Ornis Fennica 92:204–212. 2015

Unusual migratory behaviour in a newly established subpopulation of Whooper Swan (*Cygnus cygnus*) breeding in the highlands of Poland

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Received 23 October 2014, accepted 31 July 2015

The migratory behaviour of a subpopulation of Whooper Swans breeding in highlands of southern Poland was studied over a 17-year period, from 1997 to 2013. Birds ringed in their breeding area spent winters and moulting periods in the vicinity of their natal sites, and the mean distance between breeding area and wintering sites was only 149.1 ± 11.7 km. Moreover, 57.0% of all winter re-sightings were obtained within 100 km of the study area. There was an increase in winter site fidelity by individual Whooper Swans over their life-time ($R^2 = 0.09$, $p = 0.019$), reflected by a linear decrease in the distance travelled between two consecutive winters ($\beta = -0.22 \pm 0.09$). We did not find any association between winter severity and the birds' migratory behaviour, neither in the distance travelled nor the location of winter recoveries. The mean distance between the study area and the moulting site was 142.7 ± 34.6 km and c. 66.6% of ring re-sightings during the moulting period were within 100 km of the study area. During autumn many immature birds were observed close to their parents' breeding territory and this could help them reunite with parents or siblings from other seasons. The apparent reduction of migratory behaviour compared with representatives of northern populations indicates behavioural plasticity in the Whooper Swan, which may facilitate further southward expansions of the species.

1. Introduction

Over the decades, trends in the populations size of European birds has varied due to the influence of various factors, such as climate changes (global warming), habitat fragmentation, human activity (hunting, tourism) or changes in agricultural practices (e.g., Holmes & Sherry 2001, Fox *et al.* 2005, Pöysä *et al.* 2013, Carrascal *et al.* 2014). One bird species that has shown a considerable population size increase over the last few decades is the Whooper Swan (*Cygnus cygnus*; Brazil 2003),

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whose breeding range was traditionally confined to Iceland, north-east Europe and northern Asia (Cramp & Simmons 1977). Hunting depleted the breeding population in many European countries during the late 19th century (Brazil 2003), and by the early 20th century breeding pairs in the mainland Europe were confined to remote parts of Norway, Sweden and Finland (Myrberget 1981, Nilsson *et al.* 1998). Legal protection since the mid 20th century has resulted in a recovery of population size and the recolonisation of previously occupied areas (Haapanen 1991, Brazil 2003). Winter and summer counts revealed that the Fennoscandian/northwest Russian breeding population doubled its size between 1974 and 1993 (Brazil 2003). At the same time, breeding pairs appeared along the Baltic coast in Estonia, Latvia, Lithuania and Germany (e.g., Profus 1999, Luiguöje *et al.* 2002, Butkauskas *et al.* 2012, Boiko *et al.* 2014).

The first pair reported breeding in Poland was observed in 1973 (Sikora *et al.* 2012). Initially territories were established in parts of the country: the Silesian fish farms and the Podlasie lowlands, in areas traditionally used by Whooper Swans during the autumn and spring migration from north-east to western Europe. Numbers breeding in Poland increased rapidly to 80–90 pairs over the next 30 years, with breeding pairs recorded at sites across the northern and western part of the country (Sikora *et al.* 2012). The first Whooper Swan pair to nest in the highlands of Poland, recorded found in 1997, probably reflected an extension of the breeding range for the increasing number of pairs nesting in Silesia (Czyż & Woźniak 1998). A total of 18 breeding pairs now nest in the Polish highlands (Dudzik *et al.* 2014; unpubl. data).

The Whooper Swan is a migratory species, with distinct breeding and wintering grounds, and the annual return migration can take up to four months of the year (Brazil 2003). Birds breeding in northern Europe and the European part of Russia spend the winter in continental Europe (Laubek *et al.* 1998, Luiguöje *et al.* 2002), with the newly-established populations on the eastern part of the Baltic coast similarly undergoing long distance autumn and spring migrations. For example, birds breeding in Latvia spend the winter in Germany and are estimated to cover over 800 km during migration (Boiko & Kampe-Persson 2011). Little is known, however, about the migratory behaviour of birds from the southernmost parts of their breeding range.

Climate can have a strong effect on the behaviour and annual cycle of avian species, especially those frequenting in the boreal zone (Carey 2009). The short but intense period of vegetation growth at high latitudes is regarded as a main factor underlying migratory activity and the timing and duration of the breeding season for species wintering in a temperate climate (Drent *et al.* 2003, Klaassen 2003). Birds have to schedule their arrival and departure time precisely because the period in which breeding can occur is very short (Jensen *et al.* 2014, Nuijten *et al.* 2014).

Moreover, they have to travel considerable distances in order to find appropriate conditions for wintering. Species/individuals which breed in the temperate zone are not time-constrained in this way. The period of suitable weather conditions and an abundant food supply is sufficient to fulfil the requirements of growing juveniles. Winters can be mild and allow birds to reduce the migratory distance, staying in close proximity to their breeding territories. Resident individuals save on the energy demands of a long-distance flight but may be subjected to higher predatory pressure and intraspecific competition during winter. These different environmental conditions may result in a change in the behaviour of individuals occupying the southern edge of the species' home range.

Observations made of Whooper Swans breeding in central Europe provide an opportunity to test this scenario. Birds occupying territories in southern Poland have to face different environmental conditions than individuals nesting in arctic and sub-arctic regions. The aim of our study was to determine whether breeding in the temperate zone influences the location of wintering and moulting sites for Whooper Swans nesting in southern Poland. We investigated whether individuals adjust their migratory distance in relation to local weather conditions, and if this modified migratory behaviour was continued over the bird's life-time. We also assessed whether swans from our study area used different moulting and wintering sites to those used by Whooper Swans breeding further north. Re-sightings data (date and location) recorded for neck-banded individuals from 1997–2013 inclusive were used in the analyses.

2. Material and methods

Observations were made of 18 breeding pairs and their offspring, located in a 8,740 km^2 study area in the highlands of Poland (Fig. 1). Whooper Swans in the region established their breeding territories on fish farms of different sizes (40–100 hectares), at least partially surrounded with forests (Dudzik *et al.* 2014). From 1997 onwards, we recorded the annual breeding success of each pair, and also attempted to ring all fledged cygnets and breeding pairs within the study area. In total, 79 cygnets (46 males, 29 females, 4 non-sexed individuals) and 5 adult breeding birds (3 females) from 10 territories were ringed between 1997–2013 (Fig. 1). Of these, 96% of the cygnets and all of the adults were marked with neck collars. Between August 1997 and November 2013 we collected 1983 recoveries from 73 individuals. All recoveries, which were made by different observers, came from the Polish Ringing Centre database.

In order to analyse annual variation in Whooper Swan movements, the recovery data were grouped into six distinct time periods reflecting the different stages of the swans' annual cycle, based on extensive field observations carried out by Dudzik *et al.* (2014) in southern Poland: spring migration (months III–IV), onset of breeding and pre-moulting (V–VI), moult (VII–VIII), pre-migratory (IX), autumn migration (X–XI) and wintering period (XII–II). Our analyses thus focused on four distinct parts of the year connected to migratory behaviour: spring and autumn migration, moult and wintering time. In order to avoid bias caused by some sites having more observers than others, only one observation of an individual swan per location was used for each time period each year. Using this approach, we obtained a dataset of 898 location records from 73 individuals (68 cygnets and 5 adults, Table 1). Most of the data were from sightings of neck-collared birds (97.1%), while only a small proportion was obtained from swans ringed with metal rings (2.5%) and from dead birds (0.4%).

Three values were recorded to describe each sighting or recovery: the geographical coordinates of the site, distance from the ringing site and the angle of movement between ringing and sighting locations. The direction and distance of movement was calculated from the geographical coordinates using the loxodromic formula (Imboden & Imboden 1972). All distance values were log-transformed to improve normality. The mean location of the wintering/moulting grounds for the subpopulation of swans from southern Poland was calculated as the means from coordinates of particular re-sightings (Bairlein 2001). Only one observation was used to describe the location of a family group on calculating mean coordinates of the wintering site (i.e. repeat sightings of siblings/mates were omitted) because Whooper Swan cygnets usually remain with their parents throughout their first winter (Brazil 2003). In our study, for 69.8% of first winter birds, the swans' parents and/or siblings (if any) were also recorded in the same winter flock. Taking just one location measure per pair or family group was necessary to avoid any biases arising from differences in family size and the number of cygnets marked in each family. Moulting site location was based on data collected from non-breeding birds because breeders generally moult within their breeding territory (n = 37). In order to check whether birds adjust the distance to the wintering grounds according to local weather conditions, we used three variables describing winter severity based on weather data obtained from the Kielce Meteorological Station, which is situated within the study area. The following variables were used: mean winter temperature (XII–II), the NAO index for winter months and the index of winter severity (Eq. 1) calculated using the formula proposed by Meininger *et al.* (1991).

$$V = 0.000275 \times v^2 + 0.667 \times ij + 1.111 \times z \qquad (1)$$

V – winter severity index
v – number of frost days (with minimum temperature below 0°C)
ij – number of ice days (with maximum temperature below 0°C)
z – number of days with harsh climate conditions (with maximum temperature below –10°C)

In circular statistical analyses (angle of migration) we followed Batschelet (1981) and used Oriana 4.0. software. Statistical methods for linear variables (distance of migration) were based on Zar (1996) and the analysis was performed using STATISTICA ver. 10.0 software (StatSoft 2011). All values are presented as means ± SE.

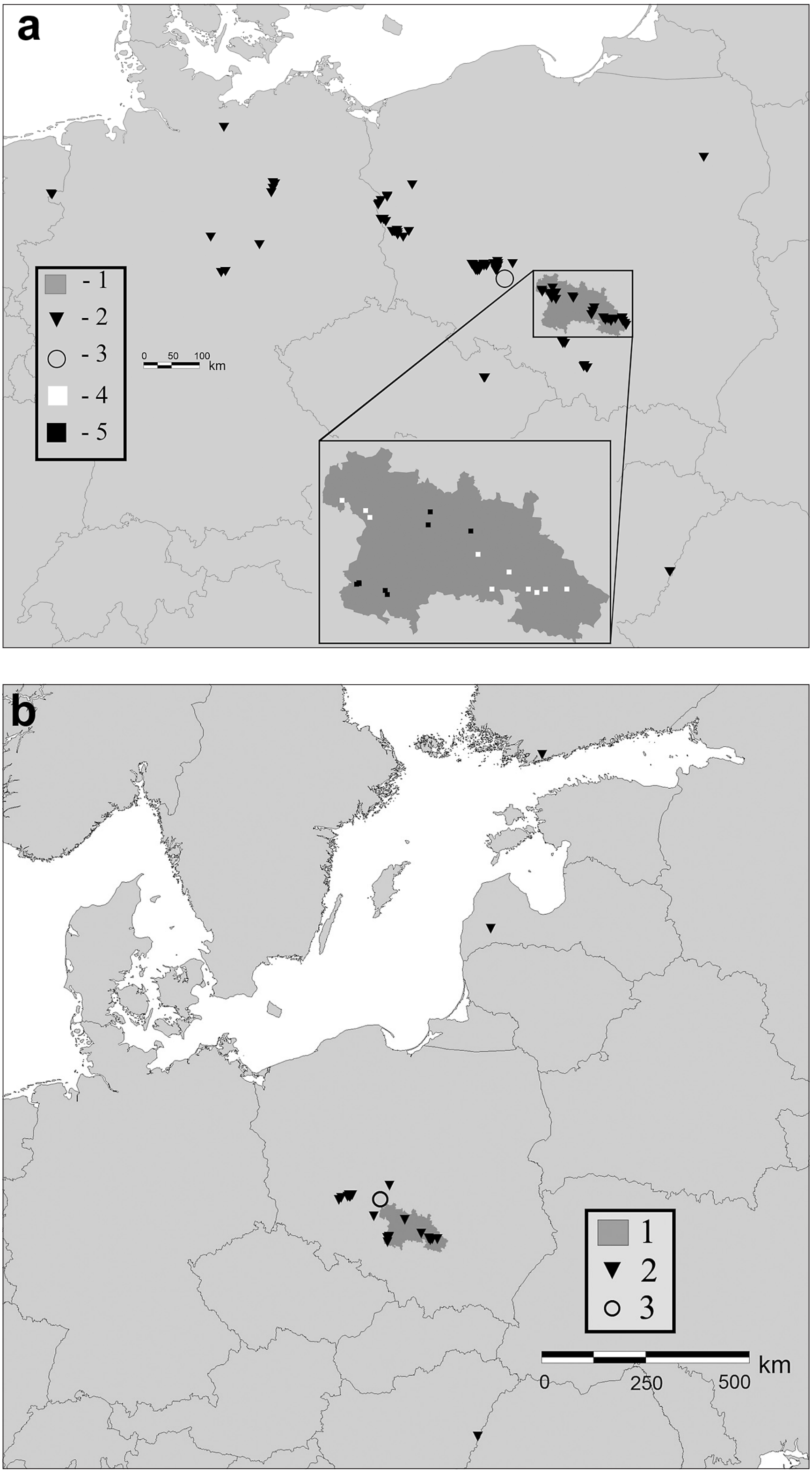

Fig. 1. Distribution of the re-sightings from wintering (a) and moulting (b) period of Whooper Swans ringed in the highlands of southern Poland (1 – study area, 2 – re-sightings, 3 – mean location of wintering/moulting re-sightings, 4 – breeding territory where birds were ringed, 5 – breeding territory without ringing activity).

3. Results

3.1. Wintering grounds

The mean location of wintering grounds for the local population was situated in south-western Poland (51°29'N, 17°56'E; Fig. 1a). The mean value of the distance travelled between the study area and wintering grounds was 149.06 ± 11.74 km. The vast majority of winter records (91.7%) were collected within Poland but reports were also received from Germany (6.5%), Hungary (1.4%) and The Czech Republic (0.4%). Overall, 57.0% of observations were collected within 100 km of the study area. The mean angle of movements between study area and wintering grounds was 307.86° and the direction of movements was not randomly distributed (Rayleigh test: Z = 29.741, $p < 0.001$), with birds moving mainly in a north-west direction. A comparison of the winter locations for birds observed over several consecutive winters showed that 57% of individuals wintered within 50 km of the wintering site from the previous year. Data obtained from birds ringed as nestlings (n = 57) indicated that winter site fidelity increased with the life-span of a bird (linear regression: $R^2 = 0.09$, $p = 0.019$), and that there was a linear decrease in the difference between the locations of two consecutive wintering sites (regression coefficient: $\beta = -0.22 \pm 0.09$, Fig. 2). Winter conditions during the study were variable, with mild weather (mean winter temperature above 0.0 °C, in 5 seasons) and severe weather (mean temperature below –2.0 °C, in 5 seasons) recorded during the course of the study. However, none of the winter severity variables influenced the distance between the ringing and winter resighting locations (multiple regression: $R^2 = 0.02$, $p = 0.12$). Moreover, the index of weather severity did not appear to have a significant effect on the latitude of the wintering site used by a swan or family group each year (linear regression: $R^2 = 0.0009$, $p = 0.74$).

3.2. Moulting grounds

The mean location of moulting sites used by birds ringed in the highlands of southern Poland was 51°16' N, 18°14' E (Fig. 1b), and the mean distance between ringing and moulting sites was 142.7 ± 34.6 km. However, 66.6% of observations during the moulting period were made within 100 km of the study area. Re-sightings during the moult time were not randomly distributed around the study area (Rayleigh test: Z = 6.465, p = 0.001), with birds observed mainly to the north-west of the ringing site (mean degree of migration: 309.28°) at this time. Only two individuals moulted in the northern part of the species' home range: one male (3R07) in southern Finland – 1,063.0 km from the study area and another male (3R03) in western Latvia – 657.6 km from the study area. In the following season, the latter (3R03) moulted in the place situated in south-eastern Hungary – 520.9 km from the study area and 1,088.0 km from the previous moulting site.

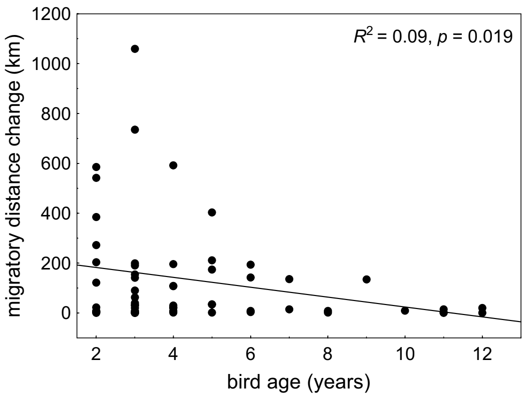

Fig. 2. Differences in wintering distance covered by birds in two consecutive winters among different age classes of Whooper Swans from highlands of southern Poland.

3.3. Autumn and spring migration

The mean distance of autumn recoveries from the study area for swans resighted or recovered in autumn was 26.2 ± 5.75 km in October and 136.6 ± 18.6 km in November. In both months the majority were within 100 km of ringing site (92.5% in October, 65.3% in November). Birds originally ringed as cygnets were often observed close to their natal area in autumn, prior to moving to the wintering grounds: 36% of the sightings recorded for non-breeding birds in October–November each year found that the birds were within 30 km of the site where they hatched. This behaviour was

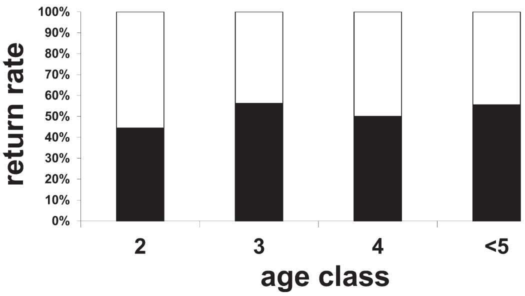

Fig. 3. Percentage of individuals that underwent migration to their natal area before winter migration (black bars) among different age classes of Whooper Swans from southern Poland.

observed in swans of all age classes from the 2nd till the 5th calendar year of life (Fig. 3). Moreover, birds were often seen with other family members (parents or siblings from the same or different years); such associations were noticed in 34% of autumn observations. Swans resighted in the spring were also mainly found close to the study area, when the mean distance between the ringing and resighting sites was 61.4 ± 17.2 km in March (i.e. at the start of spring migration) and 74.1 ± 18.7 km in April (i.e. once spring migration was more advanced). When excluding one record from bird that was observed in northern Europe the mean distance for April was 59.3 ± 11.3 km. Moreover, 83.9% of re-sightings were collected within 100 km of the study area in March and 85.4% in April.

4. Discussion

Our analyses found that Whooper Swans from the highlands of southern Poland wintered close to their breeding grounds. The mean distance between the breeding areas, where the swans were ringed, and the sites where the birds were observed in winter is very short in comparison with migration distances recorded for swans breeding at higher latitudes (Rees *et al.* 1997, Boiko & Kampe-Persson 2011). Indeed, the observed migratory distance (150 km) could be treated as a local movement, possible to travel in less than one day (Rees *et al.* 2002). The reduced migratory behaviour can be advantageous. Birds reducing migration distance can save energy and avoid risk of death by not prolonging the flight. They benefit from familiarity with local conditions: food resources, a suitable roosting place or the level of predation (Newton 2008). They can also stay close to their breeding territory and take advantage of the early arrival in spring (Kokko 1999). Some aspects of species biology predispose Whooper Swan to increased sedentary behaviour. Whooper Swans use arable land for feeding in winter and take advantage of nutritious winter crops (Rees *et al.* 1997). Unlike Mute Swans (*Cygnus olor*) or dabbling ducks, they do not depend on access to water plants during the winter months, when they use water bodies mainly as a night-time roost and also to escape from predators (Laubek *et al.* 1999). The climate in the south of Poland helps the birds to reduce their migratory activity. Rivers freeze only during severe winters and are surrounded by arable fields suitable for feeding. The fish farms also provide a possibility of sleeping and feeding till late autumn. Birds have to move further west only after long periods of harsh conditions. Evidence for the proposed scenario is provided by the lack of a correlation between the winter severity and the distance travelled for our study birds, whereas this was detected in the fully migratory populations of northern Europe (Boiko & Kampe-Persson 2011).

The winter site fidelity found in our study is commonly observed in waterbirds, swans in particular (Rees 1987, Robertson & Cooke 1999). As mentioned above, individuals benefit from spending winters in a familiar place. The winter period causes significant mortality in swans (Brown *et al.* 1992); thus overwintering at high-quality sites can considerably increase their survival rate. Additionally, wintering in suitable areas can help birds to find conspecifics in a good state of health and to mate with high quality individuals (Heitmeyer 1995). This is especially important for those waterfowl species in which pair formation occurs on the wintering grounds (Anderson *et al.* 1992). The experience from the previous wintering seasons can promote the increased site fidelity to wintering sites observed in our study. In the majority of species, immature individuals show a higher level of migratory behaviour in comparison with adult birds (Greenwood & Harvey 1982). They try to explore different areas in order to find suitable wintering grounds for the future and avoid to intraspecific competition. Adult individuals reduce

Table 1. Number of re-sightings obtained in years 1997–2013 from Whooper Swans ringed in highlands of southern Poland for each period of the annual cycle.

Period of year	Observations	Individuals observed	Seasons observed (range; mean)
Spring migration (III–IV)	147	46	1–10; 2.78
Pre-moulting period (V–VI)	121	38	1–4; 2.15
Moult (VII–VIII)	88	21	1–6; 1.79
Pre-migratory period (IX)	106	56	1–5; 1.84
Autumn migration (X–XI)	206	62	1–8; 2.40
Wintering period (XII–II)	230	53	1–10; 3.01

their own exploratory behaviour as they have experience from the previous wintering seasons. As a consequence, the increased site philopatry is expected in older age classes, compared with immature birds. In the case of swans and geese, philopatry to wintering grounds can be strengthened by the extended parental care in this group of birds. Young birds accompanied by their parents obtain a higher social status in wintering flock than solitary individuals (Kotrschal *et al.* 1993). They get access to food-rich patches and are exposed to lower aggression level (Klaassen *et al.* 2006). The prolonged parental care can be beneficial even in older age classes as the whole family has a higher chance to win in social interactions due to the positive effect of its size. In our study, we observed some evidence for extended parental care as a large proportion of the re-sightings of non-breeders from autumn migration were done in the area close to their birth place. Moreover, birds were observed with their parents or siblings. Consequently, they can reunite with their parents and spend winter together as enlarged family groups (Robertson & Cooke 1999).

Birds from the studied population moult in the areas close to their natal place. Notably, they generally do not mix with the representatives of northern populations during the moulting period. Local conditions allow birds to moult in shallow fish ponds with well-developed reed belts that provide abundant food source and shelter during the non-flight period. Moulting close to the birth place is a new finding for the Whooper Swan. For example, birds breeding in Latvia moult mainly outside the country, up to 1,455 km from the birth place (Boiko & Kampe-Persson 2012). Swans from southern Poland are, to a certain extent, isolated from birds breeding at high latitudes, however some individuals join their northern counterparts and move north for moulting (two re-sightings from northern Europe). Although Whooper Swans from the highlands of Poland contact with the “northern” individuals during both migration and wintering, the existing isolation may reduce gene flow between both populations. The proposed scenario can be supported by the presence of the pair consisting of siblings from two consecutive breeding seasons, observed within the study area (Dudzik *et al.* 2012).

To conclude, our results show that birds from the southernmost subpopulation of Whooper Swan, living on the edge of the species range, exhibit different migratory activity in comparison with representatives of northern populations. Individuals spend winter and moult in close proximity to their birth place. The majority of them did not move significant distances during the study period. All observed behavioural adaptations to warmer climate can facilitate the range expansion of the species to the south. On the other hand, the reduced migratory behaviour can have a negative effect in terms of mate choice and genetic isolation of newly established subpopulation. Moreover, nearly year-round presence of new species can cause a conflict with other waterfowl (Mute Swan) and humans (crops damage). The Whooper Swan wins in territorial conflicts with the Mute Swan, replacing it in suitable habitats (Butkauskas *et al.* 2012). However, in Poland the competition for territories can be reduced as Whooper Swans still avoid areas with intensive human activity and breed in more remote waterbodies than Mute Swans (Sikora *et al.* 2012). Feeding on fields can become a significant problem in the near future as the number of residential birds will most probably increase.

Acknowledgements. We are grateful to all participants of the fieldwork, especially Mateusz Albrycht, Tomasz Błaszczyk, Robert Dobosz and numerous members and enthusiasts of the Wildlife Research and Conservation Society. We thank one anonymous reviewer for the language corrections. We appreciate comments by two anonymous reviewers, who helped to improve earlier drafts of the manuscript. A monitoring of breeding territories was carried out as a part of a national programme dedicated to Whooper Swan, conducted during 2007–2013, organised by the Chief Inspectorate for Environmental Protection and funded by The National Fund for Environment Protection and Water Management.

Puolalainen laulujoutsenpopulaatio on lyhentänyt voimakkaasti muuttomatkaansa

Tutkimme laulujoutsenten muuttokäyttäytymistä Etelä-Puolan ylängöllä sijaitsevassa osapopulaatiossa vuosina 1997–2003. Pesimäalueillaan rengastetut linnut viettivät niin talvet kuin sulkasatonsa lähellä syntymäseutujaan. Pesimä- ja talvehtimispaikan välinen etäisyys oli keskimäärin vain 149,1 ± 11,7 km ja 57,0 % kaikista talviaikaisista havainnoista oli alle 100 km etäisyydellä pesimäalueesta. Tutkimusjakson aikana laulujoutsenyksilöt lyhensivät muuttomatkaansa keskimäärin 0,22 ± 0,09 km vuodessa. Lintujen muuttoetäisyys tai talvisten havaintojen sijoittuminen ei kuitenkaan ollut yhteydessä talven ankaruuteen. Keskimääräinen etäisyys pesimä- ja sulkasatopaikan välillä oli 142,7 ± 34,6 km ja noin 66,6 % sulkasatovaiheen rengashavainnoista oli 100 km sisällä pesimäalueesta. Syksyllä esiaikuisia lintuja havaittiin yleisesti lähellä vanhempiensa pesimäaikaisia reviirejä. Ilmeinen muuttokäyttäytymisen heikkeneminen verrattuna pohjoisempiin laulujoutsenpopulaatioihin kielii kyseisen käyttäytymispiirteen joustavuudesta. Tämä vuorossaan saattaa edesauttaa lajin levittäytymistä etelään.

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