NEW DATA ON SPAWNING SITE AND GROUP EGG LAYING
OF *Onychodactylus fischeri* (BOULENGER, 1886)
(THE SOUTHERN SIKHOTE-ALIN RANGE, RUSSIA)

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At the end of May, a permanent spawning site of *Onychodactylus fischeri* was first discovered in the gravel-stony layer under the bottom of a small river valley in the upward flows of subsurface alluvial waters (upper reaches of the Pravaya Sokolovka River, the Sikhote-Alin Range, Chuguevka rayon, Primorsky Krai). This place was located at an altitude of 650 m a.s.l. in mixed coniferous-broad-leaved forest in a narrow river valley. The primary spawning site lay beneath the bottom of a small water body that was two meters away from the main river course. The water in the breeding ground was slightly acidic and slightly mineralized. The local population of *O. fischeri* begins to reproduce in the end of May, when the water temperature inside the site reaches 6.1 – 7.9°C. This site had been used for egg laying on multiple occasions. We found 72 clutches attached to several small stones ($n = 11$). There were no large cavities between the stones, only narrow gaps. There were two recently laid clutches, 26 clutches in the late stages of embryogenesis, already empty sacs and fragments of old mucous stalks. *O. fischeri* lays paired egg sacs measuring 35.4 ± 1.9 mm (34.5 – 38.15; n = 3) in length. Egg arrangement in clutches of *O. fischeri* was varying: in one (or in two) rows in both sacs, or in one row — in one sac and in two — in the other. The mean number of eggs in each sac was 6.8 ± 1.3 (4 – 10; $n = 55$), the mean number of eggs in the clutch — 13.6 ± 2.2 (9 – 17; $n = 27$), the egg diameter — 8.08 ± 0.6 mm (6.71 – 8.9; $n = 19$). For the first time we recorded the otter (*Lutra lutra*) actively hunting adult *O. fischeri*. In late May – early July it preyed upon salamanders near the spawning site. The otter ate heads and bodies of *O. fischeri* but not tails. Perhaps, a high concentration of muciparous glands with poisonous secretion in the tails prevented the predator from eating them.

Keywords: spawning site; clutch; eggs; *Onychodactylus fischeri*; predator; otter.

INTRODUCTION

Climate change is one of the primary threats to the global diversity of amphibians (Borzée et al., 2022). A large-scale decline in the abundance of amphibians has been taking place worldwide. The monitoring data from various countries indicate that not only certain amphibian populations suffer a decline or disappear, but even some species go extinct (Vershinin, 2007; Handogy et al., 2017). At the same time, there is still little known about a number of endemic or relict species (Kuzmin, 2012; Dujsebayeva, 2013). It is impossible to objectively assess the threats affecting the number of endemic and relict

species (global climate change, anthropogenic impact etc.) and to protect them effectively without knowing their unique reproductive traits.

Active herpetological research in East Asia has resulted in a significant number of discoveries and descriptions of new tailless amphibian species, including clawed salamanders of the genus *Onychodactylus* Tschudi, 1838, from the family Hynobiidae in recent years. For a long time, this genus was believed to comprise only two species: *Onychodactylus fischeri* (Boulenger, 1886) from the Russian Far East, northeastern China, and the Korean Peninsula and *Onychodactylus japonicus* (Houttuyn, 1782) from Japan. At present the genus *Onychodactylus* consists of 12 species. *O. zhangyapingi* Che, Poyarkov, Li et Yan, 2012 and *O. zhaoermii* Che, Poyarkov et Yan, 2012 are found in northeastern China. *O. koreanus* Min, Poyarkov et Vieites, 2012 and *O. sillanus* Min, Borzée et Poyarkov, 2022 inhabit the Korean Peninsula. *O. fischeri* is

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endemic to the Russian Far East, and seven species (*O. japonicus*; *O. kinneburi* Yoshikawa, Matsui, Tanabe et Okayama, 2013; *O. nipponoborealis* Kuro-o, Poyarkov et Vieites, 2012; *O. tsukubaensis* Yoshikawa et Matsui, 2013; *O. intermedius* Yoshikawa et Matsui, 2014; *O. fuscus* Yoshikawa et Matsui, 2014; *O. pyrrhonotus* Yoshikawa et Matsui, 2022) are found in Japan (Kuzmin, 1995; Zhang et al., 2006; Yoshikawa et al., 2008, 2010a, 2010b, 2012, 2013; Poyarkov et al., 2012; Zheng et al., 2012; Yoshikawa and Matsui, 2013, 2014; Sparreboom, 2014; Borzée et al., 2022).

All members of the genus *Onychodactylus* are endemic and stenotopic species which life mode (especially reproduction) being understudied due to their secretive behavior. According to all available data on their reproductive ecology and certain morphological features, it is safe to assume that all *Onychodactylus* species have similar embryonic and early larval development.

Salamanders lay a pair of elongated egg sacs, which they attach to stones under a layer of gravel at the bottom and/or in areas of stream sources (Kuzmin, 2012; Poyarkov et al., 2012). The most complete information on the spawning sites, embryonic and early larva development is collected for only three species: *O. japonicus*, *O. kinneburi*, and *O. koreanus*. Given their hidden underground type of reproduction, there have been only single finds of spawning sites (Kudo, 1934; Sato, 1943; Iwasawa and Kera, 1980; Ohno, 1981; Akita, 1982, 1983, 1985; Hayashe and Yamane, 1982; Akita and Miyazaki, 1991; Nambu, 1996; Park, 2005; Lee et al., 2008; Iizuka et al., 2010; Yoshikawa et al., 2013). For other species of the genus *Onychodactylus*, including *O. fischeri*, there is only fragmentary or circumstantial information on their biology and ecology (Regel and Epstein, 1975; Kozik, 1991; Kozik and Truberg, 1991; Serbinova and Solkin, 1992; Griffin and Solkin, 1995; Li, 2004; Poyarkov et al., 2012; Yoshikawa and Matsui, 2014; Borzée et al., 2022).

The Ussuri Long-Tailed Salamander *Onychodactylus fischeri* (Boulenger, 1886) is one of the most understudied amphibian species in Russia. It is found only in the southern part of the Sikhote-Alin Range (Primorsky Krai). *O. fischeri* is included in the Red Data Book of Russia and the Red Data Book of Primorsky Krai (Maslova, 2005; Kuzmin and Maslova, 2021; Maslova et al., 2021). It is listed as of Least Concern by the IUCN (2004), but with population trend — Decreasing. According to the researchers, *O. fischeri* should be regarded as Vulnerable (Kuzmin and Maslova, 2005; Poyarkov et al., 2012). The timing and cyclicity of the breeding period are not known. There is no information on embryonic and early larval development. Typical spawning sites of this species remain unknown (Kuzmin, 2012; Poyarkov et al., 2012). Egg clutches of *O. fischeri* (*n* = 19)

have been found in the wild only once, in a most unusual place. They were attached to the upper side of a flat stone (50 × 30 cm), which lay by the southern riverbank. The stone extended above the water and was moistened merely with water splashes. Only one whole clutch consisted of two egg sacs containing between 3 – 7 eggs each. The sacs were jointed together with a rather elastic gelatinous stalk attached to the substrate (Kozik, 1991; Kozik and Truberg, 1991). Obviously, under normal conditions *O. fischeri* has to lay clutches in gravel and between large stones under the ground in streams sources like other members of the genus (Kuzmin, 2012). All attempts to breed this species in the laboratory or natural environment have been unsuccessful; the clutches have not developed (Regel and Epstein, 1975; Serbinova and Solkin, 1992).

The northwestern border of the distribution of *O. fischeri* is located in the basin of the Pavlovka and Sokolovka rivers (tributaries of the Ussuri River, the western macroslope of the Sikhote-Alin Range). A numerous population of this species is known from the upper reaches of the Pravaya Sokolovka River (Kuzmin and Maslova, 2005). These places have a number of geographical and climatic characteristics different from the more southern habitats of *O. fischeri*.

The western macroslope of the Sikhote-Alin Range has a mountainous terrain with altitudes ranging from 500 to 1150 m a.s.l. and a dense river branch. From the hydrogeological perspective, the area belongs to the Sikhote-Alin Hydrogeological Massif known for its wide distribution of fracture and fracture-vein subsurface waters (Shamov et al., 2021; Sibirina et al., 2022). All stream flows are composed of large pebble bed. The water temperature varies between 6.6 – 10.1°C.

The Pravaya Sokolovka basin is predominantly composed of late Cretaceous period effusives of acid composition, as well as sedimentary rocks of Jurrasic and Triassic. The elevated segments of the floodplain are composed of brown forest soil with layers of sandy-gravel deposits. Those deposits provide effective drain age preventing the soil from flooding. Mountain brown forest soil of alluvial benches and the lower parts of very shallow slopes is formed on diluvial deposits. This kind of soil is characterized by a high in profile concentration of silt fractions, which significantly increases in the underhumus horizons (Gartsman et al., 2020; Sibirina et al., 2022).

The climate is conditioned by the East-Asian monsoon of temperate latitudes. The weather in winter is dry, cloudless and cold; unlike summer, when warm and moist winds dominate the area. January is the coldest month with a mean temperature of 20 – 23°C and a mean snow depth of 30 – 50 cm. The mean temperature in July
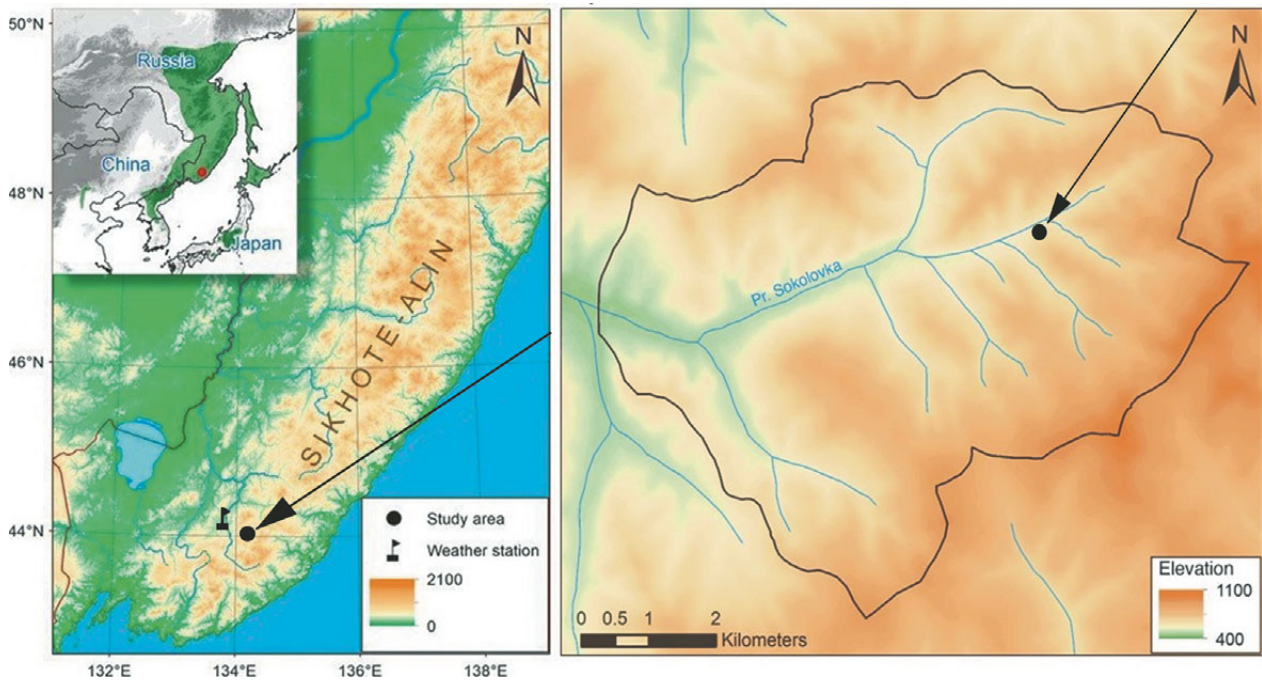
Fig. 1. Map of northeast Asia and southern part of Russian Far East showing study location [upper reaches of the Pravaya Sokolovka River, Verkhneussuriisky Biogeocenotic Station of the Federal Scientific Center of the East Asia Terrestrial Biodiversity of Far Eastern Branch of the Russian Academy of Sciences (VUS)).

is 20 – 22°C. The annual precipitation is approximately 800 mm; over 80% of which falls as rains from April until October. High runoffs are typical of local rivers in summer. The freezing depth ranges from 53 – 125 cm on average. Soil completes thawing in May — June (Gartsman et al., 2020; Sibirina et al., 2022).

In terms of vegetation, the VUS area is rather typical of the southern Sikhote-Alin Range. It may serve as an ideal model of the southern taiga dominated by coniferous-broad-leaved and spruce-fir forests (Sibirina et al., 2022).

MATERIAL AND METHODS

Our research took place on the territory of the Verkhneussuriisky Biogeocenotic Station of the Federal Scientific Center of the East Asia Terrestrial Biodiversity of Far Eastern Branch of the Russian Academy of Sciences (hereinafter — VUS) located in the upper reach of the Pravaya Sokolovka River (an Ussuri River tributary, Chuguevka rayon, Primorsky Krai) (Fig. 1). Here we have been observing a local population of *O. fischeri* in recent years.

We have measured the diameter of the stones with clutches, egg sacs' length and width, the length of mucous stalks and egg diameter. The clutches had to be measured selectively and fast in order not to damage them.

The work completed, we have returned all the stones with clutches to their places. We have also covered them with a layer of gravel and larger stones restoring the cavities between them and leaving the "springs." We use a digital water quality tester Waterproof to determine the water parameters. The clutch measurements (egg sac length and width, mucous stalk length and egg diameter) are obtained with a help of caliper Laserliner Metric Master Plus 075.510A. While searching for spawning sites, we have applied a video endoscope jProbe MX expert. On June 24, 2023, we set a camera trap Seelock 5308 to the monitor all predators near *O. fischeri* spawning site. Since there are no data on the embryogenesis for *O. fischeri*, egg and early larvae development stages are reported according to the embryonic and postembryonic development table of *O. japonicus* (Iwasawa and Kera, 1980, in Kuzmin, 1995). Numerical data were presented as ±SD.

RESULTS

The location for our research has not been chosen spontaneously. While study in the local population of *O. fischeri* in the VUS territory in 2018 – 2021, we found two their larvae in the stages that had never been previously described for this species. They were found in gravel layer in a small body of water by the Pravaya

Fig. 2. Spawning place of *Onychodactylus fischeri* in a narrow river valley at Southern Sikhote-Alin Range. Photo by I. Maslova.

Sokolovka River. In mid-September 2018, we recorded a larva of *O. fischeri* at st. 64 and another one at st. 56 – 57 in late July 2021 (Maslova et al., 2023).

This place is located at an altitude of 650 m a.s.l. in mixed coniferous-broad-leaved forest in a small river valley (44°02′19.5″ N 134°12′39.9″ E). The Pravaya Sokolovka River at the area and time (May 2023) under study was 2.3 m wide and between 0.05 – 0.08 m deep with a water temperature of 8.3 – 9.9°C. Its bottom is covered with pebbles and stones. The river valley is approximately 40 m wide with 10 m to the right and 30 m to the right. This part of the valley is covered with coniferous-broad-leaved forest. The tree layer is dominated by the Maximowicz's poplar (*Populus maximowiczii* A. Henry), the Ajan spruce (*Picea ajanensis* (Lindl. et Gord.)), the Manchurian maple (*Acer mandshuricum* Maxim.), and the Red-twig Korean maple (*A. barbinerve* Maxim.). The herb layer is predominately composed of the meadowsweet (*Filipendula* sp.), the bittercress (*Cardamine* sp.), the cacalia (*Cacalia* sp.), the Alpine Korean buckler fern (*Dryopteris crassirhizoma* Nakai) and the Forest marigold (*Caltha silvestris* Worosch.). The shrub layer is not pronounced.

The water body was round (1.2 × 1.1 × 0.15 – 0.3 m) and had a bottom of pebbles, gravel and stones. It had been formed by the upward flows of subsurface alluvial waters under the valley of the Pravaya Sokolovka River. The water body is located beneath a steep bank of a low river terrace (0.7 – 1.0 m high) two meters away from the main course of the Pravaya Sokolovka River. It's connected with the river by a narrow water-crossing allowing the water flow into the river. We marked this water body as Plot 1, it has become our permanent monitoring point (Figs. 2 and 3).

During our regular examining of Plot 1 in May 2023, we noted at the bottom in two places the movement of water similar to the pulsation of a spring. Although the bottom was more silted than in previous years, there were constant clear "spring" sources of less than 1 cm in diameter. "Springs" were 0.7 m apart from each other and 0.3 m away from the bank. The water parameters in the water body during our research were as follows: $t = 6.1 – 7.9$°C; pH = 6.1; Ec = 105; TDS = 74.9 and Salt = 48.5.
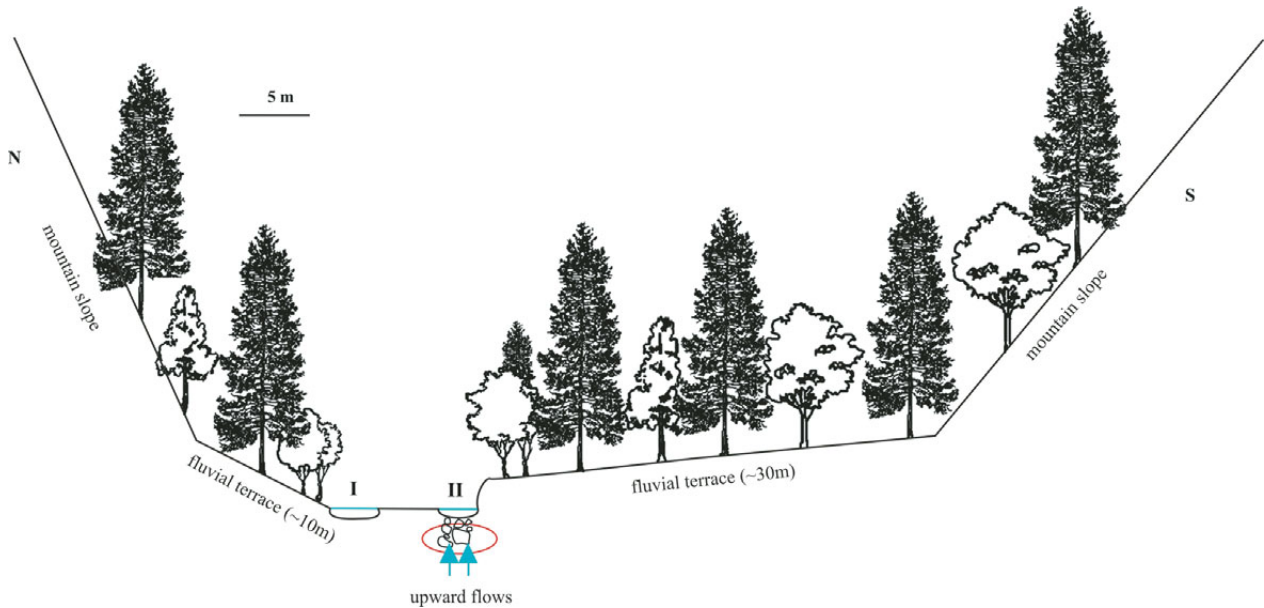
Fig. 3. Profile of the river valley and breeding site of *Onychodactylus fischeri* upper reaches of the Pravaya Sokolovka River, Sikhote-Alin Range: I, the river-bed; II, the water body over the spawning place.

In the last few days of May, we recorded males and females of *O. fischeri* under the stones along the edge and at the bottom of the water body. Their condition revealed that they were ready to breed as they had noticeably swollen cloaca, claws, prominent lateral fold on hindlegs in males and oocytes visible through the belly skin in females. Thus, on May 29 we found four salamanders under a single stone along the coastline.

After we had noticed that some *O. fischeri*, both larvae and mature individuals, emerge from the "springs", we decided to remove the upper layer of stones around those places. For three days (May 29 – 31, 2023) the stones and gravel had been carefully removed. Each day we had to take only a thin layer (ca. 10 cm) and then we were waiting for the silt and detritus suspension to settle, and the holes of the "springs" were not clogged. For the first two days there were predominantly small stones, gravel and silt, but on the third day we started to find larger stones, exceeding 10 cm in diameter. Having excavated the bottom to a depth of approximately 25 cm, we lifted a flat stone of about 22 cm in diameter and found the clutches of *O. fischeri*, attached to its bottom side (Fig. 4). Egg sacs were cylindrical or spindle in shape. Eggs were yellowish white in color. Another ten stones with either clutches or stalks from previous clutches were discovered in the following days (May 31 – June 2).

A total of 72 clutches were found under the layer of gravel and stones that was about 0.25 – 0.4 m thick. The clutches were attached to both the underside and the lat-

eral side of the stones (*n* = 11) which were different in shape and size. Only two stones were flat. The diameter of the stones varied from 69 to 310 mm; mean — 168 ± 76 mm (Table 1). The stones had only narrow gaps between them. Most of the clutches were lying sideways because of the limited space. Some egg sacs were stuck together and/or covered in silt and detritus. Nevertheless, all of them were being washed by clear water and the larvae did not stop developing.

There were from one to 38 clutches, including the stalks from previous clutches, on stones. The correlation between the size of the stones and the number of clutches laid on them was weak. The correlation coefficient is 0.298. Six stones (54.5%) had both clutches and old mucous stalks, one stone (9.15%) had exclusively clutches, another four (36.4%) had only mucous stalks (Figs. 5 – 7). We recorded empty sacs and the stalks from previous clutches with various degrees of decay on ten stones (90.9% of the total number of stones with clutches). We counted 32 mucous stalks from the clutches from previous breeding seasons.

The mean number of eggs per sac *O. fischeri* was 6.8 ± 1.3 (4 – 10; *n* = 55). The mean number of eggs per clutch was 13.6 ± 2.24 (9 – 17; *n* = 27).

26 live clutches were in the late stages of embryogenesis, similar to stages 53 – 55 of *O. japonicus* (Iwasawa, Kera, 1980). The bodies and black eyes of the larvae could be seen clearly through the sac walls. In stages 53 – 55, the length of egg sacs (mm) was 40.62 ± 4.7

Fig. 4. Many pairs of egg sacs of *Onychodactylus fischeri* on flat triangular stone No. 1 (May 31, 2023). Photo by I. Maslova.

(32.22 – 49.97; *n* = 52), the width (mm) was 13.65 ± 2.34 (8.77 – 18.07; *n* = 52), the length of the mucous stalk (mm) 10.74 ± 3.76 (5.71 — 22.04; *n* = 29) and the egg diameter (mm) was 10.17 ± 1.2 (7.1 – 13.52; *n* = 151) (Table 2).

In five clutches (19.2%) one sac had all eggs live and healthy, while in the other sac all the eggs were dead in their early stages. In some cases, a sac with live eggs con-

tained 1 – 3 dead (undeveloped) at the tip of it. Seven clutches had exclusively dead eggs; all in early stages. Five clutches were empty; some of them had the orifices which may have been made by the hatching larvae (Fig. 8).

On June 2, 2023, we discovered two clutches that had been laid recently. Eggs in these clutches were more yellow in color, than in "old." Both of them were attached to

TABLE 1. The Number of *O. fischeri* Clutches on Stones of Different Shapes and Diameters

No. of the stone	The form of the stone	The diameter of the stone, mm	The number of live clutches		The number of dead clutches with eggs	The number of old empty clutches	The number of old mucous stalks	The total number of clutches
			st. 53 – 55	st. 1 – 2				
1	Flat, triangular	220	15	0	3	3	17	38
2	Angular	190	0	0	3	0	3	6
3	Angular	100	0	0	1	0	2	3
4	Angular	125	0	0	0	0	1	1
5	Angular	240	0	0	0	0	4	4
6	Angular	230	0	0	0	2	0	2
7	Angular	160	8	1	0	0	1	10
8	Angular	85	2	0	0	0	0	2
9	Angular	120	0	0	0	0	1	1
10	Flat	310	1	1	0	0	2	4
11	Angular	69	0	0	0	0	1	1
Total		Mean = 168 ± 76	26	2	7	5	32	72

Fig. 5. Many pairs of egg sacs of *Onychodactylus fischeri* on angular shapeless stone No. 7 (June 2, 2023). Photo by I. Maslova.

the stones, where clutches were already developing at st. 53 – 55 (Figs. 9 and 10). One of new clutches had a damaged sac, possibly by some aquatic invertebrates. It had only two eggs, therefore we did not include it in our total count. The egg sacs from the two freshly laid clutches were 35.94 ± 1.94 mm ($34.5 – 38.15$; $n = 3$) in length and 9.67 ± 1.89 mm ($8.53 – 11.86$; $n = 3$) in width; the length of the mucous stalk (mm) was $5.75 – 9.53$ ($n = 2$); the number of eggs — 6 ($5 – 7$; $n = 3$) and the egg diameter (mm) — 8.08 ± 0.57 ($6.71 – 8.9$; $n = 19$).

Clutches of *O. fischeri* were consisted of 337 live eggs (82.6%) and 71 dead ones (17.4%) in total.

The eggs in the clutches at early stages were arranged in one row ($n = 2$). We have recorded the most varying egg arrangement in the live clutches in late stages of the development (st. 53 – 55; $n = 25$): in 64% of all cases the eggs lay in two rows in both sacs, 28% — in one row, 8% — one row in one sac and two rows in the other (Fig. 11).

For many years, we have been studying different habitats of *O. fischeri*, yet we have never seen any salamander remains. However, in 2023 we began finding the tails of adult *O. fischeri* among the stones in the water at Plot 1. During our first visit to the site on May 28, we found tails of three salamanders. Two of them were still contracting when touched. All the tails were intact from the tip to the cloaca. On the following days (May 29 – June 2) we found yet seven tails of adult *O. fischeri*. Three remains had saved also fragments of hindlegs (Fig. 12). The camera trap, we had installed on June 24, recorded the otter *Lutra lutra* visiting the site on multiple occasions (June 28; July 10, 12 and 13) and actively preying on *O. fischeri* (Fig. 13). The pictures demonstrated the predator dipping its head into the water and thoroughly examining the bottom above the spawning site. Aside from the otter, there were single records of a sable Martes zibellina (June 29) and an American mink Neogale vison (July 15), yet they crossed the Plot 1 without stopping and did not attempt to search for salamanders.

DISCUSSION

The spawning site of *O. fischeri* we have found is similar to the spawning sites of other species from the ge-

Fig. 6. Two pairs of egg sacs of *Onychodactylus fischeri* on small stone No. 8 (June 2, 2023). Photo by I. Maslova.

Fig. 7. Two pairs of old empty sacs of *Onychodactylus fischeri* on the stone No. 6 (June 1, 2023). Photo by I. Maslova.

TABLE 2. The Measurements of Live Clutches of *O. fischeri* at Stages 53 – 55

No. of the clutch	The egg sac length, mm (1st/2nd)	The eggs sac width, mm (1st/2nd)	The number of egg in each sac (1st/2nd)	The difference between the sacs (eggs)	The total number of eggs in the clutch
1	35.97	11.48	5	0	10
	34.63	12.54	5		
2	39.53	15.43	7	0	14
	40.49	18.07	7		
3	41.52	17.0	7	1	15
	44.82	15.99	8		
4	33.47	8.78	5	1	11
	41.1	13.85	6		
5	48.47	14.54	7	0	14
	45.54	16.03	7		
6	40.81	16.37	6	2	14
	49.97	14.71	8		
7	37.66	12.25	7	0	14
	34.77	11.87	7		
8	45.46	16.0	8	1	15
	47.07	17.24	7		
9	39.29	12.57	8	0	16
	38.16	12.71	8		
10	41.18	10.53	6	0	12
	38.44	11.53	6		
11	37.73	15.05	8	2	14
	34.17	13.2	6		
12	43.62	11.95	8	1	15
	43.31	13.82	7		
13	33.68	11.26	4	4	12
	49.47	11.33	8		
14	37.35	17.18	6	0	12
	39.46	16.57	6		
15	37.68	12.05	4	1	9
	36.58	9.08	5		
16	42.75	8.77	7	2	12
	40.0	10.64	5		
17	44.49	13.84	8	1	15
	41.02	13.03	7		
18	46.93	13.88	5	2	12
	45.24	13.97	7		
19	37.17	13.44	6	0	12
	34.32	11.19	6		
20	41.15	14.52	8	0	16
	37.03	15.65	8		
21	40.92	13.03	9	1	17
	32.22	11.39	8		
22	39.36	15.24	10	3	17
	32.68	13.44	7		
23	44.72	15.33	7	0	14
	36.94	14.29	7		
24	39.12	10.65	5	1	11
	41.93	13.72	6		
25	46.99	15.97	8	0	16
	39.52	16.81	8		
26	49.55	17.31	8	1	17
	46.72	12.53	9		
Mean	40.62	13.65	6.85	0.92	13.69
SD	4.7	2.34	1.3	1.1	2.22

nus *Onychodactylus* by a number of parameters. It is characteristic of this species to inhabit the places with relatively high, well-forested mountains in the upper reaches of small cool streams (Kuzmin, 1995; Poyarkov et al., 2012; Sparreboom, 2014; Raffaëlli, 2022).

The spawning site of *O. fischeri* is located at 650 m a.s.l. like two breeding places of *O. japonicus* at Mt. Hodatsu in Ishikawa Prefecture (at an altitude of 300 –

Fig. 8. Egg sacs of *Onychodactylus fischeri* with orifices which may have been made by the hatching larvae. Photo by I. Maslova.

Fig. 10. Two clutches of *Onychodactylus fischeri* (st. 1 – 2 and st. 53 – 55) and two mucous stalks from previous breeding season on flat stone No. 10 (June 2, 2023). Photo by I. Maslova.

Fig. 9. Close-up of a pair of egg sacs of *Onychodactylus fischeri* (st. 1 – 2). Photo by I. Maslova.

Fig. 11. The clutches of *Onychodactylus fischeri* with eggs arranging one row in one sac and two rows in the other. Photo by I. Maslova.

450 m) in Japan (Akita, 1982, 1983), a spawning site of *O. koreanus* from Hwansun-gul Cave at an altitude of 504 m in the Korean Peninsula (Park, 2005) as well as breeding sites and habitats of *O. zhangyapingi* and *O. zhaoermii* at 300 – 800 m in China (Li, 2004; Sparreboom, 2014). At the same time, most spawning sites of the species from *Onychodactylus japonicus* complex have been found at the altitudes between 1200 and 1400 m (Kudo, 1934; Ohno, 1937; Okada, 1937a; Sato, 1943; Yoshikawa et al., 2013). There are populations of *O. fischeri* in Primorsky Krai that constantly inhabit on

low altitude (180 – 500 m) on spurs of Sikhote-Alin Mountains (Maslova, 2001; Sokolova et al., 2017; Kuzmin and Maslova, 2021). The data on the altitudinal distribution of *O. fischeri* provided in the Red Data Book of Russia (Kuzmin and Maslova, 2021) contains an error "80 – 1600 m," while the original manuscript stated "180 – 1600 m." Other populations of *O. fischeri* occupy on high altitude (600 – 1600 m) (Serbinova and Solkin, 1992; Kuzmin and Maslova, 2005). We suggest that further spawning sites of *O. fischeri* may be found at various altitudes.

The breeding site of *O. fischeri* is located in mountainous mixed coniferous-broad-leaved forest, which is most typical of this species (Emelianov, 1944; Korotkov, 1977; Griffin and Solkin, 1995; Maslova, 2001; Kuzmin and Maslova, 2005). However, our recent studies demonstrated that certain populations of long-tailed clawed salamanders are able to inhabit rather light broad-leaved

Fig. 12. The tail of adult *Onychodactylus fischeri* eaten by a predator. Photo by I. Maslova.

Fig. 13. *Lutra lutra* is actively preying on adult *Onychodactylus fischeri* near their breeding place (June 28, 2023, the camera trap).

forests (lacking coniferous trees) (Sokolova et al. 2017; Maslova et al., 2018). Other *Onychodactylus* species are biotopically confined to different types of forests: mountain coniferous, mixed, broad-leaved deciduous and evergreen (Poyarkov et al., 2012). For example, Akita (1983) reported a spawning site located in a broad-leaved forest (oak and chestnut) with single pines, and Li (2004) points that *O. zhaoermii* inhabit broad-leaved deciduous forests.

Our data on temperature regime of water — 6.1 – 7.9°C (end of May – beginning of June, spawning site of *O. fischeri*) is consistent with the information of other Russian researchers, indicating that the species starts laying eggs at the of May with an increase in temperature in the water reach 6.0 – 9°C (Serbinova and

Solkin, 1992; Solkin, 1993; Kuzmin, 1995). Japanese scientists also provide the water temperature range between 6 and 11°C as a starting point for reproduction for *Onychodactylus japonicus* complex (Sato, 1943; Akita, 1982, 1985; Poyarkov et al., 2012; Yoshikawa et al., 2013). Breeding period of *O. koreanus* begins when water temperatures rise from 6 to 10.4°C (Park, 2005). Optimum temperature regime for *O. zhaoermii* is 6 – 14°C (Li, 2004; Poyarkov et al., 2012).

The water in the breeding ground of *O. fischeri* is slightly acidic and slightly mineralized: pH = 6.1; Ec = = 105; TDS = 74.9 and Salt = 48.5. Similar data are known for *O. zhaoermii* from China — the water's pH is = 5.8 (Li, 2004). The water at the site under study is slightly acidic due to the composition of underlying mining rocks: late Cretaceous period effusives of acid composition (Gartsman et al., 2020). In addition, acid soils locally associated with coniferous litter may regulate stream pH seasonally (Griffin and Solkin, 1995).

The breeding site of *O. fischeri* is located in the gravel-stony layer under the bottom of a mountain river valley in the upward flows of subsurface alluvial waters. Such location is described for the salamanders of the genus *Onychodactylus* for the first time. The first recorded spawning sites of *Onychodactylus japonicus* complex were located between large stones, in rock crevices, cavities under waterfalls or under the ground in the areas of stream sources, where the egg sacs were attached to the flat surface of large stones (Kudo 1934; Ohno, 1937; Sato, 1943). Akita discovered and described a new type of spawning sites on a steep slope of Mt. Hodatsu in the 1980s. Breeding sites were found in small underground cavities (at a depth of 50 – 60 cm), where cold springs

emerge from under the stones to form the headwaters of a mountain stream. Above the stream, flowing in parallel with the slope under the ground surface, all gaps between the stones were filled with gravel and clayish soil which provided good adhesion. The underground part was riddled with tree roots (Akita, 1982, 1983, 1985). The only breeding site of _O. koreanus_, found by far, was located in a cave within a brook. The oviposition site was on the rock wall, whose upper margin was 2 m wide and 1 m high (Park, 2005).

Despite the uniqueness of _O. fischeri_ spawning site, it is partly similar to the sites described by Akita (1982, 1983). For example, all the stones were not large and had no large empty cavities between them. Most clutches were lying sideways due to the lack of space. Some eggs sacs were stuck together and/or heavily covered with silt and detritus.

We assume that the main part of the _O. fischeri_ spawning site lies deeper, and we have only examined its uppermost layer (0.25 – 0.4 m). For example, in 1983 Akita researched breeding site of _O. japonicus_ on the depth near 1 m (Akita, 1985). We also watched the salamanders hide in the "spring" sources. Given the small diameter of those sources, we did not manage to examine the "springs" using our 15 mm video endoscope. We decided not to remove any more stones, as we felt concerned about the possible silting of the gaps between the stones used by the salamanders.

The clutches of _O. fischeri_ in their late embryogenic stages found in late May are identical to stages 53 – 55 in _O. japonicus_ (Iwasawa and Kera, 1980). This enables us to assume that they were laid last year. If the embryo of _O. japonicus_ reaches stages 53 – 55 in 118 – 135 days, then it is possible that the embryogenesis of _O. fischeri_ will last longer due to more inclement climate. Otherwise it turns out that clutches of _O. fischeri_ were laid in January – February under extreme weather events, which is unlikely. At present there are two theories concerning the spawning period in the genus _Onychodactylus_. Some researchers think that clawed salamanders breed twice in one season (April – June and late September – late December) and use different breeding sites depending in different seasons. There is evidence in favor of this theory relatively some _Onychodactylus_ species (Akita, 1983, 1985, 2011; Akita and Miyazaki, 1991; Lee et al., 2008). On the other hand, there is a hypothesis claiming that _O. fischeri_ reproduces once a year (May – July), and little larvae hatch only in spring after hibernation (Serbinova and Solkin, 1995). However, there are data on a small peak of the breeding population of _O. fischeri_ in early autumn, when adult males and females showed secondary sexual characteristics (Griffin and Solkin, 1995). We suppose that we should continue monitoring the spawning

site in autumn and winter to determine the seasonality of the breeding of _O. fischeri_. Our observations have shown that this species uses the same place of breeding always. We found in one place and old clutches (st. 53 – 55), and males and females ready to breed and fresh clutches (st. 1 – 2).

The genus _Onychodactylus_ is supposed to have species differences in the length of egg sacs and stalks, number of eggs per clutch and egg diameter (Poyarkov et al., 2012). But Kuzmin is pointed out that the clutch parameters vary among both sites and individuals (Kuzmin, 1995). According to Akita (1982, 1983), the clutch parameters may differ significantly within a single _O. japonicus_ population depending on the breeding season. The size of egg sacs changes over different stages of embryogenesis as well.

According to our data, _O. fischeri_ lays paired egg sacs measuring 35.4 ± 1.94 mm ($34.5 – 38.15$; $n = 3$) in length like to _O. koreanus_ (35.7 ± 2.6; $n = 8$) and less size than by species of _Onychodactylus japonicus_ complex (Table 3). The length of sacs in _O. fischeri_ increases during the development of eggs, which has also been recorded in _O. japonicus_ (Akita, 1982, 1983) (Table 3).

The sac width is _O. fischeri_ probably not an informative parameter for species definition. The eggs can be arranged in one as well as two rows in different species of salamanders. For instance, _O. koreanus_ has a significant sac width (15.6 ± 2.3; $n = 8$), and the photographs in Park's publication showed that all the eggs are arranged in two rows (Park, 2005). Akita (1982) reports that most of _O. japonicus_ eggs in the sacs lie in two rows. As for _O. kinneburi_, the eggs were arranged in one row or two rows in recorded clutches (Sato, 1943; Yoshikawa et al., 2013). In our research egg arrangement in clutches of _O. fischeri_ was varying like _O. kinneburi_: or in two rows in both sacs, or in one row in both sacs, or one row in one sac and two rows in the other. Therefore, the width of the egg sac varies in each clutches significantly.

Given both the resilience and extensibility of mucous stalks, we believe that their length cannot be an informative parameter for species identification. The length of the stalks may greatly change and vary during embryogenesis for the same species and the same population under the influence of different factors (water speed ets.), as for example for _O. japonicus_ from 9.0 to 56.0 mm (Akita, 1982, 1983). We noticed that the stalks generally tend to elongate during embryogenesis: st. 1 – 2 — 7.64 mm (5.75 – 9.53), st. 53 – 55 — 10.74 ± 3.76. Akita (1982, 1983) reported similar changes in _O. japonicus_: st. 10 — 16.8 ± 5.5, st. 30 – 32 -17.9 ± 7.2, st. 51 – 52 — 27.7 ± 9.2 (Table 3). The insignificant increase in the length of stalks in _O. fischeri_ may be associated with the spawning site specificity. Lo-

TABLE 3. Comparative Table of the Clutches of Genus *Onychodactylus* Species

	O. japonicus Akita, 1982, 1983	O. kinneburi Sato, 1943; Yoshikawa et al., 2013 (early stages)	O. koreanus Park, 2005 (June 13 – 28, 2004, st. 1)	O. fischeri			
				Kozik, 1991 (August 9, 1989)	Serbinova, Solkin 1992	Griffin, Solkin, 1995	Our data May 31 – June 2, 2023
Mean length of egg sacs, mm	May 27, 1982 40.7 ± 5 (33.0 – 52.1; n = 8) st. 10 December 25, 1982 46.0 ± 5.5 (32.0 – 58.9; n = 36) st. 30 – 32 March 28, 1982 61.1 ± 10.6 (50.0 – 76.2; n = 14) st. 51 – 52	June 10, 2012 66.6 (58.8 – – 72.2; n = 3)	35.7 ± 2.6; n = 8	Total length of 45 mm (including the stalk) 25 mm (without stalk)	—	—	35.4 ± 1.94 (34.5 – 38.15; n = 3) st. 1 – 2 40.62 ± 4.7 (32.22 – 49.97; n = 52) st. 53 – 55
Mean width of the egg sacs, mm	May 27, 1982 12.9 ± 0.6 (11.8 – 14.3; n = 8) st. 10 25 December, 1982 14.2 ± 1.0 (11.7 – 16.8; n = 36) st. 30 – 32 March 28, 1982 17.8 ± 1.6 (15.0 – 21.0; n = 14) st. 51 – 52	—	15.6 ± 2.3; n = 8	—	—	—	9.67 ± 1.89 (8.53 – 11.86; n = 3) st. 1 – 2 13.65 ± 2.34 (8.77 – 18.07; n = 52) st. 53 – 55
Mean length of gelatinous mucous stalks, mm	May 27, 1982 16.8 ± 5.5 (11.0 – 32.0; n = 8) st. 10 December 25, 1982 17.9 ± 7.2 (9.0 – 42.3; n = 36) st. 30 – 32 March 28, 1982 27.7 ± 9.2 (17 – 56; n = 14) st. 51 – 52	May 21, 1937 Up to 20	12.9 ± 2.25; n = 5	10 – 20	—	—	7.64 (5.75 – 9.53; n = 2) st. 1 – 2 10.74 ± 3.76 (5.71 – 22.04; n = 29) st. 53 – 55
Mean number of eggs within an egg sac	May 27, 1982 11 ± 1.6 (6 – 13; n = 16) December 25, 1982 11.8 ± 2.2 (7 – 18) March 28, 1982 11.4 ± 2.3 (7 – 15; n = 14)	May 21, 1937 2 – 12 June 10, 2012 9 (6 – 11; n = 3)	8.62 ± 1.95 (2 – 13; n = 52)	3 – 7	1 – 8	5 – 10	6.8 ± 1.3 (4 – 10; n = 55)
Mean clutch size (number of eggs per egg sac pair)	May 27, 1982 22 ± 2.6 (17 – 25; n = 8) December 25, 1982 23.6 ± 4.2 (15 – 33; n = 18) March 28, 1982 22.9 ± 3.6 (18 – 28; n = 7)	May 21, 1937 7 – 15 June 10, 2012 20 ± 2.7 (16 – 25; n = 17)	16.92 ± 2.93 (10 – 22; n = 25)	—	—	15 (n = 1)	13.6 ± 2.24 (9 – 17; n = 27)
Egg diameter, mm	May 27, 1982 5.8 ± 0, 5 (n = 21) st. 10	May 21, 1937 5.0 – 5.7 June 10, 2012 5.1 ± 0.4 (4.7 – 5.9; n = 27)	5.95 ± 0.52 (4.9 – 7.2; n = 86)	5 – 6	5 – 6	6 – 8	8.08 ± 0.57 (6.71 – 8.9; n = 19) st. 1 – 2 10.17 ± 1.2 (7.1 – 13.52; n = 151) st. 53 – 55

cal water flows haven't a lot of force even during floodings, and the lack of space in the cavities with clutches restricts clutches oscillation amplitude to a minimum. We suppose that Kozik's data (Kozik, 1991; Kozik and Truberg, 1991) on total length egg sac (+ stalk) of *O. fischeri*, are not informative because dead clutches were in extreme conditions.

Our data on the number of eggs in each sac (mean 6.8 ± 1.3 (4 – 10; *n* = 55)) confirm the little information received earlier on the fecundity of *O. fischeri* females. The only observation of the egg clutches in the wild by Kozik showed paired egg sacs containing 3 – 7 eggs each and having gelatinous stalks (Kozik, 1991; Kozik and Truberg, 1991). With artificial stimulation of spawning, female *O. fischeri* lay egg sacs in which the egg number varied from 1 to 10 eggs per egg sac (Serbinova and Solkin, 1992; Griffin and Solkin, 1995) (Table 3).

Both the mean number of eggs in each sac, and the mean number of eggs in *O. fischeri* clutch (13.6 ± 2.24 (9 – 17; *n* = 27)) are less in comparison with other species of the genus *Onychodactylus* (Table 3). For example, female *O. japonicus* lay mean 11 (6 – 18) eggs per egg sac. Average clutch size is 22 (15 – 33) (Akita, 1982, 1983). The maximum number of ovarian eggs observed in the largest female (17 cm) was 36 (Akita, 1985, in Kuzmin, 1995). The number of eggs per each sac for the species of the *Onychodactylus japonicus* complex in other reports varied: 5 – 7 (Sato 1943), 7 – 14, mean — 10.3 (Kudo, 1934), 4 – 12 (Okada, 1937) and 9 – 18 (Nakamura, 1941) (in Akita, 1982).

According to the obtained data, *O. fischeri* lays larger eggs than other *Onychodactylus* species whose egg diameter ranges between 4.5 – 5.9 mm (Kudo, 1934; Sato, 1943; Iwasawa and Kera, 1980; Akita, 1982, 1983; Yoshikawa et al., 2013), 5 – 7 mm (Okada, 1937a) and 4.9 – 7.2 mm (Park, 2005). In our case, the eggs diameter in a freshly laid clutch of *O. fischeri* was mean 8.08 ± ± 0.57 mm (6.71 – 8.9; *n* = 19). And in late stages it increased up to mean 10.17 ± 1.2 mm (7.1 – 13.52; *n* = 151) (Table 3). Our data are consistent with the results received by Griffin and Solkin, who reported the eggs of *O. fischeri* diameter of 6 to 8 mm (Griffin and Solkin, 1995). Also Korotkov was fixed the females with ovarian eggs up to 6.4 mm in diameter throughout the warm season (Korotkov, 1977). The artificial stimulation of spawning (Serbinova and Solkin, 1992) encouraged *O. fischeri* females to lay eggs where diameter varied from 5 to 6 mm which corresponded similarly to eggs size described by Kozik (1995) and Kozik and Truberg (1991), where their diameter varied from 5 to 6 mm, too. It is possible that the small size of the eggs of *O. fischeri* in the above cases is associated with certain circumstances. Sometimes, artificial stimulation encourages fe-

males to lay underdeveloped eggs. It is also possible that eggs of *O. fischeri* (outside the water, exposed to the sun) have slightly decreased in size, since Kozik and Truberg mentioned the clutch was dead (Kozik, 1991; Kozik and Truberg, 1991).

We presume that the presence of dead (either completely or partly) clutches of *O. fischeri* in spawning site is caused by a couple of factors. First, the lack of space within the cavity, with clutches often tightly pressed together, may lead to the oxygen starvation which greatly affects the embryogenesis (Iwasawa and Kera, 1980). Second, the upper part of the spawning site may be exposed to the extreme temperatures, typical of the cold season in this territory (Gartsman et al., 2020; Sibirina et al., 2022).

The Eurasian otter has not yet been listed as a predator of clawed salamanders. *Cottus poecilopus*, *Salvenius malma*, *Gloydius ussuriensis*, *G. intermedius*, and *Cinclus pallasii* are known to prey upon larvae of *O. fischeri*, while *Meles meles* and *Ursus tibetanus* eat adult salamanders (Korotkov, 1977; Solkin, 1993; Kuzmin and Maslova, 2005).

Since the otter is a predator, that feeds on the prey living in water courses, her discovery thanks to camera trap was expected. We noticed that the predator does not eat the tails of *O. fischeri*. Emelianov reported that salamanders excreted a mucous substance onto their skin to repel potential enemies. Much of this mucus is excreted by the parotids on the back, body sides and the lateral part of tail. A cat, catching a *O. fischeri* by its tail, immediately released it. A foam appeared in its mouth, and intensive salivation occurred (Emelianov, 1944). The presence of defensive granular glands in the tail area is characteristic of some lungless and true salamanders. These glands are most developed in the salamander's land stage. This increase in the size of the granular glands is probably determined by the use of this secretion for defending against predators like in many tailed amphibians (Brizzi et al., 2001). Russian researchers report that *Salamandrella keyserlingii* Dybowski, 1870 of aquatic morphotype stage had no cornified epidermis, their mucous glands were empting, and subdermal connective tissue was hypertrophied (Yartsev and Evseyeva, 2018a, 2018b). We suppose that such phenomenon can be characteristic and of *O. fischeri* during the breeding season, when adult salamanders spend much time in the underground water sources being completely inaccessible to predators. Perhaps, the otter hunts them exclusively in the period when salamanders gather in breeding grounds and move to the aquatic phase. This predator may avoid eating tails since they contain a larger concentration of defensive glands, and the poisonous secretion persists longer there than in

salamanders' bodies. Nevertheless, our assumptions require further studies.

CONCLUSIONS

At the end of May, a permanent spawning site of *Onychodactylus fischeri* was first discovered in the gravel-stony layer under the bottom of a small river valley in the upward flows of subsurface alluvial waters (upper reaches of the Pravaya Sokolovka River, the Sikhote-Alin Range, Chuguevka rayon, Primorsky Krai). This place was located at an altitude of 650 m a.s.l. in mixed coniferous-broad-leaved forest in a narrow river valley (44°02′19.5″ N 134°12′39.9″ E). The primary spawning site lay beneath the bottom of a small water body ($S = 1.32$ m^2, water level = 0.15 – 0.3 m), that was two meters away from the main river course. The water in the breeding ground of salamanders is slightly acidic and slightly mineralized: pH = 6.1; Ec = 105; TDS = = 74.9; Salt = 48.5.

The local population of *O. fischeri* begins to reproduce in the third decade of May, when the water temperature inside the site reaches 6.1 – 7.9°C. This corresponds with all available data for both this particular species and other members of the genus *Onychodactylus*.

Our study reveals that oviposition took place there on multiple occasions. We found a total of 72 clutches attached to several small stones (diameter (mm): mean 168 ± 76; 69 – 310; $n = 11$) There were 2 recently laid clutches, 26 clutches alive in the late stages of embryogenesis (stages 53 – 55, according to Iwasawa, Kera, 1980), 7 old dead with eggs, 5 already empty clutches and 32 fragments of old mucous stalks.

The clutches were attached to the underside or the lateral side of the stones which differed in shape and size. The stones had no large cavities between them. Most clutches were lying sideways due to the limited space. Although some egg sacs were stuck together and/or covered in silt and detritus, the larvae inside of them did not stop developing. There were attached from 1 to 38 clutches, including the stalks from previous clutches, on stones. The correlation between the size of the stones and the number of clutches laid on them was weak. The correlation coefficient is 0.298.

O. fischeri lays paired egg sacs measuring $35.4 \pm \pm 1.94$ mm (34.5 – 38.15; $n = 3$) in length, like *O. koreanus* (35.7 ± 2.6; $n = 8$) but less than salamanders from *Onychodactylus japonicus* complex. The mean length of egg sacs is 40.62 ± 4.7 mm (32.22 – 49.97; $n = 52$) in late embryonic stages (st. 53 – 55).

The eggs in the freshly laid clutches ($n = 2$) were lying per sacs in one row. Clutches in late stages($n = 25$) had varying egg arrangement: in 64% of all cases the eggs lay in two rows in both sacs, 28% — in one row, 8% — one row in one sac and two rows in the other.

The mean number of eggs of *O. fischeri* in each sac was 6.8 ± 1.3 (4 – 10; $n = 55$). The mean number of eggs in clutch ranged from 9 to 17 (mean = 13.6 ± 2.24, $n = = 27$), less in comparison with other members of the genus *Onychodactylus*. Diameters 19 eggs in sacs ranged 6.7 – 8.9 mm (8.08 ± 0.57), more than other members of the genus *Onychodactylus*. In the late stages of embryogenesis, the eggs diameter increased up to $10.17 \pm \pm 1.2$ mm (7.1 – 13.52; $n = 151$).

The clutches consisted of 337 live eggs (82.6%) and 71 dead ones (17.4%) in total. The presence of dead (either completely or partially) clutches of *O. fischeri* may be caused by the partial oxygen starvation damaging the embryos, as well as their exposure to the extreme freezing temperatures in winter.

For the first time we recorded the Eurasian otter (*Lutra lutra*) actively hunting adult *O. fischeri*. In late May – early July it preyed upon salamanders near the spawning site. The otter ate heads and bodies of *O. fischeri* but not tails. Perhaps, a high concentration of muciparous glands with poisonous secretion in the tails prevented the predator from eating them.

REFERENCES

Akita Y. (1982), "Notes on the egg-laying site of *Onychodactylus japonicus* on Mt. Hodatsu," *Jap. J. Herpetol.*, **9**, 111 – 117 [in Japanese].

Akita Y. (1983), "Winter reproduction of *Onychodactylus japonicus*," *Ryoseihachurui Kenkyukaishi*, **26**, 1 – 6 [in Japanese].

Akita Y. (1985), "*Onychodactylus japonicus* in Mt. Hodatsu during the reproductive period," *Ryoseihachurui Kenkyukaishi*, **31**, 1 – 6 [in Japanese].

Akita Y. (2011), "Morphometric comparisons of early summer and early winter breeding assemblages of *Onychodactylus*

japonicus from Mt. Hodatsu, North-Central Honshu, Japan," *Bull. Herpetol. Soc. Jap.*, **1**, 1 – 7.

Akita Y. and Miyazaki K. (1991), "Migration and cycle of reproduction of *Onychodactylus japonicus* in Mt. Hodatsu," *Jap. J. Herpetol.*, **14**, 29 – 38 [in Japanese].

Brizzi R., Delfino G., Jantra S., Alvarez B. B., and Sever D. M. (2001), "The amphibian cutaneous glands: some aspects of their structure and adaptive role," in: *Herpetologia Candiana*, Natural History Museum of Crete, pp. 43 – 49.

Borzée A., Shin Y., Poyarkov N. A., Jeon J. Y., Baek H. J., Lee C. H., An J., Hong Y. J., and Min M.-S. (2022), "Dwindling in the mountains: Description of a critically endangered and microendemic *Onychodactylus* species (Amphibia, Hynobiidae) from the Korean Peninsula," *Zool. Res.*, **43**(5), 750 – 755.

Duisebaeva T. N. (2013), "Monitoring of populations of *Ranodon sibiricus* Kessler, 1866 (Amphibia: Caudata: Hynobiidae) in the southern part of the range," *Tr. Zool. Inst. RAN*, **317**(2), 151 – 175 [in Russian].

Emelianov A. A. (1944), *Amphibians and reptiles of the Soviet Far East. Doctoral Thesis*, Kazakh Branch of the USSR Academy of Sciences, Alma-Ata [in Russian].

Emelianov A. A. (1947), "On the biology of *Onychodactylus fischeri*," *Zool. Zh.*, **26**, 65 – 70 [in Russian].

Gartsman B. I., Gubareva T. S., Lupakov S. Yu., Orlyakovskii A. V., Tarbeeva A. M., Shamov V. V., and Shekman E. A. (2020), "The Forms of Linear Structure of Overland Flow in Medium-Height Mountain Regions: Case Study of the Sikhote-Alin," *Water Resources. Moscow*, **47**(2), 123 – 132.

Griffin P. C. and Solkin V. A. (1995), "Ecology and conservation of *Onychodactylus fischeri* (Caudata, Hynobiidae) in the Russian Far East," in: *Proc. of the Second Asian Herpetological Meeting, September 6 – 10, 1995, Ashgabat, Turkmenistan*, Ashgabat, Turkmenistan, p. 24.

Hayase N. and Yamane S. (1982), "Life history during the aquatic life period of a salamander *Onychodactylus japonicas* (Houttuyn), at Mt. Tsukuba, Ibaraki, Japan," *Jap. J. Ecol.*, **32**, 395 – 403 [in Japanese].

Iwasawa H. and Kera Y. (1980), "Stages of normal development of *Onychodactylus japonicus*," *Jap. J. Herpetol.*, **8**, 73 – 89 [in Japanese].

Khandogiy A. V., Susha A. A., and Lopatin V. D. (2017), "Assessment of anthropogenic impact on amphibians during their reproduction," in: *Proc. of the Sakharov Readings 2017: Environmental Problems of the XXI Century: Materials of the 17th Int. Sci. Conf., May 18 – 19, 2017, Minsk, Belarus. Part 2*, Minsk, Belarus, pp. 50 – 51 [in Russian].

Korotkov Yu. M. (1977), "A contribution to the ecology of *Onychodactylus fischeri* and *Hynobius keyserlingi* in the Primorsky District," *Zool. Zh.*, **56**, 1258 – 1260 [in Russian].

Kozik S. S. (1991), "Record of the *Onychodactylus fischeri* egg-laying site," *Zool. Zh.*, **70**, 159 – 160 [in Russian].

Kozik S. S. and Truberg A. G. (1991), "*Onychodactylus fischeri*," *Priroda*, **7**, 55 – 57 [in Russian].

Kudo T. (1934), "On the egg-laying and collection of embryos of Hakone-salamander (*Onychodactylus japonicus*, Houttuyn)," *Acta Anatom. Niigata*, **4**, 1 – 8 [in Japanese].

Kuzmin S. L. (1995), *The Clawed Salamanders of Asia. Genus* Onychodactylus. *Biology, Distribution, and Conservation,* Westarp Wiss, Magdeburg.

Kuzmin S. L. (2012), *Amphibians of the Former USSR*, Association of Scientific Publications of the KMK, Moscow [in Russian].

Kuzmin S. L. and Maslova I. V. (2005), *Amphibians of the Russian Far East*, KMK Scientific Press, Moscow [in Russian].

Kuzmin S. L. and Maslova I. V. (2021), "Ussuri long-tailed salamander *Onychodactylus fischeri* (Boulenger, 1886)," in: *Red Data Book of the Russian Federation. Animals*, Moscow, pp. 408 – 409 [in Russian].

Lee J.-H., Ra N.-Y., Eom J. H., and Park D. S. (2008), "Population dynamics of the long-tailed clawed salamander larva, *Onychodactylus fischeri*, and its age structure in Korea," *J. Ecol. Field Biol.*, **31**, 31 – 36.

Li J.-L. (2004), "On the biology of *Onychodactylus fischeri* found in Xiuyan Co., and protection of its habitat," *Sichuan J. Zool.*, **23**(3), 169 – 171 [in Chinese].

Maslova I. V. (2001), "New Data on the Distribution of *Onychodactylus fischeri* in the Primorye," in: *Proc. of the 1st Meeting of the Nikolsky Herpetological Society, December 4 – 7, 2000, Pushchino*, Moscow, pp. 190 – 192 [in Russian].

Maslova I. V., Akulenko M. V., Portnyagina E. Yu., Pokhilyuk N. E., and Rogashevskaya D. A. (2021), "Rare and endangered amphibians and reptiles of Primorsky Krai (Russian Far East)," *Biota Environm. Nat. Areas*, **41**, 102 – 121 [in Russian].

Maslova I. V., Portnyagina E. Y., Sokolova D. A., Vorobyeva P. A., Akulenko M. V., Portnyagin A. S., and Somov A. A. (2018), "Distribution of Rare and Endangered Amphibians and Reptiles in Primorsky Krai (Far East, Russia)," *Nat. Conserv. Res.*, **3**(1), 61 – 72.

Maslova I. V., Rogashevskaya D. A., and Daschenko O. I. (2023), "New data on developmental biology of Ussuri long-tailed salamander *Onychodactylus fischeri* (Boulenger, 1886)," in: *Proc. of the 10th of "V. Ya. Levanidov's Biennial Memorial Meetings," March 20 – 22, 2023, Vladivostok*, Vladivostok, p. 57 [in Russian].

Nakamura D. (1941), "On the ecology of *Onychodactylus japonicus*," *Bot. Zool. Tokyo*, **9**, 422 – 426 [in Japanese].

Nambu H. (1996), "Notes on the breeding site of *Onychodactylus japonicus* from Ooyama-machi, Toyama Prefecture, central Japan," *Bull. Toyama Sci. Mus.*, **19**, 41 – 43 [in Japanese].

Ohno M. (1982), "*Onychodactylus japonicus* (Houttuyn)," in: *Distributions of Important Amphibians and Reptiles in Japan. Vol. 2*, Environment Agency of Japan, Tokyo, pp. 134 – 141 [in Japanese].

Okada Y. (1937a), "Notes on the Amphibia of the Tohoku District, Northern Japan," *Saito Ho-on Kai Mus. Res. Bull.*, **12**, 177 – 206.

Okada Y. (1937b), "On *Onychodactylus japonicus* Houttuyn," *Doubutsugaku zasshi* (*Zool. Mag. Tokyo*), **35**, 263 – 268 [in Japanese].

Park D. (2005), "The First Observation of Breeding of the Long-tailed Clawed Salamander, *Onychodactylus fischeri*, in the Field," *Curr. Herpetol.*, **24**, 7 – 12.

Poyarkov N. A., Che J., Min M.-S., Kuro-o M., Yan F., Li C., Iizuka K., and Vieites D. R. (2012), "Review of the systematics, morphology and distribution of Asian Clawed Salamanders, genus *Onychodactylus* (Amphibia, Caudata: Hynobiidae), with the description of four new species," *Zootaxa*, **3465**, 1 – 106

Raffaëlli J. (2022), *Salamanders and Newts of the World*, Penclen Édition, Plumelec, France.

Regel E. D. and Epshtein S. M. (1975), "Some peculiarities of biology of *Onychodactylus fischeri*," *Zool. Zh.*, **54**, 1515 – 1524 [in Russian].

Sato I. (1937), "A synopsis of the family Hynobiidae of Japan," *Bull. Biogeogr. Soc. Jap.*, **7**, 31 – 45.

Sato I. (1943), *A Monograph of the Tailed Batrachians of Japan*, Nippon Shuppan-Sha, Osaka [in Japanese].

Serbinova I. A. and Solkin V. A. (1992), "The Reproduction of Ussuri lungless long-tailed salamander (*Onychodactylus fischeri*)," *Zool. Zh.*, **71**(7), 68 – 73 [in Russian].

Shamov V. V., Shekman E. A., Gubareva T. S., Gartsman B. I., Lupakov S. Yu., Chelnokov G. A., Kozhevnikova N. K., Burdukovskii M. L., and Orlyakovskiy A. V. (2021), "Properties of preferential water flow paths networks and background for their genesis in the slopes of small mountain," *Hydrosphere. Hazard Proc. Phenomena*, **3**(3), 275 – 296 [in Russian].

Sibirina L. A., Gladkova G. A., Omel'ko A. M., and Barkalov V. Yu. (2022), "The Verkhneussuriiskiy Biogeocenotic Station of Federal Scientific Center of the East Asia Terrestrial Biodiversity FEB RAS," *Vestn. DVO RAN*, **4**, 85 – 100 [in Russian].

Sokolova D. A., Maslova I. V., and Manaev V. B. (2017), "On distribution of *Onychodactylus fischeri* in the southeastern part of Primorsky Krai,," in: *Proc. of XII Far Eastern conference on reserve management, October 10 – 13, 2017, Birobidzhan*, ICARP FEB RAS, Birobidzhan, pp. 114 – 115 [in Russian].

Solkin V. A. (1993), "On the ecology of the salamander *Onychodactylus fischeri* (Caudata: Hynobiidae)," *Herpetozoa*, **6**(1/2), 29 – 36.

Sparreboom M. (2014), *Salamanders of the Old World. The Salamanders of Europe, Asia and Northern Africa*, KNNV Publishing, Zeist, Netherlands.

Vershinin V. L. (2007), *Biota of Urbanized Territories*, Yekaterinburg [in Russian].

Yoshikawa N. and Matsui M. (2013), "A new salamander of the genus *Onychodactylus* from Tsukuba Mountains, Eastern Honshu, Japan (Amphibia, Caudata, Hynobiidae)," *Curr. Herpetol.*, **32**(1), 9 – 25.

Yoshikawa N. and Matsui M. (2014), "Two new Salamanders of the genus *Onychodactylus* from Eastern Honshu, Japan (Amphibia, Caudata, Hynobiidae)," *Zootaxa*, **3866**(1), 53 – 78.

Yoshikawa N., Matsui M., Nishikawa K., Kim. J.-B., and Kryukov A. (2008), "Phylogenetic relationships and biogeography of the Japanese clawed salamander, *Onychodactylus japonicus* (Amphibia: Caudata: Hynobiidae), and its congener inferred from the mitochondrial cytochrome b gene," *Mol. Phylogen. Evol.*, **49**, 249 – 259.

Yoshikawa N., Matsui M., Nishikawa K., Misawa Y., and Tanabe S. (2010a), "Allozymic variation in the Japanese clawed salamander, *Onychodactylus japonicus* (Amphibia: Caudata: Hynobiidae), with special reference to the presence of two sympatric genetic types," *Zool. Sci.*, **27**, 33 – 40.

Yoshikawa N., Matsui M., and Nishikawa K. (2010b), "Allozymic Variation and Phylogeography of Two Genetic Types of *Onychodactylus japonicus* (Amphibia: Caudata: Hynobiidae) Sympatric in the Kinki District, Japan," *Zool. Sci.*, **27**, 344 – 355.

Yoshikawa N., Matsui M., and Nishikawa K. (2012), "Genetic structure and cryptic diversity of *Onychodactylus japonicus* (Amphibia, Caudata, Hynobiidae) in northeastern Honshu, Japan, as revealed by allozymic analysis," *Zool. Sci.*, **29**, 229 – 237.

Yoshikawa N., Matsui M., Tanabe S., and Okayama T. (2013), "Description of a New Salamander of the Genus *Onychodactylus* from Shikoku and Western Honshu, Japan (Amphibia, Caudata, Hynobiidae)," *Zootaxa*, **3693**(4), 441 – 464.

Yartsev V. V. and Evseyeva S. S. (2018), "Histological Characteristics of the Skin of *Salamandrella keyserlingi*i (Caudata, Hynobiidae) Males in the Aquatic and Terrestrial Phases of Their Seasonal Cycle," *Curr. Stud. Herpetol.*, **18**(1 – 2), 54 – 63 [in Russian].

Yartsev V. V. and Evseeva S. S. (2018), "Histological Characteristics of the Skin of *Salamandrella keyserlingi*i (Caudata, Hynobiidae) Females in Aquatic and Terrestrial Phases of Seasonal Cycle," *Curr. Stud. Herpetol.*, **18**(3 – 4), 159 – 167 [in Russian].

Zhang P., Chen Y.-Q., Zhou H., Liu Y.-F., Wang X.-L., Papenfuss T. J., Wake D. B., and Qu L.-H. (2006), "Phylogeny, evolution, and biogeography of Asiatic salamanders (Hynobiidae)," *Proc. Natl. Acad. Sci. U.S.A.*, **103**(19), 7360 – 7365.

Zheng Y., Peng R., Murphy R. W., Kuro-o M., Hu L., and Zeng X. (2012), "Matrilineal Genealogy of *Hynobius* (Caudata: Hynobiidae) and a Temporal Perspective on Varying Levels of Diversity among Lineages of Salamanders on the Japanese Islands," *Asian Herpetol. Res.*, **3**, 288 – 302.