvious advantages to arriving early (Havlin 1963a, 1963b, Hori 1966).

Intersexual competition

The intersexual competition hypothesis is the most commonly proposed explanation for differential migration in duck species. Much of the support for this comes from studies which have found evidence suggesting that dominance influences habitat selection in the sexes (Paulus 1983, Hepp & Hair 1984, Alexander 1987). In the United Kingdom, Owen & Dix (1986) found that in three of the four species studied, the proportion of males increased in what were considered preferred habitats. For example, in the Pochard, rivers and associated marshes supported the highest proportion of males at 339.7 males/100 females whereas natural lakes had only 275.2 males/100 females. Marshland and riverine habitats have very high vegetation biomass and

should be preferred by this species. In the Canvasback the Pochard's ecological equivalent in North America, males made up 48% of the total number of birds in areas with low densities of food, but this increased to 74% in areas with high food densities (Alexander & Hair 1979).

Owen & Dix (1986) suggest that these patterns in distribution may be the result of intersexual aggression (see also Alexander 1983, 1987). They state "if there were inter-gender competition, and if males dominated females we would expect males to predominate on preferred habitats". These differences in habitat use occur independently of temperature and latitude, and so cannot be explained either by sex differences in cold tolerance or by distance to the breeding grounds.

Males are commonly the dominant sex in wildfowl species (Patterson 1977, Welling & Sladen 1979, Alexander & Hair 1979, Alexander 1980, 1983, 1987, Nichols & Haramis 1980, Paulus 1983, Hepp & Hair 1984, Perry & Uhler 1988, but for exception, see Perry *et al.* 1988). Choudhury & Black (1991) found that male Pochard have higher levels of aggression than females; 74% of male attacks were directed at females and this was thought to influence the number of females at feeding sites.

In the northern regions of this survey, male proportions were found to increase with flock size. Since large flocks are found in areas with high bird densities, and these areas are also likely to be high quality habitats, the tendency for male proportions to increase with flock size is believed to be a result of intersexual competition. Similar trends have been identified in a number of studies (Owen & Dix 1986, Nilsson 1970a, Nichols & Haramis 1980, Tamisier 1984).

Population Sex Ratio

Population sex ratios are difficult to assess because of sex differences in the timing of migration and patterns of settlement on a local and geographic scale (for review see Nilsson 1970b). In the Pochard, not only are there geographic differences in the distribution of the sexes, but females

appear to be found in marginal habitats at lower densities. Thus, in this species, female numbers may be underestimated by surveys which focus solely on sites of international importance. However, in the Pochard, between 60 and 80% of the total population is thought to overwinter at 12 key sites in Europe (Atkinson-Willes 1972). It is important, therefore, to obtain good sex ratio estimates from these sites. Ideally, one should sample different sized sites in proportion to their abundance, but it is difficult to obtain a good estimate of the distribution of birds without a detailed survey.

Survey coverage is likely to be biased in a number of ways (Nilsson 1970b). It is often difficult to conduct counts on major wintering sites because the size of these sites limits access to the birds. Small sites, then, may be counted preferentially. In addition, it is often extremely difficult to obtain even geographical coverage. In some areas there are few counters available. For example, in this survey few counts were made in the northeast region, however, it is very likely that the number of ducks in this area was small.

The availability of counters can also influence the types of sites sampled. In the southern regions, where fewer volunteers are available, counts tended to come from sites with high densities of birds. However, in the northwest, where far more volunteers are available, many small sites were sampled. It seems likely then, that the differences in flock size with latitude (evident in **Table 2**) do not represent true distributions of this species, but are just the result of bias in the survey. Given that there is a bias in the number of small flocks (with low male numbers) obtained in the northern regions, then the regression presented in **Figure 2**, may underestimate the effect of latitude on the proportions of males.

Given the biases in the data and the limited sample size, one can only obtain a crude estimate of population sex ratio from this study. The unweighted average sex ratio of 231.8 males/100 females (± 9.0) is within the range of 150-250 males/100 females, estimated for Pochard in the United Kingdom by Owen & Dix (1986). However, this estimate gives equal weight to all flocks, regardless of size and location. Given

that 536 counts were made in the northwest region (where male proportions are higher), as opposed to 141 in the southern regions, such an estimate may overestimate male numbers. The second sex ratio, of 149.0 males/100 females was estimated from the total sum of the expected number of males and females (based on the estimates of flock size, see methods). This method gives equal weight to each bird sampled. The best estimate probably lies between 137-232 males/100 females. Since what evidence exists indicates a 1:1 male:female ratio at hatching in ducks (Havlin 1963b), this indicates a higher mortality of females during immature or adult life. Owen & Dix (1986) suggested that this was associated with the longer migration distances and this seems likely. In Europe, more southerly areas are associated with higher shooting pressure (Tamisier 1985) and this may impose a higher mortality on females.

Ecological Implications

Female survival is likely to be affected by winter distribution. The risks of starvation and predation are higher in poor quality habitats. The increased migratory distance also increases energy demands and the likelihood of starvation (Owen & Dix 1986). In addition, Pochard survival in southern Europe may be lower due to drought and fewer restrictions on hunting (Owen & Dix 1986, Monval & Pirot 1989). These factors may reduce female survival substantially and may contribute to the overall bias in the sex ratio.

Bellrose *et al.* (1961) and Alexander & Taylor (1983) suggest that productivity in duck populations is limited by the number of females. Haramis *et al.* (1986) found that Canvasback in the eastern United States tended to have lower levels of recruitment during years when the population was heavily male biased. Therefore, it is important to improve our knowledge of factors which affect female mortality. This topic has become especially relevant given what has been described as a "worrying" decline in Pochard numbers (Ruger *et al.* 1986, Monval & Pirot 1989) in Europe in recent years.

This survey could not have been conducted without the help of the International Waterfowl and Wetlands Research Bureau and hundreds of counters and regional organisers. We are extremely grateful for their help. We would also like to thank Jean-Yves Pirot for helping to arrange the contact with the organisers. This research was funded largely by The Wildfowl & Wetlands Trust.

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