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The origin of Blackcaps *Sylvia atricapilla* wintering on the British Isles

Katarzyna Kopiec & Agnieszka Ożarowska*

K. Kopiec, Ornithological Station Museum and Institute of Zoology, Polish Academy of Sciences, Nadwiślańska 108, 80-680 Gdańsk, Poland. E-mail kasia@miiz.waw.pl
*A. Ożarowska, Bird Migration Research Station, University of Gdańsk, Al. Marszałka Józefa Piłsudskiego 46, 81-378 Gdynia, Poland. *Corresponding author's e-mail bioat@ug.edu.pl*

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A migration route leading central European breeder Blackcaps to their winter quarters in Britain and Ireland was discovered in the 1960s. This phenomenon, representing a rapid evolutionary change of migratory behavior, can be explained by a shift in migration course towards the west and north-west (as opposed to the standard south-west direction) or reverse migration. These hypotheses were evaluated by analyzing the recoveries of Blackcaps either ringed or recovered on the British Isles. Blackcaps arriving in the British Isles from Scandinavia had been ringed over two weeks later than had been birds arriving from Central Western Europe, while no significant difference was found in the recovery dates of birds from these regions. Moreover, birds ringed in Scandinavia were recovered significantly later on the British Isles than in the continental Europe. This finding suggests that two populations migrate through Scandinavia: the local breeding population (migrating towards the south) and another with an unknown origin (possibly Central European, heading towards the north and west). Thus, some of the Blackcaps ringed in Utsira on the Norwegian west coast, and ending up to the British Isles, might be of Central European origin.

1. Introduction

Genetic factors controlling various migratory traits, including migratory orientation, have been the topic of several studies (e.g., Berthold *et al.* 1992, Berthold & Helbig 1992, Berthold 1995, Helbig 1996). Genetic variation and selection pressure acting on wild birds could result in rapid evolutionary changes in migratory behavior, which have been observed in continental Blackcaps wintering in Britain and Ireland. The phenomenon of Blackcap autumn migration to the British Isles has been known to researchers for a long time. The number of Blackcaps wintering there has been increasing since the 1960s and has continued until now. Presently this phenomenon is recognized as representing the evolution and stabilization of a completely new migration route in modern times (Berthold *et al.* 1992, Berthold 1995, Langslow 2002). A small fraction of Blackcaps may have migrated in a north-westerly direction for hundreds of years (Berthold *et al.* 1992). However, weather conditions for Blackcap wintering have not consistently been favourable, and

hence the phenomenon has sometimes been overlooked by ornithologists. Only in recent decades, weather conditions in Great Britain have changed enough to enable Blackcaps to survive throughout the winter season as a result of climate warming. The increase in the wintering population of Blackcaps on the British Isles may also be the result of from the increasingly common practice of feeding wintering birds in gardens (Leach 1981, Berthold & Terrill 1988, Toms 2002, Chamberlain *et al.* 2005).

The origin of these over-winterers was earlier considered continental (Langslow 1979, Leach 1981). However, according to Berthold and Terrill (1988), the development of a north-westerly migratory direction could result from rotation of the angle of normal migration by ca. 30° north-west and an earlier end of migration period due to an exposure of migrating individuals to a shorter photoperiod. Another hypothesis was proposed by Busse (1992) who argued that Blackcaps might reach Britain and Ireland by reversed migration followed by reorientation. Busse (1992) further hypothesized that cross-breeding between two distinct Blackcap populations that differ in their average migratory directions could result in hybridisation and consequently incorrect navigation during the first autumn migration of these hybrids. The hybridization might have taken place in Central Europe (cf. Cramp1992, Shirihai *et al.* 2001), and resulted in a reversed migratory direction by 180°.

Two mechanisms are plausible. Firstly, West European individuals that reverse the normal south-eastern direction by 180° should arrive in Great Britain. Secondly, if a southern direction is reversed, individuals first reach Scandinavia where they encounter conditions unfavourable for wintering, and consequently change their migratory direction again using another inherited navigating program, i.e., head south or south-west. Hence, when following a south-westerly route from Scandinavia, Blackcaps should arrive in Great Britain in the second stage of their migration. Both mechanisms would result in birds arriving in British Isles with the possible option of overwintering. Theoretically, as the origin of these birds would be the same but the migration distance covered would differ, the timing of migration would be different. The aim of the present study was to test these hypotheses and provide insight into the possible origin and migration routes followed by continental Blackcaps to the winter quarters in the British Isles.

2. Material and methods

A total of 494 recoveries of Blackcaps ringed or recovered on the British Isles during 1961–2000 were analysed. These included individuals of the local breeding population, i.e., ringed between the beginning of May and the end of August, and individuals ringed in other parts of Europe and recovered in the British Isles during autumn and winter, i.e., between 1 August and 31 March. Individuals recovered within 15 km of the location at which they were ringed, were excluded from the analyses. Most recoveries concerned immatures (63%), while 16% were adults and 21% were of unknown age. Also, recoveries of Blackcaps ringed in Scandinavia in autumn (i.e., 1 September–30 November) and recovered later on the European continent ($N = 82$) were analyzed. Again, individuals recovered within 15 km of the location at which they were ringed, were excluded from analysis.

Additionally, recovery data of Blackcaps ringed during the breeding season in Norway, and 14 recoveries of Blackcaps ringed or recovered in Utsira, an island adjacent to the south-western coast of Norway, during the same autumn migration in 1992–2005, were used. Additional data on the daily numbers of Blackcaps captured in Utsira during autumn migration seasons 1992–2005, were included in this study.

The following analyses were performed. (1) The compass angle between ringing and recovery locations, measured in degrees, was compared between individuals ringed in Scandinavia and in western Europe using a two-sample Watson-Williams test (Zar 1999). (2) Using ringing recoveries made in Britain during the non-breeding season, comparisons were made between birds of British breeding origin and continental-breeding Blackcaps.

British non-breeding season recovery dates of Blackcaps of the local (British) population and individuals arriving from the European continent were compared. (3) Ringing and recovery dates of Blackcaps in autumn were compared to individu-

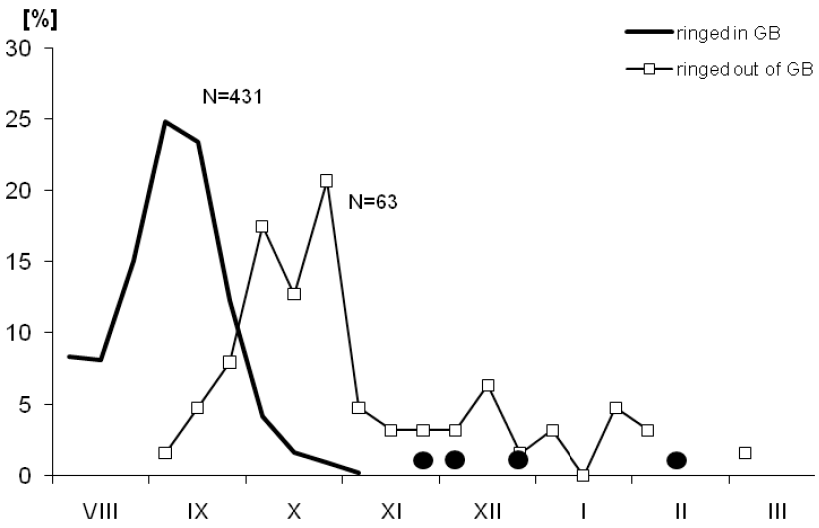

Fig. 1. Ringing recovery dates of Blackcaps reported from Great Britain (GB). Black dots represent single recoveries from the local British population; curves show percent of all recoveries.

als ringed in Scandinavia (mainly Norway) and individuals from Western Europe (mainly Belgium, the Netherlands, France and Germany). (4) Autumn (1 September–30 November) ringing dates of Blackcaps captured in Scandinavia and recovered either on the British Isles or continental Europe were also compared. These comparisons were done by applying Mann-Whitney *U* test to compare ringing and recovery dates of Blackcaps ringed or recovered either on the British Isles or the European continent.

3. Results

The departure dates of Blackcaps of the local breeding population and the arrival dates of Blackcaps from the continent differed by over a month (Fig. 1). The passage peak of British birds was noted in the first ten days of September (median date = 07.09, SD = 20), while the number of Blackcaps arriving from the continent to the British Isles peaked significantly later, i.e., in the second ten days of October (median date = 22.10, SD = 43;

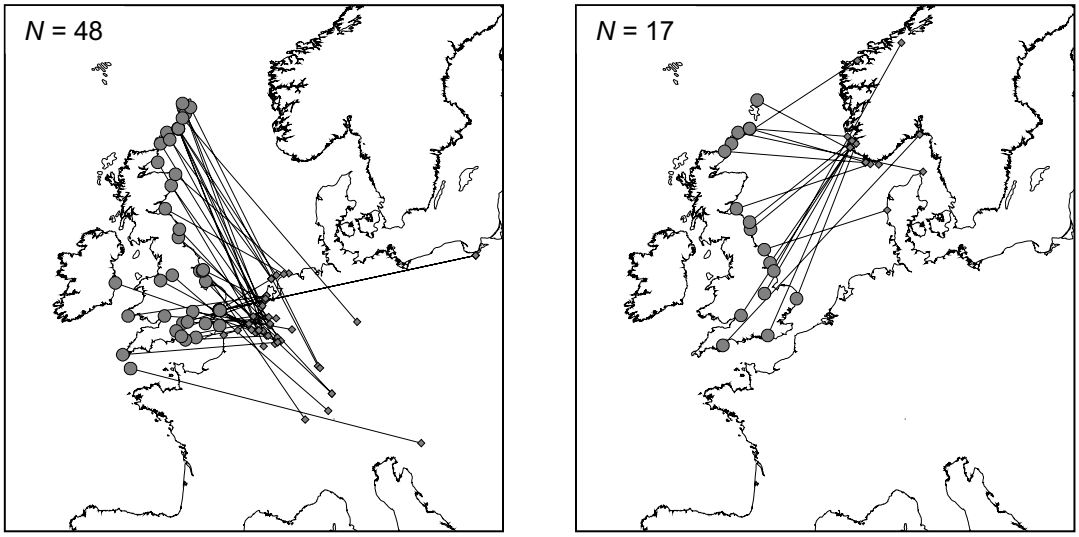

Fig. 2. The origin of Blackcaps arriving in Britain to overwinter.

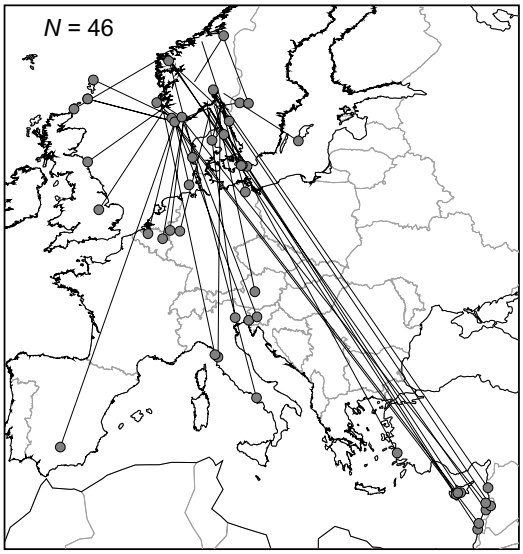

Fig. 3. Recoveries of Blackcaps breeding in Norway (birds ringed in Norway between 1 May and 31 August).

Mann Whitney *U* test $Z = -11.57$, $p < 0.01$). Four individuals from the local population were observed in Great Britain during winter, representing 0.9% of recoveries reported from this region. Blackcaps that arrived in the British Isles from continental Europe in autumn originated from two regions: Scandinavia (mainly Norway) and Western Europe (Fig. 2). Most birds arriving from Western Europe migrated to the north-west (mean angle $\alpha = 317.3°$, angular deviation s = 42.34), which was particularly clear in Blackcaps recovered in the Faeroe Islands and Scotland (Fig. 2a). Birds that arrived in Great Britain from Norway migrated mostly in a south-westerly direction ($\alpha = 231.9°$, s = 40.92°; Fig. 2b). This difference in migration direction between these groups was statistically significant (Watson-Williams test; $F = 37.7$, $p < 0.001$).

Most birds that originated from Norway (i.e., had been ringed there between the beginning of May and the end of August) followed either the southern direction and were recovered, e.g., in Italy ($n = 7$), or followed the south-eastern direction and were later recovered in Turkey, Cyprus and the Middle East ($n = 10$; Fig. 3). Another five individuals followed either the western or south-western direction and were recovered on the British Isles, and one individual was reported in Spain.

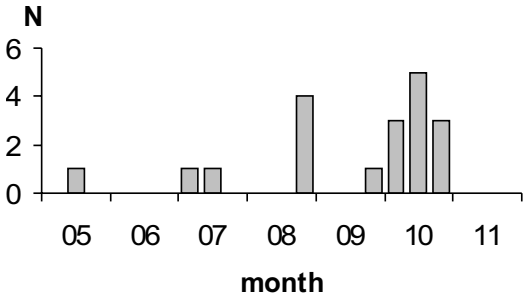

Fig. 4. Blackcaps arriving in Great Britain from Scandinavia. Number of birds ringed in Norway and Denmark in subsequent ten-day periods.

Most Blackcaps (63%) arriving from Scandinavia were ringed outside breeding season (Fig. 4). After an exclusion of potential breeders of the local population (i.e., individuals ringed between 1 May and 31 August; Fig. 5), ringing dates of birds that arrived to the British Isles from Scandinavia were significantly later than those from western Europe (n = 13 and 35, respectively; Mann-Whitney *U* test; $Z = -3.11$; $p = 0.002$). The median ringing date of Blackcaps arriving from Western Europe and Scandinavia differed by over two weeks, being 28 September (SD = 17.5) and 13 October (SD = 8.5), respectively. However, no significant difference in recovery dates between these two groups was

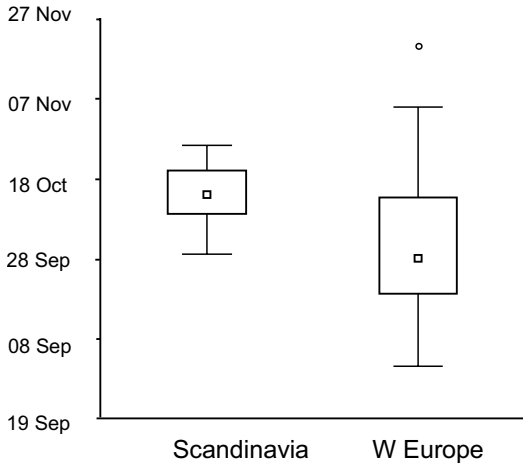

Fig. 5. Ringing dates of blackcaps in Scandinavia and western Europe, subsequently recovered in Great Britain. Median, upper and lower quartiles, 95% confidence intervals, and an outlier (circle) shown.

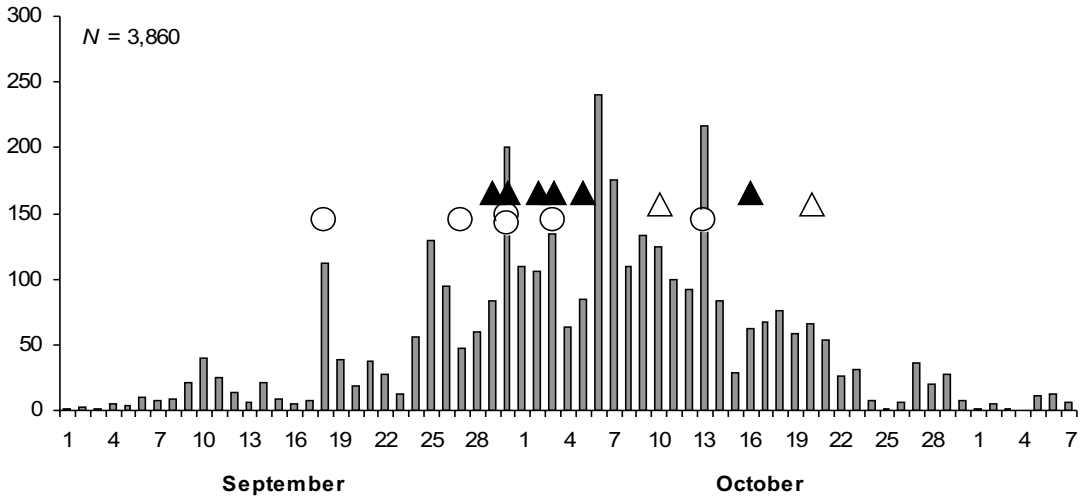

Fig. 6. Daily numbers of Blackcaps captured in Utsira, Norwegian west coast, in the autumn migration seasons of 1992–2005. Circles = birds recovered in the southerly direction; white triangles = birds recovered in the northerly direction; black triangles = birds ringed to the south from Utsira and recovered the same autumn in Utsira.

found ($Z = -0.22$, $p = 0.83$). While, ringing dates of Scandinavian birds recovered in continental Europe were significantly earlier ($n = 82$; $Z = 3.73$, $p = 0.002$) than those that had been recovered in the British Isles (median dates 1 October [SD = 14.0] and 13 October, respectively).

Temporal trends in the numbers of Blackcaps captured in Utsira indicated late passage, as the number of migrants started to increase in the last days of September and the passage was intensive in October (Fig. 6). Such pattern in the Blackcap migration at the south-western coast of Norway corresponds with ringing dates of individuals that arrived to the British Isles from Scandinavia. Of the six individuals ringed in Utsira and recovered during the same autumn to the south of the island (Fig. 7a), four were ringed in September, presumably on migration. Blackcaps that reached Utsira from the south, mainly Belgium ($n = 4$; Fig. 7b), were recorded mostly in October. Migration dates of Blackcaps heading to the south was slightly, albeit statistically non-significantly, earlier than those of birds migrating to the north ($Z = 1.48$, $p = 0.14$; Fig. 6).

4. Discussion

Ringing recoveries are valuable sources of information on bird movements, including seasonal migration. However, analyses of recovery data have to account for certain limitations, of which at least spatial and temporal variation in recovery rates are important. Bird mortality due to hunting, human population density, level of education, and even political situation influence the spatial and temporal distribution of recoveries (e.g., Payevsky 1973, Perdeck 1977, Kania & Busse 1987). In the present study Blackcap recoveries were analyzed in the western, northern and central parts of Europe, where several ringing schemes have operated since the 1960s. Consequently the recovery rate in these regions is high, and data analyses provide an insight into the possible origin and migration routes of continental Blackcaps to their winter quarters in the British Isles.

Phillips (1994) suggested that continental Blackcaps arrive in the British Isles after most local breeders have departed. However, the present ringing-recovery analysis shows that the arrival of Blackcaps from continental Europe in Britain and Ireland begins considerably earlier and occasionally continues along with the departure of birds from the local population. Blackcap migration in the British Isles nevertheless seems to consist of two peaks: the first occurs early in the autumn and probably reflects the departure of local breeders, and another peak occurs during late autumn, probably reflecting the arrival of birds that over-winter

Recovered to the South from a ringing place

Recovered to the North from a ringing place

Fig. 7. Blackcaps ringed or recovered during the same autumn in Utsira, Norwegian west coast.

on the British Isles (The County Ornithological Records Committee 1991, 1993, Marsh 1993). What is overlooked, is that the arrival of Blackcaps from continental Europe starts in mid-September, and intensifies in mid-October.

The present analysis of ringing recoveries supports the common view that Blackcaps wintering in the British Isles originate from continental Europe. The few winter recoveries of Blackcaps ringed during the breeding season in the British Isles represent only a fraction of recoveries of birds reported there (Balmer & Milne 2003). Hence, they may represent single over-wintering attempts rather than, for example, a general loss of migratory urge caused by higher winter survival due to global warming. Two groups of Blackcaps wintering on the British Isles were distinguished in this study: birds arriving from central-western Europe, and those arriving from Scandinavia. Descriptions of the migration of Blackcaps arriving to over-winter in the British Isles have mainly concentrated on the former group (Langslow 1979, Leach 1981, Berthold & Terrill 1988). Birds of that group may represent a fraction of the originally southwest-migrating population, which might have shifted its migration course towards the west and north-west (Berthold & Terrill 1988, Helbig 1996). This new migration route has a genetic basis rather than being due to increased wind drift or other environmental factors (Berthold *et al.* 1992, Helbig 1996). However, Berthold *et al.* (1992) suggested that Blackcaps may also arrive in the British Isles from a north-easterly direction, but that these individuals might represent wind-drifted migrants and not a well-developed migration strategy. Berthold (1995) suggested that birds ringed in Scandinavia and subsequently reported on the British Isles in October would most probably be migrants that do not winter on the British Isles. Scandinavian and western continental European Blackcaps migrate in a broad front and under very specific meteorological conditions and consequently many of them might migrate through the British Isles (Berthold 1995). This is a viable explanation for the observed movements of Blackcaps, including the present data. However, according to the present analysis on migratory directions of Blackcaps breeding in Norway, low numbers of

recoveries were found to the south-west, and there was only one recovery from the Iberian Peninsula.

Furthermore, a low proportion of Blackcaps reaching the British Isles from Norway were ringed as breeders. Since there recovery rates in both the British Isles and the Iberian Peninsula are typically high (Mokwa 2004; an analysis of 8,246 recoveries), Norwegian breeding Blackcaps may only exceptionally migrate in that direction. Some Norwegian breeders do migrate to the south, i.e., in the direction of the Italian Peninsula. Therefore, the simple mechanism of widening the migration front in a south-westerly direction seems less likely. If Norwegian birds follow the coastline, which is a strategy observed for many nocturnal migrants (Åkesson 1993), they may sporadically be drifted by wind and subsequently arrive to the British Isles. Other possible factors explaining the reported migration patterns are individual variation in migration direction due to genetic variability or mutations, and the possibility that more than the assumed two populations (local breeders and individuals from central Europe) migrate through Norway.

The Blackcap migration in central Europe begins in August, is most intensive in September, and ends in early- or mid-October, as shown on the Polish Baltic coast (Kopiec 1997, Kopiec-Mokwa 1999), Polish inland (Tomiałojć & Stawarczyk 2003) and at the German ringing stations Reit and Mettnau (median dates of the passage were 31 August at Reit and 20 September at Mettnau; Berthold *et al.* 1991), while the median date of autumn migration at Helgoland was 1 October (Hüppop & Hüppop 2004). In Norway, autumn migration also begins in August (Bakken *et al.* 2006), while median dates are similar to those observed in central Europe (Jomfruland: 20 September, Lista: 30 September; Hüppop & Hüppop 2004). The present study showed that the median ringing date of Blackcaps arriving to the British Isles from central-western Europe was 28 September, which is consistent with the above dates. Accordingly, the median ringing date of Scandinavian birds, ringed in autumn and recovered later in continental Europe, was 1 October, while the median ringing date of birds at the Scandinavian coast, later recovered on the British Isles, was over two weeks later, i.e., 13 October.

Moreover, most Blackcaps arriving from Scandinavia had been ringed outside the breeding season. These numbers suggest two populations migrating through Scandinavia: the local breeding population, which migrates toward the south, and another population of an unknown origin, possibly Sweden, Finland and western Russia. However, there are currently no ringing recoveries to support this hypothesis. Finnish breeding birds (n = 33) migrated exclusively toward the south-east, while two Blackcaps ringed as pulli in Russia were recorded on the Baltic coast, i.e., had flown to the west, and in Cyprus i.e., had flown to the south-west. Blackcaps ringed in Sweden migrated to the south and south-east (Fransson & Hall-Karlsson 2008) but none was recorded on the British Isles.

Nevertheless, nine out of 70 birds recovered over 100 km from the ringing site during the same autumn had migrated in a northerly direction, which might be due to migration to the north by continental Blackcaps. A recent study by Bengtsson *et al.* (2009) showed an influx of continental European Blackcaps to Scandinavia starting in late September, which is later than the migration of north European Blackcaps, with the median date being 13 October at Lista, Norway. This was the latest median date out of all studied Scandinavian observatories and similar to the results of the present study. All these facts indicate that Blackcaps arriving to the British Isles from Scandinavia may be of Central European origin. However, there is no conclusive evidence for this hypothesis, as recoveries of the same individual from both Norway and Britain are lacking.

Blackcap migration should be over by mid-October at latitudes >59° N, but the present analysis on the temporal trends in Blackcap records in Utsira indicated that the migration on the coastal Norway still continues at that time. We suggest that there is no single explanation for this phenomenon: birds migrating along the Norwegian coast in October probably originate from regions other than Norway. Recoveries from Utsira indicate that a significant proportion of Blackcaps migrating through this region in autumn arrive from the south. Moreover, during autumn migration, birds heading to the north seem to migrate through Utsira later than those moving to the south. The present results suggest no significant difference in recovery dates in the British Isles between migrants ringed in Western Europe and Scandinavia.

All these facts suggest that Blackcaps from central Europe might reverse migratory direction by 180° (Busse 1992, Helbig 1996).

The reverse-migration scenario appears a plausible explanation for the present observations: reversing of standard migratory direction is a widespread and regular phenomenon among migrants (Richardson 1978, Busse 1981, Sandberg *et al.* 1988, Fransson & Stolt 1993, Åkesson *et al.* 1996, Remisiewicz & Baumanis 1996, Zehnder *et al.* 2001, 2002, Komenda-Zehnder *et al.* 2002). However, the hypothesis has been disputed by Gilroy and Lees (2003). Blackcaps exhibit this behaviour more frequently than other passerines (Fransson & Stolt 1993). For example, the proportion of Blackcaps moving north in autumn is 35% in Belgium, while according to Kortekaas (1998; after Bengtsson *et al.* 2009) 24% of Blackcaps ringed at the Falsterbo bird observatory in autumn moved in northerly directions. Fransson and Stolt (1993) showed that birds from areas west of the migratory divide at 12–15° E primarily seemed to move towards the north or north-east, while individuals from areas east of this divide tended to travel in a north-westerly direction. This pattern supports the reverse-migration interpretation, and it might also explain the north-western migratory direction of Blackcaps from central-western Europe migrating to winter on the British Isles. The present study indicated no difference in recovery dates in the British Isles between migrants ringed in western Europe and in Scandinavia.

It remains difficult to judge whether the north-western migratory direction is an effect of reversed south-eastern direction (Busse 1992), or the widening of standard south-western migratory direction (Berthold & Terrill 1988). Nevertheless, assuming the idea of reverse migration of Blackcaps arriving in Scandinavia and subsequently reorienting to the British Isles, then a similar mechanism could work in Blackcaps arriving in the British Isles directly from central Europe. Further studies, such as stable isotope analyses, may reveal the true origin of the Blackcaps wintering in the British Isles and verify the aforementioned hypotheses.

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Brittein Saarilla talvehtivien mustapääkerttujen alkuperä

Keski-Euroopassa pesivien mustapääkerttujen (*Sylvia atricapilla*) päätyminen talvehtimaan Brittein Saarille todennettiin 1960-luvulla. Tämä ilmiö, joka edustaa nopeaa evolutiivista muutosta muuttokäyttäytymisessä, voidaan selittää muuttosuunnan muuttumisella länteen ja luoteeseen (normaalin suuntautuessa lounaaseen) tai käänteisellä muutolla. Näitä hypoteesejä tarkasteltiin analysoimalla Brittein Saarilla rengastettuja tai siellä kontrolloituja mustapääkerttuja. Skandinaviasta Brittein Saarille saapuvat mustapääkertut oli rengastettu keskimäärin kaksi viikkoa myöhemmin kuin Keski-Euroopasta saapuneet, mutta kontrollihavainnoissa ei ollut merkitsevää eroa. Skandinaviassa rengastetut yksilöt myös saapuivat Brittein Saarille merkitsevästi myöhemmin kuin Keski-Eurooppaan.

Tämä viittaa siihen, että Skandinavian kautta muuttaa kaksi populaatiota: paikallinen pesimäkanta (muuttaa kohti etelää) ja toinen, alkuperältään tuntematon (kenties Keski-Euroopasta, suuntana pohjoinen tai länsi). Siten osa Norjan Utsirassa rengastetuista mustapääkertuista, jotka päätyvät myöhemmin Brittein Saarille, voi olla peräisin Keski-Euroopasta. Nämä yksilöt mahdollisesti vaihtavat muuttosuuntaansa Norjassa ja päätyvät Brittein Saarille. Tällainen muuttostrategia voi selittyä tavanomaisen muuttosuunnan kääntymisestä kokemattomilla yksilöillä 180 astetta (väärä muuttosuunta) ja myöhemmin kauden edetessä korjaantumisesta etelää kohti (oikea suunta).

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