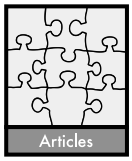

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African Odyssey project – satellite tracking of black storks *Ciconia nigra* breeding at a migratory divide

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The African Odyssey project focuses on studying the migration of the black stork *Ciconia nigra* breeding at a migratory divide. In 1995–2001, a total of 18 black storks breeding in the Czech Republic were equipped with satellite (PTT) and VHF transmitters. Of them, 11 birds were tracked during at least one migration season and three birds were tracked repeatedly. The birds migrated either across western or eastern Europe to spend the winter in tropical west or east Africa, respectively. One of the juveniles made an intermediate route through Italy where it was shot during the first autumn migration. The mean distance of autumn migration was 6,227 km. The eastern route was significantly longer than the western one (7,000 km and 5,667 km respectively). Important stopover sites were discovered in Africa and Israel. Wintering areas were found from Mauritania and Sierra Leone in the west to Ethiopia and Central African Republic in the east and south. One of the storks migrating by the eastern migration route surprisingly reached western Africa. Birds that arrived early in the wintering areas stayed longer than those arriving later. On the average, birds migrating via the western route spent 37 d on migration compared to 80 d for birds migrating via the eastern route. The mean migration speed in the autumn was 126 km/d and the fastest stork flew 488 km/d when crossing the Sahara. The repeatedly tracked storks showed high winter site fidelity.

The black stork *Ciconia nigra* is distributed in the Palearctic between 30° and 61° N with an isolated population in South Africa. In Europe, it disappeared from some western countries in the first half of the last century and it has remained endangered up to now. The majority of the European population lives in eastern countries and the black storks have reoccupied Central and western Europe in recent decades (Hagemeijer and Blair 1997). The main reason for the historical population decline is predominantly overexploitation (Del Hoyo et al. 1992). The Palearctic black stork is migratory and it enters Africa mainly through Sinai and Gibraltar (Hagemeijer and Blair 1997). The storks use soaring flight during migration. Mortality during the migration and winter period can also play an important role in the population decline (e.g. Garrido and Fernandez-Cruz 2003, Barrios and Rodriguez 2004). However, our knowledge of the black stork's migratory routes, stopovers and wintering areas have been based on the analysis of rare ring recovery data (Glutz von Blotzheim and Bauer 1966, Cramp and Simmons 1977, Creutz 1978) and no detailed information was available. Moreover, data on the individual differences in migration strategies and differences between two main migration routes of European black storks are unavailable.

The use of satellite telemetry has brought new possibilities to the study of bird migration. Today, tracking of highly mobile animals, even at the global scale, provides more detailed information about migratory routes, staging and wintering areas, behaviour, home range and habitat selection (Seegar et al. 1996). During the last decade, several birds such as cranes (e.g. Higuchi et al. 1998, Kanai et al. 2002a, b), pelicans (Izhaki et al. 2002), raptors (e.g. Meyburg et al. 1995, Hake et al. 2001, Kjellén et al. 2001), and white storks *Ciconia ciconia* (Papi et al. 1997, Berthold et al. 2001a, b, 2002) have been successfully tracked during migration.

The study of the migration and ecology of black storks became the main goal of the African Odyssey project. We combined two techniques of telemetry for the tracking of the black storks. Firstly, satellite telemetry enabled us to track the migration of storks over long distances. Secondly, conventional radiotelemetry was used to track storks at their home ranges, migratory stopover sites and wintering areas. Moreover, the study populations of storks breed at a migratory divide and they use two widely different routes and winter regions. Our research compared these two unique migration routes. The history of the African Odyssey project is presented on the website http://www.rozhlas.cz/odysea.

The aim of this study was to analyse two main migratory routes, stopover sites, wintering grounds and causes of death of black storks breeding at a migratory divide. In total, 18 black storks were fitted with transmitters in the Czech Republic in 1995–2001. We collected data about the timing of migration, speed and important feeding areas. We tracked mainly adult birds, but two families of storks were also equipped with transmitters. Furthermore, two storks were tracked during two seasons and one female during four consecutive seasons. Thus, we could compare the fidelity to the breeding places, migration routes, stopovers sites and wintering areas.

Methods

In 1995–2001, a total of 18 black storks (six adult males, five adult females and seven juveniles) were equipped with satellite (PTT) and VHF transmitters at 11 nests located in the central Bohemia, about 50 km south-west from Prague, the Czech Republic. The adults were caught with clap-nets on nests in June and July. The juveniles were provided with transmitters a few days before fledging in July. The storks were marked with plastic colour rings with the code according to the international project European Union for Bird Ringing (http://www.cr-birding.be/), and metal rings of the Prague Ringing Centre. We recaptured three adults that subsequently returned to breed in the same region, and replaced the transmitters with new ones.

The transmitters were attached to the storks as backpacks. The total weight of their whole set-up was approximately 60 g (about 2% of their total body weight). The satellite transmitters (PTT) were supplied with batteries recharged by a solar panel (the microwave Telemetry PTT 100). The signals of the transmitters are intercepted by NOAA satellites from the polar orbit and they are sent to the American-French company CLS Argos headquarters (Argos 1996, Lafuma and Ruiz 1996). The system has been described in several studies about bird tracking (see e.g. Taillade and Service Argos 1992, Fuller et al. 1995, Izhaki et al. 2002, Shamoun-Baranes et al. 2003). Argos classified the location accuracy into seven categories: 3, 2, 1, 0 and A, B, Z. For data analysis we used the categories 3, 2, 1 and 0 (for location accuracy, see Argos 1996). The location class LC 0 was included to the data showing the migratory routes, if the locations were considered appropriate from the nearest tracking times and locations. When the location estimates from LC 0-3 were not available for the period of more than 24 h, the estimates from LC A and B were used.

Terrestrial (VHF) transmitters range of a couple of kilometers and broadcast a permanent signal. The transmitters were attached to the storks as backpacks. The system and methods of terrestrial transmitters have been described in several studies (e.g. Naef-Daenzer 1993, 1994). Several expeditions following stork´s journey to the wintering areas were carried out. In the landscape, the storks were located via VHF transmitters because of behaviour monitoring. For detailed information about the project see the address http://www.rozhlas.cz/capi/resume_e.htm.

Some terms that we use in this paper are defined as follows: *Wintering period*-was counted from the day after arrival in, to the day before departure from the wintering site. *Migration*-was defined from the point when the directional movement was recorded away from the breeding site in autumn and away from the wintering site in spring with a possibility to stop at a stopover site at the distance of more than 100 km from the start of the migration. *Travelling days* – are migration d without d at stopover sites. *Stopover days* – are migrations d, when the storks rest at stopover sites. *Stopover site* – is the area where the bird stayed for at least three d and moved less than 100 km per d. *Duration of migration* (d) = travelling d + stopover d. *Migration speed*-is defined as the migration distance (km) divided by the duration of migration (d) and *Flying speed*-is defined as the migration distance (km) divided by the number of travelling d.

The distance travelled was calculated from one location estimate to the next ones as a great circle distance between the data points (Shamoun-Baranes et al. 2003). A one-way ANOVA model was used to test the travel differences between south-west and south-east migrants, and between males and the females using a JMP statistical package (SAS Institute Inc. 1995). Three adults storks were tracked during several seasons, but the data were not involved in the analysis. The map of migraton routes was developed using the GIS (ArcView GIS 3.1 and ArcGIS 9).

Results

Migration routes

Of 18 storks marked from 1995 to 2001, 11 were tracked during one migration season and three were monitored repeatedly; one female during four seasons, one female and one male during two years. Three juveniles were not possible to monitor because of transmitter failures. One juvenile stayed in the breeding area and it was transfered to Spain by air. We recieved four complete return migrations (Zuzana 95–96, Kryštof 99–00, Kristýna 96–97, David 98–99). Nine storks were tracked over the whole autumn migration route to their wintering areas, six storks only for a part of their autumnal migration and four storks for a part of their spring migration because four of them had died during the migration and the transmitters of six individuals stopped transmitting. A total of 5,076 locations were obtained and 1,571 of them were used for the data analysis. For more information about the tracked storks and their mating system see Table 1.

The autumn migration started from late August to early September. The mean departure date of the storks from the breeding area was 1 September (range 21 Aug. -18 Sep., $n = 14$). There were no significant differences between the males and females ($F = 0.54$, $df = 9$, $P = 0.48$) and the eastern and western routes ($F = 0.36$, $df = 9$, $P = 0.57$).

Mates Jakub-Kristýna left the breeding ground the same day. Mates David-Kristýna also left the breeding ground the same day, however their chick Hynek was not observed at the nest from 2 Sept. Mates Kryštof-Dominika and their offsprings Václav and Otakar departed at a different time. Female Dominika left her nest in early Aug., her chicks Václav and Otakar left their nest together on 21 Aug. and her mate Kryštof left their nest on 4 Sept. (Table 1).

Table 1. Autumn and spring migration of fourteen black storks tracked by the satellite from the Czech Republic to Africa. W = western migration route, E = eastern migration route, A = autumn, S = spring, M = male, F = female, IM = immature male, IF = immature female.

Ind./sex-age/year	Start of migration	Path	Date and site of wintering (coord.)	Arrival on breeding site	No. of travelling days A (no. of stopover days)	No.of travelling d S	Migration speed (km/d) A	Migration speed (km/d) S	Total distance (km)
Viktor, M, 95/96	30 Aug	E	26 Oct-14 Dec,Chad (12.2N,21.2E) 19 Dec-17 Mar,Central Afr.Rep.(8.2N,23.4E)	–	38 (20)	–	123	–	7135
Kristýna, F, 95/96	16 Sep	W	13 Oct-20 Feb,Senegal (13.2N,11.9W) 27Feb-16 Mar,Cote d'Ivoire (9.3N,3.9W)	–	21 (7)	–	223	–	6248
96/97	26 Aug	W	27 Oct-1 Mar,Senegal (13.0N,11.8W)	6 Apr	62	37	100	168	6223
97/98	06 Sep	W	16 Oct-14 Feb,Senegal (13.0N,11.8W)	–	40	–	155	–	6189
98/99	18 Sep	W	22 Oct-?, Senegal (13.0N,11.8W)	–	28 (7)	–	183	–	6389
Zuzana, F, 95/96	1 Sep	E	6 Dec-24 Mar,Ethiopia (12.0N,38.1E)	–	49 (48)	–	72	–	6937
96/97	26 Aug	E	25 Nov-?,Ethiopia (11.9N,38.0E)	–	66 (25)	–	60	–	5468
Oskar, M, 96/97	25 Aug	E	9 Dec-6 Mar,Cent. Afr.Rep.(5.7N,26.6E)	–	70 (36)	–	69	–	7347
Jakub, M, 97/98	05 Sep	E	5 Nov-?,Nigeria (10.6N,9.8E)	–	60	–	135	–	8113
Martin, M, 97/98	21 Aug	W	26 Oct-10 Mar, Mali (14.7N,4.1W)	–	65	–	91	–	5933
Tereza, F, 97/98	30 Aug	W	–	–	(11)	–	–	–	–
David, M, 98/99	18 Sep	W	6 Oct-4 Mar, Spain (37.0N,5.9W)	4 Apr	10 (8)	31	167	97	3011
Hynek, IM, 98/99	02 Sep	W	–	–	–	–	–	–	–
Krištof, M, 99/00	04 Sep	W	28 Oct-26 Jan, Mali (14.2N,11.8W 29 Jan-2 Mar,Sierra Leone (9.5N,12.4W)	2 Apr	43 (11)	31	117	203	6302
00/01	22 Aug	W	–	–	(11)	–	–	–	–
Dominika, F, 99/00	Aug	W	1 Oct-?, Mauritania (15.5N,12.7W)	–	(12)	–	–	–	5039
Otakar, IM, 99/00	21 Aug	W	–	–	–	–	–	–	–
Václav, IM, 99/00	21 Aug	W-E	–	–	(30)	–	–	–	–
Johana, IF, 00/01	12 Sep	E	–	–	–	–	–	–	–

Note. Mate/offspring relationships: Kristýna mate Jakub in 1997. Kristýna mate David in 1998. Dominika mate Krištof in 1999.
Hynek is a chick of Kristýna and David born in 1998. Otakar and Václav are chicks of Dominika and Krištof born in 1999.

The storks used two different migration routes to the wintering areas: (1) three males, three females and two juveniles used the western route across Germany, France and Spain. They crossed the Mediterranean Sea close to Gibraltar and continued to Africa. (2) Three males and two females migrated along the eastern route via the Balkans, Turkey and Israel to Africa. Juveniles used the same routes as their parents with the exception of Václav who started to migrate the same time as his parents on the western route. However, he turned east in Germany and continued via Austria, Switzerland, Croatia to Italy. He flew across the Adriatic Sea – a distance of 180 km, but, unfortunately, he was shot in Italy near Cosenza on 25 Oct.

The mean total migration distance of tracked storks from breeding areas to the main wintering areas was 6,227 km (range 3,011–8,113 km). The eastern route was significantly longer than the western route (7,000 km and 5,667 km, respectively, $F = 8.06$, $df = 7$, $P = 0.03$). The birds did not follow the sea coasts but were observed inland, often crossing hills and even mountains.

The storks which were monitored repeatedly flew along the same routes and wintered in the same areas every year. However the routes differed in some details. The female Kristýna passed the western parts of the Pyrenees in 1996/97, 1997/98 and 1998/99, but flew along the easterly route across the Pyrenees in 1995/96. The migration parts of Kristína through Sahara differed between the years and spanned over an area of 1,000 km in the west-eastern direction. The female Zuzana migrated on a different route through Turkey in 1996 compared to 1995.

The female Kristýna, that was tracked by our expedition step by step, flew alone and she stopped by streams in a submontane region in Europe during the migration. She foraged in the morning, and departed on migration in the afternoon.

Most of the birds made one or more stopovers (Table 2). The mean number of stopover days differed significantly between the birds travelling by the western route (8.0 ± 4.0 d, mean $\pm$ SD), and by the the eastern route (34.7 ± 5.2 d, mean $\pm$ SD, $F = 16.51$, $df = 6$, $P = 0.007$).

Wintering areas

The birds that used the western route wintered in tropical West Africa – in eastern Senegal in the Falémé river basin, Guinea, southern Mauritania, Ivory Coast, Sierra Leone and the western and the central part of Mali. The eastern route migrants wintered in northern Ethiopia, the central part of the Central African Republic in the Kotto river basin and the Mbokou river basin, Chad and north-eastern Nigeria (Table 1, Fig. 1).

The storks were stationary on the wintering ground, but three storks changed wintering area. Viktor flew from the wintering ground in Chad to the Central African Republic, Kristyna from Senegal to the Ivory Coast (in 1995/96), and Kryštof from Mali to Sierra Leone. The male David wintered in Spain. None of the three juveniles reached the wintering grounds. The signal from one of them was lost in Germany and the other two were shot by hunters in France and Italy, respectively. Mates used different wintering grounds. The tracked storks wintered in the areas of drying seasonal affluents of rivers and small water bodies in the sub-Saharan savannahs. They fed there in the morning, they had a rest in trees in the afternoon and slept in the dead trees at night. The tracked storks were observed in the assemblage of other black storks and grey herons *Ardea cinerea* there. The number of days spent on the wintering grounds varied between 87 and 148 d with an average of 127 d without significant differences between the sexes ($F = 0.003$, $df = 5$, $P = 0.96$) and the eastern and western migrants ($F = 2.91$, $df = 5$, $P = 0.15$). The individuals arriving to the wintering areas early stayed longer than the ones arriving late ($n = 7$, $r = -0.94$, $P = 0.001$).

Migration speed

On average, birds migrating along the western route spent 37 d on migration, while birds flying the eastern route spent 80 days ($F = 6.91$, $df = 6$, $P = 0.04$). Duration of the migration varied from 18 to 106 d. There was no significant difference between males and females ($F = 0.006$, $df = 6$,

Table 2. Stopover sites of tracked black storks in 1995–2001.

Ind./year	Dates of stopovers	Sites of stopovers (coord.)
Viktor/95–96	6 Sep-22 Sep	Slovakia-Hungary (47.7N,17.9E)
	14 Oct-16 Oct	Israel (32.6N,35.4E)
Kristýna/95–96	19 Sep-21 Sep	France (47.2N, 6.3E)
	30 Sep-3 Oct	Marocco-Algeria (29.6N,7.1W)
98–99	3 Oct-9 Oct	Spain (39.1N,3.7W)
Zuzana/ 95–96	1 Sep-9 Sep	Slovakia (47.7N,18.2E)
	14 Sep-15 Oct	Romania-Serbia (45.5N,21.0E)
	16 Apr-23 Apr	Turkey (39.4N,29.9E)
96–97	26 Aug-9 Oct	Serbia (45.1N,21.2E)
	3 Nov-12 Nov	Israel (33.2N,35.6E)
Oskar/96–97	10 Sep-24 Sep	Serbia-Croatia (45.8N,18.8E)
	2 Oct-18 Oct	Serbia (48.8N,21.0E)
	22 Oct-25 Oct	Egypt (24.4N,33.0E)
Tereza/97–98	11 Sep-22 Sep	France (47.0N,2.8E)
David /98–99	24 Sep-29 Sep	France-Spain (43.2N,1.1W)
Krištof/99–00 00–01	8 Oct-18 Oct	Morocco (33.0N,6.2W)
	25 Aug-4 Sep	France (46.8N,5.6E)
Dominika/99–00	2 Sep-13 Sep	Spain (40.6N,6.3W)
Václav/99–00	28 Aug-26 Sep	Germany (48.6N,9.6E)
Johana/00–01	24 Sep-?	Romania-Serbia (45.4N,20.8E)

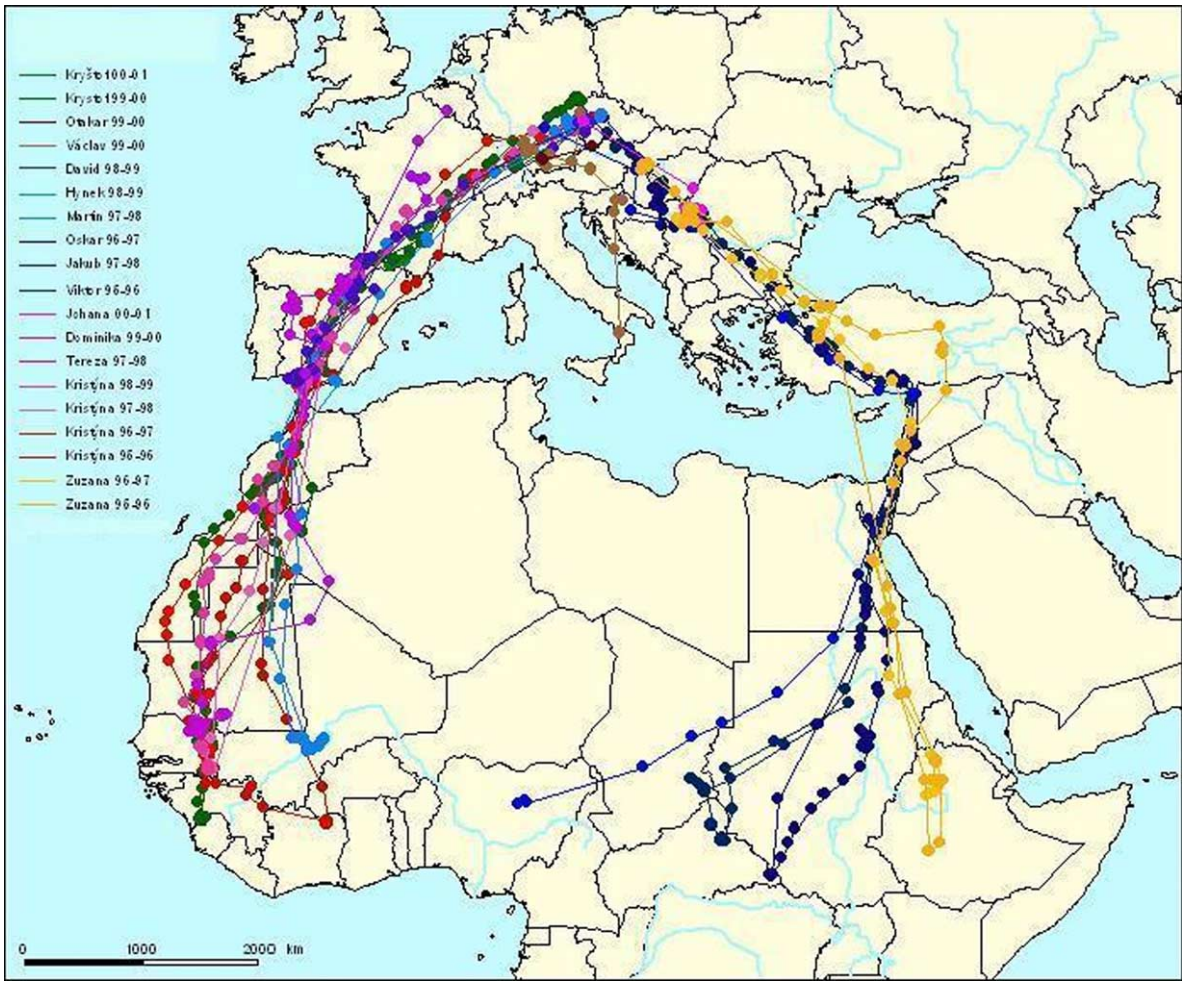

Figure 1. Autumn and spring migratory routes of 15 black storks tracked by the satellite from the breeding site in the Czech Republic to the winter quarters in Africa and Spain. Points show location of the migration course.

$P = 0.98$). The mean migration speed in autumn was 126 ± 54 km/d (mean $\pm$ SD, range 69–231 km/d, $n = 8$). There were no significant differences between males and females ($F = 0.58$, $df = 6$, $P = 0.48$) and eastern and western migrants ($F = 2.16$, $df = 6$, $P = 0.19$). Storks that started their autumn migration late migrated faster than those which started early, but this difference was not significant ($n = 11$, $r = 0.62$, $P = 0.08$). The mean flying speed in autumn was 176 ± 82 km/d (mean $\pm$ SD). The male Jakub travelled at the speed of 350 km/d during three days in Turkey. A speed over 400 km/d was reached by the female Kristýna in 1995/96 and the male Viktor in 1995/96 only during the Sahara crossing. The fastest stork was the male Kryštof reaching 488 km/d during the Sahara overflight. During the spring migration the storks used the same migratory routes as in autumn with a variation of roughly 500 km in the west-easterly direction in Africa.

Discussion

The route of the stork migration between Europe and Africa is defined by its flight strategy. The black stork as other big birds uses thermal soaring. Due to the general absence of thermals above the sea, the storks circumvent the Mediterranean Sea via southern Spain, close to Gibraltar (western route) or via Turkey and Israel (eastern route). The distribution of ring recoveries and some observations show that some black storks migrate through Italy and cross the sea via Sardinia, Sicily and Malta to reach Africa (Hudec 1994, Hagemeijer and Blair 1997, Janssen et al. 2004). This might have been the case of Václav, which was shot in Italy. The flight of soaring birds over large stretches of sea has been reported by e.g. Papi et al. (1997) and Chernetsov et al. (2004).

European black storks use both the eastern and western migration routes (Hagemeijer and Blair 1997). The black storks that breed in France, Belgium and west Germany use the western migratory route, the storks breeding in east Germany, Czech Republic and Poland use both the eastern and western migration route and storks breeding in eastern Europe and western Russia use the eastern migration route (Janssen et al. 2004). However, the exact delimitation of black storks´ migratory divide is not known. Because of the population decline of black storks in west Europe during the 20th century the majority of European storks migrate via the eastern route (Cramp and Simmons 1977). Storks from the Czech Republic use both the western and eastern migratory routes and offer uniqe opportunities to compare the eastern and western migratory routes. The eastern

migration route may possibly be more suitable from the point of view of survival during migration, or overwintering, despite of longer distance and time. But, no study has adressed this topic. The present study reveals for the first time details on the two migratory routes, stop-over sites and wintering grounds of the black storks breeding in the same area.

Also white storks use two different routes during migration via Sinai and Gibraltar. The white stork´s migration divide is situated farther west than that of the black stork (Cramp and Simmons 1977). On migration, black stork forms smaller flocks than the white stork (Hagemeijer and Blair 1997). However, we do not know if the white stork could influence black stork migration through travels in mixed species flocks that were sometimes observed during migration (Janssen et al. 2004).

The migration route is probably innate (Berthold and Terrill 1991), but surprisingly young from the same nest may migrate on different courses (Glutz von Blotzheim and Bauer 1966, Cramp and Simmons 1977). Our tracked young probably flew together with their parents or siblings. We suppose that young naive storks learn the route from their parents or, in case of the lost contact with parents, from other adult storks. The deviation of young Václav from the western route to Italy might be explained by its associations with other storks. Similarly, Chernetsov et al. (2004) assumed that the change in flight direction of young white storks during migration is explained by the fact that they encountered some late migrating storks and joined them in their flight. Chernetsov et al. (2004) suggested that naive white storks rely to a great extent on social interaction when selecting their autumn migratory route. However, white storks are highly gregarious on migration, contrary to black storks, that are mainly seen alone or in small family groups. Nevertheless, the first migration journey is very important for the young birds because many bird species demonstrate an exploratary phase in early life and they repeat this established pattern of migration movements throughout their adult life (Baker 1978 in Izhaki et al. 2002).

Except for wintering areas in Mauritania, Ivory Coast, Sierra Leone, Mali and the Central African Republic, the wintering of the male David in Spain is of great interest. The Spanish stork population is partially resident but it is not known that black storks from Central Europe winter there. On the other hand, the area is a known wintering ground for the white storks (Tortosa et al. 1995). Another interesting finding was that a stork using the eastern route reached the winter quarters in western Africa (Nigeria). A similar case was observed by Berthold et al. (2001b) for the white stork. Some ring recoveries of white storks demonstrate a mix of eastern and western populations on the wintering grounds (Brouwer et al. 2003), and our data illustrates that a similar pattern may hold for the black stork.

Black storks that were tracked repeatedly demonstrated a hight fidelity to their wintering areas. The black stork wintering strategy differs from white stork, which do not show a strong winter-site fidelity, but instead migrating to different areas from one year to the next (Berthold et al. 2002, 2004). Furthermore, the autumn migration speed differs between the two species. The mean duration of migration in autumn for the white storks was 26 d (Shamoun-Baranes et al. 2003), about a half to a third of the duration for the black stork. The black storks spent more time at stopover sites and there were also significant differences between the western and eastern migrants in mean number of stopover days. Shamoun-Baranes et al. (2003) suggested that the differences in the white stork daily migration speed were related to the wind assistance, location and season. In black storks, the difference in stopover time between the eastern and western migrants was probably related to the significant different routes with the longer eastern route mediating longer stopovers.

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