

Migratory orientation of first-year white storks (*Ciconia ciconia*): inherited information and social interactions

Nikita Chernetsov^{1,*}, Peter Berthold² and Ulrich Querner²

¹Biological Station Rybachy, Rybachy 238535, Kaliningrad Region, Russia and ²Max Planck Research Centre for Ornithology, Radolfzell 78315, Germany

*Author for correspondence (e-mail: nchernetsov@bioryb.koenig.ru)

Accepted 19 December 2003

Summary

We used satellite tracking to study the migratory orientation of juvenile white storks from the population in the Kaliningrad Region (Russia) during their first autumn migration. Two series of experiments were performed. In the first series of experiments, several groups of first-year storks were raised in an aviary, kept there until all free-living conspecifics had left the area and then released. These birds had to select their migratory route on the basis of the inherited directional information they possessed, without any chance of being guided by their experienced conspecifics. In the second series of experiments, several groups of juveniles were displaced from the Kaliningrad Region to the Volga area and to

Western Siberia. Both areas lie outside the breeding range of the white stork so the displaced birds also had to rely on their innate migratory program. Results from the differently designed experiments did not match. Nor did they match with the results of earlier experiments on the delayed departure of juvenile white storks as reported by several authors. We suggest that naïve white storks (and maybe other soaring migrants) rely on social interactions when selecting their autumn migratory route to a much greater extent than do passerine long-distance migrants.

Key words: orientation, white stork, *Ciconia ciconia*, spatiotemporal program, displacement.

Introduction

Orientation by first-time migrants is an intriguing topic in the study of avian migratory performance. How do young birds find their winter quarters when they have never been there before? Are they guided by their experienced conspecifics or do they have an orientation system that makes it possible to reach their destination independently of adults? One of the first attempts to answer this question was the series of experiments performed in the 1920s and 1930s (Thienemann, 1931; Schüz, 1949, 1950).

Juvenile white storks from East Prussia were detained in aviaries until all free-living conspecifics had left the area and were then released. Recoveries and subsequent sightings of experimental birds suggested that they generally followed the south–southeast (SSE) direction typical of white storks migrating normally from East Prussia (Schüz and Weigold, 1931). It was interpreted as evidence of the ability of young inexperienced birds to find their winter quarters without receiving aid from the adults, on the basis of an innate orientation mechanism (Thienemann, 1931; Schüz, 1949, 1951). However, as shown by Wallraff (1977) and using his notation, where α is mean vector of recoveries and \bar{a} is relative length of the mean vector, so that $\bar{a}=1$ means no directional variation and $\bar{a}=0$ means no directional preferences at all, the mean orientation of recoveries of the delayed birds ($\alpha=170.3^\circ$,

$N=19$, $\bar{a}=0.9395$, $P<0.0001$) slightly but significantly differed from the mean orientation of recoveries of the non-manipulated birds from East Prussia ($\alpha=159.3^\circ$, $N=26$, $\bar{a}=0.9737$, $P<0.0001$; the difference of 11° is significant at $P<0.05$: VWR test (Batschelet, 1965), $F=4.55$; B test (Batschelet, 1972), $U=6.71$; from Walraff, 1977). Furthermore, early releases of East Prussian storks in western Germany (before the departure of local experienced conspecifics) showed that the urge to follow other storks dominates over inherited directional information (Schüz, 1950).

Later, similar experiments were performed in Latvia (Katz, 1986). In the autumns of 1970 and 1983, juvenile white storks were detained in aviaries until late September, by which time all free-living storks had left Latvia. The mean orientation of short-distance recoveries in the adjacent Lithuania was 192° ($N=9$), while the mean direction of recoveries at distances greater than 400 km was 213° ($N=5$). The normal migratory direction of Latvian storks within Europe is 168° ($N=6$). The difference in migratory directions between the non-manipulated and the experimental birds was significant ($P<0.01$, Watson–Williams test; Katz, 1986).

Current theory suggests that inexperienced birds depart from their breeding areas flying in a certain compass direction (Berthold, 1991, 1996; Mouritsen and Mouritsen, 2000). After

some time, they change their migratory direction, if appropriate. Such spatiotemporal programming of migration brings the birds to their population-specific wintering areas. This mechanism was shown by Gwinner and Wiltschko (1978) in their experiment with hand-raised caged garden warblers, *Sylvia borin*, and was demonstrated even more convincingly by Helbig et al. (1994).

In the light of these results, we suggested a hypothesis explaining the more westerly mean direction of recoveries of detained white storks from East Prussia (Thienemann, 1931; Schüz, 1949, 1951) and from Latvia (Katz, 1986) as compared with non-manipulated individuals. We assumed that the delayed storks made the directional change that normally occurs at the Gulf of Iskenderun (Berthold et al., 2001a) at the programmed date and took the south–southwest (SSW) course while still in Europe. However, the delayed birds differed from their non-manipulated conspecifics in two respects: (1) they were travelling alone and could rely on their innate orientation mechanisms only and (2) they were travelling late in the season when their conspecifics had (nearly) reached the first part of the wintering area in Africa. In order to separate these effects, two groups of naïve storks were displaced to two different locations in Eurasia with no breeding white stork population. These displaced birds were not delayed but relied on their own orientation abilities without a chance of guiding by experienced individuals.

We expected that the delayed storks should either first migrate towards the SE and later change their flight direction towards the SSW (if they follow the migratory program with delay) or migrate towards the SW from the very start (if they just fly parallel to their free-living conspecifics). The displaced birds were expected to fly parallel to the free-living white storks from the Kaliningrad Region, at least until they encountered a major ecological barrier (a large body of water or a mountain range). If the displaced juveniles are able to navigate using an inherited ability to correct for displacements (which we thought unlikely; Åkesson, 2003 and references therein), they should select the migratory direction towards their first winter quarters in Sudan or Chad (Berthold et al., 2001b).

To test this hypothesis, it was necessary to trace the route of the detained birds using satellite tracking (Berthold et al., 1997, 2001a,b). Satellite tracking has recently been applied to study the navigational abilities of green sea turtles (Luschi et al., 2001; Åkesson et al., 2003; Hays et al., 2003) and petrels (Benhamou et al., 2003). This technology made it possible to track the animals along the whole of their route and not to rely on recoveries. It appeared possible to repeat the now classical studies of orientation and navigation in migratory birds by displacement, recently reviewed by Åkesson (2003), on a new technical level, as proposed recently (Mouritsen, 2001, 2003).

Materials and methods

Control group

In 2000, four white storks (*Ciconia ciconia* L.) from the

Kaliningrad Region of Russia were equipped with satellite transmitters while still in the nest (three on 30 June and one on 12 July). They formed the control group that was to show the route of autumn migration taken by normal, non-manipulated (albeit carrying transmitters) storks from the Kaliningrad population. Each bird in this group originated from a different nest. The nests were located in the Zelenogradsk and Gurievsk districts of the Kaliningrad Region.

Two series of experiments (detention and displacement) were performed in order to test whether inexperienced white storks follow an innate directional program of migration. In 2000–2002, several groups of young birds were taken from nests in the Kaliningrad Region of Russia [formerly East Prussia, the same area where Thienemann (1931) performed his experiments]. They were raised in an aviary at the Biological Station Rybachy (55°12' N, 20°46' E). The aviary was 23 m×4 m×4 m and housed a maximum of 18 storks simultaneously. Aviary height allowed the birds to make short training flights. Food was provided four times a day (when the birds were 5–6 weeks old) or three times a day (when they were over 6 weeks old) and mainly included fresh fish. In all cases, the amount of food given to storks was adjusted so that some pieces of fish were left until the next feeding. They were removed before the next feeding, so that only fresh food was available. Drinking water was available constantly.

Delayed birds

Ten white stork nestlings were taken from their nests in the western part of the Kaliningrad Region on 12 July 2000 at the age of ~5 weeks. All birds were taken from different nests. They were kept in the aviary until all free-flying storks had left the Kaliningrad Region (which usually happens by the end of August) and were released in three groups. Each group included two individuals carrying satellite transmitters and one or two birds without transmitters. All birds carried the usual aluminium rings for identification purposes. The first group was released on 7 September, the second group on 14 September and the third group on 21 September, all at the same site in the vicinity of Zelenogradsk, near the base of the Courish Spit (54°56' N, 20°32' E).

On 10 July 2001, nestlings were taken from the same area of the Kaliningrad Region. Six birds were released in two groups on 3 September at two different sites in the western Kaliningrad Region. Each group included two birds with transmitters and one bird without a transmitter. All released storks carried aluminium rings. In 2002, nestlings were taken from nests on 1 July. Of the 10 birds, nine carried transmitters. They were released in four groups at different sites in the western Kaliningrad Region on 5 September.

Displaced birds

In 2001 and 2002, we carried out the displacement experiments. The aim was to track the migratory route of inexperienced storks released at the normal time (not delayed) but with no chance of being guided by conspecifics. It was expected that the displaced birds, if capable, would follow their



Fig. 1. Map showing the movements of three storks equipped with transmitters in nests in 2000.

were released in two groups in the Omsk Region. One group consisting of four storks (two with transmitters) was released on 4 August 2002 on the coast of Lake Tenis ($56^{\circ}12' \text{ N}$, $72^{\circ}01' \text{ E}$), while the other group (two birds, one with transmitter) was released on 5 August near Ostrovnyaya ($56^{\circ}23' \text{ N}$, $72^{\circ}10' \text{ E}$). Omsk Region lies far to the east of the breeding range of white storks.

Details of the satellite tracking, transmitters used, ARGOS satellite-based positioning system, etc. are described by Berthold et al. (1997, 2001b). We used PTT-100 transmitters produced by Microwave Telemetry Inc. (Columbia, OH, USA). Their mass varied between 38 g (solar-powered transmitters) and 100 g (battery-powered transmitters). As the mass of a white stork is usually $\sim 3.5 \text{ kg}$, transmitters weighed less than 3% of the birds' mass in all cases.

Since the early 1990s, much work has been done on satellite tracking of white storks (e.g. Berthold et al., 2001b). Mortality during first-time autumn migration is $\sim 75\%$ in white storks (M. Kaatz, personal

communication). We have no reason to believe that mortality of storks equipped with transmitters is significantly higher than in non-manipulated birds. Mortality of the displaced individuals was high (nearly 100%). We cannot be sure but it seems that in many cases the cause of mortality was hunting or collision with power lines. Signal usually disappeared very abruptly, and it often happened when the birds reached more populated areas, often with practically non-regulated hunting activities (e.g. Batumi area in Georgia, Hassan-Kuli area in Turkmenistan, Karachi in Pakistan).

Results

Birds equipped with satellite transmitters in the nest (control group)

Of the four storks from the control group, three reached their first African winter quarters. The departure direction was SSE. Two birds started migration on 10 August and one bird on 14 August. Rapid southerly movement ended on 6, 7 and 10 September, respectively. At this point, two birds were in central Sudan and one was in eastern Chad near the Sudanese

innate migratory direction in spite of the displacement (Perdeck, 1958).

In 2001, 10 first-year white storks were transported by air to Samara on 3 August and released in the Samara Region on 4 August 2001. This was done just before the onset of the autumn migration of Kaliningrad storks. Five individuals (four of them carrying transmitters) were released in Samarskaya Luka National Park (Samara Region, $53^{\circ}13' \text{ N}$, $49^{\circ}53' \text{ E}$), and the five other birds (four with transmitters) were released to the north of Togliatti (Samara Region, $53^{\circ}42' \text{ N}$, $49^{\circ}15' \text{ E}$). Thus, the white storks were displaced nearly 30° to the east. No breeding white stork population exists in the Samara Region (Borodin, 1994; Lysenkov and Lapshin, 1997). Black storks (*Ciconia nigra*) breed in the Middle Volga region but their numbers are extremely low. In most parts of the region they are probably extinct (Lysenkov and Lapshin, 1997). The experimental birds could have joined a group of black storks and flown together with them, but this seems unlikely.

In 2002, white storks were transported by air to Omsk (southern part of Western Siberia) on 1–2 August. The birds



Fig. 2. Map showing the movements of storks released in the Kaliningrad Region in September 2000 and September 2001. Bird # 14554 is the one that crossed the Mediterranean.

border (Fig. 1). Their migration was very similar to the pattern shown by birds from NE Poland (Berthold et al., 2001a). The fourth bird stopped sending data at the beginning of August, before the onset of migration. It probably perished during the post-fledging period.

Delayed birds

All storks released in September from the Kaliningrad Region in 2000 and 2001 moved towards the SW or WSW (Fig. 2). In 2000, the birds released on 7 September moved towards the SW. The transmitter of one of the birds failed soon afterwards. The other stork (# 14554) continued flying towards the SW. On 3 October it reached the French Mediterranean coast south of Nîmes. On 7 October it took off from the vicinity of St Tropez at ~11:15 h and started its flight across the Mediterranean. At 13:44 h on the following day the bird was already on the African coast after flying a distance of 752 km. This bird spent its first winter in Tunisia. Another bird released on 7 September without a transmitter but with a metal ring (Moskwa B-60510) was found dead on 24 October 2001 in south Baden (Baden-Württemberg, Germany).

The two storks from the second group released on 14 September soon parted. Both birds took a WSW route. They moved only short distances and made long stopovers even when the weather allowed them to fly. One of the birds was found in an unhealthy condition in northern Poland on 12 October. Another bird reached Germany and was observed on 25 September near Wittenberg (Sachsen-Anhalt, Germany)

and on 26 September near Taucha (Sachsen, Germany). It was finally found dead in Bavaria.

Birds from the third group, released on 21 September, moved towards the SW only a very short distance, ~100 km. Contact with them was lost at the beginning of October when they were still in the Kaliningrad Region. The transmitter from one of the birds was found by a member of the public somewhere in the Kaliningrad Region and returned to the Biological Station Rybachy two years later (the exact date and place of finding are not known).

In 2001, six white storks were released in two groups (four of them with transmitters) on 3 September. Two tagged birds died before leaving the release site. Another two remained in the vicinity of the release site until 25 September. This may have been caused

by very rainy weather, which is unfavourable for stork migration. On 25 September, the birds started to move towards the WSW. After reaching Germany, they remained there for more than 2 months without making significant movements.

Of the birds released in September 2000 and 2001 in the Kaliningrad Region, at least four individuals (or groups) chose the SW or WSW direction independently of each other. No other pattern was recorded. In 2002, the situation was different. Nine birds were released in four groups; seven of them were successfully tracked and at least six individuals/groups were flying independently of each other. Two birds initially chose a WSW direction but five flew more or less towards the south. Moreover, five birds out of seven changed their flight direction towards the SE when in Central Europe. This change was most dramatic in bird # 36169 (Fig. 3). Together with the wide scatter of initial directions, this makes the 2002 results quite different from those of the preceding years.

Displaced birds

Of the storks released in the Samara Region in 2001, seven were tracked and one transmitter failed two days after release (Fig. 4). Five birds initially chose the SSE direction, while two (flying together) chose the SSW direction. One of the birds that initially departed towards the SSE, later changed direction and flew to the SSW.

At least until the birds reached the latitude of the Caspian Sea coast, their movements were influenced by topography. However, the initial flight directions could well have been the

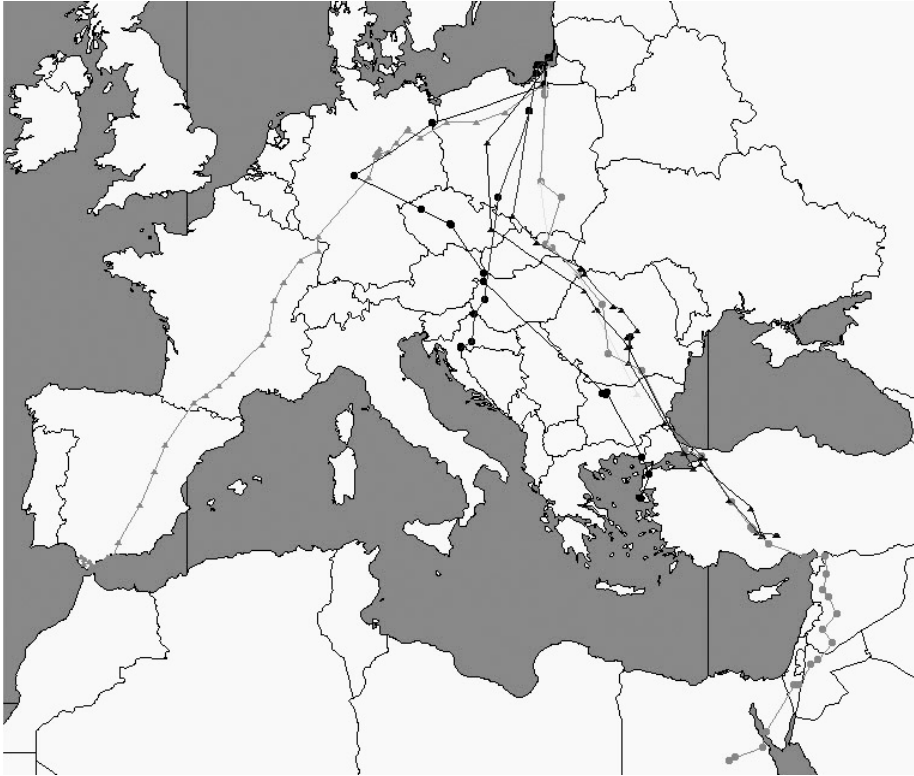


Fig. 3. Map showing the movements of storks released in the Kaliningrad Region in September 2002. Bird # 36169 is the one that sharply changed migratory direction in central Germany.

result of an innate program. It is noteworthy that the birds that moved to the SSE (the direction more or less corresponding to flight patterns of normally migrating Kaliningrad storks) left optimal habitats in the Volga valley and moved to dry steppe habitats probably not favourable for them.

Of the birds released in the forest steppe of Western Siberia, one died soon after release and two took a SSW route independently of each other (Fig. 4). Their flight pattern was clearly different from that expected on the basis of an innate program. One bird probably died in SW Iran, and the signal from the other was lost in Turkmenistan.

Discussion

The initial flight directions chosen by the delayed birds released in the Kaliningrad Region in September (2000–2002) show a wide scatter from south to WSW. The 2002 results deserve special attention. The change in flight direction shown by five out of seven birds is most probably explained by the fact that these individuals encountered some late migrating white storks and joined them in their flight towards the SE. This assumption is supported by the evidence from bird # 36169, which showed the most dramatic change in its flight path. This bird was released together with bird # 27233. They parted after several days, and bird # 27233 was one of those that never changed its flight direction and wintered in southern Spain. Bird # 36169 was found dead on the island of Lesbos (Greece, 39°14' N 26°13' E) on 27 October 2002. As reported by Mr and Mrs Peeters-Lenglet of the Lesbos Wildlife Hospital

(personal communication), it was accompanied by two other white storks, which flew away. The experimental bird must have joined these two individuals *en route*.

The results of our delaying experiments generally agree with those of Katz (1986). However, the results obtained by Thienemann (1931) and Schüz (1949) were different: only three SSW–SW and no WSW recoveries were recorded (see fig. 2B in Wallraff, 1977).

Birds released on 14 and 21 September 2000, and those released on 3 September 2001 but delayed by inclement weather until 25 September, migrated slowly and reluctantly. Delayed birds seem to be able to prolong their migratory time program

only within certain limits. Probably some of Thienemann's and Katz's birds died in the vicinity of the release site but were not detected. Katz (1986) reported that five (out of 36) of his late-released storks were found dead near his study area.

The directions taken by the displaced storks show the most variation. Flight paths shown by the birds released on the Volga could suggest that they followed an innate program guiding them towards the SSE (e.g. bird # 13105, Fig. 4). However, the birds released in Western Siberia flew as if they were navigating towards their African winter quarters (Fig. 4). From the viewpoint of the current theories (clock-and-compass vs innate navigation abilities), the results of these two similar experiments do not match.

We clearly need a theory capable of explaining the results of all the experiments. It may be suggested, following Rüppell (1937) and Rüppell and Schüz (1948), that juvenile white storks have only a rough inherited migratory direction. None of the experimental birds flew to the north, so the idea that they were completely disoriented can be rejected with certainty. However, it seems that they did not possess an exact migration map or program. This is suggested by the large directional scatter shown by the delayed birds, even when their treatment had been exactly the same (as, for example, in the 2002 experiment), and by the widely varying behaviour shown by the displaced individuals. We argue that this hypothesis can explain the results of numerous delaying experiments (Thienemann, 1931; Schüz, 1949, 1950; Wallraff, 1977; Katz, 1986; our data) and our displacement results.

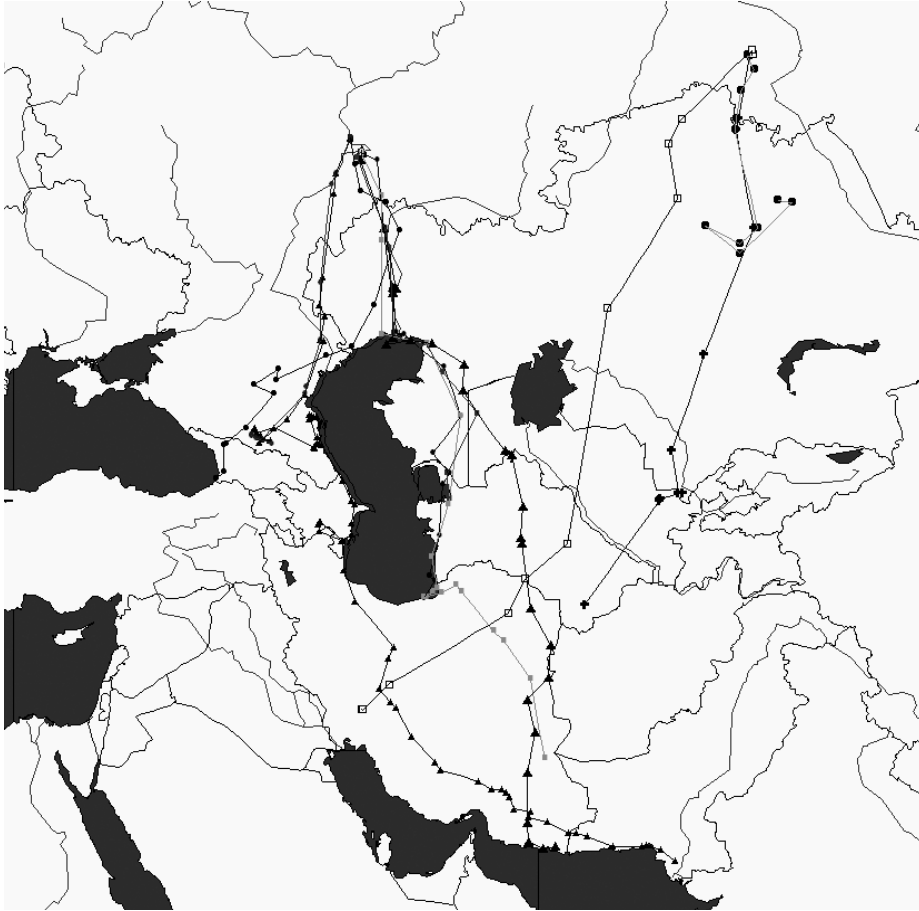


Fig. 4. Map showing the movements of the displaced storks: western site – released in the Samara Region in 2001; eastern site – released in the Omsk Region in 2002.

Three possibilities may be imagined:

(1) The genetic pool of a population contains many individual inherited directions ranging from the WSW to the SSE. Each bird has its own genetically fixed direction and follows it if it has to rely on its innate orientation abilities. The fact that each bird followed its chosen direction quite strictly and did not switch can be treated as evidence for this possibility.

(2) All individuals have more or less similar inherited directions. Random spatiotemporal factors cause the observed phenotypic variation. Generally constant individual internal flight directions may explain why the birds kept to their initially selected direction. This possibility is supported by the fact that flight directions seem to be more uniform within years than between years.

(3) The results of displacement experiments suggest a genetically determined more or less southerly direction. The southwesterly tracks of delayed birds could be the function of a temporal program (flight towards the SSW along the eastern Mediterranean coast or flight towards the WSW from Nile valley to Chad). The results of Thienemann (1931) and Schüz (1949), however, disagree with this assumption.

The hypothesis of Rüppell (1937) that naïve migrants have only a rough inherited migratory direction does not agree with more recent findings in nocturnal passerine migrants (Gwinner

and Wiltschko, 1978; Helbig et al., 1994). Much evidence is available that many bird species have an inherited spatiotemporal program that guides first-time migrants to their winter destination without any aid from the adults (for reviews, see Berthold, 1996; Mouritsen, 2003). It may be hypothesized that in soaring migrants that are heavily dependent on local topography, social contacts and observation of the performance of migrating conspecifics play a much greater role than in nocturnal migrants that usually fly individually. This may presuppose a greater role for social inheritance in the white stork and probably in other soaring migrants than in other long-distance migrants.

Juvenile white storks normally migrate in large conspecific flocks containing experienced adult individuals. Therefore, naïve storks only rarely have to use their own innate orientation mechanisms. A result of this may be that selection pressure supposed

to eliminate birds with failing orientation mechanisms may be rather weak as compared with the situation found in nocturnal passerine migrants. When we force juvenile white storks into using their innate orientation mechanisms, it may appear that comparatively many birds fail to orientate correctly.

This study benefited from kind assistance from many persons. Dr Michael Kaatz has generously shared his experience in various aspects of satellite telemetry with N.C. Vlad Kosarev, Dr Anatoly Sema and Vladimir Salikhov helped in many ways during the field phase of the experiments. Oleg Borodin and Sveta Smirnova were most helpful in organizing the logistics in the Samara Region, and the hospitality of Dr Sergei Soloviev made the trip to Omsk easy and efficient. Kaliningrad Air Enterprise kindly permitted us to transport wild (and kicking!) storks in their aircrafts. John Walder polished the English. The analysis of the data benefited a lot from the experience of Prof. Dr Hans G. Wallraff who suggested many important points, including the hypotheses about the patterns of genetic variation in the inherited migratory direction in white storks. However, the responsibility for all the possible drawbacks and deficiencies remains solely with the authors. We are most grateful to two anonymous reviewers whose comments helped to improve the manuscript a lot.

References

- Åkesson, S. (2003). Avian long-distance navigation: experiments with migratory birds. In *Avian Migration* (ed. P. Berthold, E. Gwinner and E. Sonnenschein), pp. 471-492. Berlin, Heidelberg: Springer-Verlag.
- Åkesson, S., Broderick, A. C., Glen, F., Godley, B. J., Luschi, P., Papi, F. and Hays, G. C. (2003). Navigation by green turtles: which strategy do displaced adults use to find Ascension Island? *Oikos* **103**, 363-372.
- Batschelet, E. (1965). *Statistical Methods for the Analysis of Problems in Animal Orientation and Certain Biological Rhythms*. Washington, DC: American Institute of Biological Science.
- Batschelet, E. (1972). Recent statistical methods for orientation data. In *Animal Orientation and Navigation* (ed. S. R. Galler, K. Schmidt-Koenig, G. J. Jacobs and R. E. Bellville), pp. 61-91. Washington, DC: NASA.
- Benhamou, S., Bonadonna, F. and Jouventin, P. (2003). Successful homing of magnet-carrying white-chinned petrels released in the open sea. *Anim. Behav.* **65**, 729-734.
- Berthold, P. (1991). Spatiotemporal programmes and genetics of orientation. In *Orientation in Birds* (ed. P. Berthold), pp. 86-105. Basel: Birkhäuser Verlag.
- Berthold, P. (1996). *Control of Bird Migration*. London: Chapman and Hall.
- Berthold, P., Nowak, E. and Querner, U. (1997). Eine neue Dimension der Vogelforschung: Die Satelliten-Telemetrie. *Falke* **44**, 134-140.
- Berthold, P., van den Bossche, W., Fiedler, W., Gorney, E., Kaatz, M., Leshem, Y., Nowak, E. and Querner, U. (2001a). Der Zug des Weißstorchs (*Ciconia ciconia*): eine besondere Zugform auf Grund neuer Ergebnisse. *J. Ornithol.* **142**, 73-92.
- Berthold, P., van den Bossche, W., Fiedler, W., Kaatz, C., Kaatz, M., Leshem, Y., Nowak, E. and Querner, U. (2001b). Detection of a new important staging and wintering area of the white stork *Ciconia ciconia* by satellite tracking. *Ibis* **143**, 450-455.
- Borodin, O. V. (1994). *Overview of the Avifauna of the Ulyanovsk Region*. Ulyanovsk: Moscow State University (in Russian).
- Gwinner, E. and Wiltshko, W. (1978). Endogenously controlled changes in migratory direction of the garden warbler, *Sylvia borin*. *J. Comp. Physiol.* **125**, 267-273.
- Hays, G. C., Åkesson, S., Broderick, A. C., Glen, F., Godley, B. J., Papi, F. and Luschi, P. (2003). Island-finding ability of marine turtles. *Proc. R. Soc. London B Suppl.* **270**, S5-S7.
- Helbig, A., Berthold, P. and Wiltshko, W. (1994). Migratory orientation of Blackcaps (*Sylvia atricapilla*): population-specific shifts of direction during autumn. *Ecology* **82**, 307-315.
- Katz, E. (1986). Problems concerning bird orientation according to the Sun. *Ornithologia (Moscow)* **21**, 103-112 (in Russian with English summary).
- Luschi, P., Åkesson, S., Broderick, A. C., Glen, F., Godley, B. J., Papi, F. and Hays, G. C. (2001). Testing the navigational abilities of ocean migrants: displacement experiments on green sea turtles (*Chelonia mydas*). *Behav. Ecol. Sociobiol.* **50**, 528-534.
- Lysenkov, E. V. and Lapshin, A. S. (1997). *Fauna, Ecology and Conservation of Rare Birds of the Middle Volga Region*. Saransk: MGPU (in Russian).
- Mouritsen, H. (2001). Ringing recoveries contain hidden information about orientation mechanisms. *Ardea* **89**, 31-42.
- Mouritsen, H. (2003). Spatiotemporal orientation strategies of long-distance migrants. In *Avian Migration* (ed. P. Berthold, E. Gwinner and E. Sonnenschein), pp. 493-513. Berlin, Heidelberg: Springer-Verlag.
- Mouritsen, H. and Mouritsen, O. (2000). A mathematical expectation model for bird navigation based on the clock-and-compass strategy. *J. Theor. Biol.* **60**, 283-291.
- Perdeck, A. C. (1958). Two types of orientation in migrating *Sturnus vulgaris* and *Fringilla coelebs* as revealed by displacement experiments. *Ardea* **46**, 1-37.
- Rüppell, W. (1937). Heimfindeversuche mit Staren, Rauchschnalben, Wendehälsen, Rotrückenwürgern und Habichten. *J. Ornithol.* **85**, 102-135.
- Rüppell, W. and Schüz, E. (1948). Ergebnis der Verfrachtung von Nebelkrähen (*Corvus corone cornix*) während des Wegzuges. *Vogelwarte* **15**, 30-36.
- Schüz, E. (1949). Die Spät-Auflassung ostpreussischer Jungstörche in Westdeutschland 1933. *Vogelwarte* **15**, 63-78.
- Schüz, E. (1950). Früh-Auflassung ostpreussischer Jungstörche in West-Deutschland durch die Vogelwarte Rossitten 1933-1936. *Bonner Zool. Beiträge* **1**, 239-253.
- Schüz, E. (1951). Überblick über die Orientierungsversuche der Vogelwarte Rossitten (jetzt: Vogelwarte Radolfzell). *Proc. Int. Ornithol. Congr.* **10**, 249-268.
- Schüz, E. and Weigold, H. (1931). *Atlas des Vogelzuges nach den Beringungsergebnissen bei palaearktischen Vögeln*. Berlin: R. Friedländer & Sohn.
- Thienemann, J. (1931). *Vom Vogelzuge in Rossitten*. Neudamm: J. Neumann.
- Wallraff, H. G. (1977). Selected aspects of migratory orientation in birds. *Vogelwarte* **29** (Sonderheft), 64-76.