Polar Biol
DOI 10.1007/s00300-016-1916-z

ORIGINAL PAPER

How the most northern lizard, *Zootoca vivipara*, overwinters in Siberia

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Received: 13 February 2015 / Revised: 7 January 2016 / Accepted: 27 February 2016

Abstract The common lizard *Zootoca vivipara* has the largest range of all the terrestrial reptiles which includes the subarctic regions of the Palaearctic. The species provides a unique model for studying the strategies of adaptation of a reptile to extreme low winter temperatures. The aim of our research was to determine whether this species survives the severe winters of Siberia, including Yakutia, due to its exceptional cold hardiness or due to wintering in abnormally warm places. The cold hardiness limit of lizards from the southeast of Western Siberia was lower than in conspecific European populations (−4 °C) and was the record low for all adult reptiles. In dry substrate (water content 13–14 %), 21 % of lizards survived at temperatures from −3 to −10 °C, but in wet substrate (70–80 %) none of them survived even at slightly below-zero temperatures. The survivors remained in a supercooled state until the temperature dropped to about −3 °C, and then they froze and could remain frozen for over 2 months. In most biotopes examined in the southeast of Western Siberia, soil temperatures at the depth of the lizard hibernacula (5–13 cm) were higher than −10 °C. Despite very cold air, similar winter soil temperatures were recorded in the warmest lizard habitats in Yakutia, due to the soil-heating effect of unfrozen groundwater in talik zones. Thus, extensive distribution of the common lizard in Yakutia is determined not only by its exceptional cold hardiness but also by specific hydrogeological conditions maintaining winter soil temperatures above its tolerance limit.

Keywords Cold hardiness · Hibernacula · Range · Yakutia · Talik zones

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Introduction

The common lizard *Zootoca vivipara* (Lichtenstein, 1823) is a small (body mass 2–8 g) ground-dwelling lizard. Among terrestrial reptiles, the common lizard has the largest and the most northern range. In the coverage of natural zones and the degree of expansion into the Subarctic, this lizard is similar to such northern amphibians as the North American wood frog *Lithobates sylvaticus* (*Rana sylvatica*) and the Siberian salamander *Salamandrella keyserlingii*, known for their extraordinary adaptations to cold climate including cold hardiness (Martof and Humphries 1959; Berman et al. 1984; Berman and Meshcheryakova 2012; Costanzo et al. 2013; Bulakhova and Berman 2014). The common lizard thus offers a unique possibility of studying the limits of adaptations of reptiles, and poikilothermic vertebrates in general, to extremely low winter temperatures.

In the north of Europe, with its abundant snow cover and the warming influence of the Atlantic, the common lizard can be routinely found north of the Arctic Circle. It is also widely distributed in the cold regions of Asia, including Yakutia where the species reaches 70°48′N (Borkin et al. 1984), even though the territory is famous for its severe winters. Such an extensive northern distribution, especially in the Asian part of the range, may reflect either considerable cold hardiness of the species, or a tendency to hibernate in places with exceptionally warm microclimates. Only a few findings of common lizards hibernating in natural habitats have been documented, nearly all the reports being accidental. The descriptions of the hibernacula are contradictory: According to some authors, lizards overwinter in soil at shallow depths (10–15 cm) or even at the soil surface, under the litter or in some shelters (Teplova 1957; Grenot and Heulin 1988; Tabachishin et al. 2000; Bulakhova et al. 2011); according to other reports, lizards find places where the temperature does not drop below the freezing point of their body fluids, i.e., about 40 cm deep in soil (Borkin et al. 1984; Vershinin 2007). Besides, hibernacula were reported to occur deeper in colder regions, for example, in the mountains as compared to plains (Grenot et al. 1996). However, no special study of common lizards hibernating in their natural habitats has been attempted before.

Little is known about their tolerance to negative temperatures. Field and laboratory studies performed in the European part of the species range have shown that the low-temperature tolerance limit of the common lizard lies in the range of −2.5 to −4 °C (Vasiliev and Osmolovskaya 1989; Costanzo et al. 1995; Voituron et al. 2002, 2004).

Soil temperatures at the assumed depths of hibernation in the greatest part of the species range can be estimated from the data provided by the weather station network of the Russian Federal Service for Hydrometeorology and Environmental Monitoring (Roshydromet). However, weather stations are generally scarce in the northern underdeveloped regions of Russia, and not all of them monitor soil temperatures at shallow depths in winter.

Judging by the pattern of minimum soil isotherms, in the western parts of the species range within the territory of Russia the soil remains warm enough even at a depth of 3 cm (Alfimov 2005), due to both relatively high air temperatures and the early formation of abundant snow cover. The wintering conditions change for the worse in the eastern direction, as the continentality of the climate increases, and become the most severe in Yakutia where temperatures of the upper 20 cm of soil may drop below −20 °C, due to cold air and thin snow cover (Izyumenko 1966, 1968). It is unknown how lizards overwinter under such conditions, given the cold hardiness limit of mere −2.5 to −4 °C determined for the European populations.

In view of the above, the territory of Sakha (Yakutia) Republic would certainly be the most suitable for studying the position and microclimatic parameters of hibernacula, the cold hardiness of lizards, and the effect of temperature conditions on their distribution. Since *Z. vivipara* is not only widespread but also locally abundant in this territory, which is one of the coldest regions of the Palaearctic as far as the winter temperatures are concerned, the lizards inhabiting it would probably be the most cold-tolerant. Moreover, there is a detailed list of known locations of the species for the entire territory of Sakha Republic (Borkin et al. 1984), and the network of weather stations monitoring winter soil temperatures is quite extensive there, which would make it easier to determine the relations between cold hardiness and distribution of the common lizard. However, *Z. vivipara* is listed as endangered in the Red Book of Sakha Republic, and collection of these lizards is prohibited there even for research purposes. Therefore, in two regions of Sakha Republic (the environs of Olyokminsk, southwestern Yakutia and the environs of Abyi, northeastern Yakutia) we only studied the biotopic distribution of the species and the soil temperatures in the possible wintering habitats. The main part of our work was carried out in the southeast of Western Siberia, where the winter conditions are much more severe than in Europe but milder than in Yakutia, and where the common lizard is quite abundant. There we collected lizards for cold tolerance experiments, located their hibernacula, and measured the winter temperatures in them.

The goal of this research was to determine whether common lizards inhabiting Siberia have an exceptional level of cold hardiness (similar to that in the Siberian salamander) or overwinter in abnormally warm places.

To solve this problem, the following specific tasks were set:

- to locate hibernacula of the common lizard in its natural habitats in Siberia;
- to describe the temperature conditions at the hibernation sites during the cold season;
- to determine the parameters of cold hardiness which allow the common lizard to overwinter successfully even in the coldest regions of Northern Asia;
- to describe the possible relation between cold hardiness and geographic distribution of the species.

Materials and methods

Cold tolerance experiments

Acclimation

For cold hardiness experiments, we used lizards over 1 year old, with body mass 1.2–5.6 g ($n = 121$), collected in the environs of Tomsk (southeast of Western Siberia, 56°28′N, 84°52′E) during the second half of August 2005–2010. Until the beginning of September, we kept the lizards in laboratory terrariums at room temperature (18–22 °C) in groups of 7–10 individuals of the same sex and age. The lizards were heated with 40 W light bulbs for 3–5 h every day and fed with mealworms, small cockroaches, and various insects from their natural habitats. At the beginning of September, we transferred the animals to the Laboratory of Biocenology, Institute of Biological Problems of the North (Far East Branch of Russian Academy of Sciences, Magadan), where the necessary equipment was installed. In September, additional heating was stopped and the temperature in the terrariums was kept at about 15 °C. In the second half of September, we placed the lizards singly or in pairs in 200-ml plastic containers 4 cm high, with small ventilation openings. The containers were filled with substrate taken from the lizard habitats, which consisted of a bottom layer of sandy loam soil 1.5 cm thick and a top layer of leaf litter, also 1.5 cm thick, so that approximately 1.5 cm of free space remained under the lid. During acclimation and experiments, the lizards could either burrow into the preferred substrate layer or remain on the surface.

Lizards were acclimated in TSO 1/80 SPU temperature-controlled chambers by reducing the temperature stepwise: 4 days at 10 °C and 7 days at 5 °C. Then the containers were placed in a WT 64/75 programmable temperature test chamber (Weiss Umwelttechnik GmbH) and kept there at 1 °C, 0 °C, and −1 °C (7 days at each temperature).

Determination of the temperature tolerance threshold

After acclimation, we tested the lizards at different temperatures, with the duration of exposure varying from 1 to 34 days (Table 1). Each stage of the experiment started only after obtaining the results for the preceding temperature step. The group of lizards exposed to a given temperature included the actual test sample plus all the lizards earmarked for testing at lower temperatures; therefore, the total duration of exposure and the sample size could be considerable. For example, the lizards earmarked for the planned (but not realized) testing at temperatures lower than −12 °C were kept at −10 °C and then used for testing at −10 and −12 °C.

At a temperature of −3 °C, close to the supercooling point (SCP—temperature at which ice crystallization or spontaneous freezing starts in a supercooled system, see Block 1995), the test duration was increased to 3 days for clearer differentiation between the frozen and supercooled individuals. At the minimum survivable temperature of −10 °C, lizards were kept for different periods of time to determine whether the duration of cold exposure affected the survival rate.

The cooling rate was 0.1 °C h^{-1}, which did not exceed the highest cooling rate recorded in the upper 40-cm soil layer in all the biotopes studied (see “Results”).

In addition to the built-in sensors, the temperature in the Weiss WT 64/75 chamber was additionally monitored by autonomous DS1922L iButton temperature loggers installed directly inside the containers with lizards.

The state of the lizards (frozen or supercooled) was identified by the color of their skin and the stiffness of their bodies, legs, and tails. For the lizards located within the substrate layer, these characters were assessed by gently moving some of the covering substrate aside and replacing it afterward, or by observing the lizards through the transparent walls of the container.

After exposure to the test temperature, lizards were warmed to 1–3 °C in the Weiss WT 64/75 chamber, at a rate of 0.06 °C h^{-1}. The surviving lizards started to show vital signs already at 0 °C: They resumed respiratory movements and tried to turn over when placed on their backs, but did not open their eyes. As a rule, the individuals that failed to show such signs at 0 °C did not revive after further warming. Such lizards were kept until the appearance of clear signs of death, such as necrotic spots and sunken eyes.

To assess the effect of substrate humidity on hibernation, we performed the experiments in two variants with different levels of soil water content: “wet” (70–80 %, 32 lizards tested) and “dry” (13–14 %, 89 lizards tested).

Repeated freezing of some of the surviving lizards was also attempted. One lizard previously frozen to −6 °C for 6 days and two lizards previously frozen to −8 °C for 20 days were not warmed above 1 °C but immediately

Table 1 Regimes of stepwise cooling of *Z. vivipara* during determination of the temperature tolerance thresholds (“wet”/”dry” substrate)

T (°C) tested	Duration of exposure (days) at the intermediate and final temperatures (°C)					
	−3	−4	−6	−8	−10	−12
−3	1/3	–	–	–	–	–
−4	3	1/3	–	–	–	–
−6	3	3	1/1.5 (14)*; 6 (11)	–	–	–
−8	3	3	6	1/1.5 (4); 6 (3); 20 (4)	–	–
−10	3	3	6	20	1/1.5 (7); 8 (8); 19 (8); 34 (9)	–
−12	3	3	6	20	34	1/1.5

* The size of samples for series with varying duration of cooling is given in parentheses; the size of samples for other series is given in Table 2

cooled again at a rate of 0.01 °C h^{-1} to −10 °C, at which temperature they were kept for 1.5 days.

Determination of the supercooling point (SCP)

The supercooling point (SCP) was determined in two series of experiments using different equipment: a DAQ multichannel logger (Fourier Systems Ltd.) and manganin–constantan thermocouples. In the first series, the flat sensors of the DAQ logger were fixed with heat insulating band on the bodies of four lizards (Fig. 1a) which were cooled in containers with dry substrate (water content 13–14 %). The containers, substrate composition, and temperature regimes of acclimation, freezing, and warming in a WT 64/75 test chamber were the same as those used for determination of the temperature tolerance threshold (see the corresponding section).

The second series of experiments was designed to eliminate the possible influence of the substrate on the SCP. The lizards were cooled in a specially built test chamber providing for fine adjustment of the cooling rate. The SCP values were measured with manganin–constantan thermocouples, digitized with an ADC, and recorded on a computer. After acclimation to 0 °C, six lizards were placed singly in conical glass centrifuge tubes 15 cm long and 2 cm in diameter, with plastic foam stoppers and thermocouples inserted in such a way that the thermojunction was positioned close to the lizard body (Fig. 1b). The tubes were placed in a thick-walled aluminum container filled with fine haydite to reduce the possible temperature fluctuations. The temperature inside the test chamber was maintained and monitored by a special control unit, and that inside the container was additionally monitored by autonomous DS1922L iButton temperature loggers. We cooled the animals at a rate of 0.75–1.5 °C h^{-1} until the SCP was reached, kept them at the SCP temperature for 12 h, and then warmed them at a rate of 2.5 °C h^{-1}.

In the cold tolerance experiments, we tried to imitate the wintering conditions in natural biotopes by keeping the lizards on the natural substrate and using the water content levels close to the natural ones and the cooling rates not exceeding the maximum rates recorded in the natural lizard habitats. The authors who earlier studied the tolerance of common lizards to negative temperatures carried out their research either in the field (Vasiliev and Osmolovskaya 1989; Grenot et al. 1996, 1999, 2000) or in model environments: in tubes containing damp or dry absorbent paper pads, plastic foam, or pulverized ice (Costanzo et al. 1995; Voituron et al. 2002, 2004).

Hibernation sites

The actual hibernation sites of the common lizard were studied in a cleared strip in a pine forest near Timiryazevskii (environs of Tomsk, 56°28′N, 84°52′E), where the lizards were numerous in summer. In the falls of 2009 and 2010, we thoroughly examined a land plot of about 1000 m^2 looking for lizards hibernating on the soil surface and in the litter. At the end of April 2010, we monitored the emergence of the first active lizards and determined the soil thawing depth with a graduated probing rod in a small thawed patch completely surrounded with snow. We marked the spots of emergence of the overwintered lizards, and in October 2010, we excavated them to study the exact location of the hibernating lizards. Besides the environs of Tomsk, we also studied the biotopic distribution of lizards in the environs of Podgornoe (57°47′N, 82°39′E), southeast of Western Siberia, in September 2009, in the environs of Olyokminsk (60°23′N, 120°26′E), southwest Yakutia, in July 2009, and in the environs of Abyi (68°23′N, 145°04′E), northeast Yakutia, in August 2012.

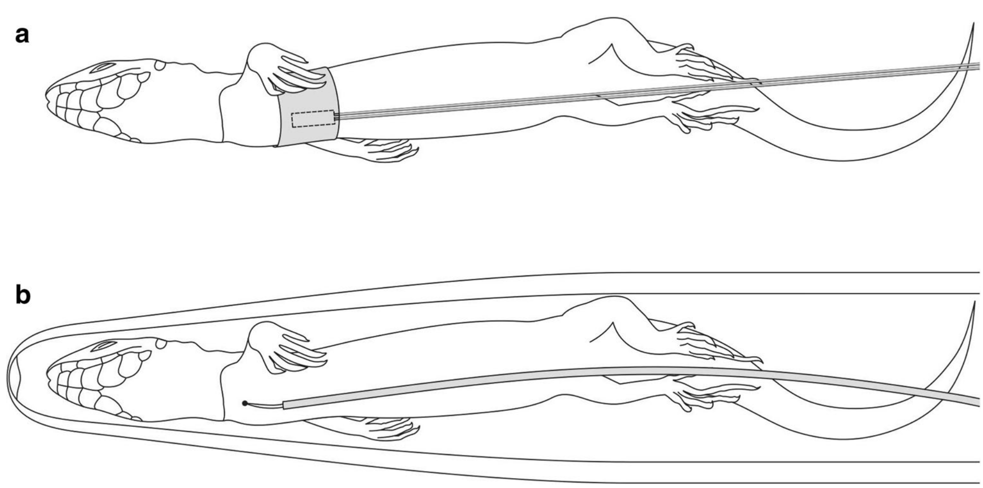

Fig. 1 Position of sensors on the lizard bodies during experimental determination of the supercooling point (SCP) using DAQ multi-channel loggers (**a**) and manganin–constantan thermocouples (**b**)

Soil water content in the immediate vicinity of hibernating lizards in the environs of Tomsk was determined by a standard method: Soil samples were collected in weighing bottles and dried to constant weight, and water content (%) was calculated based on the weight difference between the intact and dried sample.

The temperature conditions of hibernation

The temperature conditions of hibernation of the common lizard were studied in the southeast of Western Siberia: in the environs of Tomsk in 2006–2008 and in the environs of Podgornoe in 2009–2010, and in Yakutia: in the southwest (the environs of Olyokminsk) in 2009–2010 and in the northeast (the environs of Abyi) in 2012–2013. We recorded soil temperatures 2–8 times a day from September to May with DS1922L iButton temperature loggers (accurate to ±0.5 °C).

In the environs of Tomsk, we measured temperatures in 11 sites on the soil surface under grass cover, under small woody fragments, in rotten logs, and in the soil at different depths (0, 5, 15, 25 cm) in the habitats where lizards were the most abundant in summer (Fig. 2). In the environs of Olyokminsk and Podgornoe, we measured temperatures not only in the typical summer lizard habitats but also in the most common forest and meadow biotopes within different landscape elements, in order to obtain a general picture of the temperature patterns in the possible hibernation sites. In the environs of Olyokminsk, we installed loggers at seven sites: in meadows varying in humidity, at the edge of a small-leaved forest, on the side of a forest road, on a river terrace slope, in an overgrown clearing, and under the brushwood, at depths of 5, 20, and 40 cm. In the environs of Podgornoe, measurements were carried out at 17 sites: in meadows, at the edge of small-leaved, mixed and coniferous forests, in various microrelief elements, and on water banks, at depths of 0–1, 10, and 20 cm.

Fig. 2 Cleared strip in a pine forest in the environs of Tomsk where the wintering conditions of the common lizard were studied

In the environs of Abyi, we measured temperatures at six sites (in the most common biotopes within different landscape elements): in meadows varying in humidity, on water banks, and at the edge of a small-leaved forest. Since the loggers were installed at depths of 20 and 40 cm, which are the standard depths used by weather stations, our results could be compared with the long-term monitoring data.

According to the nearest weather station data, no unusual deviations from the long-term mean climatic parameters and soil temperatures were recorded in the years of our work in the above localities. Therefore, we could compare the observed values with the long-term means (Izyumenko 1966).

Results

Cold hardiness

As the temperature in the containers dropped to 5–3 °C, some lizards moved into the soil layer, some positioned themselves under the litter layer, and some, on its surface. When we tried to cover the exposed lizards with soil or dry leaves, they moved back onto the surface. At a temperature of −1 °C, the both the wet and the dry substrates froze and were covered with ice crystals.

No temperature gradients were observed inside the containers after several hours of exposure to a certain temperature, whereas the temperature in the Weiss WT 64/75 chamber strictly followed the preset pattern. Thus, it can be stated that the lizards were cooled at the specified rate and reached the specified temperatures. In the wet substrate (70–80 %), all the animals ($n = 32$) froze already after 24 h of exposure to a temperature of about −1 °C. Their bodies became rigid, and their skin acquired a bluish tint that was especially distinct on the throat and sides and was preserved after thawing (Fig. 3). All these lizards perished (Table 2).

Examination of the containers with lizards in the dry substrate (13–14 %) showed that 54 out of 89 animals were in a supercooled state at −3 °C. Such lizards could be distinguished from the frozen ones by the preserved natural coloration (without a bluish tint) and the ability to slightly change the position of the body, legs, and tail. As the temperature dropped below −3 °C, all of them froze and turned bluish, but the surviving individuals restored their natural color immediately after warming (Fig. 3). The actual share of lizards which froze in the dry substrate within the temperature interval from −1 to −3 °C may be greater than the recorded one (35 out of 89 ind.), since such

Fig. 3 Typical position of the body and coloration of integuments of living and dead wintering lizards. The surviving individuals restored their natural color immediately after thawing (*left*); the bluish tint of the dead animals persisted after thawing (*right*)

Table 2 Survival of *Z. vivipara* at different temperatures

T (°C)	Wet substrate			Dry substrate				
	Total number of ind. used	Number of ind. supercooled at −3 °C	Survived, ind.	Total number of ind. used	Number of ind. supercooled at −3 °C	Survived		
						Number of ind.	% of total number	% of supercooled ind.
−1	5	0	0	0	–	–	–	–
−3	4	0	0	5	2	2	40.0	100.0
−4	3	0	0	2	2	1	50.0	50.0
−6	6	0	0	25	16	8	32.0	50.0
−8	5	0	0	11	7	2	18.2	28.6
−10	7	0	0	32	19	3	9.4	15.8
−12	2	0	0	14	8	0	0	0

signs of freezing as changes in the body coloration probably took a certain time to develop. Correspondingly, the fraction of survivors among the supercooled lizards may be underestimated.

Almost one-third of these lizards ($n = 16$) survived the experiments. During warming, they showed vital signs already at temperatures slightly above zero (1–3 °C). The rest of the lizards (35 out of 89 ind.) froze at a temperature of about −1 °C in the same manner as those in the wet substrate; none of them revived when warmed.

The results of cooling were sometimes different for lizards cooled together in the same container, i.e., under identical conditions: One individual froze at about −1 °C, whereas the other remained in a supercooled state until −3 °C and froze during further cooling.

The mean SCP of lizards in the dry substrate, measured by flat sensors of the DAQ multi-channel logger, was -2.7 ± 0.1 °C ($n = 4$, range −2.6 to −3.1 °C). The mean SCP value measured by thermocouples (in conical glass centrifuge tubes without substrate) was -3.2 ± 0.1 °C ($n = 6$, range −2.8 to −3.6 °C). Although the mean SCP values obtained in two experiments were somewhat different, their ranges overlapped. The higher values obtained in the first experiment may be related to the possible influence of the substrate or the cooling rates.

Five out of six tested lizards died within 12 h of exposure to supercooling temperatures. The SCP of the survivor was −3.1 °C, which indicated the ability of the common lizard to endure freezing.

The minimum temperature endured by lizards was −10 °C (Table 2), at which they were kept for 1.5, 8, 19, and 34 days. A single individual survived in each variant except that with 8 days of exposure.

The longest time spent by the surviving lizard in a supercooled state (at temperatures above the SCP) was 13 days; the maximum duration of existence in a frozen state (below the SCP) was 67 days.

In the experiment with repeated freezing to −10°, one lizard survived which had been previously frozen to −8 °C. The other two lizards, which endured freezing to −6 °C at the first stage of the experiment, died at the second.

All the surviving lizards were kept in the laboratory for several months after the experiments, which proved the absence of any delayed lethal effects.

Hibernation sites

In the fall of 2009–2010, we thoroughly examined the soil surface in a plot of about 1000 m^2 in the environs of Tomsk, in the biotope where lizards were numerous in summer, but could not find any hibernating lizards in the litter or under various objects. On April 26, 2010, we recorded the first active lizards (seven adult males) in a small thawed patch of about 30 m^2, completely surrounded with snow 25–50 cm thick. The thawed patch was located on the periphery of a meadow with sparse coppice of birch, aspen, and pine, adjoining a small thawed segment of a forest road. The patch contained no tree stumps, snags, fallen twigs, or similar plant remains which could serve as epigeic hibernacula. By the date of the observation, the soil had thawed to no more than 15 cm in the meadow and to 30 cm on the sandy roadside bank. We could therefore assume that lizards in this particular habitat hibernated in soil at depths no greater than 30 cm.

Fig. 4 Half of the hibernating lizards in the environs of Tomsk was found in the empty burrows of the dung beetle (*A. stercorosus*)

We marked the boundaries of this thawed patch, and after the end of the lizards' active season in the fall of the same year, we excavated about 65 m^2 of this patch to a depth of 30 cm. As a result, we discovered seven hibernacula containing eight mature males of *Z. vivipara* in exactly the same area where the first emerging lizards had been observed on April 26. Two more hibernacula containing two immature lizards were discovered on the opposite end of the meadow.

The hibernacula were situated 0.8–9 m apart. The lizards in them were found at depths varying from 5–6 to 13 cm. We did not find any lizards in the sandy roadside bank which thawed to the greatest depth (30 cm) in spring. Half of the hibernating lizards occupied empty burrows of the dung beetle *Anoplotrupes stercorosus* Scriba, 1791, which was a common insect in the area (Fig. 4). The burrows were shaped as almost vertical tunnels up to 30 cm long and 1–1.5 cm in diameter. The lizards were positioned in them 5–10 cm from the soil surface, with their heads up and the tail curled around the trunk, or with the end of the tail coiled around its basal portion. Besides, we found two lizards inside a rotten birch (*Betula pendula*) root less than 1.5 cm in diameter, buried about 13 cm deep in soil; two more, in narrow soil fissures along the aspen (*Populus tremula*) and pine (*Pinus sylvestris*) roots, at a depth of 7–10 cm; and one, inside a tussock of moss (*Polytrichum*), cowberry (*Vaccinium vitis-idaea*) and sedge (*Carex*) at a depth of 7–8 cm below the surface. The mean water content of the soil near the hibernating lizards was 15.1 ± 0.6 % ($n = 16$, range 11.5–18.4 %), and the soil temperature was 4.1–6.1 °C.

Temperature conditions of wintering

Before the snow cover formation in fall, the greatest daily temperature variation (from 0.7 to −3.9 °C) within the hibernation plot in the environs of Tomsk was observed on the soil surface and in small epigeic shelters (under litter, grass tufts, bark, and board fragments). The transition from fall to winter (i.e., from positive to stably negative temperatures) took no less than 5 days at the surface level, which was also characterized by the highest rates of temperature change (up to 1.2 °C h^{-1} in fall and up to 0.3 °C h^{-1} after the snow cover formation). The thermal

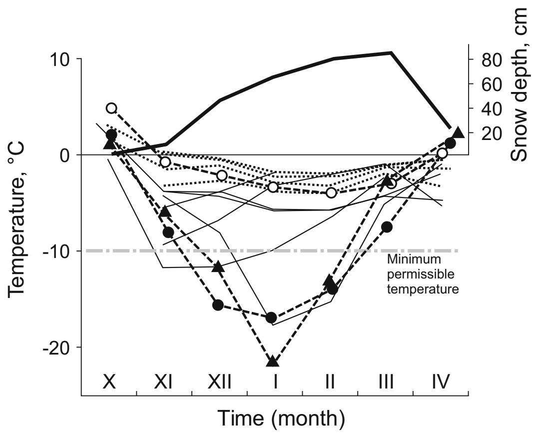

Fig. 5 Seasonal dynamics of snow cover thickness and minimum soil temperatures in habitats of the common lizard *Z. vivipara* in the environs of Tomsk (southeast of Western Siberia) in the winter of 2007–2008 (*dotted lines* at the hibernation sites). The long-term mean temperatures: Air (*filled circles*), soil at a depth of 20 cm (*empty circles*), and the mean air temperatures for the period of observations (*triangles*) are based on data of Tomsk weather station

regime in the soil, even at a small depth (5 cm), was milder, with transition from positive to negative temperatures occurring within 1–1.5 days and the rate of temperature change not exceeding 0.1 °C h^{-1}. At the beginning of winter, negative temperatures at a depth of 15 cm were recorded 6–7 days later than at a depth of 5 cm.

According to the Tomsk weather station data, the soil temperatures of the coldest month (January) are formed under the following conditions: the mean air temperature of −19.3 °C (the mean absolute minimum being −41 °C) and the mean snow thickness of 49 cm. As a result, the long-term mean January soil temperature at a depth of 20 cm is −3.1 °C (Pahknevich 1965; Kukharskaya 1969). Soil temperatures in the lizard habitats varied widely (Fig. 5). The minimum temperatures in areas with a thin snow cover were low (−11.7 to −17.9 °C) even at depths of 15–20 cm. Somewhat higher values were recorded in the litter and in epigeic shelters, but they were still much lower than those recorded in the European part of the species range (Vasiliev and Osmolovskaya 1989; Grenot et al. 1996). The minimum soil temperatures at depths of 5–15 cm varied from −1.9 to

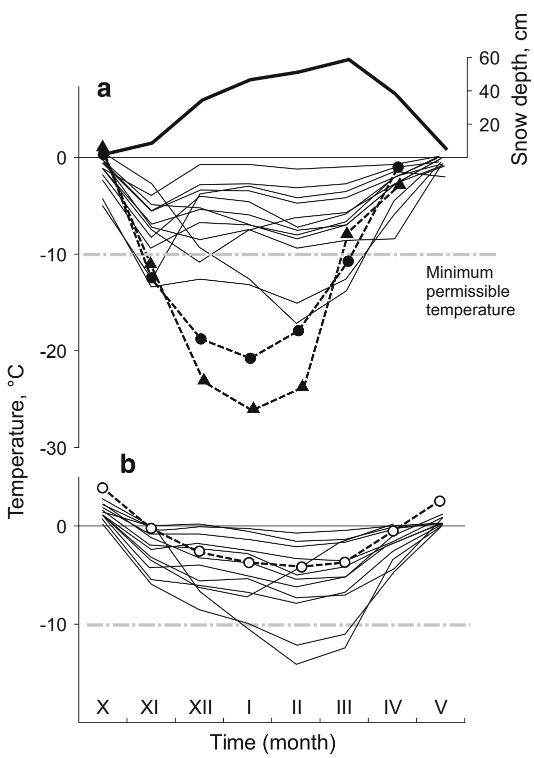

Fig. 6 Seasonal dynamics of snow cover thickness and minimum soil temperatures at a depth of 2 cm (**a**) and 20 cm (**b**) in 12 common lizard habitats in the environs of Podgornoe (southeast of Western Siberia) in the winter of 2009–2010. The long-term mean temperatures: Air (*filled circles*), soil at a depth of 20 cm (*empty circles*), and the mean air temperatures for the period of observations (*triangles*) are based on data of Podgornoe weather station

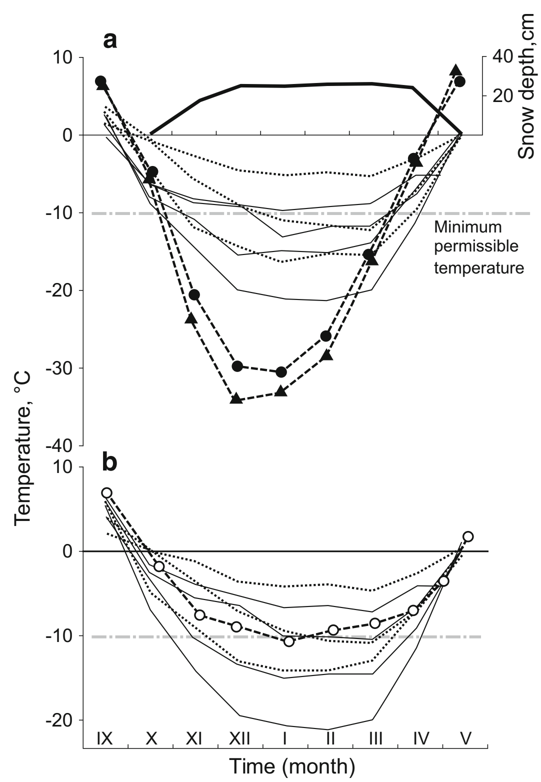

Fig. 7 Seasonal dynamics of snow cover thickness and minimum soil temperatures at a depth of 2 cm (**a**) and 20 cm (**b**) in seven biotopes in the environs of Olyokminsk (southwest of Yakutia) in the winter of 2009–2010 (*dotted lines* in the lizard habitats). The long-term mean temperatures: Air (*filled circles*), soil at a depth of 20 cm (*empty circles*), and the mean air temperatures for the period of observations (*triangles*) are based on data of Olyokminsk weather station

−5.8 °C in different areas. In some hibernation sites, the lowest temperatures were recorded in late fall—early winter, in others, in the middle of winter, depending on the thickness and dates of formation of the snow cover and the intensity of frost. The number of frost days was 170–176 days, only slightly varying among the studied localities.

In the environs of Podgornoe, 300 km NW of Tomsk, the minimum air temperatures in the winter of 2009–2010 were close to the long-term mean, but the snow cover was 7–10 cm thicker than average. Correspondingly, the minimum soil temperatures recorded by us (Fig. 6) deviated by 1–2 °C from the long-term means (Shulgin 1972). The minimum temperatures at a depth of 20 cm were found to be lower than −10 °C only in two of all the biotopes studied in this region (Fig. 6).

In the environs of Olyokminsk, southwestern Yakutia, lizards occurred in undisturbed and mown meadows on the Lena river terrace, in an abandoned holiday village, and on the sides of forest roads, i.e., they occupied essentially the same biotopes as in Western Siberia. The highest winter soil temperatures at a depth of 20 cm were recorded there in the so-called talik zones with non-freezing ground waters “heating” the soil (Yershov 1998). The minimum temperatures in the talik zones did not drop below −4.5 °C, whereas in the nearby permafrost areas they were as low as −15.0 °C (Fig. 7). It should be noted that these data were obtained during a relatively severe winter, when the temperatures of November and February were 3 °C lower than the long-term means.

In northeastern Yakutia, there are two isolated localities of the common lizard positioned far to the north of its main range (Fig. 8): the northernmost Asian locality, near

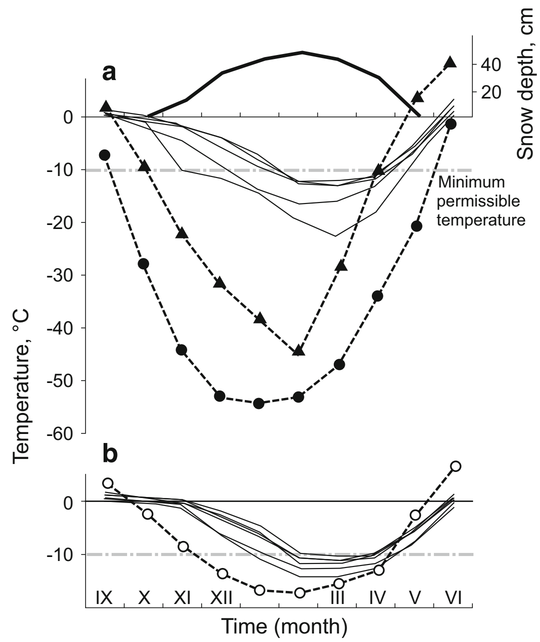

Fig. 9 Seasonal dynamics of snow cover thickness and minimum soil temperatures at a depth of 5 cm (**a**) and 20 cm (**b**) in six biotopes in the environs of Abyi (northeast of Yakutia) in the winter of 2012–2013. The long-term mean temperatures: Air (*filled circles*), soil at a depth of 20 cm (*empty circles*), and the mean air temperatures for the period of observations (*triangles*) are based on data of Belaya Gora weather station

Khaiyr (70°48′N, 133°30′E) and the easternmost one, near Abyi (68°23′N, 145°04′E) (Borkin et al. 1984). We did not find any lizards in the examined environs of Abyi, although local residents showed us the places where lizards had occurred recently. According to the logger data, the winter

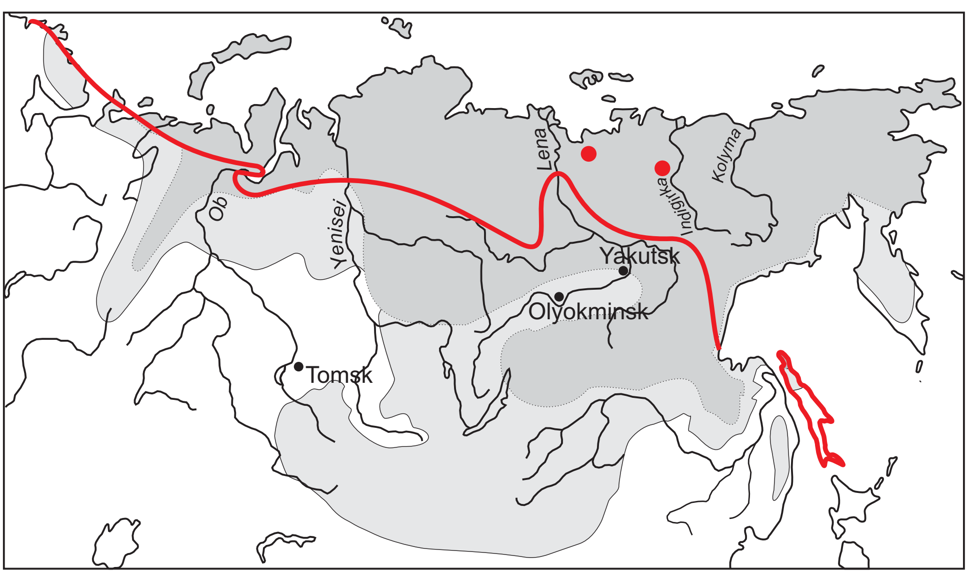

Fig. 8 Northern boundary of *Z. vivipara* range (*line*) and the permafrost area (*dark color fill* continuous permafrost, *light* insular permafrost) in Northern Eurasia. *Points* the northernmost findings of *Z. vivipara* near the settlements of Abyi and Khaiyr

temperatures of the upper soil layer (20 cm) in this locality were quite high (Fig. 9), though somewhat lower than the threshold level of −10 °C.

The soil freezing rate at a depth of 20 cm in late fall and early winter may be zero in case of high water content. The freezing rate of drier soil with few large organic inclusions may be much higher, up to 0.1 °C h^{-1}. This value was observed at depths of 2–40 cm in the lizard habitats in the environs of Tomsk, Podgornoe and Olyokminsk. The mean rate of soil freezing (from 0 °C to the minimum recorded at each site) varied between the studied biotopes: In Tomsk and Podgornoe, it was about 0.0017 °C h^{-1} at the surface, about 0.0013 °C h^{-1} at a depth of 20 cm, and about 0.0009 °C h^{-1} at 40 cm, and in Olyokminsk, 0.0069, 0.0064, and 0.0043 °C h^{-1}, respectively.

Discussion

Tolerance to sub-zero temperatures

The cold hardiness of common lizards from the southeast of Western Siberia was estimated at −10 °C; this is the record value for adult reptiles (see Storey 2006; Costanzo and Lee 2013). The temperature limit of lizards from the populations of Western Europe (Voituron et al. 2002, 2004) and Moscow region (Vasiliev and Osmolovskaya 1989) appears to be 6–7.5 °C higher.

All the lizards which survived in our experiments (16 ind.) remained in a supercooled state, which could be determined by their coloration, until the temperature reached −3 °C, and froze as the temperature dropped below this value. In this case, they could potentially endure the extremely low temperature, down to −10 °C. The same sequence is probably realized under the natural conditions of the region: Lizards survive small sub-zero temperatures in a supercooled state and lower temperatures in a frozen state. The fact that some lizards could survive freezing if they supercooled to about −3 °C before ice began to form, but none could survive freezing if they began to freeze at higher subzero temperatures contradicts to the major cryobiological tenet, namely, that freezing at a higher temperature facilitates subsequent survival (Storey and Storey 1988). We cannot explain this phenomenon at present; however, even with the closest scrutiny we could not find any methodological error in our experiments which would produce such a false result. A detailed study of this phenomenon is a matter for the future. However, according to Grenot et al. (1999, 2000), lizards from the highland populations of France can endure sub-zero temperatures in either a supercooled or a frozen state, depending on the physiological conditions of a particular individual. The use of both strategies by the same lizard during one winter was considered a rare phenomenon by the cited authors.

In our opinion, the possible differences in the cold hardiness strategy may be explained by different SCP values of lizards from the Western Siberian and European populations. The mean SCP of lizards from the Western Siberian population was −3.0 ± 0.1 °C, which was somewhat higher than the values determined for the European highland population (−4.1 ± 0.4 °C: 1450 m, Cévennes mountains, France) as well as for the oviparous form of the species (−3.9 ± 0.3 °C) from the mountain (900–1100 m, Tarvisio Valley, north-eastern Italy; 900 m, Ossau Valley, southwestern France) and plain (350 m, Ossau Valley) populations (Voituron et al. 2004). At such SCP values, lizards from the European populations can probably hibernate in a supercooled state, since under the mild winter conditions, the temperatures in their hibernacula do not drop below −4 °C. In Siberia, at lower temperatures, lizards hibernate in a frozen state.

The common lizard was characterized by considerable individual variation in SCP: 1.0 °C ($n = 10$) in our material and up to 2.5 °C ($n = 23$) according to Voituron et al. (2002). Given such variation, one of the two lizards sharing a hibernaculum may be in a supercooled state, and the other, in a frozen state; this situation was probably observed by Grenot et al. (2000).

The lizards studied by us were highly susceptible to inoculative freezing: All the individuals placed on a substrate with 70–80 % water content froze already at −1 °C. None of the tested lizards ($n = 32$) survived under such conditions. By contrast, in the experiments of Grenot et al. (2000) many lizards remained supercooled in their hibernacula with an almost 100 % humid substrate, even at lower temperatures and in direct contact with ice crystals.

Although the minimum endurable temperature determined in our experiments was quite low (for reptiles), the fraction of surviving lizards was quite small (about 43 %) even in dry substrate at temperatures higher than −4 °C. Moreover, many lizards (more than 40 %) froze already at −1.0 to −1.2 °C even in dry substrate. It is still unknown why some animals froze and died at small sub-zero temperatures (not reaching the SCP), while others remained in a supercooled state, froze at about −3 °C, and survived further freezing. This is certainly a very important problem which requires further research; when solved, it may help one to improve the design of cold tolerance experiments.

The actual cold hardiness of lizards of the Yakutian population may be even greater than the presently recorded level of −10 °C, since the temperatures are generally lower in Yakutia than in the studied territory of Western Siberia.

High mortality of lizards in our experiments even at small sub-zero temperatures (see Table 2) may reflect some flaws in the experiment technique, such as imperfect living conditions of animals before the experiment, the substrate used for acclimation and testing, the freezing, and thawing rates, etc. The latter factor seems to be particularly important: According to Costanzo et al. (1995), cooling at 0.1 °C h^{-1} within the near-SCP temperature range is stressful and may contribute to higher mortality.

The ability of the common lizard to survive repeated freezing after complete thawing also indicates a high degree of cold hardiness and endurance. This phenomenon was previously observed in the northern amphibians: the European common frog *Rana temporaria* and the Siberian salamander *S. keyserlingii* (Pasanen and Karhapaa 1997; Berman and Meshcheryakova 2012). This ability may have adaptive significance for amphibians in cold regions. We have repeatedly observed that Siberian salamanders can freeze when caught by the night frost during their spring migration to the spawning ponds, then thaw, and reactivate as the temperature rises. In areas with relatively mild winters, the ability to survive multiple freeze–thaw cycles must be important for poikilotherms during periods of thawing weather. Common lizards inhabiting cold regions may rely on this adaptation to survive prolonged cold spells in spring, after their emergence from hibernation.

Costanzo et al. (2013) showed that wood frogs *L. sylvaticus* from Interior Alaska, near the northern distribution boundary of the species, revealed "distinct, prehibernal changes in physiology and a substantially greater capacity for freeze tolerance compared with conspecifics from more temperate regions," and supposed that such differences might have a genetic basis. By analogy with geographic variation in cold hardiness of wood frogs, common lizards from Yakutia may be even more tolerant to cold than those from Western Siberia, and their adaptation may have a genetic or physiological basis.

Although we did not specially attempt to determine the maximum possible duration of existence in a frozen state, the duration observed in our experiments established a record. For all the reptiles studied in this respect (see Storey 2006), freezing for 3–11 days at temperatures close to −3 °C is considered an outstanding result. In the experiments of Voituron et al. (2004), lizards of the ovoviviparous form of *Z. vivipara* endured freezing for no more than 24 h, which was attributed to their limited ability to stabilize the ice content at about 50 %. However, successful freezing for 67 days observed in our experiment is not at all extraordinary as compared to the natural situations, since in some cold regions the soil horizons where lizards hibernate may remain frozen below −4 °C for half a year (see Figs. 5, 6, 7).

The position of the hibernacula

Our systematic study of common lizards hibernating in the nature seems to be the first of its kind. Although data on the hibernacula of this species are very scarce, no special attempts at finding them have been previously made. Not counting the reports of lizards found in anthropogenic habitats (mostly vegetable gardens), on the soil surface or at a depth of 15–25 cm (Vasiliev and Osmolovskaya 1989; Garanin 2006; Bulakhova et al. 2011), all the published descriptions of common lizards hibernating under natural conditions were based on accidental findings. Such were, for example, brief but specific reports of Shcherbakov (1905) and Fellenberg (1983). In the former case, one hibernating lizard was discovered in early spring in Moscow region, under a pile of plant and other debris which had accumulated during the spring flood of the Oka and remained there for several years. In the latter case, two lizards were found in February in the mountain part of South Westphalia, under a small flat boulder on a rocky slope.

The wintering conditions of the common lizard in the European part of its range were described in greater detail only in a few publications. Teplova (1957) described two accidental findings of hibernating lizards in the soil under moss tussocks, in an old clearing in a swampy birch–spruce forest (Komi Republic, 61°50′N, 56°50′E): The first, hibernaculum contained three adult lizards and, the second, 12 individuals of different ages. Grenot and Heulin (1988) described lizard hibernacula in a specially fenced peat bog plot in the lowland of Paimpont (Brittany, France, about 48°N). Lizards overwintered there in the soil at a depth of 2–10 cm, in grass sod mats, old rodent burrows, and under forest litter or moss cover. In a similar fenced peat bog plot in the mountain population (850 m, Jura Mountains), hibernacula were found at a greater depth: 10–20 cm (Grenot et al. 1999).

As for the Asian part of its range, there is only one detailed description of the common lizard hibernating in a natural habitat (the northern taiga of Western Siberia, about 63°N) (Bulakhova et al. 2011). The lizard was found in an oval hibernaculum matching the size of the curled animal, positioned about 10 cm deep in a layer of humid peat with partially decomposed roots and wood debris, in a clearing in a birch–pine forest.

It is often assumed in the literature that in the European part of the range lizards hibernate under a thin layer of litter or lodged grass, in moss or tussocks (Bannikov et al. 1977; Bauwens 1981; Tabachishin et al. 2000, etc.). However, despite thorough examination of the marked plot in the environs of Tomsk during two fall seasons, we did not find any lizards hibernating on the surface.

The hibernacula found by us in the environs of Tomsk had several common traits. First, all of them without a single exception occurred in various distinct cavities: beetle burrows, tunnels left behind by decomposed roots, etc. No hibernating lizards were found in areas with loose soil. The presence of small and stable cavities may be a necessary condition for hibernation.

The second characteristic trait of the hibernacula found by us was low water content of the substrate: 15.1 ± 0.6 %. However, in summer the common lizard is associated with humid and even swampy biotopes within its entire range. Although lizards can be commonly found in such biotopes in the environs of Tomsk in summer, it is unknown whether they also hibernate in humid places in this region (or in similar biotopes of other regions) or migrate to drier places for wintering.

The third common trait of the hibernacula found in the environs of Tomsk was their shallow position (on average at 8–10 cm). Together with the previous documented findings (Teplova 1957; Bulakhova et al. 2011, etc.), our new data suggest that hibernation at shallow depths in the soil, probably not deeper than 15 cm, may be typical of common lizards occupying natural biotopes in these cold regions.

The conditions at hibernation sites

Contrary to intuitive expectations based on the common notion of extremely cold Siberian winters, we observed rather mild conditions in the soil of the biotope where lizards hibernated, in the environs of Tomsk in 2007–2008. Of the ten sites examined, the temperatures at the depth of the hibernacula were lower than −10 °C only at two sites, whereas at six sites they did not drop below −4.0 °C, which is the threshold value for the common lizard in the European part of its range in the opinion of Grenot et al. (2000) and Voituron et al. (2002). It should be noted that the winter of 2007–2008 was close to "average" as concerned the date of snow cover formation and the monthly winter temperatures. Thus, the soil temperatures recorded by us can be considered typical of the region.

The thermal conditions at the hibernation sites of the common lizard are milder in the European part of its range, even in the mountain areas. These regions are characterized by warm winters or a thick snow cover (more than 100 cm) ensuring favorable temperature conditions in the upper soil horizons. For example, the soil temperature at the level of the hibernacula of a highland French lizard population (10 cm deep in soil and under almost 40 cm of snow) was close to 0 °C and only rarely dropped to −4 °C (Grenot et al. 2000).

A characteristic feature of the hibernation sites found by us in the environs of Tomsk was low substrate water content (15.1 ± 0.6 %). Voituron et al. (2004) noted that lizards from the European populations hibernating in dry substrate froze at −4 °C, whereas in humid substrate inoculative freezing occurred already at −2 °C. In our experiments with a considerably wet substrate, lizards also froze at about −1 °C, and 100 % of them perished within merely 12 h of exposure to that temperature. Therefore, we may reasonably assume that hibernation at high water content is possible only in those regions where the temperature in the hibernacula remains above zero or drops slightly below zero for a short period only. Selecting relatively dry places for hibernation may be one of the possible mechanisms of survival of the species in cold regions.

The soil temperature conditions were somewhat more severe in the environs of Podgornoe, where lizards were also abundant. The mean and minimum air temperatures are 1–3 °C lower in Podgornoe than in Tomsk, while the snow cover is thinner by almost one-fourth (38 cm); correspondingly, according to the nearest weather station data, the long-term mean soil temperature at a depth of 20 cm in January is −3.9 °C, which is almost 1 °C lower than in Tomsk (Izyumenko 1966). Nevertheless, in a year with average weather parameters, the thermal wintering conditions in the studied localities of the southeast of Western Siberia are far from being extreme as compared to the survivable temperature of −10 °C (Figs. 5, 6). Hibernation at depths of 5–13 cm could have evolved in the common lizard in the environs of Tomsk due to a small temperature differential within the soil layer 10–20 cm deep. The gradient of minimum temperatures in this layer is several times smaller than that in the upper 0–10 cm and only rarely exceeds 0.1 °C cm^{-1}, which means that the temperatures at depths of 10 cm and 20 cm differ by no more than 1 °C (Pavlov 1979; Berman et al. 2010; Alfimov et al. 2012).

In the environs of Olyokminsk (southwest of Yakutia), the snow cover thickness is close to that in the southeast of Western Siberia (differing by only 2 cm between Podgornoe and Olyokminsk), whereas the mean absolute minima of air temperature are 7–10 °C lower. However, air temperature is not the only factor determining the minimum soil temperatures in this region; there are two more essential factors. First, Olyokminsk lies in the zone of transition from permafrost-free regions to those of continuous permafrost and is characterized by mosaic distribution of permafrost and seasonally frozen soils. Permafrost occurs there on gentle north-facing slopes, under moss–lichen larch forests and in other cold places, occupying up to 20 % of the total area (Ershov 1989). Second, the region is characterized by abundant talik zones, i.e., areas with shallow non-freezing ground waters (unfrozen lakes, river drainage waters, deep groundwater discharge areas, etc.) which "heat" the ground in winter. Due to these two factors (the absence of continuous permafrost and the warming effect of ground waters within talik zones), the minimum soil temperatures at a depth of 20 cm in the warmest biotopes of southwestern Yakutia, as well as in the southeast of Western Siberia, still fall within the common lizard's tolerance limits (Figs. 7, 8, 10), despite the severe climatic conditions.

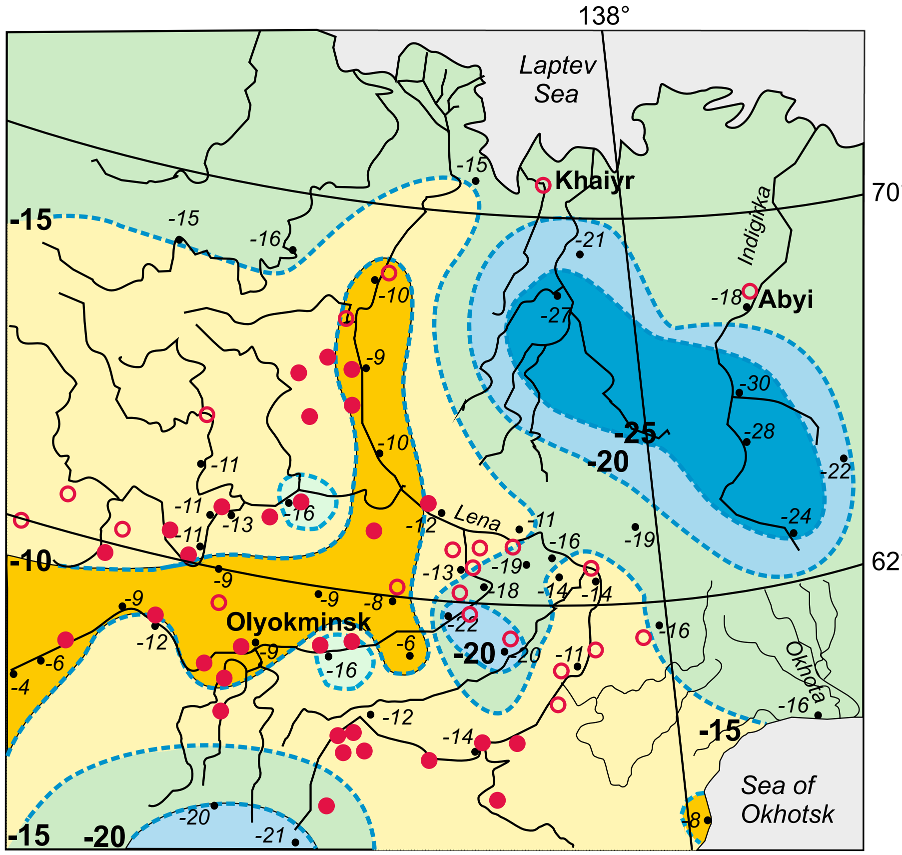

Fig. 10 Temperature conditions of wintering of the common lizard in Yakutia. Soil temperatures of the coldest month at a depth of 20 cm, based on weather station data, are shown in italics; isotherms are shown as *dashed lines* (after Alfimov et al. 2012). *Filled circles* localities where the species is common; *empty circles* localities where the species is rare (after Borkin et al. 1984)

The published data on the hibernation sites of the common lizard are scarce. Assuming that we have studied the typical wintering habitats, the following preliminary conclusions can be made: (1) The hibernation sites are located in mesophytic plots; (2) the depth of the hibernacula does not exceed 13 cm; (3) in the transitional zone between the regions of seasonally frozen soils and permafrost, lizards probably occur in the non-permafrost biotopes and talik zones; (4) in the zone of continuous permafrost, lizards can exist only in talik zones.

The wintering conditions and distribution of the common lizard in Siberia

The common lizard is widely distributed in the subpolar regions of Northern Asia. It extends beyond the Arctic Circle in the north of Western and Middle Siberia (along the Yenisei valley). In Yakutia, the species occurs as far northward as 68°43′N in the Lena valley, but it is rare in Central Yakutia. The northernmost (for both the northeast of Asia and the range as a whole) and easternmost isolated localities are the settlements of Khaiyr (70°48′N) and Abyi (68°N, 145°E), respectively (Borkin et al. 1984).

Judging by the weather station data (Pahknevich 1965; Shumakova 1965), soil temperatures similar to those observed at the hibernation depth in the environs of Tomsk and Podgornoe are typical of the entire Ob–Yenisei interfluve area, from the northern boundary of the forest-steppe zone (55–56°N) to the Arctic Circle. We may therefore conclude that soil temperatures are suitable for hibernation of the common lizard in the greater part of Western Siberia.

Similar thermal conditions are to be observed in the greater part of Southern Yakutia, except for the lower Amga–Lena interfluve area. Southern Yakutia is characterized by the presence of insular permafrost whose southern boundary passes there, and also by widespread talik zones. Therefore, the minimum soil temperatures at a depth of 20 cm recorded by weather stations in this region do not drop below −10 to −12 °C, which certainly indicates that much warmer habitats should also be present there (Alfimov et al. 2012). The frequency of lizard findings is correlated with such conditions (Borkin et al. 1984).

The common lizard is also known from localities positioned much farther to the north and east (Borkin et al. 1984), within the territories mostly occupied by continuous permafrost. Despite the abundant snow cover, the minimum soil temperatures at a depth of 20 cm drop to −15 to −20 °C and even lower, making the existence (more exactly, successful wintering) of the species seemingly impossible. Temperatures exceeding the lizards' tolerance limit can be found there only in the talik zones, which are the most common in the Vilyui and Lena valleys upstream of their confluence and in the interfluve area of these rivers (Ershov 1989). However, fairly high soil temperatures were also recorded by weather stations in the Lena valley downstream of the Vilyui outfall, due to extensive snow cover (1.5 times as thick as in the south-west of Yakutia) and abundant talik zones. This fact explains why the range of the common lizard extends so far northwards along the Lena valley, one of the extremely cold regions of Yakutia.

In addition, two known localities of the common lizard isolated from its main range should be mentioned: the easternmost one, near Abyi (68°N, 145°E), and the northernmost one, near Khaiyr (70°48′N). Although the climatic conditions of these localities require a separate study, it is essential to note that they both lie in lacustrine plains with numerous thermokarst lakes of varying size (Fig. 9). The larger lakes remain partly unfrozen, whereas under and around them there are talik zones with relatively high winter soil temperatures. This fact may probably explain the existence of lizards in these areas, despite the extremely cold winters. The minimum winter temperatures recorded by us were somewhat lower than the lizards' hardiness limit, which may be due to the small number and/or inadequate placement of the loggers. Within these regions, lizards are most likely to be found on peninsulas of large thermokarst lakes, i.e., in land areas "heated" on three sides by unfrozen waters. We did not, however, monitor soil temperatures in such areas due to the shortage of equipment.

In general, most findings of the common lizard in Yakutia (Borkin et al. 1984) were made in regions where soil temperatures at a depth of 20 cm do not drop below −15 °C in the coldest month. Lizards are rare in the territories where these temperatures vary from −15 to −20 °C, and are completely absent in the zone of still lower temperatures (Fig. 10).

Overall, our original assumption about the exceptional cold hardiness of the common lizard, allowing this species to hibernate at extremely low temperatures in Siberia (similar to the Siberian salamander), was only partly confirmed by our experiments. The minimum temperature endured by the common lizard (−10 °C) proved to be much higher than that previously determined for the Siberian salamander (−35 °C) (Berman et al. 1984). The cold hardiness of the salamanders allows them to hibernate in the upper soil layer in virtually any territory. The observed cold hardiness of the lizards ensures their successful wintering in shallow hibernacula (no deeper than 15 cm in soil) in the greater part of Western Siberia. The temperatures of this soil horizon were found to be much higher than −10 °C in most biotopes examined, which means that they do not limit the distribution of the common lizard in the region. It should be emphasized that the minimum temperature endured by common lizards from the Western Siberian populations (−10 °C) is 2.5 times as low as that of conspecific lizards from Europe; so far, this is the record level of cold hardiness for adult reptiles. It may be even lower in some other populations of the common lizard, by analogy with geographic variation in the cold hardiness of wood frogs revealed by Costanzo et al. (2013).

It may seem that the observed level of cold hardiness would not be sufficient for the common lizard to survive under the extreme winter conditions of Yakutia. However, the minimum soil temperatures in the warmest habitats of southwestern Yakutia and probably the entire Southern Yakutia are close to those in the southeast of Western Siberia (−4.5 to −7.0 °C), since lower air temperatures in Yakutia are compensated for by the soil-heating effect of the non-freezing ground waters. Such thermal anomalies are quite abundant in the south of Yakutia (but not in other parts of Yakutia), which determines the broad distribution of the common lizard in this region. The observed level of cold hardiness (−10 °C) is sufficient for the lizards to survive in these territories. Thus, considerable cold hardiness of the common lizard and favorable hydrogeological conditions of some territories (the presence of talik zones) determine the wide distribution of the species in the extremely cold regions of Siberia.

Acknowledgments The study was financially supported by the Russian Foundation for Basic Research (Grants 10-04-00425-a, 13-04-00156-a, 16-04-00082-a). We are also grateful to V.K. Zinchenko (ISEA SB RAS, Novosibirsk) for identification of the dung beetle, to A.N. Leirikh (IBPN FEB RAS, Magadan) for discussion of the methods of studying cold hardiness, to A.A. Poploukhin (IBPN FEB RAS, Magadan) for the flawless work of the refrigeration equipment, and to N.P. Zhornyak, O.Yu. Rozhkova (Olyokminsk), and the Solomov family (Abyi) for their help during field work. We are grateful to the anonymous reviewers for their comments, which resulted in substantial improvement of the manuscript. All the procedures were carried out in accordance with the *International Guiding Principles for Biomedical Research Involving Animals* (Council for International Organizations of Medical Sciences, 1985).

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