

RESEARCH ARTICLE

Orientation in the European common frog *Rana temporaria* during the first wintering migration

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ABSTRACT

The orientation of naive animals during their first migration is extensively studied in birds and sea turtles, whereas the data for other groups such as amphibians are still scarce. To date, it is unknown whether young-of-the-year anurans perform a random or directional search for the hibernation sites, and what cues (global or local) they use. We conducted a series of field experiments to study the orientation behavior of juvenile common frogs during their first wintering migration. We captured 1614 froglets from two subpopulations with different directions of migration and assessed their orientation in large circular outdoor arenas (20 m in diameter) on the opposite sides of the river. Before the migration, froglets used local cues and moved back towards the forest (summer habitat). At the start of migration, the froglets did not move randomly: they navigated towards the river using local cues. Later, however, before approaching the hibernation site, they memorized the compass direction of migration and followed it using global cues. Orientation along a memorized compass heading begins to dominate in the hierarchy of orientation mechanisms, and this predominance is maintained even after reaching the hibernation site. Unlike in birds, no innate direction of migration was found.

KEY WORDS: Orientation, Local cues, Compass heading, Global cues, Circular arena, Anuras

INTRODUCTION

Migration behavior is widespread among vertebrates (Alerstam et al., 2003; Dingle, 1996). When searching for the migration route, animals can use both global and local orientation cues. Global cues allow them to determine a route or choose a direction without direct sensory contact with the goal, e.g. celestial cues and Earth's magnetic field. Local cues are associated with the final location itself, e.g. smell, humidity gradient and visual landmarks (Chernetsov, 2017; Lohmann et al., 1999; Morandi-Raikova et al., 2020; Mouritsen, 2018; Wells, 2007). The processing of different cues is a difficult task that requires experience; thus, the methods utilized by naive animals to choose a path during their first migration remains a key question in animal behavior (Able, 2001; Berthold, 1991; Chernetsov et al., 2004; Mouritsen, 2018).

The young of many bird species use vector navigation/clock-and-compass strategy, i.e. an innate compass heading and information

on the distance towards the population-specific winter range (Able, 2001; Berthold, 1991; Mouritsen and Larsen, 1998), or even assume some inherited mechanisms of controlling their position on the migration route (Chernetsov, 2016; Thorup et al., 2010). However, it was demonstrated that young birds, unlike adult ones, are not always capable of assessing the displacement from the migration route and compensating for it, and continue to fly in the initial direction of migration (Perdeck, 1958; Thorup et al., 2007). In sea turtles, the navigation program includes several stages: hatchling turtles must first find the sea and swim away from the coast to enter a current using the local cues (Lohmann and Lohmann, 1996). Later, they can either completely rely on the current (Hays et al., 2010) or adjust their course according to the global cues based on an innate map (Lohmann et al., 2012; Putman et al., 2012). Other groups of animals are studied to a lesser extent, including amphibians, which, as the first terrestrial vertebrates, are an important group for understanding the evolution of these innate programs.

Most adult amphibians of the temperate regions have three types of migration: to the breeding site, to the summer habitat and to the hibernation site (Sinsch, 1990; Wells, 2007). They have been shown to rely on multiple different cues (local and global) that are used in a hierarchical manner depending on the relative availability (Adler, 1982; Ferguson, 1971; Russell et al., 2005; Sinsch, 1990, 2019). Young amphibians usually undertake only two types of long-distance movements: dispersion of the metamorphosed young from a native water body and the first wintering migration.

Research so far has mainly focused on dispersal, showing that juvenile amphibians can find favorable habitats using local cues (Dole, 1971; Popescu et al., 2012; Timm et al., 2007; Vasconcelos and Calhoun, 2004; Vasconcelos et al., 2008). For example, juvenile ambystomatid salamanders and American toads emigrating from the pools at the forest edges showed significant preference for the forest versus another possible site, the open field (Rothermel and Semlitsch, 2002), while the success of orientation depended on the distance from the forest edge (Rothermel, 2004). In addition, the metamorphosed individuals are known to be sensitive to humidity and the odor of the native water body learnt during their development (Bastakov, 1992; Hepper and Waldman, 1992; Ogurtsov, 2005; Reshetnikov, 1996). This can be utilized for orientation both near the water body and at the beginning of dispersal (Bastakov, 1991; Ogurtsov, 2012; Shakhparonov and Ogurtsov, 2005). Cases when the juveniles dispersed in a certain compass direction maintained by global cues were also described (Dole, 1972a; Miaud and Sérandour, 2003; Patrick et al., 2007; Tracy, 1971).

To date, orientation of the young during migration towards hibernation sites has been experimentally studied only in one work, by Pasanen and Sorjonen (1995). Froglets of the European common frog captured during migration to the wintering lake and released 200 m from it oriented back towards to the lake (Pasanen and Sorjonen, 1995). Previously, Pasanen et al. (1994) suggested that the adult frogs remember the hibernation site and navigate towards

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it, while the froglets remain close to their native water body, and it is therefore easy for them to return for wintering. Yet, some froglets disperse further and find wintering places by chance (Pasanen et al., 1994). However, Pasanen and Sorjonen (1995) experimented with the population where reproduction and main wintering occurred in the same water body, and their hypothesis does not explain how migration is established in amphibian populations where reproduction and wintering constantly occur in different water bodies, which is much more common. For example, many populations of common frog and marsh frog that breed in stagnant water bodies tend to winter in a river (Kuzmin, 2013). Presumably, some other mechanisms must be involved in discovering a river as a wintering water body, such as an innate direction of migration. In addition, Pasanen and Sorjonen (1995) released the froglets only on the side of the lake where they were captured during migration; this setup does not allow one to hypothesize on the type of utilized migration cues. It is unclear how froglets would behave on the opposite side of the lake: using the local cues to orient towards the lake (like adults) or global cues to continue moving in the direction of migration, as was shown for young birds.

The goal of the present study was to achieve a better understanding of how young-of-the-year frogs that reproduce and winter in different water bodies orient during their first wintering migration, and what types of cues they utilize: local (smell of the water, humidity gradient or visual landmarks) or global (celestial cues and Earth's magnetic field). We chose the European common frog *Rana temporaria* Linnaeus 1758 as a model species: its biology is well studied, and the species itself is abundant enough to allow large-scale experiments to be conducted. Creating a cue conflict (Able, 1993) between global and local cues was implemented as the main study approach. The froglets were released into circular arenas constructed on the opposite sides of a river (the wintering site of the adults). Therefore, for the froglets on their native river side, river-associated local cues coincide with the direction of migration available from the global cues; however, on the side opposite to the capture site, the local and global cues will contradict each other. Conducting the experiment before and at various stages of migration allowed us to study this process and possible alterations in the hierarchy of orientation cues. As it is not always possible to capture a large number of animals at a single time, we conducted additional studies on animals after a short-term captivity (several days), and assessed how it impacted both the development of migration behavior and motivation. The results will improve the experiment design for the research of specific orientation

mechanisms in juvenile individuals and provide missing links in our understanding of the evolution of orientation mechanisms in young animals.

MATERIALS AND METHODS

Studied populations

The experiments were conducted at the Zvenigorod Biological Station of the Moscow State University (Moscow Oblast, Russia; 55.700, 36.723) and its vicinity in 2013 and 2015–2018 with European common frogs from two populations inhabiting the left and right sides of the Moskva River (Fig. 1).

The right-side population, which was used in the majority of experiments, is rather well studied: frogs breed mainly in pond nos 1 and 4, and spend the summer in the spruce–broad-leaved forest. Most adults winter in the Moskva River and migrate north to reach the water (Chugunov, 1966; Khmelevskaya, 1989; Severtsov et al., 1998). After metamorphosis, the froglets of this population seem to disperse into the same habitat as the adults (Khmelevskaya, 1989). They were found to winter in the Moskva River and in a stream near pond no. 1 (Khmelevskaya, 1989; Lyapkov, 1997a); however, this stream became shallow and was no longer suitable for the wintering. Some researchers assume that the terrestrial wintering is equally probable (Khmelevskaya, 1989; Lyapkov, 1997a). In the winter and spring of 2019, we conducted our own survey of the possible hibernation sites: a stream and Bardinskii gully at location F1, the river and ponds (Table S2).

The left-side population has not been previously studied; according to our own observations, spawning occurs in the water body near the village of Ustye, 900 m from the Moskva River, and frogs migrating south to the Moskva River through the field can be found in the autumn.

Experimental setup

To determine the direction chosen by the frogs, we used a circular arena, 20 m in diameter, enclosed by a translucent polyethylene wall, 150 μm thick and 50 cm high, supported by 36 wooden stakes (Fig. 2). The grass inside the arena was mowed to a length of 5–10 cm. A 15 cm wide and 10 cm deep groove was dug around the inside perimeter of the arena. A total of 16 cylinder traps made of 6 l bottles was dug neck down in the groove every 22.5 deg. The area of the arena construction did not have a constant slope towards any of the cardinal points (confirmed using a 3 m long board and the incline sensor of Bosh GLM 80).

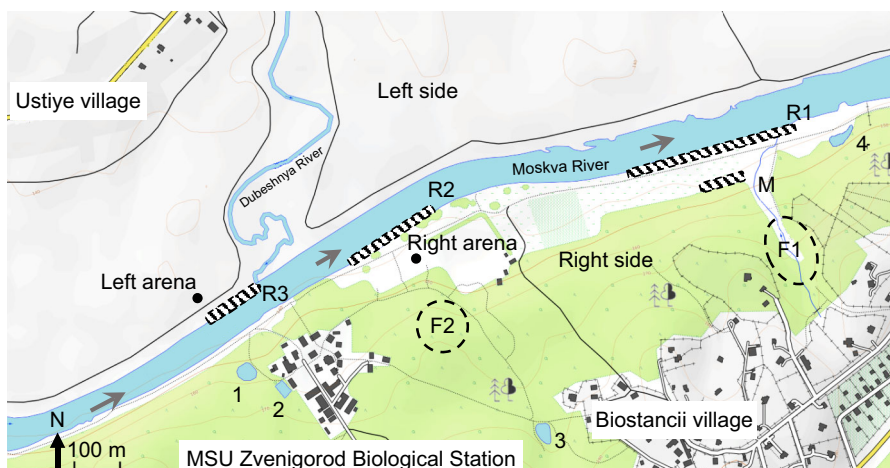


Fig. 1. Map of the study area. 1–4, water bodies (ponds) of MSU Zvenigorod Biological Station; F1 and F2, collection sites in the forest; M, collection site in the meadow along the forest edge; R1–R3, collection sites along the river bank. Labelled black dots indicate the locations of the circular arenas. The map was made with data provided and copyrighted by ©OpenStreetMap-Mitwirkende, SRTM | Kartendarstellung: OpenTopoMap (CC-BY-SA; <https://www.openstreetmap.org/copyright>).



Fig. 2. Circular arena for the experiments. Overall view (A) and construction (B). 1, wooden stake; 2, polyethylene wall; 3, groove; 4, trap.

We assume that our setup did not interfere with the usage of any available orientation cues, and the froglets were able to choose a direction under conditions close to natural. The 20 m diameter was chosen based on experiments that used a spool and line tracking method for another Ranidae species, the marsh frog *Pelophylax ridibundus*, which also winters in rivers. The adult marsh frogs traveled approximately 10 m before their compass heading towards the hibernation site became apparent (Shakhparonov and Ogurtsov, 2008). Therefore, we assume that the young-of-the-year common frogs would also have sufficient distance to successful navigation.

To test what type of cues (global or local) frogs use during the migration, two arenas were constructed, one on either side of the Moskva River (Fig. 1). In one arena, the information from local and global cues will be co-directional; in the other, they will be opposite (cue conflict). Thus, if the froglets use river-associated local cues (smell of the water or humidity gradient) while traveling towards it, they will orient towards the river in both arenas. If the migratory direction is determined by global cues, the froglets will choose the same direction in both arenas independent of the position of the river. This chosen direction should be different in frogs from the two studied populations, as the animals from the right side migrate north, towards the river, while the left-side frogs migrate south. The left arena was built in an open field; the right arena was built in a meadow between the river and the forest. The distance from the center of the arena to the water was 60 m in both cases. The distance towards the edge of the forest from the center of the right arena was 40 m southeast; individual trees closest to the arena were located in the northeast. According to our assumption, at these distances, the froglets should perceive the stimuli from both the river and the forest well. Adult common frogs have no issues with orientation even at a greater distance, towards both the spawning (Elmberg and Lundberg, 1988) and the wintering water bodies (Pasanen and Sorjonen, 1995). In the experiments by Pasanen and Sorjonen (1995), froglets were also released at a greater distance of 200 m.

Release procedure and survey

The frogs were transported in closed opaque containers to prevent the use of visual cues. At the site of release, containers were rotated in different directions for approximately 1 min to disrupt orientation by path integration. Then, the froglets were placed in the center of the arena in a plastic basin, 40 cm in diameter with 8 cm high walls, covered with two containers and allowed to calm down for a couple of minutes. After that, two researchers simultaneously removed the containers and left in different directions: north and south. The froglets were released in groups of 31–119 animals. According to our observations they did not appear to travel as a group or follow

one another. Previous studies of other authors conducted in the outdoor arenas with large groups of anurans also demonstrated their independent choice of direction (Ferguson et al., 1965, 1968; Gorman et al., 1970; Landreth and Ferguson, 1967a). To monitor the weather conditions, we used the Vantage Vue weather station (Davis Instruments).

At northern latitudes, the frogs' activity shifts from night to day hours in autumn, before and during the migration (Bannikov, 1940; Koskela and Pasanen, 1974; our own observations). This phenomenon is associated with the nightly temperatures dropping in September; during the day, not only are the temperatures higher but also the humidity remains at a level sufficient for the frogs. Thus, the majority of experiments were conducted during the day.

The froglets were released at 12:00 h and surveyed for the first time at 20:00 h (after sunset), the second time at 23:00 h, and at 11:00–12:00 h the next day. Most frogs were recaptured during these surveys. If more than five animals remained in the arena, we would not start the next release and carefully search for them. The analysis of the movement directions included only individuals caught inside the groove and traps.

Many other species of amphibians migrate on rainy nights (Wells, 2007) when a different set of cues is available: celestial cues are not available, and less wind means worse olfaction, but the magnetic field is more stable. We conducted additional experiments on relatively warm nights with 100% cloud coverage to test how the froglets would navigate under these conditions (see 'Experiments conducted', below).

In surveys, the froglets were collected from each trap separately, their body length (snout–urostyle length) was measured with a caliper with an accuracy of 1 mm, and they were weighed (Massa k model bk 600.1 scales) with an accuracy of 0.02 g. According to the literature, in this population, the maximum size of the froglets before first wintering is 41 mm, and the minimum size before the second wintering is 37–40 mm (Lyapkov, 1997b; Smirina, 1980). We used 38 mm as a threshold value, and all larger specimens were excluded from the analysis as possible 2 year olds. In our experiments, only 45 and 29 specimens out of 1614 frogs that we used in the final sample set were 37 and 38 mm long, respectively; thus, the probability of 2 year old individuals being included in the sample set was minimal.

Experiments conducted

A total of 1790 frogs were captured. The total number of frogs in each experiment is presented in Table 1; certain experiments included more than one release and were repeated in different years. The dates of all 30 releases, the number of froglets and the wind direction are listed in Table S1.

Table 1. Experiments conducted and total number of froglets released in each

Site of capture	Left arena		Right arena	
	N	Years	N	Years
Experiments before the start of migration				
Right-side forest, 14–17 days before migration	84	2017	45	2017
Right-side forest, 1–3 days before migration	64	2016	130	2016, 2017, 2018
Experiments after the start of migration				
Right-side forest	84	2016	100	2018
Right-side meadow	119	2018	101	2018
Right river bank	188	2015, 2016, 2018	140	2016, 2018
Left-side meadow	42	2017	42	2017
Left river bank	81	2017, 2018	82	2018
Right river bank, night experiments	158	2016, 2017, 2018	121	2016, 2018
Experiments with froglets released after captivity				
Captured in the right-side forest before and released after the start of migration	69	2015	65	2013
Captured at the right river bank after the start of migration and released in 3 days	58	2016	59	2016

The date and the number of the frogs in each release are given in Table S1. N, total number of froglets captured for the experiment and released in the arena.

Experiments with froglets captured and released before the start of migration

Before the start of migration (Fig. 3A), the froglets were at their feeding sites (probably their summer home range) and had no motivation to search for hibernation sites; thus these experiments can be considered as controls for those conducted during the

migration. The experiments can be divided into two groups, conducted 14–17 days and 1–3 days before the start of mass migration. According to Bannikov (1940), the behavior of froglets in the forest changes several days before the migration: they start to group in locations close to the hibernation sites and the first individuals can begin migration. We wanted to test whether this phenomenon would affect the choice of direction. Froglets were caught in the right-side forest (location F1; Fig. 1) and released on the day of capture in both arenas.

Experiments with froglets captured and released after the start of migration

Determination of the start of migration

The start of migration (assuming mass migration rather than the appearance of the first migratory individuals) was determined by a sharp increase in the number of froglets registered on the survey route along the edge of the Moskva River, 1400 m on the right bank and 900 m on the left. The migration of the froglets began after repeated decreases of the air temperature to +3–0°C and rain, which is in agreement with literature data on the common frog (Bannikov, 1940; Koskela and Pasanen, 1974; Kutenkov, 2009) and similar to findings for other brown frogs (Miwa, 2018). In 2013, mass migration began on 21 September; in 2015, on 27 September; in 2016, on 20 September; in 2017, on 7–13 October; and in 2018, on 23 September.

Experiments with froglets from the right-side population

After the start of migration (Fig. 3B), the froglets were caught in three locations: in the forest (animals that presumably are at the very start of migration or intend to winter in the forest), in the meadow near the forest edge (animals in the process of migration that exit from the forest to the meadow near the river) and at the river bank, in the water or 3 m from it (animals that have completed the migration). Froglets were collected in F1, M, R1 and R2 locations (Fig. 1) and released on the day of capture in both arenas.

According to the literature, the start of migration can be protracted in brown frogs (Bannikov, 1940; Koskela and Pasanen, 1974;

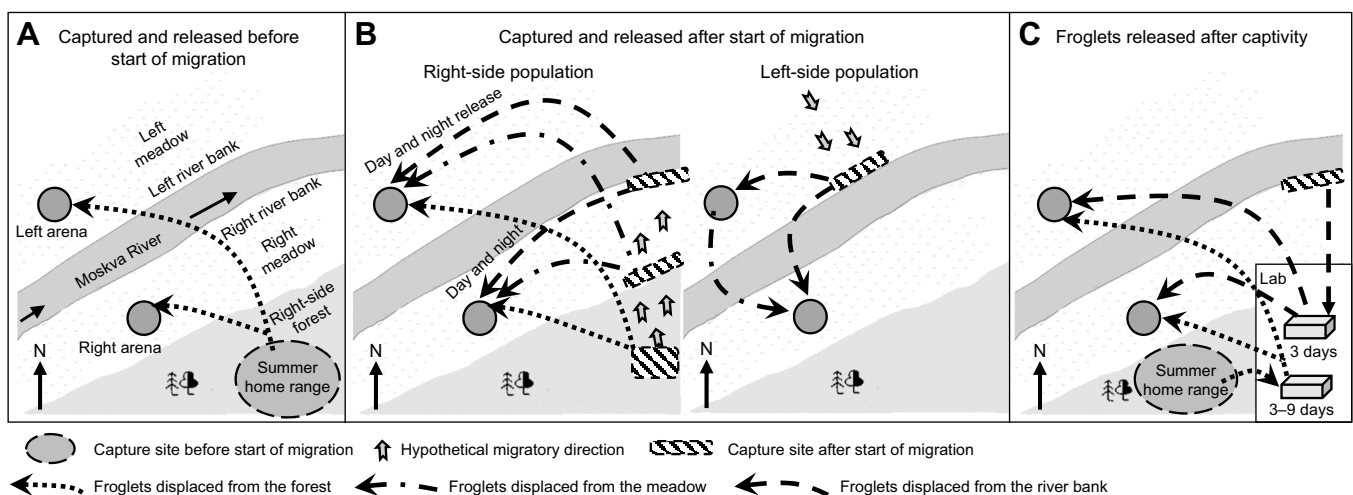


Fig. 3. Principal scheme of the conducted experiments. Dotted lines denote translocation of the frogs captured in the forest; dash-and-dot lines indicate froglets captured in the meadow; dashed lines indicate froglets captured at the river bank. (A) Experiments with froglets captured and released 14–17 and 1–3 days before the start of migration (right-side population). (B) Experiments with froglets captured and released after the start of migration with both populations (right and left side) and cases where not only day but also night releases were conducted. (C) Experiments with froglets captured in the forest, held in captivity and then released after the start of migration and froglets captured at the river bank after the start of migration, held captive and then released. In A and B, froglets were released on the day of capture. Number of specimens in each experiments is listed in Table 1. Details are given in Materials and Methods.

Miwa, 2018); thus, the animals caught in the forest may differ in their motivation: some froglets had already started migration, while others had not. This fact complicates the interpretation of the results; for example, the froglets may choose the direction towards the forest not as the hibernation location but because they have not begun the migration yet. This heterogeneity, however, must level out with time; thus, we repeated the release in the right arena (3–8 day captivity interval), where the froglets had a choice between two possible hibernation sites: the forest and the river.

Experiments with froglets from the left-side population

The froglets caught on the left side of the Moskva River were used as a control group (Fig. 3B), as they can have an opposite direction of migration. As these froglets inhabit the territory of the village during summer, we could not capture the animals that correspond to the sample set from the forest for the right-side population. We collected only the froglets that traveled through the field during migration and reached the river.

In 2017, the fence of the left arena was accidentally disrupted (blown by the wind), and its traps became exposed. The froglets migrating through the field towards the river at the time – a total of 42 animals – were caught. As the collapse of the fence occurred from different angles, the distribution of the froglets that got inside could be considered methodologically reliable, and it was taken into account in the general analysis. These froglets were collected from the traps and released in the right arena.

Froglets captured at the left river bank near the water's edge were collected in location R3 and released on the day of capture in both arenas.

Night experiments

To investigate the night-time orientation (Fig. 3B), the froglets were caught at the right river bank (location R1) after the start of migration from 17:00 h to 19:00 h and released after the end of astronomical twilight (from 20:20 h to 22:00 h on different days) on relatively warm nights with 100% cloud coverage. They were checked for the first time 30 min before sunrise; after that, we waited until the eleventh day and collected all the froglets remaining in the arena. Only animals collected during the first check were included in the analysis.

Froglets released after captivity

This series of experiments was conducted to observe whether the migration behavior could develop in captivity (Fig. 3C). We caught the froglets in the right-side forest at locations F1 and F2, 2–8 days before migration, kept them in a terrarium and released them after the start of migration. As a control, in order to understand how captivity can affect the behavior of froglets, we caught a group on the right river bank at location R1 after the start of migration, kept them in captivity for 3 days, divided them into two groups, and released them in both arenas.

Collection of the froglets

In the forest and at the river bank, the froglets were captured by hand in the grass and under the foliage or using a net in the water, then placed in opaque bags and brought to the laboratory. We used polyethylene fences with traps (a total length of 60 m) constructed 1.5 m from the forest edge to capture the froglets that migrate through the right-side meadow.

Before and after the experiment, the froglets were kept in 80×30×40 cm terrariums. After completing all the experiments in a year, the froglets were returned to the capture locations.

Compliance with ethical standards

The research was conducted in accordance with the laws of the Russian Federation and the requirements of the Committee for BioEthics of Lomonosov Moscow State University (GOST 33219-2014). The 'Guidelines for accommodation and care of animals' of the European Convention for the Protection of Vertebrate Animals used for Experimental and other Scientific Purposes (ETS No. 123) and the 'Guidelines for the treatment of animals in behavioural research and teaching' by the ASAB Ethical Committee/ABS Animal Care Committee (2012) were also followed.

Statistical analysis of the results

To analyze the distribution of frogs in the arena, we used Rayleigh's uniformity test (Batschelet, 1981; Humphreys and Ruxton, 2017). In cases where we assumed a bimodal distribution, we used the angle doubling procedure (Batschelet, 1981; Landler et al., 2018). To analyze the preferred direction (if there was any), we used the mean vector and its 95% confidence interval (Batschelet, 1981; Mardia and Jupp, 2000). The χ^2 test was used as a two-sample test (Batschelet, 1981). In the majority of cases, to ensure that most or all the expected frequencies used in the calculation will be greater than 5 when using the χ^2 test, we had to decrease the number of sectors to 8 by merging them in pairs (N+NNE; NE+ENE; E+ESE, etc.). Cases where all 16 sectors were utilized for the comparison are noted separately. To counteract the multiple comparisons problem, we used the Bonferroni correction (Lehner, 1996). In accordance with that, for night experiments and experiments conducted before the start of migration, $\alpha=0.025$; in other cases, $\alpha=0.0125$. To understand what caused the differences, we compared the 95% confidence interval, length of the mean vector and the circular standard deviation of the datasets (Batschelet, 1981). If the 95% confidence intervals of the two samples overlapped, the differences were due to the scatter of data (Batschelet, 1981). If the 95% confidence intervals did not overlap, then the differences were in the direction of movement under a comparable vector length. The calculations were performed in Oriana 4.0 (1994–2011 Kovach Computing Services).

Non-parametric criteria were used to analyze the portion of froglets captured in the first check in the experiments during different stages of migration. In particular, the Mann–Whitney *U*-test and Kruskal–Wallis ANOVA on ranks were used for pairwise comparisons and multiple group comparisons, respectively. The Wilcoxon signed-rank test was used to compare the scatter in the first check and the total dataset. Spearman rank order correlations was used to determine the influence of weather conditions. The calculations were performed in Statistica 8.0 (Statsoft Inc. 1984–2007).

RESULTS

Out of 1790 froglets released in the arenas, 1719 were recaptured, 1661 of them matched our criteria for young-of-the-year frogs, and 1614 of the latter were caught in traps inside the groove and used for direction analysis. The raw data for each experiment are given in Table S1.

Behavior before the start of migration

Right-side population

The froglets captured in the right-side forest 14–17 days and 1–3 days before the start of migration and released in the right arena oriented SE, i.e. towards the forest. We did not observe orientation directly towards the capture site F1 (a distance of 800 m). The scatter of directions was small in the first case (circular standard deviation CSD=36.1 deg), but increased in the second

(CSD=107 deg), creating a nearly uniform distribution (Fig. 4C,D) (no differences were found between the results of the experiments of 2016, 2017 and 2018: $\chi^2_{14}=11.01$, $P=0.69$). On the opposite side of the river (left arena), the froglets caught at 14–17 days oriented S but the distribution had a large scatter (CSD=93.9 deg) and was close to uniform (Fig. 4A); 1–3 days before the migration, the distribution by sectors did not differ from uniform (Fig. 4B).

Behavior after the start of migration

Right-side population

Froglets captured in the right-side forest after the start of migration changed their behavior. We observed a bimodal distribution for the right arena: a portion of the froglets chose the SE direction towards the forest, but half of the frogs traveled NW towards the river (Fig. 5F). During the repeated release of these froglets together with some of the frogs captured before the start of migration (3–8 days captivity interval), the majority of the them oriented towards the

Moskva River (Fig. 5F). On the opposite side (left arena), froglets moved SSW, also towards the river (Fig. 5A).

Froglets captured in the right-side meadow during migration oriented NW (towards the river) on the same side (right arena), as did the froglets caught in the forest in the repeat experiment (Fig. 5G). However, in the left arena, the froglets unexpectedly moved NNE, from the river, instead of S, towards it (as did the animals collected in the forest). The scatter of direction choice in this case was small (CSD=55.7 deg) (Fig. 5B).

Froglets captured at the right river bank near the water edge chose the same NNW direction on both river sides (95% confidence interval of the average vectors overlaps, Fig. 5C,H). This coincided with the direction towards the river on the right side, but not on the left side. The statistically significant differences between these experiments were due to the scatter, which was greater in the left arena (CSD=84 deg versus 66.3 deg). There were no differences found between the results of experiments conducted in 2015, 2016 and 2018 in the left arena and in 2016 and 2018 in the right arena: $\chi^2_{14}=16.35$, $P=0.29$ and $\chi^2_7=6.72$, $P=0.46$, respectively.

Left-side population

Froglets captured in the left-side meadow during migration oriented SSW, towards the river, in the left arena (Fig. 5D). When the same froglets were released at the opposite river side in the right arena, they also oriented south (Fig. 5I), but in this case, this coincided with the direction away from the river.

Froglets captured at the left river bank near the water and released into the left arena oriented towards the river (SE) and the location of capture (E) (Fig. 5E), and in the right arena, they were oriented south (Fig. 5J) (same as the froglets captured in the meadow). Thus, the selected directions, although similar, were different (95% confidence intervals of the average vectors did not overlap, with a comparable scatter of data).

Night experiments

The froglets caught after the start of migration at the right river bank and released during the night in the right arena oriented NW, similar to the froglets released during the day (Fig. 6C,D). In the left arena, the froglets released at night oriented from the river, the same as during the daytime experiments (Fig. 6A,B); however, the mean direction was NNE, not NNW (the same NNE direction was registered in the froglets captured in the right-side meadow). The scatter of directions in the night experiments was generally greater than in the daytime (CSD=83.6 deg versus 68.6 deg for the left arena and CSD=67.2 deg versus 51.2 deg for the right arena). There were no significant differences found between the results of experiments conducted in 2016 and 2018 in the right arena: $\chi^2_7=12.63$, $P=0.08$. For the left arena, the number of animals caught at night in 2016 and 2017 was not enough to analyze.

Froglets released after captivity

The froglets captured in the right-side forest before migration and released after migration started oriented towards the river in both arenas (Fig. 7A,C). It is important to note that very few oriented towards the forest in the right arena. In the left arena, the scatter of directions was significantly smaller compared with that for the froglets captured after the start of migration (CSD=68.6 deg versus 96.3 deg; $\chi^2_7=23.66$, $P=0.001$). No significant differences were found for the right arena from the repeated experiment with froglets captured after the start of migration ($\chi^2_7=12.78$, $P=0.08$); however, scatter of directions was also smaller (CSD=65.8 deg versus 78.7 deg).

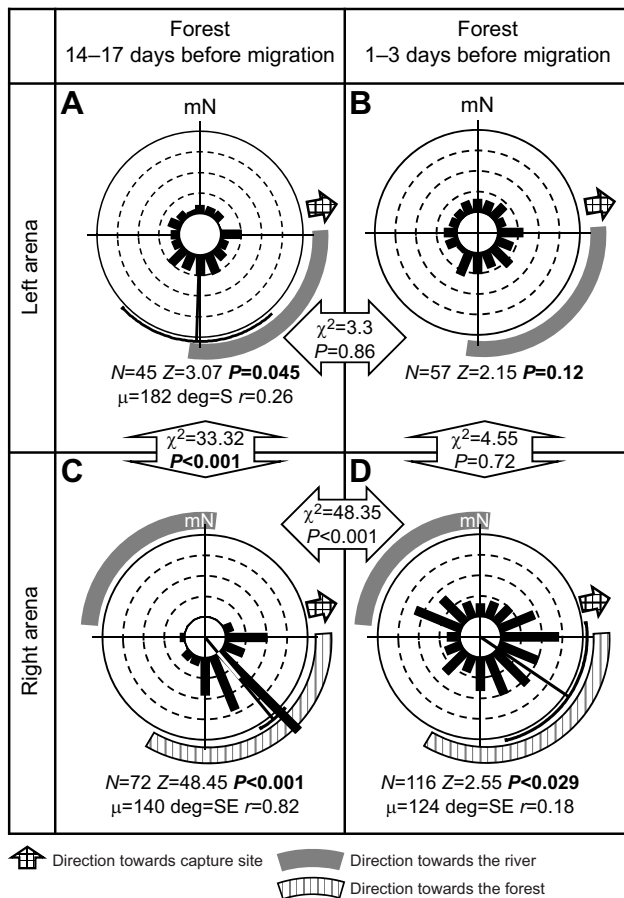


Fig. 4. Orientation of froglets in circular arenas before the start of wintering migration. Froglets captured and released 14–17 days (A,C) and 1–3 days (B,D) before migration in the right-side forest are individuals that dispersed into these habitats after metamorphosis. Experiments repeated in different years were combined into a single graph. mN, magnetic north. Bars show the number of froglets reaching the trap every 22.5 deg (1/16 perimeter). Dashed lines on circular diagrams denote 5 specimen intervals. The mean vector and its 95% confidence interval are shown in cases of unimodal distribution. *N*, number of froglets collected from arena traps with body length ≤ 38 mm; μ , mean vector and compass direction (e.g. N for north, SW for southwest, NNE for north-north-east, etc.); *Z*, Rayleigh test statistics; *r*, length of mean vector. Bold indicates significant differences; d.f.=7 for all χ^2 tests.

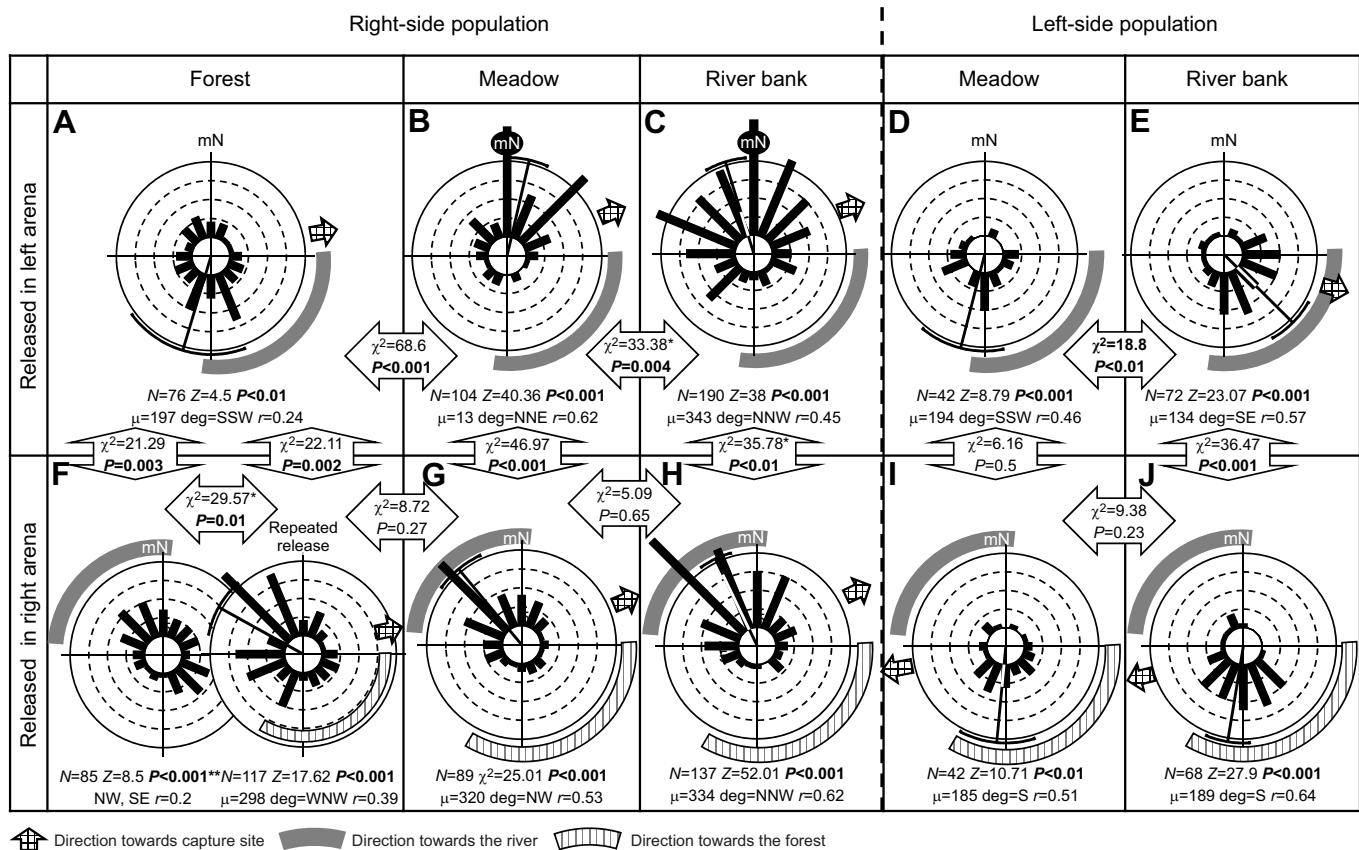


Fig. 5. Orientation of froglets in circular arenas captured and released after the start of wintering migration. Data are shown for the right-side population (A,F, forest; B,G, meadow; and C,H, riverbank) and left-side population (D,I, meadow; E,J, river bank). Froglets captured in the forest are those that we were able to find in the forest after the start of migration; froglets captured in the meadow are those caught in the traps while traveling towards the river; froglets captured along the river bank are the specimens that migrated to the river (hibernation site of adult frogs) from the forest and were collected in the water or 3 m from it. Experiments repeated in different years were combined into a single graph. mN, magnetic north. Bars show the number of froglets reaching the trap every 22.5 deg (1/16 perimeter). Dashed lines on circular diagrams denote 5 specimen intervals. The mean vector and its 95% confidence interval are shown in cases of unimodal distribution. *N*, number of froglets collected from arena traps with body length ≤ 38 mm; μ , mean vector and compass direction; *Z*, Rayleigh test statistics; *r*, length of mean vector. Bold indicates significant differences; χ^2 tests with d.f.=15, in other cases d.f.=7; **bimodal distribution, Rayleigh test applied after doubling the angle.

Froglets captured at the right river bank after the start of migration and kept in captivity for 3 days oriented NNW in the right arena and N in the left arena (Fig. 7B,D), thus demonstrating the same pattern as the froglets that were released on the day of capture ($\chi^2_7=5.24$, $P=0.63$ for the left arena and $\chi^2_7=15.35$, $P=0.03$ for the right arena).

Influence of the wind on behavior of released froglets

The potential influence of the wind on the behavior of the froglets was assessed based on two instances with drastically differing wind conditions. (1) Froglets collected in the right-side forest 1–3 days before the migration had a near-uniform distribution in the right arena; no differences were found between the results of the experiments in 2016 (N wind), 2017 (S wind) and 2018 (SW wind): $\chi^2_{14}=11.01$, $P=0.69$. (2) Froglets collected at the right river bank after the start of migration and released in the right arena in 2016 and 2018 oriented NNW (pairwise comparison $\chi^2_7=6.72$, $P=0.46$) despite the calm air during the 2016 release and the WNW wind in 2018. Thus, presumably, the wind did not have a significant effect on the behavior of froglets.

Comparison of the first and subsequent checks

As the majority of the frogs were collected from traps in the first check, we decided to analyze whether their behavior was different

from that of the froglets collected at later stages. The sample size was sufficient for the analysis in four experiments (Table 2). The general behavior of frogs in the first and subsequent checks was similar. However, in the experiments conducted after the start of migration with specimens captured at the river bank, it appears that froglets collected in the second and third checks had a greater scatter of selected directions than those in the first check (especially in the arena located on the opposite river side). In other cases, this pattern was achieved indirectly: in cases where distribution was unimodal, the scatter (CSD) in the first check was lower than in the total dataset ($N=21$, $t=40$, $Z=2.62$, $P=0.008$ according to the Wilcoxon signed-rank test).

We also analyzed the influences on the number of froglets caught during the first check. No statistically significant correlation was found between the portion of froglets caught during the first check from the total number caught in the experiment and the weather conditions (minimum and maximum temperature, relative humidity, atmospheric pressure) ($N=30$; *R* ranged -0.21 to 0.13 ; $P>0.2$ in all cases, based on Spearman's rank correlation). The percentage of froglets captured in the first check during the night-time and daytime experiments also did not differ ($P=0.42$ according to Mann–Whitney test). However, the portion of froglets caught in the first check changed depending on the stage of migration (Fig. 8). It

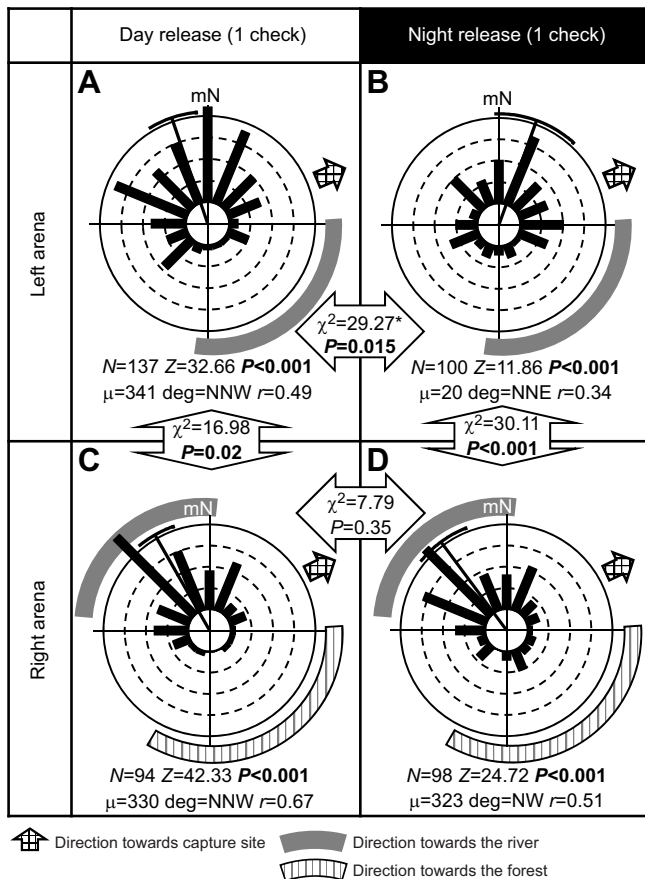


Fig. 6. Orientation of froglets released in the daytime and night-time. All froglets were captured at the right river bank after the start of migration. (A,C) Daytime release was at 12:00 h and checked at twilight (first check). (B,D) Night-time release was after dusk and checked 30 min before sunrise. Experiments repeated in different years were combined into a single graph. mN, magnetic north. Bars show the number of froglets reaching the trap every 22.5 deg (1/16 perimeter). Dashed lines on circular diagrams denote 5 specimen intervals. The mean vector and its 95% confidence interval are shown in cases of unimodal distribution. *N*, number of froglets collected from arena traps with body length ≤ 38 mm; μ , mean vector and compass direction; *Z*, Rayleigh test statistics; *r*, length of mean vector. Bold indicates significant differences; χ^2 tests with d.f.=15, in other cases d.f.=7.

increased after the start of migration and could decrease in animals that completed it (i.e. reached the river). For the froglets that did not complete the migration, captivity led to an increase in the number of active individuals (in repeated releases of the froglets captured in the forest, all 117 specimens were caught during the first check); in the animals that reached the river and finished their migration, captivity reduced this number.

DISCUSSION

General behavior model in froglets and the goal of migration

The following dynamic of froglet behavior can be drawn from the experiments conducted in this study. Two weeks before migration, the froglets captured in the forest and released in the arena on the same river side moved towards the forest. We did not observe orientation directly towards the capture site: the distance of 800 m appeared too great for the animals. The first animals oriented towards the river appeared 1–3 days before the migration. In the arena on the opposite river side, the froglets caught in the forest 2 weeks before migration were oriented south with a large scatter;

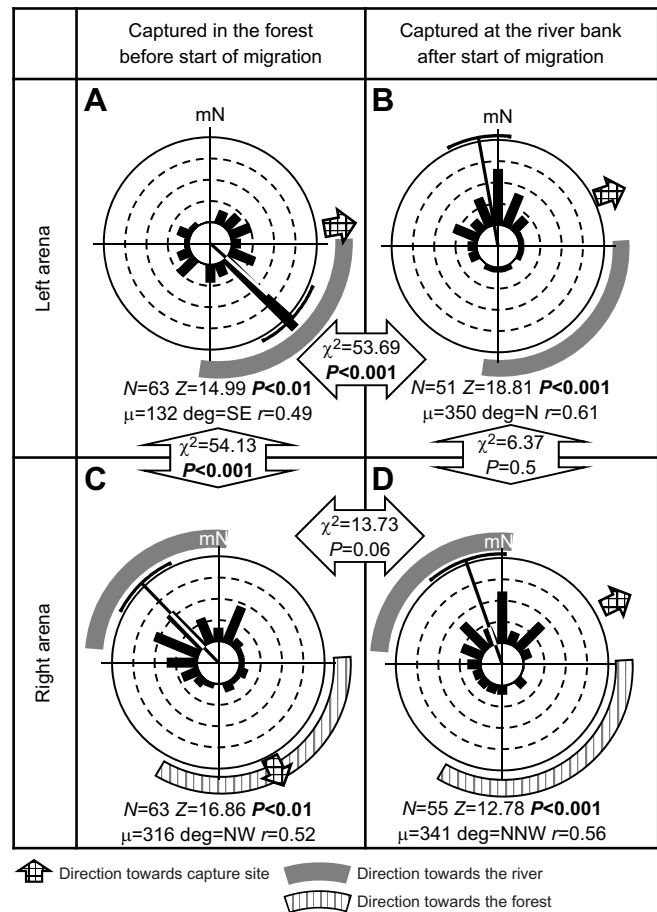


Fig. 7. Orientation of froglets in circular arenas after the start of migration, after 3–9 days in captivity. (A,C) Froglets were captured in the forest before migration and kept in captivity for 3–9 days. (B,D) Froglets were captured at the river bank after the start of migration and kept in captivity for 3 days. mN, magnetic north. Bars show the number of froglets reaching the trap every 22.5 deg (1/16 perimeter). Dashed lines on circular diagrams denote 5 specimen intervals. The mean vector and its 95% confidence interval are shown in cases of unimodal distribution. *N*, number of froglets collected from arena traps with body length ≤ 38 mm; μ , mean vector and compass direction; *Z*, Rayleigh test statistics; *r*, length of mean vector. Bold indicates significant differences; d.f.=7 for all χ^2 tests.

however, 1–3 days before migration, froglets were disoriented. After the beginning of migration, the froglets captured in the forest oriented to the river in the arena on the opposite side and demonstrated a bimodal distribution (towards the river and the forest) in the arena on the side of capture. This distribution became unimodal towards the river for the animals kept in captivity. The froglets captured in the meadow and at the river bank near the water oriented in the same direction in the two arenas: towards the river on the capture side and from the river on the opposite side of the river. Froglets from right- and left-side populations chose the opposite directions.

Therefore, when the froglets were in their summer habitats (e.g. the forest), they tried to return there if removed. As the froglets were not oriented towards the place of capture, their behavior can be described not as homing but as a return to their habitat. The presence of froglets moving towards the forest after the start of migration was associated with heterogeneous motivation within the group (some individuals had started migration, others had not) rather than with hibernation in the forest. As we predicted, the froglets kept in

Table 2. Comparison of orientation of froglets collected during the first and subsequent checks

Site of capture	Site of release	First check				Subsequent (second+third+fourth) checks				
		N	Rayleigh test Z; P	μ (deg)	r (CSD) (deg)	N	Rayleigh test Z; P	μ (deg)	r (CSD) (deg)	χ^2 ; P
Experiments before the start of migration										
Right-side forest, 1–3 days before migration	Right arena	71	2.92; 0.054	–	0.2 (102.3)	45	2.16; 0.12	–	0.22 (99.9)	9.42; 0.22
Experiments after the start of migration										
Right river bank	Right arena	94	42.33; <0.001	330	0.67 (51.2)	43	11.18<0.001	346	0.51 (66.5)	7.25; 0.4
Right river bank	Left arena	137	32.66; <0.001	341	0.49 (68.6)	53	5.26 0.005	352	0.32 (87.1)	5.82; 0.56
Left river bank	Left arena	37	18.26; <0.001	125	0.7 (48.2)	35	7.07<0.001	151	0.45 (72.5)	8.66; 0.28

N, number of froglets collected from arena traps with body length ≤ 38 mm; μ , mean vector; r, length of mean vector; CSD, circular standard deviation.

captivity became uniform in their motivation and travel towards the river. The number of animals that oriented towards the forest did not exceed that in the groups caught in the meadow or at the river bank. In our experiments, captivity did not disrupt the drive towards the hibernation site; consequently, if a portion of froglets had intended to hibernate in the forest, the distribution would remain bimodal. The preference for the water during the first hibernation is also consistent with laboratory experiments, where the young-of-the-year common frogs preferred water over land during artificial hibernation (Laitinen and Pasanen, 1998). Common frogs of any age do not survive even short-term freezing (Pasanen and Karhapää, 1997); thus, they tend to choose the largest flowing water body – the river, as it has a much lower chance of freezing. Our survey of wintering sites (Table S2), as well as previous data (Bannikov, 1940), confirm this.

We can therefore conclude that: (1) the froglets do not select the hibernation site randomly and thus the hypothesis of Pasanen and co-authors (1994), which states random selection of hibernation

sites by froglets that do not winter in their native water body, has not been confirmed; and (2) the river in particular (not the forest) is the final goal of migration.

Global and local cue hierarchy and possible orientation mechanism in froglets

The experiments conducted on both sides of the river allowed us to evaluate the contribution of global and local cues to the orientation behavior. For the froglets on their native river side, local cues from the river coincided with the direction of migration available from global cues, whereas froglets on the side opposite to the capture side experienced a cue conflict (Able, 1993).

Mechanism of orientation towards the forest before migration

The froglets inhabiting the forest presumably used local cues, as they clearly oriented towards the forest only in the arena on their native side; on the opposite side, where the forest was not visible and the horizon was uniform, they were poorly oriented or disoriented. The latter case is similar to behavior of adult amphibians of various species and ecology that were displaced from their home site over great distances (Dole, 1968, 1972b; Sinsch, 1986) or through biological barriers (Pašukonis et al., 2014).

Among the local cues, the visual appearance of trees was presumably the least valuable for the froglets, as in the right arena, where we observed a clear orientation towards the forest, the individual trees closest to the arena were situated northeast, but the froglets did not move in this direction. Rather, we assume that the forest itself, which determines the elevation of the horizon, served as a cue. Such a mechanism (but with an ‘opposite’ reaction) is known for hatchling turtles that recognize the direction to the sea based on both illumination levels and a mainly low horizon, as opposed to a high horizon on the side of land vegetation (Godfrey, 1995; Salmon et al., 1992). Similar mechanisms of orientation towards the forest can apparently be used by metamorphosed juvenile ambystomatid salamanders and American toads migrating from their pool (Rothermel, 2004; Rothermel and Semlitsch, 2002). In our case, we also cannot exclude the use of the odor of the forest litter, as it is known to be attractive to adult frogs inhabiting the forest (Khmelevskaya and Deulina, 1972). The smell carried by separate gusts of the south wind could potentially orient some of the frogs towards the forest in the arena on the opposite side in the experiment 2 weeks before the start of migration. Had the frogs used any global cues, they would have oriented themselves just as successfully as in the arena on the familiar side.

Mechanism of orientation towards the river after the start of migration

At the beginning of migration, the froglets captured in the forest oriented towards the river on both sides, which indicates the use of

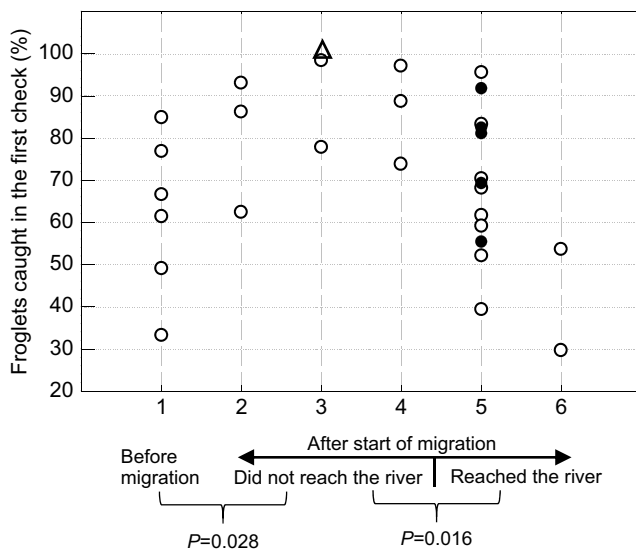


Fig. 8. Percentage of froglets captured in the arena in the first check. Data are presented as the percentage of the total number of animals caught in the arena in all checks during the experiments conducted at various stages of migration. 1, experiments conducted before migration; 2, froglets captured in the forest; 3, froglets captured in the forest before migration and released after the start of migration (kept in captivity); 4, froglets captured in the meadow; 5, froglets captured at the river bank; 6, froglets captured at the river bank and released after captivity. Open circles, daytime releases; filled circles, night-time releases; triangle, repeated release. Mann–Whitney U-test.

local cues directly from the river. In contrast, the froglets caught on their migration route in the meadow or those that reached the river chose a similar direction in the two arenas: froglets from the right-side population oriented north, and froglets from the left-side population oriented south. Thus, in the process of migration, orientation towards the river switched to a compass heading that corresponds to the direction of migration into the river. This phenomenon is similar to that observed in young birds that continue to fly in the compass direction when they are displaced from the migration route (Mouritsen and Larsen, 1998; Perdeck, 1958). As the choice of direction does not depend on the position of the river, it has to be based on global cues, and this system dominates over the previously utilized local cues. The global cues continue to prevail for the froglets that reached the river, even though they could have memorized its smell and use that to determine the correct direction. River-associated local cues appeared to be used only at the native river side when they were consistent with the direction obtained from global cues. For example, the froglets captured at the right river bank oriented with a smaller scatter in the right arena than in the left arena. In the experiments with froglets from the left river bank in the left arena, we observed a correction of orientation towards the site of capture. The froglets captured in the second and subsequent checks demonstrated the best results only under the most favorable conditions, i.e. on their native side of the river, possibly as a result of weaker motivation.

The use of such compass orientation is sufficiently adaptive for the animals that hibernate in the river as it is enough to take the correct azimuth for the resulting path to definitely cross the shore. In general, this is similar to 'y-axis orientation', in which an animal orients in a learned direction (the so-called y-axis) which bisects a shoreline (the x-axis) at right angles (Adler, 1970; Ferguson and Landreth, 1966). However, in our case, the observed direction was established before contact with the river. Thus, even though similar learning mechanisms can be utilized, this is not y-axis orientation *sensu stricto*; it is unclear at what moment the direction is chosen and memorized, what is used as its basis, and what serves as a trigger for switching to another type of orientation. It is possible that frogs fix the direction chosen according to local cues when they leave the forest for an open space, where the odor gradients should be less stable because of the blowing wind. It is also possible that the compass direction itself is based on a perpendicular to the edge of the forest. A surface slope usually present near the river is unlikely to be a reference for direction, as it is absent at the left side of the Moskva River.

If we compare the orientation behavior of froglets with that of adult frogs, the latter have greater plasticity. They use local cues to orient towards the wintering pond at short distances (hundreds of meters), and only switch to compass heading when these cues either are not available or do not provide directional information. Adult common frogs orient towards the wintering lake from a distance of up to 230 m, regardless of the side of the lake they were released on (Pasanen and Sorjonen, 1995). Marsh frogs moved to their hibernation site, the river, after being displaced by 450 m; at a distance of 1 km, the frogs moved using the stereotype compass heading, which corresponded to that of their autumn migration (Shakhparonov, 2012; Shakhparonov and Ogurtsov, 2008). In adult common frog, behavior similar to compass heading was observed in experiments conducted 140 km from the hibernation site (Pasanen et al., 1994), although the authors themselves did not interpret their results this way. In general, this case is similar to that of birds: behavior of the juveniles obeys program stereotypes, while the adults are able to register their deviation from the route and return to

it using true navigation (Chernetsov et al., 2017; Perdeck, 1958; Wiltshcko, 2017).

Possible cues during migration

Local cues

Similar to Pasanen and Sorjonen (1995), we assume that the moisture gradient is unlikely to be used, as the main migration occurs during high humidity. In laboratory tests, frogs cannot use it even at 65–68% humidity (Brändle and Lázár, 1994); in our experiments, the froglets from the forest oriented towards the river in the left arena after a light rain and under 98% humidity. It is most likely that froglets use the odor of water composed by the river flora and fauna to detect the river (unlike hydrotaxis, odor perception does not deteriorate under increasing humidity: Kuehn et al., 2008; Philpott et al., 2004; Stevens et al., 1988). The possible use of odor raises at least two questions: (1) do froglets recognize the odor of a river before migration; and (2) is the odor of a river more attractive than the odor of the native pond or any other stagnant water body? Of course, froglets can simply choose the strongest source of the odor, i.e. the river. Likewise, marsh frogs from the southern populations prefer the river instead of small floodplain ponds (Shakhparonov, 2011). The main weakness of the odor hypothesis is that the froglets caught in the forest still oriented towards the river after the start of migration both in calm weather and with the wind from the opposite direction. Seismic noise caused by the river current can also potentially direct frogs to its location. Unlike stagnant water bodies, even small lowland rivers produce seismic noise at an approximate frequency of 1 Hz (0.1–1 Hz) (Barrière et al., 2013). Unfortunately, this phenomenon is poorly studied, as vibration sensitivity in frogs has been tested only for frequencies above 10 Hz (Christensen-Dalsgaard and Buhl Jørgensen, 1988; Jørgensen and Christensen-Dalsgaard, 1991). These hypotheses need additional research.

Global cues

To find a compass heading, amphibians can use the sun (Ferguson et al., 1968; Landreth and Ferguson, 1967b; Taylor and Ferguson, 1969; Tracy, 1971), stars (Diego-Rasilla and Luengo, 2002; Ferguson et al., 1965), polarized light (Taylor and Adler, 1973) and Earth's magnetic field (Diego-Rasilla et al., 2013; Pail et al., 2020; Phillips et al., 2010; Schlegel, 2008; Shakhparonov and Ogurtsov, 2017).

The ability of the frogs to orient in the compass direction even at night with an overcast sky supports possible usage of the Earth's magnetic field. However, the froglets orient better during the day, even though the magnetic field is less stable (Kirschvink et al., 1985), which also supports use of the sun compass.

Previously, we noted the same compass direction (NNE) observed in the froglets caught in the meadow near the forest edge (i.e. those that had just left the forest canopy) and in the specimens released at night that were captured near the river, while the froglets caught at the river bank during the daytime experiments oriented NNW. It is therefore possible that froglets learn the direction based on the sun compass in an open space, as its usage is hindered under the forest canopy. Before learning or in the absence of the sun compass, froglets utilize the magnetic compass that provides a slightly different direction. We did not observe such differences in orientation of the specimens from the left-side population caught at the river bank and in the meadow in a similar experiment. These frogs were caught in the meadow closer to the river and had traveled a great distance across an open field, where the celestial compass is readily available. Thus, although this

explanation appears reliable, it is still unknown why the compasses provide different directions and are not calibrated against each other as in birds (Pakhomov and Chernetsov, 2020). Additional studies are required to identify the true mechanism.

Motivation and migratory condition

We found that individuals collected in the first check oriented 'better' than those that were collected afterwards. Considering the fact that the froglets can easily travel the distance from the center to the edges of an arena during the experiment (for some froglets, this took only 30 min; V.V.S., A.P.G., E.E.G. and A.A.B., unpublished data), the individuals captured in subsequent checks were most likely less motivated and therefore began to move later and orient less efficiently than more motivated froglets. Presumably, we can consider the number of individuals caught at the first check as the general level of motivation in froglets. We found that a portion of these most motivated froglets in our experiments did not depend on the weather conditions, possibly because of their small variation. However, this correlation was most likely obscured by another factor: the stage of migration. Froglets before the migration or those that had already completed it were less active and motivated to move during the experiments. The specimens captured in the forest after the start of migration or on their way to the river (i.e. those that did not complete migration) were the most active. Thus, frogs apparently have some kind of migratory condition; we observed its manifestation as an increase in activity and orientation towards the wintering sites. This was also confirmed by the onset of 'migratory conditions; in the froglets that were kept in the laboratory and an increase in the number of active individuals in the repeat experiment with the frogs caught in the forest after the start of migration. To date, we do not have sufficient data to compare the migratory condition of frogs with the migratory disposition in birds, which includes a specific set of physiological and behavioral adaptations triggered by photoperiod and controlled by endogenous rhythm and endocrine regulation (Berthold, 1996; Dolnik, 1975). However, the search for similarities between them may become a new direction for further research on the matter.

Conclusions

Our data demonstrate the following pattern of behavior of young-of-the-year common frogs. Before the migration, froglets attempt to return to their habitat using local cues. They migrate towards the river to hibernate after several temperature drops and the onset of migratory condition. At the beginning of migration, the froglets orient towards the river using local cues, i.e. unlike birds, they apparently have no innate direction of autumn migration. Later, before reaching the hibernation site, froglets memorize the direction of migration and maintain it utilizing global cues such as the sun compass and Earth's magnetic field. Orientation along a memorized compass heading begins to predominate in the hierarchy of orientation mechanisms, even after reaching the hibernation site. Such a program includes several stages with different systems of orientation, where the local cues dominate at first and followed by global cues, resembling this phenomenon in reptiles. Sea turtles, in particular, utilize local cues as well; this stage is followed by use of the global systems of orientation after reaching the water current (Hays et al., 2010; Lohmann and Lohmann, 1996). However, because they cover large distances, turtles possess innate fixed points that help them remain in the appropriate latitudes (Lohmann et al., 2012; Putman et al., 2012). Short-term captivity does not disrupt the motivation of froglets; its vector and level correspond to that observed in nature.

Thus, despite short migration distances and the absence of innate directional/positional components, the presence of a program that assumes several stages with different systems of orientation and some kind of migratory condition shows that the amphibian migration is not a simple response to the environment but a complex process with features similar to that of long distance migrants.

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Competing interests

The authors declare no competing or financial interests.

Author contributions

Conceptualization: V.V.S., A.P.G.; Methodology: V.V.S., A.P.G.; Validation: V.V.S.; Formal analysis: V.V.S., A.P.G.; Investigation: V.V.S., A.P.G., E.E.G., A.A.B.; Resources: V.V.S.; Writing - original draft: V.V.S., A.P.G.; Writing - review & editing: V.V.S., A.P.G.; Supervision: V.V.S.; Project administration: V.V.S.; Funding acquisition: V.V.S.

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References

- Able, K. P. (1993). Orientation cues used by migratory birds: a review of cue-conflict experiments. *Trends Ecol. Evol.* **8**, 367-371. doi:10.1016/0169-5347(93)90221-A
- Able, K. P. (2001). The concepts and terminology of bird navigation. *J. Avian Biol.* **32**, 174-183. doi:10.1034/j.1600-048X.2001.320211.x
- Adler, K. (1970). The role of extraoptic photoreceptors in amphibian rhythms and orientation: A Review. *J. Herpetol.* **4**, 99. doi:10.2307/1562884
- Adler, K. (1982). Sensory aspects of amphibian navigation and compass orientation. *Vertebr. hungarica Musei Hist. Hungarici* **21**, 7-18.
- Alerstam, T., Hedenström, A. and Åkesson, S. (2003). Long-distance migration: evolution and determinants. *Oikos* **103**, 247-260. doi:10.1034/j.1600-0706.2003.12559.x
- ASAB Ethical Committee/ABS Animal Care Committee (2012). Guidelines for the treatment of animals in behavioural research and teaching. *Anim. Behav.* **83**, 301-309. doi:10.1016/j.anbehav.2011.10.031
- Bannikov, A. G. (1940). The ecological conditions of the hibernation of the grass-frog (*Rana temporaria* L) in Moscow distr. *J. Students Sci. Work. Moscow state Univ. Zool.* **16**, 41-64.
- Barrière, J., Oth, A., Schenkluhn, R. and Krein, A. (2013). Joint analysis of seismograms and hydroacoustic data for bedload transport monitoring in a small lowland river. In International workshop of acoustic and seismic monitoring of bedload and mass movements, p. Swiss Federal Research Institute WSL, Birmensdorf, Switzerland.
- Bastakov, V. A. (1991). Chemosensory spatial orientation of anuran amphibians. In *The Problems of Chemical Communication in Animals*, pp. 256-263. Moscow: Nauka [in Russian].
- Bastakov, V. A. (1992). Experimental study of the memorizing of pond odor during larval development of two anuran species. *Zool. Zhurnal* **71**, 123-127.
- Batschelet, E. (1981). *Circular Statistics in Biology*. London: Academic Press.
- 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 & Hall.
- Brändle, K. and Lázár, G. (1994). Hygrostatic orientation of frogs in the laboratory. *Amphib-Reptilia* **15**, 285-295. doi:10.1163/156853894X00065
- Chernetsov, N. S. (2016). Orientation and navigation of migrating birds. *Biol. Bull.* **43**, 788-803. doi:10.1134/S1062359016080069
- Chernetsov, N. (2017). Compass systems. *J. Comp. Physiol. A Neuroethol. Sensory Neural Behav. Physiol.* **203**, 447-453. doi:10.1007/s00359-016-1140-x
- Chernetsov, N., Berthold, P. and Querner, U. (2004). Migratory orientation of first-year white storks (*Ciconia ciconia*): inherited information and social interactions. *J. Exp. Biol.* **207**, 937-943. doi:10.1242/jeb.00853
- Chernetsov, N., Pakhomov, A., Kobylkov, D., Kishkinev, D., Holland, R. A. and Mouritsen, H. (2017). Migratory Eurasian reed warblers can use magnetic declination to solve the longitude problem. *Curr. Biol.* **27**, 2647-2651.e2. doi:10.1016/j.cub.2017.07.024

- Christensen-Dalsgaard, J. and Buhl Jørgensen, M. (1988). The response characteristics of vibration-sensitive saccular fibers in the grassfrog, *Rana temporaria*. *J. Comp. Physiol. A* **162**, 633-638. doi:10.1007/BF01342638
- Chugunov, Y. D. (1966). On the polyphase rhythm of the diurnal activity of *Rana temporaria* L. *Zool. Zhurnal* **45**, 1692-1697.
- Diego-Rasilla, J. and Luengo, R. (2002). Celestial orientation in the marbled newt (*Triturus marmoratus*). *J. Ethol.* **20**, 137-141. doi:10.1007/s10164-002-0066-7
- Diego-Rasilla, F. J., Luengo, R. M. and Phillips, J. B. (2013). Use of a light-dependent magnetic compass for y-axis orientation in European common frog (*Rana temporaria*) tadpoles. *J. Comp. Physiol. A* **199**, 619-628. doi:10.1007/s00359-013-0811-0
- Dingle, H. (1996). *Migration: The Biology of Life on the Move*. New York, Oxford: Oxford University Press.
- Dole, J. W. (1968). Homing in leopard frogs, *Rana pipiens*. *Ecology* **49**, 386-399. doi:10.2307/1934105
- Dole, J. W. (1971). Dispersal of recently metamorphosed leopard frogs, *Rana pipiens*. *Copeia* **1971**, 221. doi:10.2307/1442821
- Dole, J. W. (1972a). Evidence of celestial orientation in newly-metamorphosed *Rana pipiens*. *Herpetologica* **28**, 273-276.
- Dole, J. W. (1972b). Homing and orientation of displaced toads, *Bufo americanus*, to their home sites. *Copeia* **1972**, 151-158. doi:10.2307/1442791
- Dolnik, V. R. (1975). *Migratory Disposition of Birds*. Moscow: Nauka.
- Elmberg, J. and Lundberg, P. (1988). Navigation in breeding-migrating *Rana temporaria*: a simple translocation common frogs experiment. *Amphib-Reptilia* **9**, 169-173. doi:10.1163/156853888X00567
- Ferguson, D. E. (1971). The sensory basis of orientation in amphibians. *Ann. N. Y. Acad. Sci.* **188**, 30-36. doi:10.1111/j.1749-6632.1971.tb13087.x
- Ferguson, D. E. and Landreth, H. F. (1966). Celestial orientation of Fowler's toad *Bufo fowleri*. *Behaviour* **26**, 105-123. doi:10.1163/156853966X00047
- Ferguson, D. E., Landreth, H. F. and Turnipseed, M. R. (1965). Astronomical orientation of the southern cricket frog, *Acris gryllus*. *Copeia* **1965**, 58. doi:10.2307/1441240
- Ferguson, D. E., McKeown, J. P., Bosarge, O. S. and Landreth, H. F. (1968). Sun-compass orientation of bullfrogs. *Copeia* **1968**, 230. doi:10.2307/1441746
- Godfrey, M. H. (1995). Beach vegetation and sea finding orientation of turtle hatchlings. *Biol. Conserv.* **74**, 29-32. doi:10.1016/0006-3207(95)00011-R
- Gorman, R. R., Ferguson, J. H., Herpetologica, S. and Mar, N. (1970). Sun-compass orientation in the western toad, *Bufo boreas*. *Herpetologica* **26**, 34-45.
- Hays, G. C., Fossette, S., Katselidis, K. A., Mariani, P. and Schofield, G. (2010). Ontogenetic development of migration: Lagrangian drift trajectories suggest a new paradigm for sea turtles. *J. R. Soc. Interface* **7**, 1319-1327. doi:10.1098/rsif.2010.0009
- Hepper, P. G. and Waldman, B. (1992). Embryonic olfactory learning in frogs. *Q. J. Exp. Psychol. Sect. B* **44**, 179-197.
- Humphreys, R. K. and Ruxton, G. D. (2017). Consequences of grouped data for testing for departure from circular uniformity. *Behav. Ecol. Sociobiol.* **71**, 167. doi:10.1007/s00265-017-2393-2
- Jørgensen, M. B. and Christensen-Dalsgaard, J. (1991). Peripheral origins and functional characteristics of vibration-sensitive VIIIth nerve fibers in the frog *Rana temporaria*. *J. Comp. Physiol. A* **169**, 341-347.
- Khmelevskaya, N. V. (1989). Spatial structure of the grass frog population, *Rana temporaria*, and its temporal dynamics. In Amphibians and reptiles of the Moscow region. Proceedings of the meeting on herpetofauna in Moscow and Moscow region, pp. 124-133.
- Khmelevskaya, N. V. and Deulina, T. O. (1972). On the role of the sense of smell in the life of anura. *Zool. Zhurnal* **51**, 764-767.
- Kirschvink, J. L., Jones, D. S. and MacFadden, B. J. (eds). (1985). *Magnetite Biomineralization and Magnetoreception in Organisms*, 1st edn. Boston: Springer.
- Koskela, P. and Pasanen, S. (1974). The wintering of the common frog, *Rana temporaria* L., in northern Finland. *Aquil. Ser. Zool.* **15**, 1-17.
- Kuehn, M., Welsch, H., Zahnert, T. and Hummel, T. (2008). Changes of pressure and humidity affect olfactory function. *Eur. Arch. Oto-Rhino-Laryngology* **265**, 299-302. doi:10.1007/s00405-007-0446-2
- Kutenkov, A. P. (2009). *Ecology of common frogs (Rana temporaria L 1758) in the North-West of Russia*. Petrozavodsk: PetrGU. [In Russian].
- Kuzmin, S. L. (2013). *The Amphibians of the Former Soviet Union*. 2nd Revise. Sofia, Moscow: Pensoft Publishers.
- Laitinen, M. and Pasanen, S. (1998). Wintering site selection by the common frog (*Rana temporaria*) and common toad (*Bufo bufo*) in Finland: A behavioural experiment. *Ann. Zool. Fennici* **35**, 59-62.
- Landler, L., Ruxton, G. D. and Malkemper, E. P. (2018). Circular data in biology: advice for effectively implementing statistical procedures. *Behav. Ecol. Sociobiol.* **72**, 128. doi:10.1007/s00265-018-2538-y
- Landreth, H. F. and Ferguson, D. E. (1967a). Movements and orientation of the tailed frog, *Ascaphus truei*. *Herpetologica* **23**, 81-93.
- Landreth, H. F. and Ferguson, D. E. (1967b). Newts: Sun-compass orientation. *Science (80-)*. **158**, 1459-1461. doi:10.1126/science.158.3807.1459
- Lehner, P. N. (1996). *Handbook of Ethological Methods*, 2nd edn. Cambridge: Cambridge University Press.
- Lohmann, K. and Lohmann, C. (1996). Orientation and open-sea navigation in sea turtles. *J. Exp. Biol.* **199**, 73-81. doi:10.1242/jeb.199.1.73
- Lohmann, K. J., Hester, J. T. and Lohmann, C. M. F. (1999). Long-distance navigation in sea turtles. *Ethol. Ecol. Evol.* **11**, 1-23. doi:10.1080/08927014.1999.9522838
- Lohmann, K. J., Putman, N. F. and Lohmann, C. M. F. (2012). The magnetic map of hatchling loggerhead sea turtles. *Curr. Opin. Neurobiol.* **22**, 336-342. doi:10.1016/j.conb.2011.11.005
- Lyapkov, S. M. (1997a). Peculiarities of growth in *Rana temporaria* and *Rana arvalis* in the first years of terrestrial life. Influence of size on survival during wintering. *Zool. Zhurnal* **76**, 356-363.
- Lyapkov, S. M. (1997b). Variation of growth rate in *Rana temporaria* and *Rana arvalis* in the first years of terrestrial life. *Zool. Zhurnal* **76**, 199-205.
- Mardia, K. V. and Jupp, P. E. (2000). *Directional Statistics*. West Sussex: John Wiley & Sons Ltd.
- Miaud, C. and Sérandour, J. (2003). Preliminary results on the genetic control of dispersal in common frog *Rana temporaria* froglets. In *Herpetologica Petropolitana* (ed. N. Ananjeva and O. Tsinenko) (Saint-Petersburg), Proc. 12th Congress of SHE, pp. 193-197.
- Miwa, T. (2018). Conditions controlling the timing of the autumn migration to hibernation sites in a Japanese headwater frog, *Rana sakuraii*. *J. Zool.* **304**, 45-54. doi:10.1111/jzo.12495
- Morandi-Raikova, A., Vallortigara, G. and Mayer, U. (2020). The use of spatial and local cues for orientation in domestic chicks (*Gallus gallus*). *Anim. Cogn.* **23**, 367-387. doi:10.1007/s10071-019-01342-6
- Mouritsen, H. (2018). Long-distance navigation and magnetoreception in migratory animals. *Nature* **558**, 50-59. doi:10.1038/s41586-018-0176-1
- Mouritsen, H. and Larsen, O. N. (1998). Migrating young pied flycatchers *Ficedula hypoleuca* do not compensate for geographical displacements. *J. Exp. Biol.* **201**, 2927-2934. doi:10.1242/jeb.201.21.2927
- Ogurtsov, S. V. (2005). Basis of native pond fidelity in anuran amphibians: the case of chemical learning. *Russ. J. Herpetol.* **12**, 198-200.
- Ogurtsov, S. V. (2012). A problem of multicross interaction in studying the chemical orientation of juveniles of terrestrial amphibian species. *Zool. Zhurnal* **91**, 1330-1339.
- Pail, M., Landler, L. and Gollmann, G. (2020). Orientation and navigation in *Bufo bufo*: A quest for repeatability of arena experiments. *Herpetozoa* **33**, 139-147. doi:10.3897/herpetozoa.33.e52854
- Pakhomov, A. and Chernetsov, N. (2020). A hierarchy of compass systems in migratory birds. *Biol. Commun.* **65**, 262-276. doi:10.21638/spbu03.2020.306
- Pasanen, S. and Karhapää, M. (1997). Can boreal common frog (*Rana temporaria* L.) survive in frost? *Ann. Zool. Fennici* **34**, 247-250.
- Pasanen, S. and Sorjonen, J. (1995). An orientation experiment conducted during autumn migration of the common frog (*Rana temporaria*). *Memo. Soc. Fauna Flora Fenn.* **71**, 113-117.
- Pasanen, S., Sorjonen, J., Martikainen, S. and Olkinuora, P. (1994). Orientation of the common frog to the wintering place. *Ann. Zool. Fennici* **31**, 279-282.
- Pašukonis, A., Warrington, I., Ringler, M. and Hödl, W. (2014). Poison frogs rely on experience to find the way home in the rainforest. *Biol. Lett.* **10**, 20140642. doi:10.1098/rsbl.2014.0642
- Patrick, D. A., Calhoun, A. J. K. and Hunter, M. L. (2007). Orientation of juvenile wood frogs, *Rana sylvatica*, leaving experimental ponds. *J. Herpetol.* **41**, 158-163. doi:10.1670/0022-1511(2007)41[158:OOJWFR]2.0.CO;2
- Perdeck, A. C. (1958). Two types of orientation in migratory starlings, *Sturnus vulgaris* L., and chaffinches, *Fringilla coelbes* L., as revealed by displacement experiments. *Ardea* **46**, 1-37.
- Phillips, J. B., Jorge, P. E. and Muheim, R. (2010). Light-dependent magnetic compass orientation in amphibians and insects: candidate receptors and candidate molecular mechanisms. *J. R. Soc. Interface* **7** Suppl. 2, S241-S256.
- Philpott, C., Goodenough, P., Passant, C., Robertson, A. and Murty, G. (2004). The effect of temperature, humidity and peak inspiratory nasal flow on olfactory thresholds. *Clin. Otolaryngol. Allied Sci.* **29**, 24-31. doi:10.1111/j.1365-2273.2004.00760.x
- Popescu, V. D., Brodie, B. S., Hunter, M. L. and Zydlewski, J. D. (2012). Use of olfactory cues by newly metamorphosed wood frogs (*Lithobates sylvaticus*) during emigration. *Copeia* **2012**, 424-431. doi:10.1643/CE-11-062
- Putman, N. F., Verley, P., Shay, T. J. and Lohmann, K. J. (2012). Simulating transoceanic migrations of young loggerhead sea turtles: merging magnetic navigation behavior with an ocean circulation model. *J. Exp. Biol.* **215**, 1863-1870. doi:10.1242/jeb.067587
- Reshetnikov, A. N. (1996). Hygrotactic and olfactory orientation in juvenile common toads (*Bufo bufo*) during the postmetamorphic period. *Adv. Amphib. Res. Former Sov. Union* **1**, 181-190.
- Rothermel, B. B. (2004). Migratory success of juveniles: A potential constraint on connectivity for pond-breeding amphibians. *Ecol. Appl.* **14**, 1535-1546. doi:10.1890/03-5206
- Rothermel, B. B. and Semlitsch, R. D. (2002). An experimental investigation of landscape resistance of forest versus old-field habitats to emigrating juvenile amphibians. *Conserv. Biol.* **16**, 1324-1332. doi:10.1046/j.1523-1739.2002.01085.x

- Russell, A. P., Bauer, A. M. and Johnson, M. K.** (2005). Migration in amphibians and reptiles: An overview of patterns and orientation mechanisms in relation to life history strategies. In *Migration of Organisms*, pp. 151-203. Berlin/Heidelberg: Springer-Verlag.
- Salmon, M., Wyneken, J., Fritz, E. and Lucas, M.** (1992). Seafinding by hatchling sea turtles: role of brightness, silhouette and beach slope as orientation cues. *Behaviour* **122**, 56-77. doi:10.1163/156853992X00309
- Schlegel, P. A.** (2008). Magnetic and other non-visual orientation mechanisms in some cave and surface urodeles. *J. Ethol.* **26**, 347-359. doi:10.1007/s10164-007-0071-y
- Severtsov, A. S., Lyapkov, S. M. and Surova, G. S.** (1998). Comparative analysis of ecological niches of common frog (*Rana temporaria* L.) and moor frog (*Rana arvalis* Nilss.) (anura, amphibia). *J. Gen. Biol.* **59**, 279-301.
- Shakhparonov, V. V.** (2011). Patterns of Orientation Behavior in Marsh Frogs (*Rana ridibunda* Pall.) of Southern Populations. *Izv. Akad. Nauk Ser. Biol.* **38**, 614-618.
- Shakhparonov, V. V.** (2012). The influence of repeated experiments on the behavior of the marsh frog (*Rana ridibunda*) in field experiments of spatial orientation. *Zool. Zhurnal* **91**, 1340-1350.
- Shakhparonov, V. V. and Ogurtsov, S.** (2005). The role of the native pond odor in orientation of the green toad (*Bufo viridis* Laur.) young-of-the-year. *Herpetol. Petropolitana. Proc. 12th Ord. Gen. Meeting Soc. Eur. Herpetol.*, August 12-16, 2003, St Petersburg, Russia. *J. Herpetol.* **12**, Suppl., 209-212.
- Shakhparonov, V. V. and Ogurtsov, S. V.** (2008). Seasonal and geographical variability of orientation behavior in the marsh frog (*Rana ridibunda*) in search of its own water body. *Zool. Zhurnal* **87**, 1062-1076.
- Shakhparonov, V. V. and Ogurtsov, S. V.** (2017). Marsh frogs, *Pelophylax ridibundus*, determine migratory direction by magnetic field. *J. Comp. Physiol. A Neuroethol. Sensory, Neural, Behav. Physiol.* **203**, 35-43. doi:10.1007/s00359-016-1132-x
- Sinsch, U.** (1986). Migratory behaviour of the toad *Bufo bufo* within its home range and after displacement. In *4. O.G.M. Societas Europea Herpetologica*, pp. 361-364.
- Sinsch, U.** (1990). Migration and orientation in anuran amphibians. *Ethol. Ecol. Evol.* **2**, 65-79. doi:10.1080/08927014.1990.9525494
- Sinsch, U.** (2019). Amphibia: Orientation and Migration. In *Encyclopedia of Animal Behavior*, pp. 598-604. Elsevier.
- Smirina, E. M.** (1980). On growth rate and survival of common frogs (*Rana temporaria*) during the first years of life. *Zool. Zhurnal* **59**, 1831-1840.
- Stevens, J. C., Cain, W. S. and Burke, R. J.** (1988). Variability of olfactory thresholds. *Chem. Senses* **13**, 643-653. doi:10.1093/chemse/13.4.643
- Taylor, D. H. and Adler, K.** (1973). Spatial orientation by salamanders using plane-polarized light. *Science (80-)* **181**, 285-287. doi:10.1126/science.181.4096.285
- Taylor, D. H. and Ferguson, D. E.** (1969). Solar cues and shoreline learning in the southern cricket frog, *Acris gryllus*. *Herpetologica* **25**, 147-149.
- Thorup, K., Bisson, I.-A., Bowlin, M. S., Holland, R. A., Wingfield, J. C., Ramenofsky, M. and Wikelski, M.** (2007). Evidence for a navigational map stretching across the continental U.S. in a migratory songbird. *Proc. Natl. Acad. Sci. USA* **104**, 18115-18119. doi:10.1073/pnas.0704734104
- Thorup, K., Holland, R. A., Tøttrup, A. P. and Wikelski, M.** (2010). Understanding the migratory orientation program of birds: Extending laboratory studies to study free-flying migrants in a natural setting. *Integr. Comp. Biol.* **50**, 315-322. doi:10.1093/icb/icc065
- Timm, B. C., McGarigal, K. and Jenkins, C. L.** (2007). Emigration orientation of juvenile pond-breeding amphibians in Western Massachusetts. *Copeia* **2007**, 685-698. doi:10.1643/0045-8511(2007)2007[685:EOOJPA]2.0.CO;2
- Tracy, C. R.** (1971). Evidence for the use of celestial cues by dispersing immature California toads (*Bufo boreas*). *Copeia* **1971**, 145-147. doi:10.2307/1441608
- Vasconcelos, D. and Calhoun, A. J. K.** (2004). Movement patterns of adult and juvenile *Rana sylvatica* (LeConte) and *Ambystoma maculatum* (Shaw) in three restored seasonal pools in Maine. *J. Herpetol.* **38**, 551-561. doi:10.1670/157-03A
- Vasconcelos, D., Calhoun, A. J. K., Walston, L. J. and Mullin, S. J.** (2008). Variation in amount of surrounding forest habitat influences the initial orientation of juvenile amphibians emigrating from breeding ponds. *J. Herpetol.* **38**, 141-146.
- Wells, K. D.** (2007). *The Ecology and Behavior of Amphibians*. Chicago and London: The University of Chicago Press Chicago.
- Wiltshcko, R.** (2017). Navigation. *J. Comp. Physiol. A* **203**, 455-463. doi:10.1007/s00359-017-1160-1

Table S1. Results of all experiments conducted with froglets

Year	Date of capture	Date of release	Location of capture	Location of arena, side of the river	N of released	Number of check	Total N of recaptured*	N of Y-O-T-Y froglets**	Exact N***	Rayleigh Z;P	r (CSD)	μ (°)	N in first check	Rayleigh Z;P	r (CSD)	μ (°)	Wind direction
<i>Froglets from right side population, captured and released 14-17 days before start of migration</i>																	
2017	September 21	September 21	F1	left	45	4	48 ^a	45	45	3.07; 0.045	0.26 (93.9)	182	30	3.09; 0.044	0.32 (86.4)	202	N
2017	September 20	September 20	F1	right	39	4	39	39	39	24.08; <0.001	0.79 (39.8)	140	30	22.93; <0.001	0.87 (29.7)	137	Calm
2017	September 23	September 23	F1	right	45	4	33	33	33	24.47; <0.001	0.86 (31.3)	140	28	19.84 <0.001	0.84 (33.6)	143	Calm
2017 pooled sample			F1	right	84	4	72	72	72	48.45; <0.001	0.82 (36.1)	140	58	42.66 <0.001	0.86 (31.8)	140	---
<i>Froglets from right side population, captured and released 1-3 days before start of migration</i>																	
2016	September 18	September 18	F1	left	64	5	57	57	57	2.15; 0.12	0.19 (103.7)	---	28	0.23; 0.8	0.09 (125.9)	---	N
2016	September 19	September 19	F1	right	54	3	49 ^b	48	39	2.46; 0.085	0.25 (95.3)	---	16	2.06; 0.13	0.36 (82)	---	N
2017	October 5	October 5	F1	right	44	2	44	44	44	0.49; 0.62	0.11 (121.6)	---	27	0.99; 0.37	0.19 (104)	---	S
2018	September 20	September 20	F1	right	32	2	34	33	33	1.15; 0.32	0.19 (104.9)	---	28	0.68; 0.51	0.16 (110.6)		SW
2016+2017+2018, 1-3 days before migration, pooled sample			F1	right	130	2-3	127	125	116	2.55; 0.029	0.18 (107)	124	71	2.92 0.054	0.2 (102.3)	---	---
<i>Froglets from right side population, captured and released after start of migration</i>																	

2016	September 21	September 21	F1	left	84	4	77	77	76	4.5; 0.01	0.24 (96.3)	197	48	4.31; 0.01	0.3 (88.96)	194	Calm
2018	September 23	September 23	F1	right	64	3	59	57	56	2.29; 0.1	0.2 (102.4)	---	53	1.8; 0.17	0.18 (105.4)	---	WNW
2018	September 25	September 25	F1	right	36	2	29	29	29	1.46; 0.23	0.23 (99)	---	25	2.35; 0.095	0.31 (88.1)	---	W
2018, pooled sample			F1	right	100	2- 3	88	86	85	8.5; <0.001 ****	0.2 (102)	NW, SE	78	5.99 0.002 ****	0.22 (100.2)	N W, SE	
2018	September 20, 23, 25	September 28	F1	right (repeated release)	118	1	117	117	117	17.62; <0.001	0.39 (78.8)	298	-/-	-/-	-/-	-/-	WNW
2018	September 23	September 23	M	left	119	2	107	104	104	40.36; <0.001	0,62 (55,7)	13	101	42.84; <0.001	0,65 (53)	13	WNW
2018	September 26	September 26	M	right	101	3	98	89	89 ^c	25.01; <0.001	0,53 (64,6)	320	73	21.21; <0.001	0,54 (63,7)	328	NW
2015	October 1	October 1	R2	left	54	4	60	60	60	10,47; <0.001	0.42 (75.7)	354	37	11.1 <0.001	0.55 (62.9)	354	W
2016	September 20	September 20	R1	right	70	3	69	69	69	29.82; <0.001	0.66 (52.5)	337	36	17.85; <0.001	0.7 (47.9)	332	Calm
2016	September 20	September 20	R1	left	65	3	69	69	67	14.89; <0.001	0.47 (70.3)	319	47	16.1; <0.001	0.59 (59.3)	312	NW
2018	September 24	September 24	R1	right	70	2	70	70	68	22.56; <0.001	0.58 (60.2)	331	58	24.58 <0.001	0.65 (53.1)	329	WNW
2018	September 28	September 28	R1	left	69	3	66	64	63	16.73; <0.001	0.52 (65.9)	356	45	12.46; <0.001	0.53 (64.9)	358	NW
2015+2016+2018, pooled sample			R2 +R1	left	188	3	194	193	190	38; <0.001	0.45 (72.7)	343	137	32.66; <0.001	0.49 (68.6)	341	
2016+2018, pooled sample			R1	right	140	2- 3	139	139	137	52.01; <0.001	0.62 (56.4)	334	94	42.33; <0.001	0.67 (51.2)	330	

<i>Froglets from right side population, captured and released at night after start of migration</i>																	
2016	September 22	September 22	R1	left	48	2	48	47	29 ^d	7; <0.001	0.49 (68)	284	26	6.57; 0.001	0,5 (67.2)	286	Calm
2017	October 13	October 13	R1	left	45	2	44	39	36	10.86; <0.001	0.55 (62.7)	63	27	7.43; <0.001	0.53 (65)	65	W
2018	September 26	September 26	R1	left	65	2	62	57	54	14.21; <0.001	0.51 (66.2)	23	47	13.77; <0.001	0.54 (63.5)	27	W
2016	September 21	September 21	R1	right	51	3	53	53	53	6.5; 0.002	0.35 (82.9)	336	43	3.52; 0.029	0.29 (89.5)	341	Calm
2018	September 27	September 27	R1	right	70	2	69	60	57	25.9; <0.001	0.67 (50.9)	317	55	25.79; <0.001	0.69 (49.9)	317	Calm
2016+2017+2018, pooled sample			R1	left	158	2	154	143	119	13.84; <0.001	0.34 (84)	21	100	11.86; <0.001	0,34 (83.6)	20	
2016+2018, pooled sample			R1	right	121	2-3	122	113	110	28.82; <0.001	0.51 (66.3)	324	98	24.72; <0.001	0.5 (67.2)	323	Calm
<i>Froglets from left side population, captured and released after start of migration</i>																	
2017	October 7	found in arena A*****		left		1	46	42	42	8.79; <0.001	0.46 (71.7)	194	Only one check			---	
2017	October 7	October 8	arena A	right	42	2	44	42	42	10.71; <0.001	0.51 (66.9)	185	31	14.11; <0.001	0.68 (50.8)	175	Calm
2017	October 10	October 11	R3	left	50	4	46	44	44	17.73; <0.001	0.64 (54.62)	108	26	16.26; <0.001	0.79 (39.3)	107	SSW
2018	September 30	September 30	R3	left	31	3	31	28	28	14.64; <0.001	0.72 (46.1)	173	11	7.37; <0.001	0.82 (36.3)	170	W
2018	September 29	September 29	R3	right	82	4	77 ^c	68	68	27.9; <0.001	0.64 (54.1)	189	65	27.88; <0.001	0.66 (52.7)	190	Calm
2017+2018, pooled sample			R3	left	81	3-4	78	72	72	23.07; <0.001	0.57 (61.1)	134	37	18.26; <0.001	0.7 (48.2)	125	
<i>Froglets from right side population, captured before and released after start of migration (kept in captivity)</i>																	
2013	September 13-20	September 21	F2	right	65	3	63	63	63	16.86; <0.001	0.52 (65.78)	316	49	13.07; <0.001	0.52 (65.9)	312	N

2015	September 20-25	September 28	F1 & F2	left	69	3	63	63	63	14.99; <0.001	0.49 (68.6)	132	62	16.18; <0.001	0.51 (66.4)	132	WNW
<i>Froglets from right side population, captured and released after start of migration, but kept in captivity for 3 days before release</i>																	
2016	September 21	September 24	R1	right	58	3	57	56	55	12.78; <0.001	0.56 (61.7)	341	30	8.42; <0.001	0.53 (64.6)	1	Calm
2016	September 21	September 24	R1	left	59	3	54	54	51	18.81; <0.001	0.61 (57.2)	350	16	9.93; <0.001	0.79 (39.5)	354	Calm

Notes: F, captured in forest; M, captured in the meadow; R, captured at the river bank near water.

μ , mean vector or compass directions (e.g. N for North, SW for Southwest, NNE for North-North-East, etc.); r, length of mean vector; CSD, circular standard deviation in degrees; significant differences are highlighted in bold.

* Total number of recaptured froglets, includes individuals with body length >38 mm and froglets recaptured inside the arena outside of the groove with traps.

** Total number of recaptured young-of-the-year froglets with body length \leq 38 mm includes individuals recaptured inside the arena outside of the groove with traps.

*** Number of froglets with body length \leq 38 mm and recaptured only in traps. These specimens were included in further analysis.

**** Since we suspected a bimodal distribution, the Rayleigh test was used after the doubling the angles procedure (Batschelet 1981).

***** Froglets that were found in the traps of arena A (left side of the river) after arena wall was broken by the wind; these froglets correspond to those caught in the meadow.

^a three of two-year-old specimens from left side population were captured.

^b Nine specimens were captured near the center.

^c A large number of two-year-old specimens were captured.

^d The majority of the froglets was found outside of traps.

Table S2. Survey of potential hibernation sites of the froglets in winter and spring of 2019

Site	Environmental remarks	Result of revisions
Bardinskii gully (capture site F1)	The slopes and bottom of the gully are formed by soft and moist soil that did not freeze during the winter under snow (January 25, the temperature dropped to -26°C) and was inhabited by insect larvae. Notably, the number of froglets in the gully, where they apparently come to eat, increases 2 weeks before the start of migration.	On April 6 (snow did not melt completely), we found two young froglets in the ground at approximately 10 cm depth; they were very inactive and most likely spent the winter there. No adult specimens were found. Like Bannikov (Bannikov, 1940), we interpret these young individuals as the specimens "late" for migration into the river before the final temperature drop. This delay can be associated with accumulation of fat essential for the hibernation. Such correlation between the start of migration and storing fat was observed in birds (Dolnik and Blyumental, 1967; King and Farner, 1963; Sandberg, 2003). Assembling in humid places before migration makes it possible for "late" frogs to survive the winter by burrowing into moist soil, where the temperature would not drop below zero due to the decay processes.
Stream in the Bardinskii gully	The stream had running water under ice even after severe frosts (-26°C); during five surveys (January-March),	We were unable to find young-of-the-year common frogs. However, the wintering in general is possible, since on March 30 (snow did not melt), a young-of-the-year common toad and numerous live insect larvae were found in soil of the bottom of the stream (12 cm depth).
Moskva River	The ice on the Moskva River broke up in late March.	on April 6, the first adult frogs appeared on the river bank opposite of the pond 4 and traveled in its direction; on April 9, we found the first froglets (approx. a dozen specimens) emerging from the river and moving towards the forest.
Ponds		We found no froglets emerging from the ponds.