**Ornis Fennica 85:73–81. 2008**

# Scandinavian and central European subspecies of White-throated Dipper *Cinclus cinclus* interbreed in an isolated population in northern Poland

Arkadiusz Sikora & Grzegorz Neubauer

*A. Sikora, Ornithological Station, Museum and Institute of Zoology, Polish Academy of Sciences, Nadwiślańska 108, 80-680 Gdańsk, Poland. sikor@miiz.waw.pl*
*G. Neubauer, corresponding author: Grzegorz Neubauer, Ornithological Station, Museum and Institute of Zoology, Polish Academy of Sciences, Nadwiślańska 108, 80-680 Gdańsk, Poland. grechuta@miiz.waw.pl*

*Received 12 January 2008, revised 27 February 2008, accepted 15 April 2008*

Breeding ranges of Scandinavian and central European subspecies of the White-throated Dipper (*Cinclus cinclus cinclus* and *C. c. aquaticus*) are geographically separated by uninhabited lowlands. Between 1990 and 2006, 25 confirmed and 4 probable breeding cases of 23 individual dipper pairs were recorded in northern Poland. Dippers breeding in Northern Poland represented the Scandinavian *cinclus* phenotype in most cases (76% of males and 89% of females), while a minority phenotypically resembled the Carpathian *aquaticus* (24% and 12%, respectively). Offspring of a phenotypically mixed pair – two males from the same brood – displayed an intermediate phenotype. Ringing recoveries confirmed that immigrants from both ranges breed in N Poland. In 15 out of 23 breeding pairs, both mates represented the *cinclus* phenotype, one breeding attempt was by a pure *aquaticus* pair, and interbreeding pairs (*cinclus* × *aquaticus*) occurred in 7 out of 23 cases. Most breeding attempts were successful, and pair composition had only little if any effect on breeding success. A single individual hatched in Northern Poland was subsequently found breeding in Sweden. Out-of-range populations, such as the studied Northern Polish one supported by individuals from allopatric ranges, may promote the gene flow between allopatric subpopulations, contributing to the high morphological variability and the reported low genetic differentiation between the two studied subspecies.

## 1. Introduction

The polytypic genus *Cinclus* consists of five species distributed in Eurasia and the New World (Tyler & Ormerod 1994). In the Western Palaearctic, the only breeding species is the White-throated Dipper *Cinclus cinclus* with 2 to 17 formally recognized subspecies (Ormerod & Tyler 2005). White-throated Dipper has a patchy distribution, restricted to high mountains (Tyler & Ormerod 1994). In Europe, *C. c. cinclus* (hereafter referred to as *cinclus*) breeds in Scandinavia, and exhibits migratory habits with regular south-west, south, and south-east wintertime movements up to a few hundred km (Andersson & Wester 1976, Lehikoinen & Hakala 1988, Sikora 1993, Vuorinen & Tyrberg 1994). Central European subspecies *C. c. aquaticus* (hereafter referred to as *aquaticus*) is a short-distance or vertical migrant (Zink 1981, Glutz & Bauer 1985). The winter range of Scandinavian *cinclus* nearly overlaps with the breeding range of *aquaticus* in the German Lowland, yet interbreeding is unconfirmed despite a few suggested cases (Creutz 1986, Bink 1992).

Morphologically, the coloration of head, hind neck and breast are reddish brown in *aquaticus* and blackish brown in *cinclus*. Dippers from Central Europe are also smaller and tend to have paler legs than do Scandinavian dippers (Cramp 1988, Tyler & Ormerod 1994). There is no indication of genetic differentiation between these subspecies, and other European subspecies also show little differentiation that could be reasonably linked to their geographic distribution (Lauga *et al*. 2005). White-throated Dippers of *cinclus* type have also been assigned to areas of central France, north-western Spain, Corsica and Sardinia (Niethammer 1965). However, despite the fact that the breeding ranges of *aquaticus* and *cinclus*-like birds largely overlap in Spain (Campos *et al*. 2005a), no evidence for interbreeding has been reported. The occurrence of dark, *cinclus*-like individuals within Central European populations of *aquaticus* still lacks an explanation. Either they originate from Fennoscandian birds that migrate to Central Europe to overwinter there, or they represent aberrant individuals within *aquaticus* subspecies (von Burg 1924, Greenway & Vaurie 1958, Balat 1961, Spitznagel 1995a, 1995b).

Breeding habitat for White-throated Dippers is scarce between the mountain ranges of Central Europe (breeding range of *aquaticus*) and Scandinavia (breeding range of *cinclus*). Therefore, lowlands of Central Europe are only exceptionally inhabited. In the early 1990's, an isolated population of dippers, consisting of 1–5 breeding pairs, was discovered in Northern Poland. This area is a regular winter range of Scandinavian *cinclus* (Sikora 1993). Alternatively, *aquaticus* is solely a short-distance migrant; hence, we predicted that (1) Northern Poland would be mostly inhabited by individuals originating from Scandinavia rather than from Central Europe. We evaluated this hypothesis by comparing the phenotypic characteristics of birds from Scandinavia, Carpathians and Northern Poland. Due to the high within-population morphological variability of the species, we also used information obtained from ringing recoveries to corroborate the origin of Northern Polish breeders. Furthermore, because reproductive barriers between subspecies are unlikely due to the similar ecological requirements and low genetic divergence, we predicted that (2) if some *aquaticus* immigrants would occur, they would mate and successfully reproduce with *cinclus*, thus confirming interbreeding between the two subspecies. By validating these two hypotheses, we aimed at clarifying whether such an out-of-range population could act as a bridge between allopatric populations, promoting gene flow and contributing to the low genetic differentiation between subspecies of the White-throated Dipper in Europe.

## 2. Methods

We conducted field surveys in Pomeranian and Masurian Lakelands, Northern Poland (53°30'N–54°50'N, 16°50'E–20°40'E; Fig. 1). These districts consist of moraine hills, reaching up to 329 m a.s.l., which create a diverse relief with relative heights up to 100 m (Kondracki 2002). Field surveys were carried-out on 1,400 km of fast-flowing streams and rivers with a gradient in excess of 1‰. Using distribution data of wintering White-throated Dippers during the preceding winter (Sikora 1993) and their behaviour (e.g., displaying pair, singing individual, or birds with nest material), we explored selected rivers to search for breeding pairs in March–June, between 1990 and 2006. Where possible, we collected data on breeding success.

We measured birds from the subspecies *cinclus* and *aquaticus*. We obtained morphological data on *cinclus* ($n$ = 49; 21 females and 28 males) from birds wintering in Northern Poland, between 1993 and 2003. We used only individuals for which ringing recoveries had confirmed their Scandinavian origin; they had thus been recorded within *cinclus* breeding range in Scandinavia (58°20'N–64°50'N, 06°00'E–15°20'E; Fig. 1). Breeding in Scandinavia was confirmed for 29 of these birds, whereas the remaining 20 individuals had also been recorded within the breeding range of *cinclus*, though not during breeding season (not mapped); all these individuals are considered to represent *cinclus*.

We trapped specimens of *aquaticus* ($n$ = 27; 16

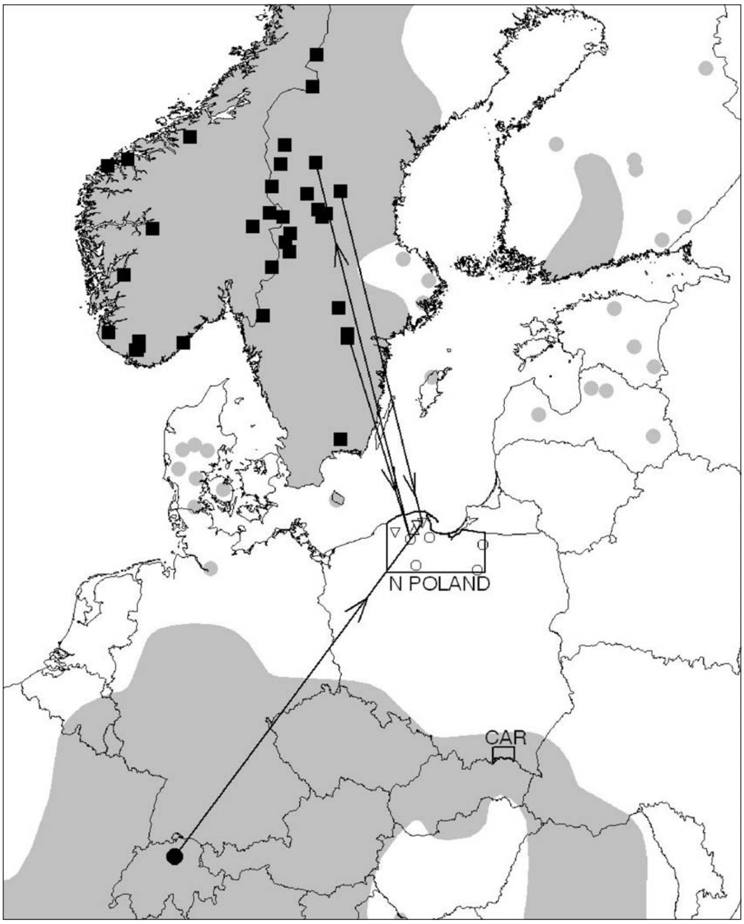

Fig. 1. The distribution of the White-throated Dipper populations (shaded sections; updated from Hagemeijer & Blair 1997), and the study areas (boxes; Northern Poland [N POLAND] and the Carpathians [CAR]). Breeding localities in Northern Poland are shown as open circles for pairs with both birds displaying *cinclus* phenotype, down-triangles for phenotypically mixed pairs, and up-triangles for pairs with both birds displaying *aquaticus* phenotype. Black squares in Scandinavia indicate breeding localities of birds used as a reference population of *cinclus*; arrows join ringing and breeding locations.

females and 11 males) in Beskid Niski mountain range, South-Eastern Poland (49°20'N–49°40'N, 21°00'E–21°50'E; Fig. 1) in September 2002. Because this subspecies is a short-distance or vertical migrant, we consider these individuals to represent a local population of *aquaticus*.

We also mist-netted, ringed and measured adult White-throated Dippers breeding in an out-of-range population in Northern Poland (*n* = 34; 18 females and 16 males). Between 1990 and 1999, we marked dippers using unique combinations of color rings, allowing for individual identification during the subsequent seasons. For each individual, we ascertained its breeding status. We trapped 34 and visually identified two individuals, making up a total of 23 breeding pairs (four males and two females were involved in more than one breeding pair); a single breeding male remained unidentified as it was not recorded when its female was incubating eggs and feeding young at the nest. Subspecific identification of two other individuals was based on visual observations in their breeding territories. Based on classic subspecific features, these two individuals could safely be identified as *cinclus*-like. Two White-throated Dippers, ringed as nestlings in Northern Poland, were re-trapped as adults.

We measured the trapped dippers according to Svensson (1992): wing length (maximum flattened chord), tarsus length, total head length, bill length (feathering to tip) and bill depth at the distal edge of nostrils. Additionally, we measured bill length to distal edge of nostrils. All measurements were taken by the author A. S. to the nearest 0.1 mm. We weighted birds to the nearest g. We also evaluated three color-based variables under ambient light conditions: (1) the amount of reddish-brown feathers on the breast, classified using a four-step scale (0%, 1–30%, 31–60%, >60%), (2) the color of the head and hind neck, classified using a three-step scale (dark brown, intermediate, brown) and (3) the leg color, classified using a three-step scale (dark, intermediate, pale). These three categorical variables were polarized so that high scores corresponded to *aquaticus* and low scores to *cinclus*.

In Northern Poland, birds showing *cinclus* coloration were initially sexed by wing length (Svensson 1992). Individuals with *aquaticus*-like coloration were sexed according to Bub (1984) and to Schmid and Spitznagel (1985): birds with wing length less than 92 mm were considered females, and larger ones males. Because body mass appears to be a good predictor of sex (Esteban *et al.* 2000, Campos *et al.* 2005b), we also plotted body mass against wing length. By obtaining two nearly discrete groups of points we confirmed that a combination of wing length and body mass allows reliable sexing of individuals. According to the equation of Esteban *et al.* (2000),

$$Y = \text{body weight} + (2 \times \text{wing length in mm}) = 243 \quad (1)$$

individuals with $Y > 243$ are considered males and those with $Y < 243$ females. Of the 243 studied Northern Polish breeding females, three were misclassified and one was unclassified when this equation was applied. We suggest that this was because these represented the Scandinavian *cinclus*, which are bigger and heavier than other European dippers. In these cases, sex could be verified by comparing measurements of their mates — males are consistently bigger than females — and by observing the behavior of individuals within their breeding territories; all these birds indeed appeared to be females. We calculated the repeatability of measurements (intra-class correlation coefficients derived from ANOVA) following Lessels and Boag (1987), using data on White-throated Dippers captured during winters of 1991/1992 and 2005/2006 in Northern Poland. These individuals were measured 2–10 (mean 3.3 ± 1.6 SD) times.

### 2.1. Statistical analysis

To classify phenotypes of dippers breeding in Northern Poland, we performed standardized Principal Component Analysis (PCA) using a correlation matrix on the morphological data of 112 White-throated Dippers (55 females, 55 males, and two males ringed as nestlings in the nest of a phenotypically mixed pair). Prior to the analysis, we log-transformed continuous variables to approach normal distributions and ranked the discrete variables (Siegel & Castellan 1988). Sexes were analyzed separately to emphasize differences between subspecies rather than between sexes. In univariate comparisons we used Student's *t* test (Sokal & Rohlf 1995). We carried out the statistical analyses using SPSS 15.0.

The phenotypic assignment of Northern Polish breeders was based on the PCA scores of each individual along the first principal component (PC1) axis. Data from Scandinavia and South-Eastern and Northern Poland were used in this analysis. North Polish individuals with PC1 scores falling within the PC1 scores of the Carpathian individuals were considered as representing *aquaticus*, and a respective protocol was applied for *cinclus*. North Polish individuals with PC1 scores falling between the *aquaticus* and *cinclus* scores were considered as representing an intermediate phenotype.

Table 1. Repeatability of measurements of 48 White-throated Dippers in Northern Poland.

| Measurement | Repeatability | *F* | df | *P* |
|---|---|---|---|---|
| Wing length | 0.99 | 232.86 | 47; 113 | <0.0001 |
| Head length | 0.90 | 31.95 | 45; 105 | <0.0001 |
| Bill length | 0.79 | 13.82 | 47; 113 | <0.0001 |
| Bill: from tip to nostrils | 0.80 | 14.47 | 47; 109 | <0.0001 |
| Bill depth | 0.81 | 15.28 | 47; 112 | <0.0001 |
| Tarsus | 0.94 | 54.51 | 47; 113 | <0.0001 |

## 3. Results

### 3.1. Phenotypic divergence between *aquaticus* and *cinclus*

All measurements were highly repeatable (Table 1). Carpathian individuals were smaller than Scandinavian ones in most measurements, and patterns

Table 2. Measurements of White-throated Dippers from the Carpathians (*aquaticus*), Northern Poland, and Scandinavia (*cinclus*). Mean values ± 1 SD (all in mm).

| | Males | | | Females | | |
|---|---|---|---|---|---|---|
| Measurement | Carpathians $n = 11$ | N Poland $n = 16$ | Scandinavia $n = 28$ | Carpathians $n = 16$ | N Poland $n = 18$ | Scandinavia $n = 21$ |
| Wing length | 95.5 ± 1.6 | 97.8 ± 1.6 | 98.4 ± 1.6 | 87.5 ± 1.5 | 89.9 ± 1.6 | 90.2 ± 1.3 |
| Tarsus length | 29.6 ± 0.6 | 30.0 ± 0.9 | 29.8 ± 0.8 | 27.7 ± 0.6 | 27.9 ± 1.0 | 28.3 ± 0.6 |
| Head length | 46.7 ± 0.8 | 47.2 ± 0.6 | 47.2 ± 0.7 | 45.0 ± 0.7 | 45.5 ± 0.6 | 45.9 ± 0.6 |
| Bill length | 16.4 ± 0.4 | 16.3 ± 0.4 | 16.3 ± 0.5 | 15.6 ± 0.4 | 15.5 ± 0.6 | 15.4 ± 0.5 |
| Bill: from tip to nostrils | 15.3 ± 0.6 | 15.5 ± 0.5 | 15.7 ± 0.5 | 14.9 ± 0.6 | 14.8 ± 0.5 | 14.9 ± 0.5 |
| Bill depth | 4.9 ± 0.2 | 4.8 ± 0.2 | 4.8 ± 0.2 | 4.6 ± 0.2 | 4.5 ± 0.2 | 4.5 ± 0.2 |
| PC1 score | 1.560 ± 0.194 | 0.020 ± 0.967 | –0.649 ± 0.309 | 1.331 ± 0.388 | –0.429 ± 0.639 | –0.647 ± 0.467 |
| PC2 score | –0.259 ± 1.095 | –0.069 ± 1.053 | 0.082 ± 0.940 | 0.220 ± 0.959 | –0.285 ± 1.141 | 0.076 ± 0.886 |

Table 3. Coloration of breast, head and legs of White-throated Dippers from the Carpathians (*aquaticus*), Northern Poland, and Scandinavia (*cinclus*). Breast = the amount of reddish-brown feathers on the breast; Head = color of head with hind neck; Legs = leg color (all in percentages).

| | Males | | | Females | | |
|---|---|---|---|---|---|---|
| Feature | Carpathians $n = 11$ | N Poland $n = 16$ | Scandinavia $n = 28$ | Carpathians $n = 16$ | N Poland $n = 18$ | Scandinavia $n = 21$ |
| *Breast* | | | | | | |
| More than 60% | 100.0 | 33.3 | 0 | 87.5 | 11.1 | 14.3 |
| 31–60% | 0 | 20.1 | 10.3 | 12.5 | 16.7 | 14.3 |
| 1–30% | 0 | 13.3 | 41.4 | 0 | 38.9 | 47.6 |
| 0% | 0 | 33.3 | 48.3 | 0 | 33.3 | 23.8 |
| *Head* | | | | | | |
| Brown | 100.0 | 26.7 | 0 | 100.0 | 15.8 | 4.8 |
| Intermediate | 0 | 0.0 | 0 | 0 | 10.5 | 4.8 |
| Dark brown | 0 | 73.3 | 100.0 | 0 | 73.7 | 90.4 |
| *Legs* | | | | | | |
| Pale | 81.8 | 26.7 | 0 | 81.2 | 5.6 | 4.8 |
| Intermediate | 18.2 | 0 | 0 | 18.8 | 5.6 | 0 |
| Dark | 0 | 73.3 | 100.0 | 0 | 88.8 | 95.2 |

of morphological divergence were similar in males and females (Table 2). Carpathian birds also tended to have paler legs, more reddish breast coloration, and paler head and hind neck (Table 3). PCA was initially performed separately for males and females, but the sexes did not differ in PC scores within any population (Scandinavia, PC1: $t_{(47)} = 0.02$, $P = 0.98$, PC2: $t_{(47)} = –0.02$, $P = 0.98$; Northern Poland, PC1: $t_{(32)} = –1.60$, $P = 0.12$, PC2: $t_{(32)} = –0.56$, $P = 0.58$; Carpathians, PC1: $t_{(25)} = –1.79$, $P = 0.09$, PC2: $t_{(25)} = 1.20$, $P = 0.24$). Therefore, the sexes were pooled in subsequent comparisons. The scores of Carpathian and Scandinavian individuals did not overlap along PC1 axis (sexes pooled, PC1: $t_{(74)} = 23.63$, $P < 0.0001$; Fig. 2), mainly due to the high contribution of color-based traits and wing length to PC1 (Table 4). The scores along PC2 were similar between Carpathian and Scandinavian individuals ($t_{(74)} = –0.24$, $P = 0.81$, Table 2). The first two axes explained 64.9% and 66.2% of the total variance in males and in females, respectively (Table 4).

Table 4. Results of a standardized principal component analysis on morphological data of 112 adult White-throated Dippers from the Carpathians (*aquaticus*), Northern Poland, and Scandinavia (*cinclus*).

| | PC1 | | PC2 | |
|---|---|---|---|---|
| | Males | Females | Males | Females |
| Eigenvalues | 3.49 | 3.61 | 2.35 | 2.35 |
| Variance explained (%) | 38.82 | 40.13 | 26.06 | 26.08 |
| *Component loadings* | | | | |
| – wing length | –0.72 | –0.81 | –0.11 | 0.08 |
| – bill length | 0.26 | 0.06 | 0.79 | 0.68 |
| – bill: from tip to nostrils | –0.21 | –0.10 | 0.88 | 0.88 |
| – bill depth | 0.44 | 0.35 | 0.21 | 0.24 |
| – head length | –0.28 | –0.61 | 0.86 | 0.72 |
| – tarsus length | 0.01 | –0.43 | 0.35 | 0.56 |
| – breast color | 0.89 | 0.78 | 0.13 | 0.31 |
| – head color | 0.96 | 0.92 | –0.05 | 0.22 |
| – leg color | 0.94 | 0.90 | –0.02 | 0.28 |

### 3.2. Phenotypic composition of the North Polish population

PC1 scores for the White-throated Dippers breeding in Northern Poland fell within the range of *cinclus* in 76% of the cases for males and in 89% for females, whereas those with PC scores suggesting *aquaticus* were less numerous (24% of males and 11% of females). No intermediate individuals were recorded among breeding adults, but two male offspring of a phenotypically mixed pair were intermediate; their PC1 scores fell between the range of Carpathian and Scandinavian birds (Fig. 2).

Two ringing recoveries confirmed that White-throated Dippers originating from Scandinavia have bred in Northern Poland (Fig. 1). Additionally, an individual with *cinclus* phenotype, ringed as a nestling in Northern Poland, had been subsequently recorded breeding in central Sweden, showing that natal dispersal between Scandinavia and Northern Poland occurs in both directions. A recovery from an *aquaticus* ringed as a nestling in the Alps (near Zurich, Northern Switzerland, 47°17'N, 08°32'E; Fig. 1) and recorded breeding in Northern Poland (Hegelbach & Koch 1994, Sikora 1994) indicates that this subspecies may at least occasionally breed far from its regular breeding range.

### 3.3. Distribution, composition and breeding success in Northern Poland

Between 1990 and 2006, we recorded 25 confirmed and four probable breeding attempts of 23 pairs of White-throated Dippers in Northern Poland. The probable breeders represent pairs displaying or building a nest early in the season but without the breeding confirmed later on. All but two breeding cases were recorded on six sites in the western (Pomeranian) part of the North Polish study area on the rivers Słupia (54°14'N, 17°45'E), Bielska Struga (53°39'N, 17°59'E), Bolszewka (54°35'N, 18°08'E), Radunia (54°16'N, 18°30'E), Łeba (54°32'N, 18°01'E) and Skotawa (54°22'N, 17°10'E). In the Masurian Lakeland, single pairs bred on the Marózka (53°29'N, 20°22'E) and Symsarna (54°07'N, 20°35'E) rivers (Fig. 1).

Of 34 individual birds, four males and two females paired more than once. For example, the Swiss-ringed *aquaticus* male bred with three different females during five successive breeding seasons in Northern Poland: with a ringed (Swedish) *cinclus* female in 1994–95, with another *cinclus*-like female in 1996 and with an *aquaticus*-like female in 1997–98. Because five individual pairs bred in more than one year, and to avoid pseudo-replication, these were incorporated into analysis once only. Therefore, we trapped or identified both partners for 23 pairs in total, including four probable breeding cases. Most frequently, both mates had *cinclus* phenotype (65%; 15 pairs), whereas mixed pairs with mates showing different phenotypes constituted about one-third (30%; 7 cases), all with males of *aquaticus* and females of *cinclus* phenotype. Interbreeding between *aquaticus* and *cinclus* in Northern Poland was further confirmed by ringing recoveries: the above-mentioned Swiss male and a ringed Swedish female bred in 1994 and in 1995. In a single case, both birds represented *aquaticus* phenotypes, and in an additional case an *aquaticus*-phenotype female bred with an unknown partner.

Most breeding attempts of White-throated Dippers in Northern Poland were successful.

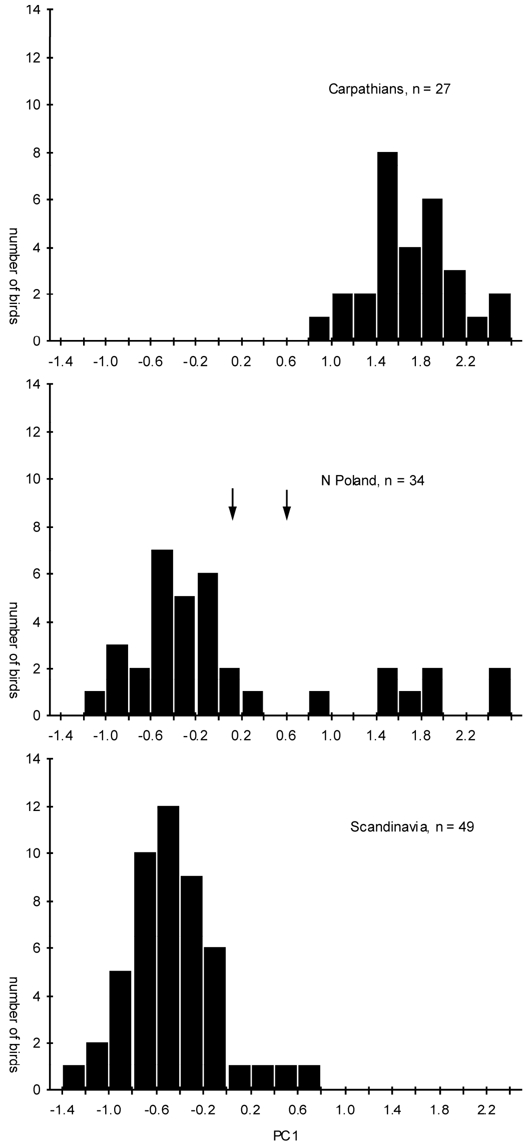

Fig. 2. The frequency distribution of PC1 scores from principal component analysis based on nine morphological traits measured in 112 White-throated Dippers from Carpathians, Scandinavia and Northern Poland (sexes pooled). The arrows show PC1 scores of two male White-throated Dippers that are offspring of a phenotypically mixed pair from Northern Poland.

Among 12 broods of pairs with both mates representing *cinclus* phenotype (breeding in successive seasons included), ten attempts were followed by us and eight were successful, indicated by recorded nestlings or recently fledged young near nests. Similarly, among ten breeding attempts of phenotypically mixed pairs, nine attempts were studied, and six of these proved successful. In 2004, a phenotypically mixed pair successfully raised two broods: fledglings were observed near nest on 30th April, and two nestlings were found in the same nest on 29th May. Two unsuccessful broods of mixed pairs contained non-fertilized eggs; one mixed pair failed to produce young for an unknown reason. Two broods of the same pair of *aquaticus* phenotype were successful in both years with 4 and 6 young raised, respectively. Although the sample size is limited by the small population size, the data seem to indicate that no apparent reproductive barrier exists between the subspecies of White-throated Dipper in Northern Poland.

## 4. Discussion

We showed that the White-throated Dipper population breeding in Northern Poland involves two subspecies that were previously thought to be reproductively isolated. However, *cinclus* and *aquaticus* also co-occur in the Cantabrian Mountains and Western Pyrenees (Campos *et al.* 2005a). Further studies are necessary to evaluate whether *aquaticus* and *cinclus* interbreed regularly in some parts of their breeding ranges, or whether the situation in Northern Poland is unique. As could be expected by their migratory habits, the out-of-range population in Northern Poland was established predominantly by *cinclus* individuals that had remained within their regular winter range and by *aquaticus* individuals that had dispersed unusually far from the Central European mountain ranges. These two subspecies occasionally form mixed pairs in Northern Poland, although most pairs in that area represent pure *cinclus.* There are a few confirmed and probable breeding records from the German Lowland, but it remains unknown to which subspecies these breeding birds belong (Creutz 1986, Bink 1992, Nicolai 1993).

Compared to *aquaticus*, Scandinavian *cinclus* is more likely to breed far from its regular breeding range due to its migratory habits. Movements of Scandinavian *cinclus*, documented by ringing recoveries, reach 1,000 km (Andersson & Wester 1976). Such distances exceed the distance between the breeding ranges of *cinclus* and *aquaticus*. For example, less than 500 km separates the breeding range of the Norwegian *cinclus* population and that of *aquaticus* in Germany (e.g., Harz Mountains). Similarly, the breeding range of Southern Swedish *cinclus* and Southern Polish (Sudetes) *aquaticus* are separated by 500–600 km. Thus, we suggest that a few *cinclus* may at least occasionally migrate to and breed within Central European populations of *aquaticus*. More surprisingly, the 1,055-km long movement of *aquaticus* from Switzerland shows that northward natal dispersal from Central Europe does happen (Sikora 1994).

Our results showed that color-based traits readily separate the two subspecies (Fig. 2). Scandinavian *cinclus* shows considerable variation in coloration of breast feathers, with a minority of birds being similar to Carpathian *aquaticus* in this respect (Table 3). This finding indicates that the breast color alone, traditionally believed to be diagnostic and used to separate subspecies in some studies (e.g., Campos *et al*. 2005a), may not be sufficient to distinguish between subspecies. Furthermore, White-throated Dipper shows extensive within-population variation in plumage coloration, influenced by habitat, sex and age (Balat 1961, Spitznagel 1995a, b). With these facts in mind, a special caution is necessary during assignment of individual birds. Therefore, although separation of subspecies in our sample was clear, we recommend to use the term “phenotype” instead of “subspecies”. However, it seems extremely unlikely, that the observed distribution of phenotypes in the studied North Polish dipper population would not, at least partially, reflect the presence of two subspecies. Finally, the obtained ringing recoveries undisputedly confirmed immigration and interbreeding between two subspecies of White-throated Dipper. Such an exchange of individuals between populations, with subsequent gene flow, may contribute to maintaining high color variability in dipper populations and reduce their genetic differentiation (Lauga *et al*. 2005).

The two male White-throated Dipper offspring of a subspecifically mixed pair appeared phenotypically different. One was similar to its mother (*cinclus* phenotype), whereas the other was reminiscent of its father (*aquaticus* phenotype). Clearly, the use of multiple morphological characters may not help much in identification of such subspecific hybrids. Thus, their “genetic history” will remain undiscovered unless molecular markers are used to assign individuals.

The situation in Northern Poland suggests that gene flow between subpopulations and subspecies may not necessarily be a rare phenomenon, even if subspecies are separated by a geographical barrier. Gene flow may occur even if the population is fragmented and/or some subpopulations show sedentary habits. The documented exchange of individuals partially explains the high morphological variability reported in Central European dipper populations, and the low genetic differentiation between subspecies.

*Acknowledgements.* We thank Marcin Dziedzic and Witold Michalczyk for assistance in trapping dippers in the Beskid Niski Mountains, and Marek Jędra for organizing accommodations. We also thank Zenek Rohde for preparing the map and two anonymous referees for their helpful comments.

## Skandinavian ja Keski-Euroopan koskikarojen *Cinclus cinclus* alalajit pesivät sekapareina eristyneessä populaatiossa Pohjois-Puolassa

Skandinaviassa ja Keski-Euroopassa pesivien koskikaran (*Cinclus cinclus*) *cinclus*- ja *aquaticus*-fenotyypit ovat asumattoman alavan maan toisistaan eristämiä. Pohjois-Puolassa todettiin 1990–2006 kaikkiaan 23 koskikaraparilla 25 varmaa ja neljä todennäköistä pesintää. Valtaosa alueen koskikaroista edusti Skandinavian *cinclus*-fenotyyppiä (76 % koiraista ja 89 % naaraista), ja vähemmistö muistutti Karpaattien seudun *aquaticus*-yksilöitä (vastaavasti 24 ja 12 %). Fenotyyppisen sekaparin kaksi saman pesyeen koirasta oli ulkoisesti välimuotoisia.

Rengaslöytöjen avulla varmistui, että molempia fenotyyppejä pesii Pohjois-Puolassa. Puhtaita *cinclus*-fenotyypin pareja oli 15, puhtaita *aquaticus*-pareja yksi, ja fenotyyppien sekapareja (*cinclus* x *aquaticus*) todettiin seitsemän. Valtaosa pesimäyrityksistä onnistui, eikä parin fenotyyppikoostumus näyttänyt vaikuttavan asiaan. Yksi Puolassa syntynyt yksilö löytyi myöhemmin pesivänä Ruotsista. Päälevinneisyysalueen ulkopuoliset – kuten tutkittu puolalainen – populaatiot, joihin liittyy allopatristen alueiden yksilöitä, voivat toimia siltana ja ylläpitää geneettistä vaihtelua sekä tässä tutkimuksessa raportoitua vähäistä geneettistä eriytymistä alalajien välillä.

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