J Ornithol
DOI 10.1007/s10336-008-0367-x

ORIGINAL ARTICLE

Within-winter movements: a common phenomenon in the Common Pochard *Aythya ferina*

Irene Keller · Fränzi Korner-Nievergelt · Lukas Jenni

Received: 16 October 2007 / Revised: 30 November 2008 / Accepted: 4 December 2008

Abstract Waterbirds are often observed to move between different wintering sites within the same winter—for example, in response to food availability or weather conditions. Within-winter movements may contribute to the spreading of diseases, such as avian influenza, outside the actual migration period. The Common Pochard *Aythya ferina* seems to be particularly sensitive to infection with the highly pathogenic avian influenza virus H5N1 and, consequently, could play an important role as vectors for the disease. We describe here the within-winter movements of Pochards in Europe in relation to topography, climate, sex and age. We analysed data provided by the EURING data bank on 201 individuals for which records from different locations from the same winter (December–February) were available. The distances and directions moved within the winter varied markedly between regions, which could be ascribed to the differing topography (coast lines, Alps). We found no significant differences in terms of distances and directions moved between the sexes and only weak indications of differences between the age classes. In Switzerland, juveniles moved in more westerly directions than adults. During relatively mild winters, winter harshness had no effect on the distances travelled, but in cold winters, a positive relationship was observed, a pattern possibly triggered by the freezing of lakes. Winter harshness did not influence the directions of the movement. About 41% (83/201) of the Pochards that were recovered at least 1 km from the ringing site had moved more than 200 km. A substantial number of birds moved between central/southern Europe and the north-western coast of mainland Europe, and between the north-western coast of mainland Europe and Great Britain, whereas no direct exchange between Great Britain and central/southern Europe was observed. Within-winter movements of Pochards seem to be a common phenomenon in all years and possibly occur as a response to the depletion of food resources. This high tendency to move could potentially contribute to the spread of bird-transmitted diseases outside the actual migration period.

Keywords Distances and directions of winter movements · Exchange of Pochards between European regions within winter · Ring recovery analysis · Waterbird · Winter harshness

Introduction

In addition to their regular movement between the breeding sites and the winter quarters, birds may perform other forms of movements, such as moult migration, juvenile dispersal on the breeding grounds and movements within the wintering grounds, often associated with the depletion of food or adverse weather conditions (Alerstam 1990; Berthold 2000).

Within-winter movements of birds in central Europe are of particular interest in bird species, such as the Common Pochard *Aythya ferina* (Pochard), that are potential vectors of avian influenza viruses (Delany et al. 2006). In order to assess the likelihood that Pochards could contribute to the

Communicated by F. Bairlein.

I. Keller · F. Korner-Nievergelt (✉) · L. Jenni
Schweizerische Vogelwarte, Sempach 6204, Switzerland
e-mail: fraeni.korner@oikostat.ch

Present Address:
I. Keller
Eawag, Department of Aquatic Ecology and Department of Fish Ecology and Evolution, Überlandstrasse 133, 8600 Dübendorf, Switzerland

spread of these viruses outside the actual migration period, it is important to understand to what extent, in which situations and in which directions within-winter movements occur.

It seems likely that the movement patterns show some regional, temporal or individual variation. On a large geographical scale, the directions and distances moved by wintering Pochards may be influenced by coastlines or mountain ranges, while the local availability of suitable habitats will be important on a smaller scale. Sex-specific differences also seem likely, but detailed predictions are difficult. On the one hand, males may be physiologically better adapted to low temperatures and, consequently, might be less prone to move when temperatures drop (Sayler and Afton 1981). On the other hand, males normally winter farther north than females (Perdeck and Clason 1983; Owen and Dix 1986; Carbone and Owen 1995; Kershaw 2002) where they may experience stronger or more frequent cold spells that could trigger longer within-winter movements. Age-specific differences in movement patterns may result from differences in the level of experience between juveniles and adults. Specifically, juveniles cannot rely on previous experience and may show higher movement activity in order to explore the wintering area and find profitable wintering sites. Finally, waterfowl have been observed to move towards warmer regions as a response to cold spells (Nilsson 1984; Ridgill and Fox 1990; Lovvorn 1994; Scott and Rose 1996; Kershaw 2002); this is especially true for juvenile ducks (Owen and Dix 1986).

In the context of a potential spread of avian influenza by Pochards, it is of particular interest to determine whether different European regions harbour discrete wintering populations or whether they are connected through regular within-winter movements. It has been proposed that the Pochards wintering in Europe can be subdivided into a north-western population wintering around the North Sea and a south-eastern population wintering in central Europe and around the Mediterranean and Black Seas (Monval and Pirot 1989; Blums and Baumanis 1990; Rose and Scott 1994). However, there may be some overlap of the winter distribution of these two putative populations—for example, in the region of the pre-Alpine lakes in Switzerland and Austria (Scott and Rose 1996)—and their breeding areas seem to largely coincide (Wernham et al. 2002; Hofer et al. 2006). Hofer et al. (2006) found that individuals ringed while wintering on the pre-Alpine lakes of Switzerland were occasionally recovered on the British Isles in subsequent winters. The frequency of such movements within the same winter, however, is unknown.

We describe here the patterns of within-winter movements of Pochards based on ring recovery data from 201 individuals compiled in the Euring database. Specifically, we investigated how these patterns differ depending on (1) the region within Europe, (2) the sex or age of an individual and (3) winter harshness. We also investigated a fourth factor—to what extent are the different postulated wintering populations within Europe connected—which we based on a description of the exchange of individuals within the same winter. An estimate of the exchange rate could facilitate an risk assessment of the spread of a bird-transmitted disease, such as avian influenza outside the migration period.

Materials and methods

Study species

The breeding range of the Common Pochard extends from Western Europe through Central Asia to Lake Baikal. Most birds are long-distance migrants and winter in several geographically distinct areas from Western Europe to Japan (del Hoyo et al. 1992).

The Netherlands, the lakes north of the Alps, the southern coast of the Baltic Sea, the western coast of the Black Sea and the coasts of the Caspian Sea are particularly important wintering areas for Pochards, but large numbers are also observed in Germany, France, Spain and the Great Britain (Scott and Rose 1996). Autumn migration takes place between September and November, and in the spring, Pochards leave their wintering grounds mainly in March (Bezzel 1959; Willi 1970; Wernham et al. 2002; Hofer et al. 2006; Heine et al. 1999). Males tend to winter further north than females, which often leads to uneven sex ratios within sites (Owen and Dix 1986). Pochards forage for animal (e.g. Zebra Mussel *Dreissena polymorpha*, larvae of chironomids, *Tubifex*) or plant material down to depths of about 4.5 m (Willi 1970; Glutz von Blotzheim et al. 1985). Common Pochards seem particularly susceptible to infection with the highly pathogenic avian influenza virus H5N1 (Delany et al. 2006). In Switzerland, for example, 25% of the infected wild birds of the outbreak in the winter 2005/2006 identified to species level were Common Pochards (Federal Veterinary Office 2007).

Ring recovery data

Data for this analysis were available for all European countries (excluding Russia) and were obtained from the Euring database. We selected only recoveries with known finding circumstances and a finding date accurate to within 1 month. We then selected all birds with two records from the same winter (December–February), resulting in 201 observations on as many different individuals. Only within-winter movements >1 km were included, as local recoveries were not recorded consistently by the different schemes. The first observation was either the ringing occasion (99%) or a recapture (1%); the second observation in the winter was a recapture (2.5%) or a dead recovery, mainly from hunted birds (97.5%). The geographical distribution of the first observations was very patchy due to the small number of countries where Pochards have been ringed in large numbers. Only four countries contributed more than ten first observations (Great Britain, Switzerland, the Netherlands, Italy), while only one within-winter movement each was recorded from Denmark and Sweden. For most of the analyses, these two records were pooled with those of the Netherlands. The second observations were somewhat more widely distributed, with records from ten different European countries, including France with many shot birds.

Data analysis

The distance (in kilometres) and direction (in degrees) between the two observations was calculated along a path of constant bearing (i.e. a loxodrome) following Imboden and Imboden (1972).

Birds were considered to be juveniles during their first year of life (up to 30 June of the year following hatching). All older birds were considered to be adults. The age was unknown for 75 of the 201 birds.

Mean daily temperatures over the study period (1953–2005) were downloaded from http://eca.knmi.nl/ for weather stations in north-western (Great Britain, the Netherlands) and central Europe (Switzerland, northern Italy) and in the Baltic Sea area (Sweden, Finland, Estonia, Russia). For each station, we computed the Hellmann index (Ijnsen 1988), which is defined as the absolute value of the sum of all negative mean daily temperatures between December and February. This index provides a measure of both the duration and the intensity of cold periods. The values were correlated across all stations, but cluster analysis showed them to be particularly similar within each of the three regions of north-western Europe, central Europe and the Baltic Sea area. A principal component analysis (PCA) based on the covariances was performed on the regional mean Hellmann indices. The first principal component (PC1) explained 94% of the variance and was correlated negatively with all regional Hellmann indices. We therefore interpreted PC1 as an overall measurement for winter harshness in Europe.

An analysis of covariance (ANCOVA) was used to investigate the effect of different variables on the log-transformed distance between two within-winter observations. Of the 201 movements, 76 had to be omitted because of missing sex or age data. The full model included the age and sex of the individual, the date of the first observation, the country of first observation, winter harshness and all two-way interactions between these variables. Terms were dropped from the model in a stepwise manner if this did not cause a significant increase in residual variance. As the final model did not include sex and age, we re-included the 76 observations with undefined age or sex and present the results for the whole data set.

Because the relationship between winter harshness (PC1 see above) and distances moved was non-linear, we fitted threshold models for varying threshold values between −400 and 200. We then used the threshold value of the model with the lowest Akaike's information criterion (AIC).

Only movements above 50 km were included in the analysis of movement directions, resulting in 108 available observations because movements over shorter distances may be more strongly influenced by local topography. We assessed the significance of the mean direction with a Rayleigh test of uniformity (Batschelet 1981) implemented in the R package CircStats (Agostinelli 2006). If this test was significant, the mean direction was calculated following Fisher (1993). To compare groups of individuals, we computed the angular distance between two mean directions following Batschelet (1981) and tested for significance using a randomisation procedure. Specifically, all individuals were randomly reassigned to two groups, and the angular distance between the group means was re-computed. This was repeated 10,000 times to produce a simulated distribution of the angular distance under the null hypothesis. Because the observed mean directions depended on the country of first observation (see below), the effects of sex, age and winter harshness were investigated for each country separately.

To assess the exchange of individuals between different European regions, we assigned all first and second observations to one of three areas: (1) Great Britain, (2) the north-western coast of mainland Europe and (3) central and southern Europe, including the pre-Alps and the Mediterranean. We then quantified the movements from each region to the other two regions as percentages of all first observations in that region. This quantification is highly dependent on the probability of recovery and thus on hunting pressure. We detected a significant effect of the interaction between region and month on the proportion of recoveries from hunted birds (likelihood ratio = 17.3, $df = 4$, $P = 0.002$; Table 1). In southern Europe, the proportion of recoveries from hunted birds stayed continuously high over all 3 months, whereas in the Great Britain and central Europe, these proportions dropped in February (Table 1). As a consequence, recoveries from the south in February are likely to be overrepresented in our data. There are additional factors as well that could potentially bias the quantification of movements based on ringing recovery analysis (see Perdeck 1977 and Discussion).

Table 1 Percentage of recoveries from hunted individuals per region and month

Region	December	January	February
Great Britain	84.8 (61.5, 100)	82.5 (71.9, 91.2)	0 (0, 0)
	$n = 13$	$n = 57$	$n = 5$
North-western coast of mainland Europe	100 (100, 100)	96.6 (89.7, 100)	58.3 (33.3, 83.3)
	$n = 6$	$n = 29$	$n = 12$
Central/southern Europe	83.3 (50.0, 100)	70.6 (56.9, 82.4)	72.7 (54.5, 90.9)
	$n = 6$	$n = 51$	$n = 22$

The 95% confidence interval (inverted binomial test) is given in parenthesis. *n*, Total number of recoveries per month and region

The statistical software R ver. 2.4.1 was used for all plots and analyses ® Development Core Team 2006).

Results

Regional differences in movement patterns

About 41% of all birds recorded twice from different locations within the same winter moved more than 200 km (59% moved 1–200 km). Due to unequal ringing effort, our observation on within-winter movements mainly started in Great Britain, Switzerland, the Netherlands and, in smaller numbers, in Italy. In Fig. 1, the observations are broken down according to the month of first observation and the month of second observation. Temporal patterns were difficult to identify because the observations were quite unevenly distributed throughout the winter. More than two-thirds of all second observations were from January, 20% from February and only approximately 10% from December.

Birds first observed in Great Britain (open circles, Fig. 1) tended to stay within the British Isles with occasional movements to the European mainland, mainly to northern France. The majority of the birds that moved out of the Netherlands (filled triangles, Fig. 1) moved in the direction of the coastline into northern or western France, but two second observations were also reported from southeast England and one from the south of France. In December, all second observations of birds from Switzerland (filled squares, Fig. 1) were reported from southern and western France. The second observations from the following 2 months were more widely scattered but showed a concentration in Switzerland, southern Germany and eastern France. Some longer distance movements from Switzerland to northern or western France or to the Adriatic coast were also observed.

The distance travelled differed significantly between the countries of first observations ($F_{3,196} = 7.474$, $P < 0.001$; Table 2). The distances were longer for individuals from Switzerland (mean = 206 km, $n = 74$) and the Netherlands (mean = 218 km, $n = 34$) than for birds from Great Britain (mean = 125 km, $n = 83$) or Italy (mean = 44 km, $n = 10$). A detailed comparison of the distances covered in the different regions revealed differences in the proportion of short-distance movements (i.e. <200 km; Fig. 2). In Great Britain, approximately 80% of the movements were in the range <200 km. In contrast, of the birds first observed in mainland Europe, about 40% moved distances >200 km. Distances >500 km were more frequent in the birds first observed at the Baltic or North sea coast.

The observed directions between two within-winter reports also depended on the country of first observation. Individuals first observed in Great Britain moved in all directions, and no significant preferred direction was discernible (Rayleigh test, $P = 0.55$; Fig. 3). Movements out of Switzerland were mainly towards the south-west, and less frequently towards the north-west, with a significant preferred direction of 253° (SSW; Rayleigh test, $P < 0.001$). Birds from the Netherlands followed a mean direction of 229° (SW; Rayleigh test, $P < 0.001$). Individuals from Italy were excluded from the analysis as only three movements >50 km had been observed.

To summarise, distances and directions moved within winters varied strongly between regions.

Influence of sex and age on distance and direction

There was no significant effect of sex on movement distance (ANCOVA, $F_{1,114} = 2.44$, $P = 0.12$). Sex-specific differences in movement direction were detected for birds first observed in Switzerland but not in the other regions. In Switzerland, males preferentially moved towards the west (mean direction 258°, Rayleigh test, $P < 0.001$, $n = 35$; Fig. 3), while females exhibited no significant preferred direction (Rayleigh test, $P = 0.47$, $n = 17$).

The analysis of variance revealed no significant effect of the age of a bird on movement distance ($F_{1,105} = 1.29$, $P = 0.26$). The influence of the age of a bird on movement direction could be investigated for Great Britain and Switzerland only because the age was unknown for most of the individuals first observed in the Netherlands. In Great Britain, the movements of both age classes showed no significant preferred direction, while in Switzerland juveniles moved in more westerly

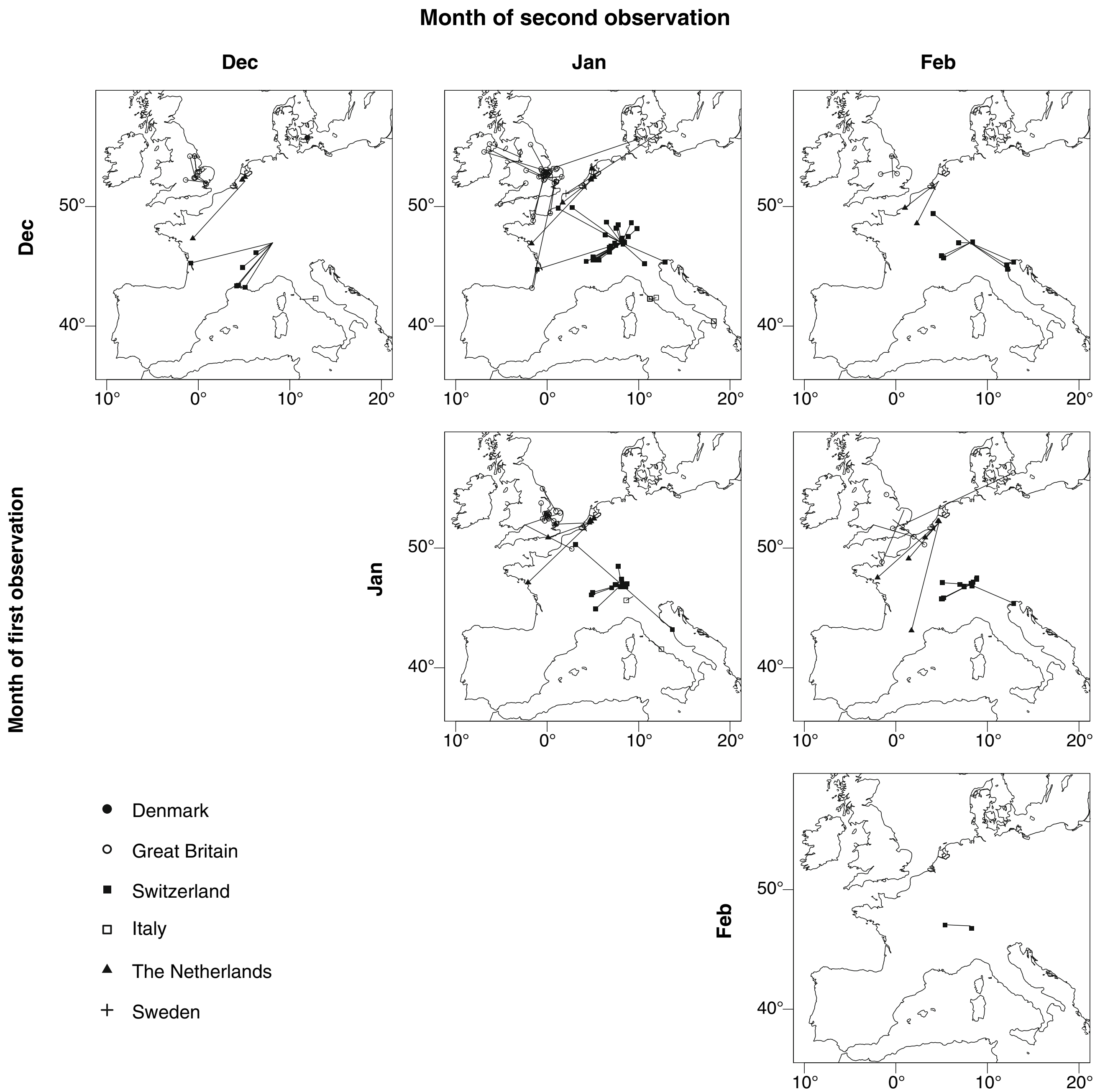

Fig. 1 Ring recoveries of Pochards ringed and recovered within the same winter in Western Europe. The first (mostly ringing) and second observations (mostly recoveries) for an individual are connected by a *line* with a *symbol* indicating the location of the second observation. The *symbols* indicate the country of first observation

directions (266°, Rayleigh test, $P < 0.001$, $n = 23$) than observed for adults (215°, Rayleigh test, $P = 0.007$, $n = 13$), and this difference was significant (permutation test, $P = 0.02$).

To summarise, there was no significant difference in distances and directions moved between the sexes and, in Switzerland, juveniles moved in more westerly directions than adults.

Influence of winter harshness on distances and directions

The distances travelled increased significantly with winter harshness (linear model, $F_{1,196} = 10.44$, $P = 0.001$; Table 2, Fig. 4). The non-parametric smoother in Fig. 4 suggested that an increase in movement distances may occur below a threshold level of winter temperatures. In

Table 2 Results of the *F* tests for the terms in the final ANCOVA model predicting log (distance)

Term	*df*	RSS	AIC	*F* value	*P*
Full final model		320.44	103.74		
Country of first observation	3	360.05	121.17	8.077	<0.001
PC1 (Hellmann index)	1	337.51	112.18	10.443	0.001

ANCOVA, Analysis of covariance; AIC, Akaike's information criterion

The full starting model contained sex, age, country of first observation and principal component 1 (PC1; Hellmann index) and all two-way interactions as predictors. The model was simplified by omitting, in a stepwise manner, nonsignificant terms according to the *F* test from the model comparison of the models with and without the specific term. The model fit was started with 125 observations. After sex and age had been omitted from the model, individuals with unknown age or sex were re-included, resulting in 201 observations

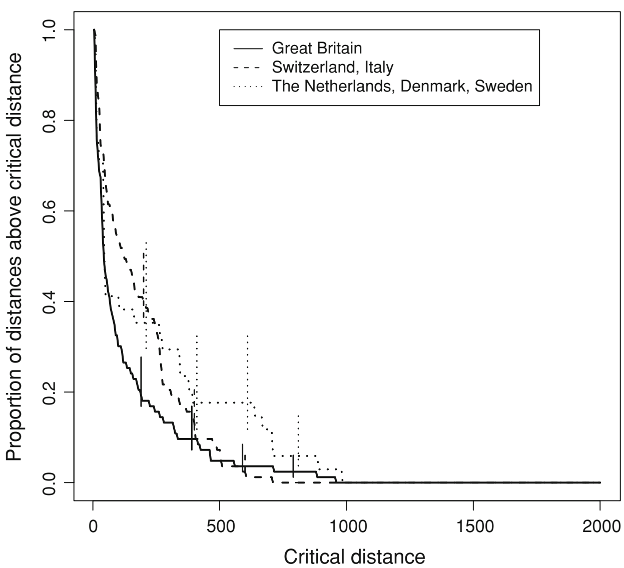

Fig. 2 Proportion of movements ≥ the critical distance (in kilometres) specified on the *x-axis* for movements starting in Great Britain (*solid line*), Switzerland/Italy (*dashed line*) and the Netherlands, Denmark or Sweden (*dotted line*). *Vertical lines* indicate the 95% confidence intervals for proportions

fact, the AIC of a model where the response was held constant for PC1 > -60, and was dependent on PC1 below this threshold, was slightly lower than that of a model which assumed a linear relationship between the response and PC1 (AIC = 671.00 vs. AIC = 671.03). The proportion of variance explained (adjusted R^2) increased from 0.0417 in the linear model to 0.0418 in the threshold model. Movement distances increased during harsh winters for mainland Europe, whereas this increase was less pronounced in Great Britain (Fig. 5).

For birds first observed in Switzerland, directions did not differ significantly between harsh and mild winters (harsh = PC1 < -60; mild = PC1 > -60; randomisation test: $P = 0.89$, $n = 53$). Birds first observed in Great Britain did not show a significant preferred direction, and birds first observed in the Netherlands were not tested due to an insufficient number of observations.

To summarise, distances travelled increased with the harshness of the winter, whereas no influence of winter harshness on movement directions was found.

Exchange of individuals between different European regions

We found no within-winter movement between central/southern Europe and Great Britain. About 7.1% of the birds first observed in central/southern Europe moved to the north-western coast of mainland Europe, whereas only 2.9% of the birds first observed at the north-western coast of mainland Europe moved to central/southern Europe (Table 3, Fig. 6). About 12% of the birds first observed in Great Britain were later observed on the north-western coast of mainland Europe, and 5.9% of the birds first observed there moved to Great Britain (Table 3, Fig. 6). As a consequence, the proportion of birds first observed in a different region among the recoveries at the north-western coast of Europe is higher than in Great Britain and in central/southern Europe (Fig. 6).

Discussion

Long-distance movements of Common Pochards are not restricted to the migration period but may occur frequently on the wintering grounds. Based on ring recovery data, we show that 41% of all observed within-winter movements cover a distance >200 km. Unfortunately, little is known about such within-winter movements in other species (Owen and Black 1990) although waterbird census data suggest that they may be common in many species (Keller 2005). In Mallards *Anas platyrhynchos*, the proportion of birds moving >200 km within the same winter was very high in Sweden (>90%). Further south-west, this proportion was between 10 and 30%, with the lowest movement activity in Great Britain (<10%; Sauter et al. in preparation). Among Tufted Ducks *Aythya fuligula* ringed in Switzerland, 22% of all recorded within-winter movements were >200 km (own unpublished data).

Regional differences in movement patterns

The distance and direction of within-winter movements was strongly affected by the country where the bird was first observed (Figs. 1, 2, 3). The movement directions differed depending on the geographical features of an area. In the Netherlands, the vast majority of movements occurred

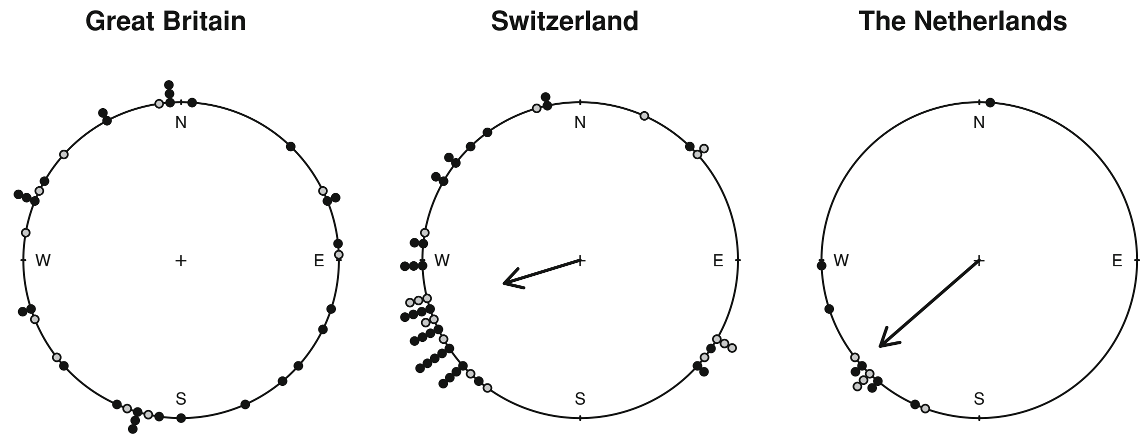

Fig. 3 Directions of movements >50 km by birds first observed in Great Britain, Switzerland and the Netherlands. Males are shown in *black*, females in *grey*. Overall significant mean directions are indicated by *arrows*. The *length of the arrow* is the standardised length of the mean vector (r)

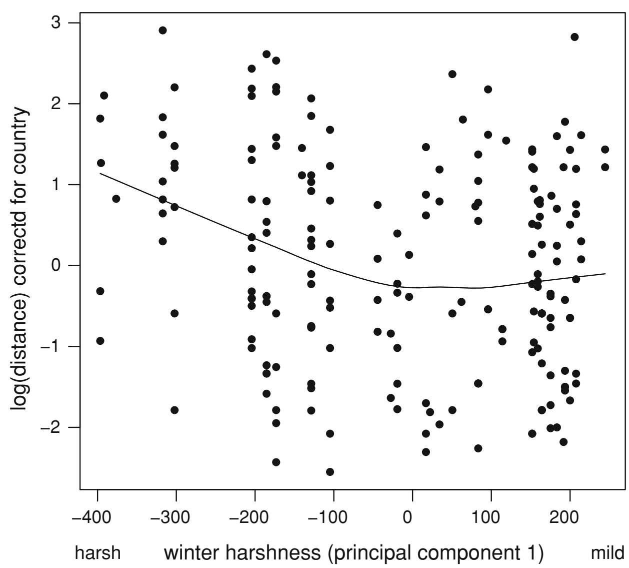

Fig. 4 Relationship between winter harshness and the distance travelled between first and second observation. Winter harshness is expressed as the first principal component based on Hellmann indices from central, north-western and north-eastern Europe (see text for details). The distances are corrected for the country of first observation (i.e. residuals from a linear model involving distance and country). A nonparametric smoother is given

along a SW–NE axis parallel to the coast of the European mainland while directions were much more variable in Switzerland and Great Britain, where most or all of the first observations were from inland sites. The absence of movements towards the south in Switzerland (Fig. 3) can probably be ascribed to the barrier effect of the Alps.

The regional characteristics of within-winter movements are likely also to be determined by small-scale features of the landscape, in particular, the distribution of a suitable habitat. In Great Britain, for example, many observations are from East Anglia where water bodies are common. Consequently, Pochards may only have to travel short distances to move between different suitable wintering sites. The situation is different in Switzerland. Most of the Swiss first observations were from Lake Sempach in central Switzerland where the food supply is very poor (lack of Zebra Mussel *Dreissena polymorpha* until 2000; Kinzelbach 1992; Kestenholz 1995; Turner et al. 1998; first record 2000, Josef Hofer personal communication). As a consequence, Pochards may stay only briefly before moving on to more suitable wintering sites, such as the larger Swiss lakes where food availability is significantly better due to the abundance of Zebra Mussels and macrophytes. Furthermore, in contrast to Great Britain, Switzerland lies in the centre of the wintering area of Pochards (Scott and Rose 1996). Therefore, birds first caught in Switzerland have a wider range of possible travel distances and directions than birds first caught in Great Britain.

Influence of sex and age on distance and direction

We found no significant differences in distances and directions moved by the two sexes, but we cannot exclude the possibility that sex-specific differences exist but were too small to be detected with the available data.

Similarly, we may not have found any difference in movement distances between age classes due to low statistical power. However, juveniles showed more westerly directions than adults in Switzerland, which may indicate different movement behaviour between the age classes. In Pochards, males normally leave their females when she is still breeding, and females leave their young when they are 8–9 weeks old (Bezzel 1969). Therefore, winter movements of juveniles probably take place independently of adults. Adults may be more tolerant of cold weather than juveniles and therefore less likely to move within winters (Hepp and Hines 1991). Furthermore, juveniles cannot rely on previous

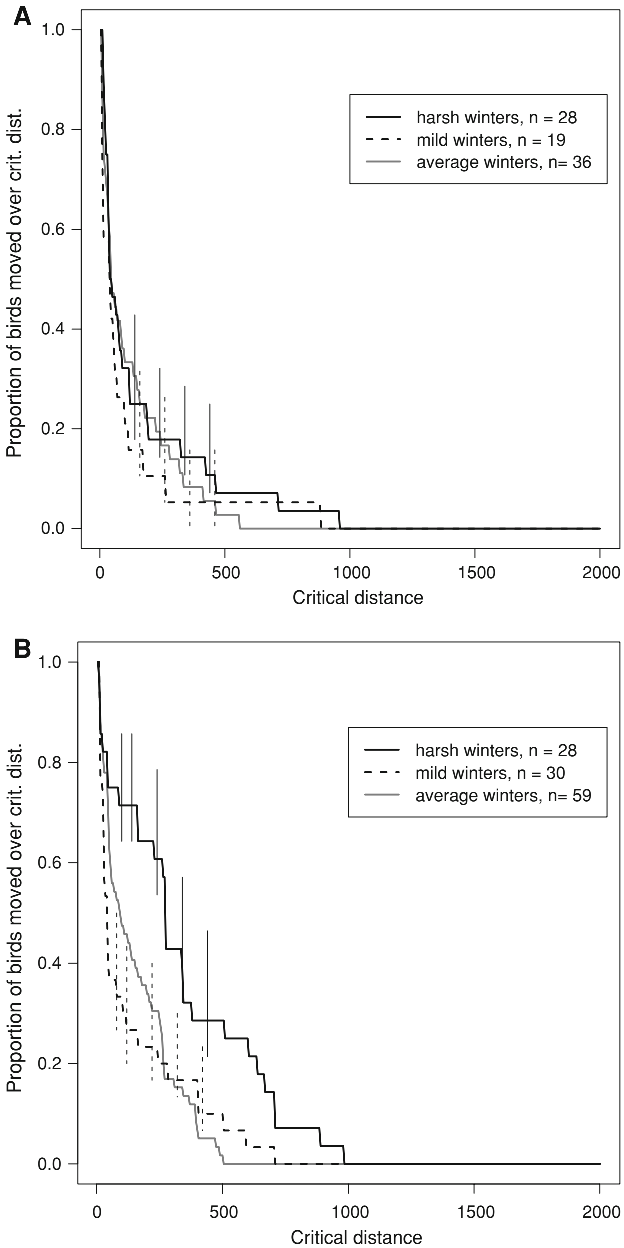

Fig. 5 Proportion of movements above the critical distance specified on the *x*-axis in cold (*black solid line*), average (*grey line*) or mild (*dashed line*) winters. **a** First observation in Great Britain, **b** first observation in mainland Europe (the Netherlands, Sweden, Denmark, Switzerland or Italy). *Vertical bars* indicate the 95% confidence intervals. Harsh winters were defined as the coldest 20%, and mild winters as the warmest 20% of all winters based on PC1

experience and may have to move around to explore the wintering area and find profitable wintering sites.

Influence of winter harshness on distances and directions

The high movement activity in all years suggests that within-winter movements are a common phenomenon in both mild and cold winters. Similarly, radar observations in Switzerland showed that the level of nocturnal flight activity of diving ducks in a mild mid-winter period is comparable to that observed during the autumn migration (Kestenholz 1995, 1999). It seems likely that such a high movement activity of wintering Pochards in all years could be an adaptation to continual changes in the winter environment such as, for example, the gradual depletion of food resources in the course of the winter (Suter 1982; Lovvorn 1989; Hamilton et al. 1994; Keller 2005; Werner et al. 2005) or the desiccation of water bodies during droughts (Owen and Black 1990; Ridgill and Fox 1990). The depletion of food resources may be a common phenomenon even in good overwintering habitats. At Lake Constance, for example, the wintering flocks move downstream along the lake and the river Rhine as mussel banks further upstream are depleted (Suter 1982). At a larger scale, the results of monthly waterbird counts indicate a gradual shift of Pochards from eastern to western Switzerland during the course of the winter (Keller 2005). A similar behaviour was observed in Canvasback Ducks *Aythya valisineria* (Lovvorn 1989) where birds move further south as food resources in the north are depleted.

The increase in movement distance below a certain threshold temperature (Fig. 4) suggests that Pochards are forced to leave an area because all available habitat freezes over. Alternatively, it is possible that the birds leave cold areas even when open water is still available because they are no longer able to meet their energy demands. However, in this case, we would expect a more gradual increase in movement distances with winter harshness, which is inconsistent with our results. Punctual events of mass migration as a reaction to cold spells rather than a gradual increase in movement rates with decreasing temperatures have been described by several authors (Impekoven 1965; Ogilvie 1981, 1982; Ridgill and Fox 1990; Suter and Van Eerden 1992; Lovvorn 1994 and Rustamov 1994).

Ridgill and Fox (1990) described dramatic cold weather movements of Pochards out of the Baltic and Waddensee towards the south and the west. In contrast, we did not find any differences in movement directions between mild and cold winters. This can potentially be ascribed to the generally high movement activity in all years in birds wintering in Western Europe. This discrepancy may suggest regional differences in the response of wintering Pochards to adverse weather conditions.

Exchange of individuals between different European regions

We found no direct exchange of individuals between Great Britain and central/southern Europe (Fig. 6). However, a relatively high movement rate (12.0 and 7.1%,

Table 3 Number of ringed and recovered birds moving between the different regions of Europe

Region of first observation	Region of second observation		
	Great Britain	Northern Europe	Central and southern Europe
Great Britain	73 (97.3/88.0%)	10 (21.3/12.0%)	0
Northern Europe	2 (2.7/5.9%)	31 (66.0/91.2%)	1 (1.3/2.9%)
Central and southern Europe	0	6 (12.8/7.1%)	78 (98.7/92.9%)

Numbers in parentheses are: (1) percentage per column = the value indicates where the birds of each region came from (pies in Fig. 6); (2) percentage per row = the value indicates where the birds of each region moved to (arrows in Fig. 6)

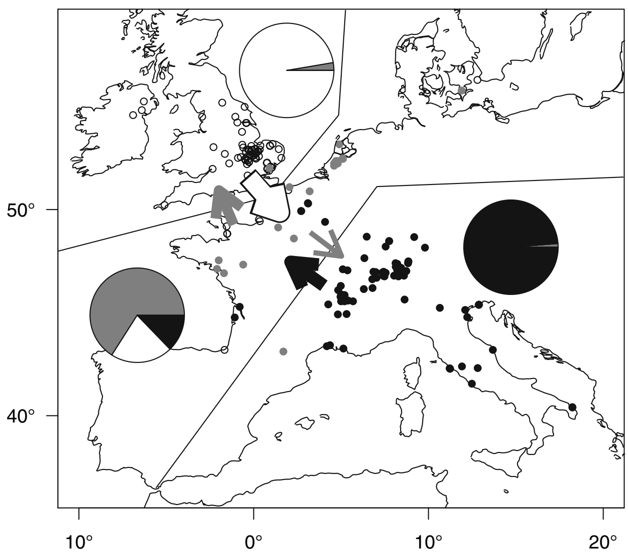

Fig. 6 Within-winter movements between regions. *Symbols* indicate the locations of the second observations. The *shade* of the symbols indicates the region of the first observation (*white* Great Britain, *grey* north-western coast of mainland Europe, *black* central and southern Europe). *Pies* Provenance of the birds in each region, *arrows* where the birds of each region move to (*size of arrow* indicates the proportion of emigrants per region; see also Table 3). There was no movement between central/southern Europe and Great Britain. The actual numbers are given in Table 3

respectively) towards the north-western coast of mainland Europe was observed from both regions, while movements in the opposite direction seemed to be slightly rarer (to Great Britain: 5.9%; to central/southern Europe: 2.9%; Table 3, Fig. 6). If we assume the wintering populations comprise 85,000 individuals in Great Britain (Baker et al. 2006), 200,000 at the north-western coast of mainland Europe and 300,000 in central/southern Europe (Delany et al. 2006), we can estimate the absolute numbers of individuals moving between the regions from the proportion of within-winter movements observed in the ring recovery data (Table 3). These numbers were 10,000 (95% confidence interval taking into account the uncertainty in the estimated movement rates but not taking into account the uncertainty in estimated population sizes: 5,000–18,000) and 21,000 (8,000–45,000) moving from Great Britain and southern Europe, respectively, towards the north-western coast of mainland Europe. Movements in the opposite direction seemed to be slightly rarer [to Great Britain: 12,000 (1000–39,000) individuals; to central/southern Europe: 6,000 (100–31,000) individuals]. These numbers should be considered with care, since the uncertainty is very high. Furthermore, note that the number of birds moving towards central/southern Europe may be overestimated due to potentially elevated ring recovery probabilities in this region (Table 1).

Interestingly, movements from the mainland to Great Britain and from the north-western coast to central/southern Europe were only observed during harsh winters (PC1 < 0), whereas movements in the opposite directions were also observed in mild winters (PC1 > 0).

Methodological issues

The probability that a ring is found and reported (reporting rate) differs strongly between countries and varies over time. This can lead to large biases in the quantifications of bird movements based on ring recoveries (Perdeck 1977). No appropriate methodology is available at the present time to correct for variations in reporting rates, since there are too many influencing factors (Thomson and Conroy 2007). The results we present here are all based on the assumptions that the reporting rate is constant both in the geographical sense and over time. We performed a series of post hoc tests in order to assess whether these assumptions were met. About 78% of our second observations were from hunted individuals, leading to a putatively strong dependence of local recovery probabilities on hunting activity.

First, we found a higher proportion of recoveries from hunted birds in southern Europe in February than in Great Britain and central Europe (see Materials and methods). Secondly, we found no significant differences in the proportion of recoveries from hunting between the different age and sex classes (log-linear model, likelihood ratio test, for sex: likelihood ratio = 1.3, $df = 1$, $P = 0.25$, for age: likelihood ratio = 0.3, $df = 1$, $P = 0.59$) even though females tend to winter further south in areas with higher hunting pressures (Tamisier 1985). This could indicate that the influences of different factors cancel each other out. Finally, we found that the proportion of recoveries from hunting did not differ significantly between the coldest and warmest 20% of all winters ($\chi^2 = 0.50$, $df = 1$, $P = 0.48$). These findings suggest that our conclusions are not systematically biased by sex-, age- or weather- dependent variation in the susceptibility to hunting.

We omitted observations within 1 km of the ringing site, where the detection probability is much higher than elsewhere and different between the countries (because of the differing catching efforts of the ringers and inconsistent recording habits of local recaptures between countries). The drawback of this method is that we have no information on those individuals that stayed within 1 km of the ringing site. However, Pochard movements between feeding and roosting sites or between different parts of the lake in response to wind directions normally cover distances >1 km (Kestenholz 1999; Keller and Burkhardt 2007). Therefore, we can reasonably assume that Pochards staying at the same wintering site (within the same lake) have the same detection probability as the ones moving to a different lake even if we exclude the recoveries within 1 km.

Conclusions

Within-winter movements of Pochards were commonly observed in all years with an increase in the frequency of long movements only in particularly cold winters. This suggests that within-winter movements mainly occur in response to environmental factors other than temperature (e.g. food availability). It further indicates that a disease transmitted by Pochards could be spread across Europe not only during the migration period but also during winter. The speed of such a spread may be elevated in particularly cold winters.

Previously postulated European subpopulations of wintering Pochards were, to some extent, confirmed but found to overlap considerably. This overlap mainly occurs along the north-western coast of mainland Europe rather than along the northern edge of the Alps as previously suggested (Scott and Rose 1996). Between years, some exchange between Great Britain and central/southern Europe was observed, but the majority of Pochards tend to return to the same wintering region (own unpublished data). These regions overlap considerably along the north-western coast of mainland Europe. The consequences of this porous substructure on the wintering grounds for population dynamics and the genetic structuring of European Pochards are currently unclear. Evidence from ringing data suggests that the breeding areas of birds wintering in Great Britain and Switzerland overlap to a large extent, particularly on the West Siberian Plain (own unpublished data). As Common Pochards mainly pair on their breeding grounds (Bezzel 1959; Glutz von Blotzheim and Bauer 1991), high levels of gene flow between the two European wintering “populations” seem likely.

Zusammenfassung

Winterwanderungen: Ein häufiges Phänomen bei der Tafelente *Aythya ferina*

Anhand von Ringfunden beschreiben wir Wanderungen innerhalb desselben Winters bei Tafelenten, die in Europa überwintern. In der EURING-Datenbank gibt es Daten von 201 Tafelenten, die im selben Winter (Dezember–Februar) zwei Mal von verschiedenen Orten gemeldet wurden (Beringung, Kontrolle oder Ringfund). Richtung und Distanz dieser Verschiebungen werteten wir im Hinblick auf Unterschiede zwischen den Regionen, den Geschlechtern und Altersklassen aus. Ebenso korrelierten wir die Distanzen und Richtungen mit der Temperatur (Winterhärte). Zuletzt quantifizierten wir den Austausch von Individuen zwischen den verschiedenen Subpopulationen der überwinternden Tafelenten in Europa.

Wir beobachteten eine relativ hohe Wanderrate. Bei 41% der Tafelenten, die innerhalb desselben Winters zwei Meldungen aufwiesen, lagen diese über 200 km auseinander. Da in Großbritannien, den Niederlanden und in der Schweiz intensiv Tafelenten beringt wurden, stammten die Erstmeldungen hauptsächlich aus diesen drei Ländern, während die Zweitmeldungen über ganz Europa verstreut lagen. Richtungen und Distanzen unterschieden sich signifikant zwischen den drei Ländern. Während die niederländischen und schweizerischen Tafelenten im Schnitt gut 200 km weit zogen, betrug diese Strecke in Großbritannien nur 125 km. Die Richtungen streuten in Großbritannien stark, während sie in den Niederlanden eindeutig entlang der Küstenlinie und in der Schweiz ansatzweise entlang der Alpen ausgerichtet waren. Wir fanden keine Geschlechtsunterschiede in Richtung und Distanz und nur schwache Altersunterschiede. In der Schweiz zogen Erstjährige nordwestliche Richtungen vor, während Adulte eher südwestliche Richtungen einschlugen. Für milde Winter bestand kein Zusammenhang zwischen Distanzen und Winterhärte, unter einem Schwellenwert stiegen die Distanzen jedoch mit zunehmender Winterhärte an. Das Zufrieren von Seen könnte einen solchen Zusammenhang bewirken. Die Richtungen unterschieden sich nicht zwischen kalten und warmen Wintern.

Ein beträchtlicher Anteil der zweimal im selben Winter gemeldeten Tafelenten zog von Großbritannien (12%) und von Zentral-und Südeuropa (7%) an die Nordwestküste

Europas. Ein fast so hoher Anteil (6%) zog von der Nordwestküste Europas nach Großbritannien, während ein kleinerer Anteil (3%) von der Nordwestküste nach Zentral- oder Südeuropa zog. Wir beobachteten keinen direkten Austausch zwischen Zentral- bzw. Südeuropa und Großbritannien. Die generell hohe Wanderrate innerhalb einer Wintersaison bei Tafelenten wird auf die Erschöpfung der Nahrungsquellen zurückgeführt. Die Beschreibung des Austauschs zwischen den Subpopulationen von in Europa überwinternden Tafelenten ist im Hinblick auf eine Verschleppung des Vogelgrippevirus wichtig.

Acknowledgments We thank Euring and, in particular, Chris du Feu, for providing the data. We are grateful to Marc Kéry, Michael Schaub, Annette Sauter, Dominik Thiel, Elisabeth Wiprächtiger and Arie van Noordwijk for their support and helpful discussions. Verena Keller, Barbara Tschirren and an anonymous reviewer provided valuable comments on an earlier draft of this manuscript.

References

Agostinelli C (2006) Circular statistics. R package: circular statistics. In: Jammalamadaka SR, SenGupta A (eds) Topics in circular statistics. World Scientific, Singapore

Alerstam T (1990) Bird migration. Cambridge University Press, Cambridge

Baker H, Stroud DA, Aebischer NJ, Cranswick PA, Gregory RD, McSorley CA, Noble DG, Rehfisch MM (2006) Population estimates of birds in Great Britain and the United Kingdom. Br Birds 99:25–44

Batschelet E (1981) Circular statistics in biology. Academic Press, London

Berthold P (2000) Vogelzug, Eine aktuelle Gesamtübersicht. Wissenschaftliche Buchgesellschaft, Darmstadt

Bezzel E (1959) Beiträge zur Biologie der Geschlechter bei Entenvögeln. Anz Ornithol Ges Bayern 5:269–355

Bezzel E (1969) Die Tafelente (*Aythya ferina*). Die neue Brehm-Bücherei, vol 405. A. Ziemsen-Verlag, Wittenberg Lutherstadt

Blums P, Baumanis J (1990) Migration and geographical distribution of Pochard and Tufted Duck populations in the USSR. In: Vìcksne J, Vilks I (eds) Baltic birds 5, ecology migration and protection of Baltic birds, vol I. Publisher Riga, Riga, pp 49–57

Carbone C, Owen M (1995) Differential migration of the sexes of Pochard *Aythya ferina*: results from a European survey. Wildfowl 46:99–108

del Hoyo J, Elliot A, Sargatal J (1992) Handbook of the birds of the world, vol 1: Ostrich to ducks. Lynx Editions, Barcelona

Delany S, Veen J, Clark J (2006) Urgent preliminary assessment of ornithological data relevant to the spread of avian influenza in Europe. Wetlands International. Available at: http://ec.europa.eu/environment/nature/nature_conservation/focus_wild_birds/avian_influenza/index_en.htm

Federal Veterinary Office (2007) Schweizer Zoonosebericht 2006. BVET Magazin 3:12–14

Fisher NI (1993) Statistical analysis of circular data. Cambridge University Press, Cambridge

Glutz von Blotzheim UN, Bauer KM (1991) Handbuch der Vögel Mitteleuropas 12/1(3). AULA, Wiesbaden

Glutz von Blotzheim UN, Bauer K, Bezzel E (1985) Handbuch der Vögel Mitteleuropas, vol 10/1. AULA, Wiesbaden

Hamilton DJ, Ankney CD, Bailey RC (1994) Predation of Zebra Mussels by diving ducks: an exclosure study. Ecology 75:521–531

Heine G, Jacoby H, Leuzinger H, Stark H (1999) Die Vögel des Bodenseegebietes. Vorkommen und Bestand der Brutvögel, Durchzügler und Wintergäste. Ornithol Jahreshefte Baden-Württemberg 14/15:847

Hepp GR, Hines JE (1991) Factors affecting winter distribution and migration distance of Wood Ducks from southern breeding populations. Condor 93:884–891

Hofer J, Korner-Nievergelt F, Korner-Nievergelt P, Kestenholz M, Jenni L (2006) Herkunft und Zugverhalten von in der Schweiz überwinternden oder durchziehenden Tafelenten *Aythya ferina*. Ornithol Beob 103:65–86

Ijnsen F (1988) Het karakterisieren van winters. Zenit 15:50–58

Imboden C, Imboden D (1972) Formel für Orthodrome und Loxodrome bei der Berechnung von Richtung und Distanz zwischen Beringungs- und Wiederfundort. Vogelwarte 26:336–346

Impekoven MZ (1965) Verbreitung und Fluchtmigration von Krickenten in den kalten Wintern 1956 und 1962/63: Eine vergleichende Analyse der Rückmeldungen in la Tour du Valant. Trans Conf Int Union Game Biol 6:293–307

Keller V (2005) Entwicklung der Wasservogelbestände in den Wasservogelreservaten von internationaler Bedeutung 1992/93–2002/03: Eine Bilanz. Schweizerische Vogelwarte, Sempach

Keller V, Burkhardt M (2007) Monitoring Überwinternde Wasservögel: Ergebnisse der Wasservogelzählungen 2005/06 in der Schweiz. Schweizerische Vogelwarte, Sempach,

Kershaw M (2002) Common Pochard (Pochard) *Aythya ferina*. In: Wernham C, Toms M, Marchant J, Clark J, Siriwardena G, Baillie S (eds) The migration atlas movements of the birds of Britain and Ireland. T&A D Poyser, London, pp 204–207

Kestenholz M (1995) Movements and roosting behaviour of diving ducks (*Aythya fuligula* and *A. ferina*) wintering in Switzerland. Philosophisch-Naturwissenschaftliche Fakultät, Universität Basel

Kestenholz M (1999) Mid-winter movements: a behavioural strategy of diving ducks wintering in a changing environment. Ring 21:26

Kinzelbach R (1992) The main features of the phylogeny and dispersal of the Zebra Mussel *Dreissena polymorpha*. Gustav Fischer Verlag, Stuttgart

Lovvorn JR (1989) Distributional response of Canvasback Ducks to weather and habitat change. J Appl Ecol 26:113–130

Lovvorn JR (1994) Nutrient reserves, probability of cold spells and the question of reserve regulation in wintering Canvasbacks. J Anim Ecol 63:11–23

Monval JY, Pirot JY (1989) Results of the IWRB international waterfowl census 1967–1986. International Waterfowl Research Bureau special publication no. 8. IWRB, Slimbridge

Nilsson L (1984) The impact of hard winters on waterfowl populations of south Sweden. Wildfowl 35:71–80

Ogilvie MA (1981) Hard weather movements of *Anas crecca* ringed in western Europe—a preliminary computer analysis. In: Proc IWRB Symp. International Waterfowl Research Bureau, Alushta

Ogilvie MA (1982) Winter 1978/79 hard weather movements and mortality of ducks ringed in the United Kingdom. In: Proc 2nd Tech Meet Western Palearctic Migratory Bird Manage. International Waterfowl Research Bureau, Paris

Owen M, Black JM (1990) Waterfowl ecology. Chapman & Hall, New York

Owen M, Dix M (1986) Sex ratios in some common British wintering ducks. Wildfowl 37:104–112

Perdeck AC (1977) The analysis of ringing data: pitfalls and prospects. Vogelwarte 29[Sonderheft]: 33–44

Perdeck AC, Clason C (1983) Sexual differences in migration and winter quarters of ducks ringed in the Netherlands. Wildfowl 34:137–143

R Development Core Team (2006) R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria

Ridgill SC, Fox AD (1990) Cold weather movements of waterfowl in Western Europe. International Waterfowl Research Bureau special publication 13. IWRB, Slimbridge, pp 1–89

Rose PM, Scott DA (1994) Waterfowl population estimates. International Waterfowl Research Bureau special publication 29. IWRB, Slimbridge

Rustamov EA (1994) The wintering waterfowl of Turkmenistan. Wildfowl 45:242–247

Sayler RD, Afton AD (1981) Ecological aspects of Common Goldeneyes *Bucephala clangula* wintering on the upper Mississippi River. Ornis Scand 12:99–108

Scott DA, Rose PM (1996) Atlas of Anatidae populations in Africa and Western Eurasia. Wetlands International Publication, Oxford

Suter W (1982) Die Bedeutung von Untersee-Ende/Hochrhein (Bodensee) als wichtiges Überwinterungsgewässer für Tauchenten (*Aythya*, *Bucephala*) und Blässhuhn (*Fulica atra*). Ornithol Beob 79:73–96

Suter W, Van Eerden MR (1992) Simultaneous mass starvation of wintering diving ducks in Switzerland and the Netherlands: a wrong decision in the right strategy? Ardea 80:229–242

Tamisier A (1985) Hunting as a key environmental parameter for the Western Palearctic duck population. Wildfowl 36:95–103

Thomson D, Conroy M (2007) EURING 2007, Technical meeting. January 14–20 2007, Dunedin, New Zealand

Turner H, Kuiper JGJ, Thew N, Bernasconi R, Rüetschi J, Wüthrich M, Gosteli M (1998). Mollusca, Atlas. Centre Suisse de Cartographie de la Faune (CSCF/SZKF), Neuchâtel

Werner S, Mörtl M, Bauer HG, Rothhaupt KO (2005) Strong impact of wintering waterbirds on Zebra Mussels (*Dreissena polymorpha*) populations at Lake Constance, Germany. Freshw Biol 50:1412–1426

Wernham C, Toms M, Marchant J, Clark J, Siriwardena G, Baillie S (2002) The Migration Atlas: movements of the birds of Britain and Ireland. T.& A.D, Poyser, London

Willi P (1970) Zugverhalten, Aktivität, Nahrung und Nahrungserwerb auf dem Klingnauerstausee häufig auftretender Anatiden, insbesondere von Krickente, Tafelente und Reiherente. Ornithol Beob 67:141–217