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Migration of Black Storks *Ciconia nigra* at a migratory divide: two different routes used by siblings from one nest and two different routes used by one individual

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ABSTRACT

Black Storks *Ciconia nigra* breeding in Europe use two main migratory routes to winter in Africa: a western route over Gibraltar and an eastern route through Turkey and Israel. A broad area of migratory divide exists in central Europe. We examined cases from the Czech Republic wherein siblings from one nest used different migration routes. We found 20 such cases associated with 18 nests distributed throughout the entire territory of the Czech Republic. Moreover, one bird hatched in 2007 used the western migration route in 2007 and the eastern one in 2009. The actual geographical position of a juvenile Black Stork from an area of migratory divide in the autumn period of migratory restlessness (after the dispersal period) influences the decision to choose the western or eastern direction of migration. We also propose that Black Storks that are older than one year and therefore with experience of past migrations could decide their direction of autumn migration and be followed by inexperienced juvenile Black Storks. Siblings originating from an area of migratory divide can commonly use both main migration routes.

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Black Storks (*Ciconia nigra*) breed across the whole Palearctic, but mostly in the zone 20–60°N, and have an isolated population in South Africa (Elliott 1992). Their European population is estimated at between 9 800 and 13 900 breeding pairs (BirdLife International 2015). European Black Storks migrate around the Mediterranean and winter in sub-Saharan Africa, usually not crossing the equator (Elliott 1992). Although generally they use a western migration route via Gibraltar or an eastern one via Turkey and Israel, a few observations suggest that some birds migrate to Africa through Italy, Sicily and Malta (Janssen *et al* 2004, Bobek *et al* 2008, Vrezec *et al* 2015, www.trektellen.nl/site/totals/1594/2016 – accessed 7 December 2016) and through Greece (the Peloponnese–Kythira–Antikythira–Crete route) (Janssen *et al* 2004, H. Alivizatos pers comm). To generalise, Black Storks that breed in western Europe use the western route, birds from central Europe use both western and eastern routes, and the birds from eastern Europe use the eastern migration route.

In the Czech Republic, Black Storks inhabit forested areas from lowlands to altitudes up to 1100 m asl. The number of breeding pairs was estimated at 300–400 pairs during 2001–03 and has continued to increase since that time (Šťastný *et al* 2006). The whole of the Czech Republic, with western Slovakia, falls within a migratory divide between the western and eastern main European migration routes (Bobek *et al* 2008, Cepák *et al* 2008). Totals of 24 and 17 Black Storks ringed with metal rings within the territory of the Czech Republic and Slovakia used western and eastern routes respectively (Cepák *et al* 2008). Of 14 Black Storks breeding in the Czech Republic and equipped with satellite transmitters from 1995 to 2001 (Bobek *et al* 2008), eight birds (six adults and two juveniles) used a western route across Germany, France and Spain, crossed the Mediterranean Sea via Gibraltar, and continued on to Africa; five birds (all adults) used the eastern route via the Balkans, Turkey and Israel to Africa; and one juvenile started to migrate on the western route but turned in Germany and continued through Austria, Switzerland and Croatia to Italy, where it was shot. The birds that used the western route wintered in Senegal, Mauritania, Mali, Côte d'Ivoire and Sierra Leone. Those using the eastern route wintered in Ethiopia, Central African Republic, Chad and Nigeria.

Based upon their study using telemetry to track four siblings from one nest in France, Larue *et al* (2016) rejected the idea that Black Stork siblings remain together on their first migration but concluded that additional tests were needed to confirm this finding. Towards that end, we analysed autumn migration

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routes of siblings from individual nests in the Czech Republic obtained from a database of results from all ringing activities of Black Storks in the Czech Republic. We focused on those cases in which siblings used different (western *v* eastern) routes in the autumn migration, asking, first, whether such cases exist in the large area of migratory divide within the Czech Republic and, second, what are their number and territorial range. If such cases existed, we could confirm the results published by Larue *et al* (2016) and support their idea that Black Stork siblings might not remain together on their migration. Moreover, we could contribute to knowledge of the migration strategy of Black Storks.

Material and methods

We reviewed all available data about Black Storks ringed in the Czech Republic with metal as well as with coloured plastic rings. A total of 6722 Black Storks were ringed using metal rings between 1934 and 2015 (Klvaňa & Cepák 2016), including 3800 Black Storks ringed with coloured plastic rings during 1994–2015. Data were checked for results from ringing siblings from individual nests. Those cases in which siblings had used different migration routes during autumn migration were selected and analysed further. We chose only the nests from which the siblings had been observed at distances greater than 400 km, in order to exclude birds observed during a dispersal phase after breeding. During their first flights juvenile Black Storks remain within 7 km of the nest and return to be fed by parents and to roost at the nest (Larue *et al* 2016). A flight-learning phase lasting several days is followed by a dispersal phase in which birds depart the nest in various directions to distances as great as hundreds of kilometres (Janssen *et al* 2004, Larue *et al* 2016). Finally, there then occurs an autumn migration, using in Europe western, southern (exceptionally), and eastern migration routes (Janssen *et al* 2004, Bobek *et al* 2008, Larue *et al* 2016).

We classified birds using the following age categories: juvenile (1cy: from hatching to the end of the first calendar year of the bird's life), immature (2cy, 3cy: birds in their second or third calendar years) and adult (4cy or older).

Results

We uncovered 20 cases from across the entire territory of the Czech Republic wherein siblings from a single nest used different migration routes (Table 1, Figure 1). These cases were associated with 18 nests, because this scenario occurred twice in the cases of two nests (N3 in 2005 and 2007, N4 in 2005 and 2012). We recorded eight nests from which siblings used different routes in the same years (2004, twice in 2005, 2007, 2008, 2011, 2012 and 2014). By the end of 2015 a total of 2498 records had been obtained from colour-ringed birds. Only 77 of these recoveries involved cases of siblings from one nest migrating along the same route.

One bird hatched in 2007 in N3 (metal ring B27751, coloured ring 61V9; Table 1) used the western migration route in 2007 and the eastern route in 2009. This bird had been ringed at the nest on 22 June 2007 and relocated on its first autumn migration in Germany (21°42′N 7°55′E, 574 km from the nest, azimuth 291°) on 9 September 2007 and in Spain (36°29′N 6°8′W, 2 312 km, 237°) on 25 October 2007 (and confirmed again at the same place on 14 March 2008). When it was two years old (3cy), it was seen in Israel (32°24′N 35°32′E, 2 558 km, 133°) on 30 September 2009. Therefore, it had used alternately both western and eastern migration routes.

Discussion

Migration routes used by Black Stork pairs and kin have been analysed in a telemetry study by Bobek *et al* (2008). In one case, both parents used the western route as did their single offspring. In another case, both parents again used the same western route as their two offspring, although one of these offspring changed the direction of its migration while in Germany and headed for Italy. In two cases, both parents used the same (western) route. In one case in 1997, a female migrated by the western route but the male by the eastern route.

No case wherein a sibling from one nest used a different (western *v* eastern) route was observed in the study by Bobek *et al* (2008). Nevertheless, such cases have been observed in studies of Black Storks marked with metal and especially with coloured plastic rings. The first was noted as early as 1925 in Denmark (Skovgaard 1926). In that instance, five nestlings were ringed at a nest and, whereas two of them used a western route (being found in the Netherlands and France), two others used an eastern route (Hungary and Romania). Three more cases are known from eastern Germany. Kuhk (1939) had reported a case of two siblings ringed in 1934, one of which migrated westwards to France and the other eastwards to Hungary. More recently, Creutz (1982) described three siblings ringed at a nest in 1951 of which two passed

Table 1. Black Stork siblings originating from nests in the Czech Republic which used different migration routes (W western, E eastern) during autumn migration.

Nest(number of pulli), ringer, coordinates	Year of ringing at nest	Metal ring number	Year of migration studied	Route	Site where observed on post-breeding migration (country, km, azimuth)
N1 (4), F. Pojer, 49°09′N 13°58′E	1997	BX3057	1997	W	France (1 607, 277°)
		BX3060	2009	E	Israel (2 489, 126°)
			2012	E	Israel (2 586, 128°)
N2 (4), T. Růžička, 49°21′N 16°33′E	2004	BX14535	2004	W	Spain (2 276, 241°)
		BX14536	2004	E	Israel (2 453, 133°)
		B14537	2007	E	Israel (2 445, 133°)
			2009	E	Israel (2 454, 133°)
			2010	E	Israel (2 458, 133°)
			2011	E	Israel (2 440, 133°)
			2012	E	Israel (2 439, 133°)
N3a (4), R. Hampl, 50°04′N 15°40′E	2005	B32079	2010	W	Spain (2 266, 239°)
		B32081	2007	E	Hungary (419, 148°)
			2008	E	Hungary (419, 148°)
N3b (5), R. Hampl	2007	B27751	2007	W	Germany (574, 291°)
			2007	W	Spain (2 312, 237°)
			2009	E	Israel (2 558, 133°)
		B27754	2008	E	Israel (2 543, 133°)
N4a (3), J. Grúz, 50°35′N 15°40′E	2005	BX15233	2005	E	Israel (2 586, 133°)
		BX15234	2005	W/E	Italy (1 203, 170°)
N4b (5), J. Grúz	2012	BX20881	2012	E	Israel (2 590, 134°)
		BX20882	2013	W	Spain (2 290, 238°)
N5 (5), J. Šimek, 50°07′N 14°25′E	2005	BX14451	2005	W	Switzerland (624, 237°)
		BX14453	2005	E	Hungary (598, 133°)
N6 (4), F. Pojer, 49°10′N 13°42′E	2007	BX17774	2014	E	Israel (2 591, 127°)
		BX17775	2008	W	Spain (1 664, 241°)
			2009	W	Switzerland (586, 246°)
			2010	W	Spain (1 298, 235°)
N7 (3), V. Beran, 49°52′N 16°55′E	2007	BX18167	2009	E	Bosnia-Herzegovina (664, 182°)
		BX18169	2007	W	France (1 161, 238°)
N8 (4), J. Vrána, 50°35′N 16°07′E	2007	BX17819	2007	E	Israel (2 563, 134°)
		BX17822	2007	W	The Netherlands (719, 286°)
N9 (5), J. Jahelka, 49°31′N 14°54′E	2008	BX19500	2009	E	Israel (2 553, 130°)
		BX19498	2010	W	Spain (2 038, 243°)
			2011	W	Germany (467, 277°)
N10 (4), P. Benda, 50°43′N 14°16′E	2008	BX17231	2009	E	Israel (2 678, 131°)
		BX17232	2008	W	Germany (1 801, 286°)
N11 (2), P. Kurka, 50°39′N 14°26′E	2008	BX18519	2008	W	Spain (2 220, 235°)
		BX18520	2008	E	Israel (2 653, 132°)
N12 (4), V. Kovář, 49°34′N 13°34′E	2009	BX13236	2009	E	Israel (2 630, 128°)
		BX13237	2010	W	France (1 321, 271°)
N13 (4), K. Broulík, 50°31′N 15°06′E	2010	BX18798	2011	E	Israel (2 624, 132°)
			2012	E	Israel (2 608, 132°)
		BX18799	2014	W	Senegal (4 932, 226°)
N14 (4), J. Zajíc, 50°14′N 15°52′E	2011	BX3193	2011	W	Spain (2 067, 241°)
		BX3196	2011	E	Israel (2 545, 133°)
N15 (4), P. Kafka, 49°32′N 18°15′E	2011	BX21153	2011	W/E	Italy (883, 219°)
		BX21154	2013	E	Hungary (223, 203°)
N16 (3), F. Pojer, 50°07′N 13°22′E	2012	BX21901	2012	W	France (660, 250°)
		BX21902	2012	E	Israel (2 687, 129°)
N17 (3), J. Procházka, 50°11′N 14°26′E	2014	YC525	2014	W	Spain (2 139, 233°)
		YC527	2014	E	Hungary (551, 123°)
N18 (4), P. Benda, 50°43′N 14°15′E	2014	BX21116	2016	E	Israel (2 674, 131°)
		BX21117	2014	W	France (1 373, 266°)
			2015	W	France (760, 253°)

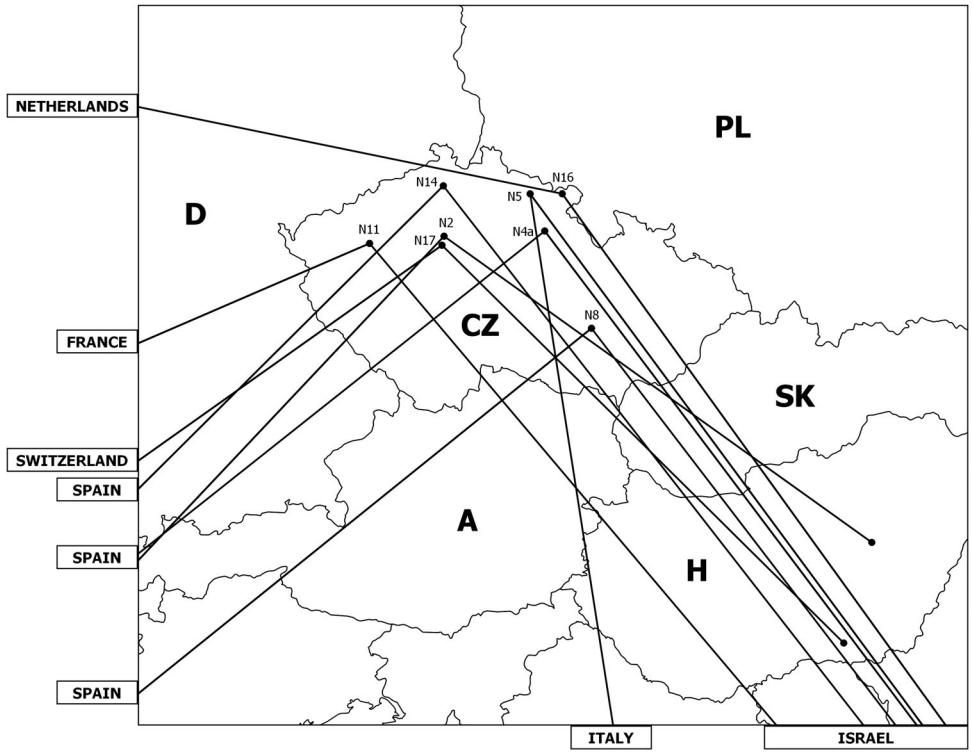

Figure 1. Positions of nests and migration routes of Black Stork siblings which used different migration routes within the same autumn period. See Table 1 for details regarding each nest.

through Italy and one used an eastern route (Bulgaria). Creutz (1982) further reported the case of another two siblings ringed at a nest in 1955, of which one migrated to France and the other to Egypt. We hereby add a substantial number of such cases from the Czech Republic to the list of siblings known to have followed different migration routes across Europe. These cases originated from a relatively broad territorial belt of migratory divide for Black Storks that includes Denmark, the eastern part of Germany, Poland, the Czech Republic and western Slovakia (Janssen *et al* 2004, Cepák *et al* 2008, Dudzik *et al* 2016). Unfortunately, suitable data from Austria are lacking (Schmidt *et al* 2014).

We suppose that, after leaving the nest, juveniles go through a flight-learning phase near the nest lasting about a week and then disperse randomly in various directions over dozens to hundreds of kilometres from the nest to suitable wetland locations with food sources. Black Storks, White Storks *Ciconia ciconia* and herons aggregate at these locations, especially when food is abundant. The dispersal phase starts in the Czech Republic between mid-July and the beginning of August. Black Storks aggregate at suitable locations at the beginning of September. Their groups contain adult, immature and juvenile birds, whether members of individual families or not, and reach numbers into the dozens and, exceptionally, hundreds of individuals (Janssen *et al* 2004).

The migration period follows a dispersal (and sometimes aggregative) period and it is conditioned by migratory restlessness. A young Black Stork originating from a migratory divide must decide which migration route will be used, whether the western, eastern or less frequently used southern route. We consider that migratory movement in the autumn is genetically conditioned and directed in the broad arc from south-east to south-west. The actual geographical position of a Black Stork from an area of migratory divide in the period of migratory restlessness (after the dispersal period) presumably influences the decision regarding migration direction. In more westerly or easterly positions, the predominant decision should be to go via the south-western or south-eastern migration route respectively. Moreover, we consider that Black Storks with experience of previous migrations could influence the decisions of juvenile Black Storks over the direction of their autumn migration during their period of migratory restlessness. Experienced, older Black Storks could be followed by juvenile, inexperienced Black Storks. In areas of migratory divide, the autumn groups should consist of Black Storks experienced with both migratory routes alongside young inexperienced birds. Here, juveniles can randomly use either the

western or eastern route when following the more experienced Black Storks. Direct observations of Black Storks tagged with telemetry devices on their autumn migration do not, however, confirm the notion that Black Storks migrate in groups, with the exceptions of their aggregation at food sources or when they pass migration bottlenecks such as at Gibraltar (Bobek *et al* 2008). Moreover, young Black Storks tend to make longer and more frequent stopovers during their autumn migration than adults, the latter flying shorter daily distances and spreading their migration time over a greater number of days of active flying (Jadoul *et al* 2003). Hence, the young to adult ratio and the composition of groups must be changing during the autumn migration.

Bobek *et al* (2008) concluded that young Black Storks tracked by telemetry probably flew together with their parents. Moreover, they explained the deviation of one young Black Stork from the western route to Italy by its association with other storks. Our results confirm the conclusions of Larue *et al* (2016), and we support their idea that Black Stork siblings might not remain together on their migrations. Siblings commonly use different migration routes. Although Bobek *et al* (2008) observed that each parent from an individual nest in an area of migratory divide would repeatedly use its own western or eastern route for autumn migration, we found a case of a Black Stork once using the western and another time the eastern route (having been confirmed in Spain and Israel).

Similarly as we propose for Black Storks, Chernetsov *et al* (2004) suggested that naive White Storks (a closely related species) rely to a great extent on social interaction when selecting their autumn migration route. It seems that the first migratory journey is very important for young birds among both Black Storks and White Storks, because this presumably constitutes an exploratory phase in early life and they usually, but not always, repeat this established pattern of migration throughout their adult lives.

Assortative mating has been proposed as a mechanism for rapid evolution of a migratory divide in central Europe in the small passerine Blackcap *Sylvia atricapilla* (Bearhop *et al* 2005) and a newly evolved migratory behaviour in this species had a genetic basis (Berthold *et al* 1992). Moreover, assortative mating in this Blackcap population could further be favoured by strong selection against the offspring of hybrid pairings, because they inherit migration directions and distances intermediate between those of their parents (Berthold *et al* 1992, Bearhop *et al* 2005). We propose a different scenario in the evolution and maintenance of a migratory divide for large bird species such as Black Storks in central Europe, with greater emphasis on cognitive skills and the memory of individual birds.

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