



Migratory programme of juvenile pied flycatchers, *Ficedula hypoleuca*, from Siberia implies a detour around Central Asia

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Field studies suggest that in autumn, passerine Siberian-African migrants make a detour around Central Asia. We tested whether it results from an innate spatiotemporal programme. We hand-raised juvenile pied flycatchers from Europe and western Siberia in captivity and studied their migratory orientation by testing in Emlen funnels. The birds were kept outdoors in the local natural magnetic field throughout the experiment. Siberian birds showed a purely westerly orientation in mid August–mid September, before changing direction in late September. These data suggest that juvenile Siberian pied flycatchers indeed have an innate spatiotemporal programme that brings them to Europe before migration to West African winter quarters. Siberian pied flycatchers displaced to the Baltic area as nestlings, raised and tested there showed no significant second-order orientation vector in August; in September their mean orientation direction was south-southwestern (202°) and differed significantly from the western direction shown by their conspecifics in Siberia in August–mid September. A possible explanation is that the displaced birds detected displacement on the basis of the innate knowledge of some signposts. They may have ‘skipped’ the section of the route from Siberia to Europe and ‘switched on’ their migratory programme when in Europe, already towards the south-southwest.

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Some long-distance avian migrants, for example willow warblers, *Phylloscopus trochilus*, or yellow-breasted buntings, *Emberiza aureola*, have breeding ranges much extended across longitude, especially in temperate and northern Palaearctic (the so-called Rapoport’s rule, Rapoport 1982). In the aforementioned species, all birds spend their winter in rather limited areas, even though some populations may have potentially suitable areas much closer (in SE Asia for willow warblers and in Africa for yellow-breasted buntings). Such evolutionary stasis might be explained by small genetic variation together with strong

natural selection of spatiotemporal programmes, and by serious ecological barriers between breeding and potential wintering areas (Merilä et al. 2001; Pulido 2007). On the other hand, several cases of rapid evolutionary change of migratory routes have been reported from different species (Sutherland 1998; Fiedler 2003; Bearhop et al. 2005). For a better understanding of conservatism of some migratory programmes and rapid evolution of others, population studies of reaction norm in migratory traits are indispensable (van Noordwijk et al. 2006).

The pied flycatcher is a typical long-distance migrant with the breeding range extended from the west to the east. It colonized western Siberia in the early 1900s (Rogacheva 1992), but birds from all breeding populations still winter in West Africa (Fig. 1). Currently, migratory routes of the easternmost populations are unexplored. Two possible routes may be hypothesized: a shortcut across arid and mountainous regions of Central Asia or a detour to avoid them (Fig. 1).

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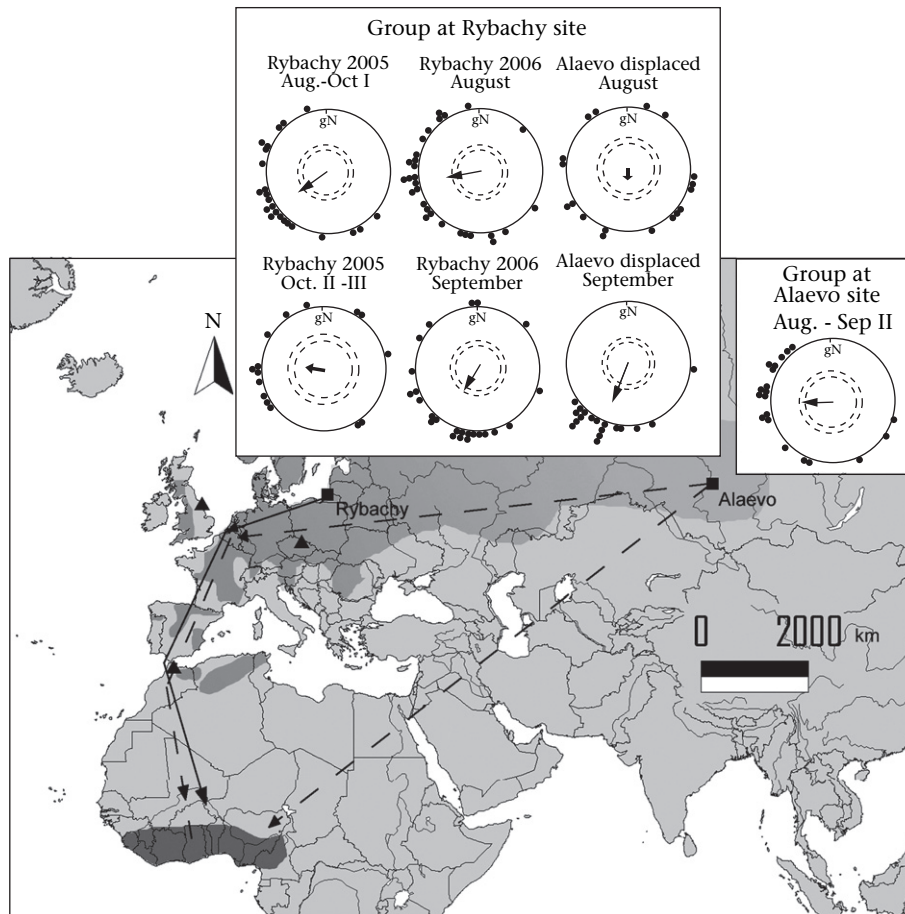


Figure 1. Orientation directions of first-autumn pied flycatchers during their migration in the Baltic region (Rybachy, 2005–2006) and western Siberia (Alaevo, 2006). The filled symbols at the periphery of the circles mark the mean headings of individual birds for the given period of time; arrows represent grand mean vectors, with their length proportional to the radius of the circle = 1; gN means geographical North. The two inner circles are the 5% (broken) and 1% significance borders of the Rayleigh test. The triangles indicate recoveries of the birds ringed in Siberia and found later during the same year (UK) or later (Czech Republic and Morocco). The solid line from Rybachy indicates migratory route of Baltic birds based on recoveries. The two dash lines from Alaevo indicate hypothesized migratory routes of western Siberian birds. The breeding range is shaded light grey; the wintering range is shaded darker grey.

It has been recently suggested that Siberian-African passerine migrants, the pied flycatcher including, do not cross Central Asia during autumn migration but rather make a detour from the north and northwest and migrate via Western Europe (Bolshakov 2002, 2003). This hypothesis is based on scarcity of these migrants in autumn captures in Central Asian oases and the very few ring recoveries (Bolshakov 2002; Fig. 1). However, ring recovery patterns should be treated with caution as reporting probability strongly depends on density and cultural traditions of human population that varies broadly across Eurasia. Moon-watching data from northwestern Kazakhstan showed a very high density of passerine nocturnal migrants heading towards African winter quarters in autumn (Bulyuk & Chernetsov 2005). Unfortunately, moon-watching data do not allow specific identification of small passerines (Bolshakov 1985).

In this paper we report the first experimental evidence that pied flycatchers make a detour around Central Asian deserts and highland that is a part of their innate spatiotemporal migratory programme. We studied autumn

migratory directions in hand-raised birds from western Siberia (northern Kemerovo Region) by testing them in Emlen funnels. For comparison, we also tested migratory directions in pied flycatchers from the Baltic area (Kaliningrad Region), and in Siberian birds raised in the Baltic area. We tested the hypothesis that in August–September Baltic birds should show a southwesterly, and Siberian birds a westerly migratory direction. We also tested whether displacement to the Baltic area influences the development of migratory programme in Siberian pied flycatchers.

METHODS

Study Sites and Species

The pied flycatcher is a common passerine in the forest zone of Europe and Western Siberia (Lundberg & Alatalo 1992). Birds from the entire breeding range spend their winter in Western Africa (Borrow & Demey 2001). Pied flycatchers are nocturnal migrants (Bolshakov 1977)

with a complex migratory route (Fig. 1). This species has several times been used in the studies of spatiotemporal programmes (Beck & Wiltschko 1988; Weindler et al. 1995, 1998) and is common at both our study sites: on the Baltic coast (Kaliningrad Region, Russia) and in northern Kemerovo Region (western Siberia). In both areas, pied flycatchers mainly breed in nestboxes provided by the Biological Station Rybachy and the Zoological Museum of Tomsk State University, respectively.

Study in the Baltic area was conducted at Fringilla field station of the Biological Station Rybachy (55°05'N, 20°44'E) in 2005–2006. In western Siberia, the study has been done in the village of Alaevo, Yurga district, Kemerovo Region (56°08'N, 84°53'E) in 2006. The distance between these sites is 4027 km (Fig. 1).

Experimental Birds

Siberian pied flycatchers were divided into two groups. Eighteen birds were tested in the natal area. Among them, nine birds, aged 9–11 days, were taken from nests near Alaevo on 28 June 2006 and hand-raised at the natal site. Nine more birds were mist-netted in the same area in August 2006 at early stages of body moult indicating their origin from the near vicinity. Hand-raised birds were kept indoors until 23–25 days old (until 11 July) when they were transferred to an outdoor aviary. They were kept there until the end of the experiment on 26 September. Eighteen more pied flycatchers from the same Siberian population were taken from nests on 25 June 2006 and on the next day, at the age of 10–13 days, transported by air to the Baltic area. During transportation, they were kept in an artificial nest. Food and drinking water were provided to the nestlings continuously during the flights (Tomsk–Moscow and Moscow–Kaliningrad) and when changing flights in Moscow. The displaced Siberian pied flycatchers were kept in a common garden experiment with Baltic birds.

In the Baltic area, we raised 51 birds in 2 study years. In 2005, nestlings were taken from their nests at the age of 8–12 days between 14 and 23 June ($N = 23$). They were hand-raised and kept indoors until 23–34 days old (until 7 July) when they were transferred to an outdoor aviary and kept there until late October. These birds had access to natural celestial and geomagnetic cues at their natal site. In 2006, Baltic nestlings were taken from nests when 7–12 days old between 20 and 22 June ($N = 28$). They were kept indoors until 35–40 days old (until 18 July) and then transferred to outdoor aviaries. All birds were kept in the experiment until late October.

The birds were fed ad libitum by mealworms and ant pupae. They always had access to fresh drinking water with vitamins added. Since fledging, the birds were kept in cages (120 × 100 × 100 cm) inside outdoor aviaries (3.5 × 3.0 × 2.2 m), with 7–10 birds per cage. In every cage, four perches were available to the birds. A part of cage roof was covered with transparent plastic that provided shelter from rain. In cases of heavy rain, the whole aviary was covered by plastic wrapping. Experimental birds never showed any signs of aggression caused by overcrowded conditions.

After the experiments, most birds were killed by asphyxia by quickly rising carbon dioxide concentration. These birds were hand-raised and therefore could not be released, and we had no funds and facilities available to keep them in captivity throughout their lives. At the moment of writing, five Siberian-born individuals were still kept in captivity at the Zoological Museum of Tomsk State University.

Orientation Tests and Statistics

We used modified Emlen funnels (Emlen & Emlen 1966) identical to those used by Mouritsen & Larsen (1998) made of PVC. Emlen funnels are circular orientation cages (top diameter 300 mm, bottom diameter 100 mm, slope 45°) with the top opening covered by a fine-meshed plastic net, allowing the birds to see the sky. The maximum view of the sky for the birds was 168°. Each test was performed during 1 h after the beginning of astronomical twilight, that is when the Sun was at least 12° below the horizon and no glow from the Sun could be seen. The tests were done when at least 50% of the starry sky was visible, in most cases it was 95–100%. The cages were placed on a sand dune (on the Baltic coast) or in a large forest clearing near Alaevo (in Siberia). The birds could not see any landmarks. Each bird was tested until a significant direction was obtained that was included into analysis irrespectively of direction. If some bird was inactive or showed random circular activity it was tested again; if this occurred 2–3 times in succession, no further tests were done during the given 10-day period.

The directionality of the birds' activity was recorded as scratches left by the birds' feet in the pigment of Tipp-Ex typewriter correction paper when they hopped in the funnels. The entire wall of the funnels was covered with typewriter correction paper or transparent plastic sheet, and scratches were counted in each of the 36 10° sectors. The result of a given experiment was only included only if at least 40 scratches were visible on the funnel paper and a unimodal mean direction was apparent. When put into the funnel, the birds showed no signs of distress. Their escape behaviour was limited to several (often none, always less than 10) hops in the funnel. After several minutes of rest, they started to hop towards the preferred migratory direction. When put back into their cage after testing, pied flycatchers showed no distress, either and immediately sat on the perches.

From the mean directions of each individual, a sample mean direction and vector length were calculated using vector addition (Batschelet 1981). When pooling the data across time windows, we calculated the mean direction and vector length from each bird's individual mean vector across this interval. This means that each individual bird contributed only one data point to the sample mean vector to avoid pseudoreplication. The graphical representations and calculations of the circular data were made using a custom-designed computer program. Differences in mean direction between experimental groups were analysed using the nonparametric Mardia–Watson–Wheeler (MWW) test. Difference from an a priori assumed direction was tested by V test (Batschelet 1981), results for which

$P > 0.05$ were regarded as nonsignificant. Statistical tests were performed with Oriana 2.0 (www.kovcomp.com).

RESULTS

Orientation of European Pied Flycatchers

In the Baltic area, direction of migratory activity was tested in each bird at least once in 10 days between 3 August–23 October 2005 and 9 August–25 September 2006. In 2005, we performed 10 test sessions (four in August, three in September and October each) with 23 birds and obtained 119 significant directions. In August–early October 2005, the mean direction across this season was 245° (95% confidence interval [CI] 223 – 268° , $N = 23$, $r = 0.64$, $P < 0.001$, Fig. 1). During the two last sessions in mid and late October, no significant second-order directions were obtained, even though nocturnal activity of individual birds was directed ($N = 15$, $r = 0.35$, $P = 0.16$, Fig. 1).

In 2006, we conducted four sessions (two each in August and September) with 28 local birds and recorded 85 significant directions. In August 2006, the mean direction was 252° (95% CI 230 – 273° , $N = 28$, $r = 0.61$, $P < 0.001$, Fig. 1). This was not significantly different from the direction shown in August–early October 2005 (MWW test: $W = 1.29$, $P = 0.52$). The mean direction shown in September 2006 was 212° (95% CI 183 – 241° , $N = 24$, $r = 0.52$, $P = 0.001$, Fig. 1) and differed from the one observed in August ($W = 6.57$, $P = 0.037$), despite overlapping 95% CIs.

Orientation of Siberian Pied Flycatchers

In Siberia, we performed six test sessions between 12 August and 25 September 2006 (two in August and four in September) and obtained 109 significant directions. Hand-raised pied flycatchers and birds mist-netted after fledging showed similar preferred directions (MWW test was not applicable because of small sample sizes; Watson U^2 test: $U^2 = 0.125$, $N_1 = N_2 = 8$, $P > 0.10$ for mid August–mid September; $U^2 = 0.037$, $N_1 = 8$, $N_2 = 7$, $P > 0.50$) and were pooled for analysis. The mean direction pooled over the period from mid August to mid September was 269° (95% CI 241 – 296° , $N = 20$, $r = 0.58$, $P < 0.001$, Fig. 1). The mean direction in late September was strikingly different: 80° (95% CI 37 – 123° , $N = 15$, $r = 0.48$, $P = 0.031$; MWW test: $W = 15.46$, $P < 0.001$). CIs did not overlap (Table 2).

The mean direction in Siberia during the most part of the experiment (late September excluded) was not significantly different from directions shown by Baltic birds in August–early October 2005 (MWW test: $W = 5.22$, $P = 0.074$) and in August 2006 ($W = 1.95$, $P = 0.378$). When the Baltic birds changed their orientation in September 2006 as compared with August (see above), this new direction differed from the one shown by Siberian birds in Siberia ($W = 11.35$, $P = 0.003$).

Five test sessions were performed with Siberian pied flycatchers raised in the Baltic area between 9 August and 25

September 2006 (two in August and three in September), with 63 significant directions obtained. The mean direction shown by these birds pooled over August was not significant ($r = 0.19$, $N = 18$, $P = 0.51$). The mean direction in September was 202° (95% CI 189 – 216° , $N = 18$, $r = 0.87$, $P < 0.001$) and differed significantly from the direction shown by their conspecifics in Siberia in August–mid September (MWW test: $W = 16.86$; $P < 0.001$; 95% CI did not overlap).

DISCUSSION

Migratory Orientation of Baltic Pied Flycatchers

Baltic pied flycatchers showed orientation of their nocturnal activity that was generally similar to flight directions of their free-living conspecifics within Europe, that is during the first half of their autumn migration. The ringing recoveries of birds marked in the eastern Baltic in subsequent years ($N = 4$) show the southwestern direction of 232° (Kishkinev et al. 2006). Orientation of Baltic experimental birds was not significantly different from that direction in either year (V test: 2005: $V = 0.618$; 2006: $V = 0.593$; $P < 0.001$ in both cases).

Mean orientation showed by pied flycatchers from the Courish Spit in August–early October 2005 and August 2006 (245° and 252° , respectively) was more western than the one shown by birds from Latvia raised in the local natural geomagnetic field under a rotating planetarium sky (215° , $r = 0.59$, $N = 18$; Weindler et al. 1995) or under the natural sky (232° , $r = 0.60$, $N = 16$; Weindler et al. 1995). The difference was not significant with our 2005 data (MWW test: $W = 1.91$, $W = 4.92$, respectively, $P > 0.05$) and marginally insignificant with 2006 data ($W = 5.77$, $P = 0.056$; $W = 1.07$, $P > 0.05$, respectively). It should be, however, stressed that unlike our birds, Latvian pied flycatchers were tested with the geomagnetic field as the only directional clue.

In 2005, experimental birds showed mean directions varying between the southwest (239°) and west-northwest (295°) in individual test sessions (mean 245°) until early October (Table 1). In mid and late October, no significant second-order direction was recorded, even through activity of individual birds remained directed. In 2006, pied flycatchers significantly changed their direction in September (south-southwest 212°) as compared with August (west-southwest 252°). We assume that this corresponds to changing flight directions of free-living conspecifics that at this time are making stopovers in the Iberian Peninsula before crossing the Sahara (Bibby & Green 1980). This shift was not observed in 2005.

It is worth noting that our birds throughout the experiment were kept in natural magnetic conditions of their natal site. In other studies, seasonally appropriate changes in orientation direction occurred only when magnetic conditions (field inclination and intensity) were gradually altered imitating movements along the presumed migratory route (Beck & Wiltschko 1982, 1988). It cannot be ruled out that our experimental birds lost

Table 1. Results of orientation tests in Emlen funnels of pied flycatchers hatched in the Baltic area

Group	Testing session	Dates	N	Mean vector (°)	r	95% CI	Significance (Rayleigh test)
Rybachy 2005	August 1	3–9 August	14	252	0.58	218–286°	0.007
Rybachy 2005	August 2	16–18 August	11				NS
Rybachy 2005	August 3	21–25 August	13	243	0.69	215–270°	0.001
Rybachy 2005	August 4	28 August–1 September	14				NS
Rybachy 2005	September 1	4–7 September	13				NS
Rybachy 2005	September 2	11–17 September	12	295	0.67	265–325°	0.003
Rybachy 2005	September 3	22–27 September	11	263	0.83	240–287°	<0.001
Rybachy 2005	Oct 1	2–7 Oct	11	239	0.72	207–271°	0.002
Rybachy 2005	Oct 2	11–17 Oct	10				NS
Rybachy 2005	Oct 3	18–21 Oct	10				NS
Rybachy 2006	August 2	9–10 August	12	244	0.61	209–279°	0.009
Rybachy 2006	August 3	21–28 August	25	256	0.65	235–277°	<0.001
Rybachy 2006	September 2	17–21 September	21	199	0.51	167–231°	0.003
Rybachy 2006	September 3	23–25 September	23	217	0.41	179–256°	0.02

N, sample size of birds that showed significant orientation in the given session; r, length of the mean vector; NS, orientation does not differ significantly from the random circular one.

orientation in October 2005 because they had not reached a natural (e.g. magnetic) signpost. The innate orientation programme of pied flycatchers has been shown to depend on magnetic signposts more strongly than in, for example garden warblers, *Sylvia borin* (Gwinner & Wiltschko 1978; Beck & Wiltschko 1988).

Migratory Orientation of Siberian Pied Flycatchers in Siberia

Siberian pied flycatchers showed in their natal area autumn migratory orientation that indicated passage through Western Europe (Fig. 1). In late September, they abruptly changed direction of their activity from a westerly direction to an easterly one. This could either be a somewhat distorted reflection of a directional change from west to south or south-southeast seen in their free-living conspecifics, or a reflection of the last part of migration when passerine migrants after crossing the Sahara might possibly fly towards the east or southeast along the West African coast (Hilgerloh 1989, 2001). Another possibility is that this behaviour resulted from their failure to reach

a certain signpost on the migratory route (cf. disorientation of European birds in October). We could not continue our tests in Siberia into October because of weather conditions that did not permit to keep the birds outdoors.

Our data suggest that first-autumn pied flycatchers from western Siberian populations have a spatiotemporal programme including migration towards the west during August and most September. This programme brings them to Central or Western Europe from where they migrate to West Africa across the Sahara by the same way as European pied flycatchers. This is supported by the few available recoveries of Siberia-ringed pied flycatchers (Fig. 1). It should be stressed that this complex migratory route results from realization of an innate spatiotemporal programme, as shown from our tests with caged inexperienced migrants.

One may argue that this spatiotemporal programme results from evolutionary conservatism and recapitulates the route of expansion of pied flycatchers to Siberia. It has been claimed that migrants have more difficulty to colonize new breeding areas than sedentary species, possibly because of their rigid migratory programmes (Bensch 1999). However, rapid evolutionary changes of migratory

Table 2. Results of orientation tests in Emlen funnels of pied flycatchers hatched in Western Siberia

Group	Testing session	Dates	N	Mean vector (°)	r	95% CI	Significance (Rayleigh test)
Alaevo	August 2	12–18 August	14				NS
Alaevo	August 3	24–27 August	15				NS
Alaevo	September 1	1–10 September	16				NS
Alaevo	September 2	12–15 September	16				NS
Alaevo	September 3	16–19 September	17	260	0.55	228–292°	0.004
Alaevo	September 4	22–25 September	15	80	0.48	37–123°	0.031
Alaevo disp	August 2	9–16 August	8				NS
Alaevo disp	August 3	21–28 August	18				NS
Alaevo disp	September 1	2 September	6	171	0.72	122–220°	0.037
Alaevo disp	September 2	11–17 September	15	200	0.84	181–219°	<0.001
Alaevo disp	September 3	21–25 September	14	208	0.83	188–229°	<0.001

Group 'Alaevo' was tested at the natal site; group 'Alaevo disp' was displaced to the Baltic area and tested there.

N, sample size of birds that showed significant orientation in the given session; r, length of the mean vector; NS, orientation does not differ significantly from the random circular one.

directions causing the development of novel winter quarters have been reported in passerine migrants (Berthold et al. 1992; Hill et al. 1998; Fiedler 2003; Bearhop et al. 2005). Siberian pied flycatchers have not replaced their complex orientation programme by another one that might have enabled them to change their wintering range from West Africa into southern or southeastern Asia. Detours are costly (Alerstam 2001), and if they occur in extant populations, they must bring some benefits, that is making shortcuts must carry costs. In the case of Siberian pied flycatchers, this cost is probably crossing the deserts of western Central Asia that are a serious ecological barrier for migrants in autumn (Chernetsov et al., in press).

Orientation of Siberian Pied Flycatchers Displaced to Europe

Siberian birds displaced to the Baltic area showed no significant direction either in individual test sessions (Table 2) or when the data are pooled across August. In September, their south-southwestern direction differed from the western direction shown in Siberia. A possible explanation is that the displaced birds detected displacement on the basis of the innate knowledge of some astronomical and/or magnetic signposts along the migratory route. They may have 'skipped' the section of the route from Siberia to Europe and 'switched on' their migratory programme when in Europe, already towards the south-southwest. These triggers could be magnetic ones, as a similar mechanism was reported from a German pied flycatcher population (Beck & Wiltschko 1982, 1988); from thrush nightingales, *Luscinia luscinia*, that sharply increased their fuel stores when magnetic conditions typical of North Africa were simulated in the laboratory (Fransson et al. 2001; Kullberg et al. 2003); and from loggerhead turtles that corrected their orientation in a way that allows them to remain in North Atlantic gyre (Lohmann & Lohmann 1994, 1996; Lohmann et al. 2001). When travelling from Siberia to Europe, magnetic intensity changes in a regular pattern and may theoretically be used as a basis for one-coordinate magnetic map (Freake et al. 2006).

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References

- Alerstam, T. 2001. Detours in bird migration. *Journal of Theoretical Biology*, **209**, 319–331.
- Batschelet, E. 1981. *Circular Statistics in Biology*. London: Academic Press.
- Bearhop, S., Fiedler, W., Furness, R. W., Votier, S. C., Waldron, S., Newton, J., Bowen, G. J., Berthold, P. & Farnsworth, K. 2005. Assortative mating as a mechanism for rapid evolution of a migratory divide. *Science*, **310**, 502–504.
- Beck, W. & Wiltschko, W. 1982. The magnetic field as reference system for the genetically encoded migratory direction in pied flycatchers, *Ficedula hypoleuca*. *Zeitschrift für Tierpsychologie*, **60**, 41–46.
- Beck, W. & Wiltschko, W. 1988. Magnetic factors control the migratory direction of pied flycatchers (*Ficedula hypoleuca* Pallas). *Proceedings 19th International Ornithological Congress*, pp. 1955–1962.
- Bensch, S. 1999. Is the range size of migratory birds constrained by their migratory program? *Journal of Biogeography*, **26**, 1225–1235.
- Berthold, P., Helbig, A. J., Mohr, G. & Querner, U. 1992. Rapid microevolution of migratory behaviour in a wild bird species. *Nature*, **310**, 668–670.
- Bibby, C. J. & Green, R. E. 1980. Foraging behaviour of migrant pied flycatchers, *Ficedula hypoleuca*, on temporary territories. *Journal of Animal Ecology*, **49**, 507–521.
- Bolshakov, C. V. 1977. Study of nocturnal bird migration (methodological aspect). In: *Methods of Bird Migration Research* (Ed. by V. D. Iljichev), pp. 77–96. (Moscow) [in Russian].
- Bolshakov, C. V. 1985. Moon-watch method for quantitative studying of nocturnal bird passage (collection, calculation and analysis of data). In: *Spring Nocturnal Bird Passage Over Arid and Mountain Areas of Middle Asia and Kazakhstan* (Ed. by V. R. Dolnik), pp. 14–36. Leningrad: Zoological Institute [in Russian].
- Bolshakov, C. V. 2002. The Palaearctic-African bird migration system: the role of desert and highland barrier of western Asia. *Ardea*, **90**, 515–523.
- Bolshakov, C. V. 2003. Nocturnal migration of passerines in the desert-highland zone of Western Central Asia: selected aspects. In: *Avian Migration* (Ed. by P. Berthold, E. Gwinner & E. Sonnenschein), pp. 225–236. Berlin, Heidelberg: Springer.
- Borrow, N. & Demey, R. 2001. *Birds of Western Africa*. London: Christopher Helm.
- Bulyuk, V. N. & Chernetsov, N. 2005. Nocturnal passage of passerines in Western Kazakhstan in autumn. *Journal of Arid Environments*, **61**, 603–607.
- Chernetsov, N., Bulyuk, V. N. & Ktitorov, P. In press. Migratory stopovers of passerines in an oasis at the crossroad of the African and Indian flyways. *Ringling and Migration*.
- Emlen, S. T. & Emlen, J. T. 1966. A technique for recording migratory orientation of captive birds. *Auk*, **83**, 361–367.
- Fiedler, W. 2003. Recent changes in migratory behaviour of birds: a compilation of field observations and ringing data. In: *Avian Migration* (Ed. by P. Berthold, E. Gwinner & E. Sonnenschein), pp. 21–38. Berlin/Heidelberg: Springer.
- Fransson, T., Jakobsson, S., Johansson, P., Kullberg, C., Lind, J. & Vallin, A. 2001. Magnetic cues trigger extensive refuelling. *Nature*, **414**, 35–36.
- Freake, M. J., Muheim, R. & Phillips, J. B. 2006. Magnetic maps in animals: a theory comes of age? *Quarterly Review of Biology*, **81**, 327–347.
- Gwinner, E. & Wiltschko, W. 1978. Endogenously controlled changes in migratory direction of the garden warbler, *Sylvia borin*. *Journal of Comparative Physiology*, **125**, 267–273.

- Hilgerloh, G. 1989. Der Singvogelzug über die Iberische Halbinsel ins afrikanische Winterquartier. *Naturwissenschaften*, **76**, 541–546.
- Hilgerloh, G. 2001. Migration patterns in the western Mediterranean Region inferred from radar observations. *Avian Ecology and Behaviour*, **7**, 119–126.
- Hill, G. E., Sargent, R. R. & Sargent, M. B. 1998. Recent change in the winter distribution of rufous hummingbirds. *Auk*, **115**, 240–245.
- Kishkinev, D., Chernetsov, N. & Bolshakov, C. V. 2006. Migratory orientation of first-year pied flycatchers (*Ficedula hypoleuca*) from the Eastern Baltic. *Ornithologia*, **33**, 153–160 (Moscow) [in Russian].
- Kullberg, C., Lind, J., Fransson, T., Jakobsson, S. & Vallin, A. 2003. Magnetic cues and time of season affect fuel deposition in migratory thrush nightingales (*Luscinia luscinia*). *Proceedings of the Royal Society of London, Series B*, **270**, 373–378.
- Lohmann, K. J. & Lohmann, C. M. F. 1994. Detection of magnetic inclination angle by sea turtles: a possible mechanism for determining latitude. *Journal of Experimental Biology*, **194**, 23–32.
- Lohmann, K. J. & Lohmann, C. M. F. 1996. Detection of magnetic field intensity by sea turtles. *Nature*, **380**, 59–61.
- Lohmann, K. J., Cain, S. D., Dodge, S. A. & Lohmann, C. M. F. 2001. Regional magnetic fields as navigational markers for sea turtles. *Science*, **294**, 364–366.
- Lundberg, A. & Alatalo, R. V. 1992. *The Pied Flycatcher*. London: T. & A. D. Poyser.
- Merilä, J., Sheldon, B. C. & Kruuk, L. E. B. 2001. Explaining stasis: microevolutionary studies in natural populations. *Genetica*, **112–113**, 199–222.
- Mouritsen, H. & Larsen, O. N. 1998. Migrating young pied flycatchers *Ficedula hypoleuca* do not compensate for geographical displacements. *Journal of Experimental Biology*, **201**, 2927–2934.
- van Noordwijk, A. J., Pulido, F., Helm, B., Coppack, T., Delingat, J., Dingle, H., Hedenström, A., van der Jeugd, H., Marchetti, C., Nilsson, A. & Pérez-Tris, J. 2006. A framework for the study of genetic variation in migratory behaviour. *Journal of Ornithology*, **147**, 221–233.
- Pulido, F. 2007. The genetics and evolution of avian migration. *BioScience*, **57**, 165–174.
- Rapoport, E. H. 1982. *Areography. Geographical Strategies of Species*. Oxford: Pergamon.
- Rogacheva, H. 1992. *The Birds of Central Siberia*. Husum: Husum Druck u. Verlagsges.
- Sutherland, W. J. 1998. Evidence for flexibility and constraint in migration systems. *Journal of Avian Biology*, **29**, 441–446.
- Weindler, P., Beck, W., Liepa, V. & Wiltshko, W. 1995. Development of migratory orientation in pied flycatchers in different magnetic inclinations. *Animal Behaviour*, **49**, 227–234.
- Weindler, P., Böhme, F., Liepa, V. & Wiltshko, W. 1998. The role of daytime cues in the development of magnetic orientation in a night-migrating bird. *Behavioral Ecology and Sociobiology*, **42**, 289–294.