HERPETOZOA 6 (1/2): 29 - 36
Wien, 30. Juli 1993

On the ecology of the salamander *Onychodactylus fischeri* (BOULENGER, 1886) (Caudata: Hynobiidae)

Zur Ökologie des Salamanders *Onychodactylus fischeri* (BOULENGER, 1886) (Caudata: Hynobiidae)

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KURZFASSUNG

In der vorliegenden Arbeit wurden Untersuchungen zur Populationsökologie von *Onychodactylus fischeri* (BOULENGER, 1886) durchgeführt. Angaben zur räumlichen Verteilung, täglichen und jahreszeitlichen Aktivität, Populationsgröße, Fortpflanzung sowie Beobachtungen über die Ortstreue und die natürlichen Feinde des Salamanders werden gemacht. Die mittlere Länge der täglichen Wanderstrecke beträgt 0,52 m (maximal 2,5 m), die der Wanderungen im Verlaufe eines Jahres 154 m (maximal 280 m). Die bevorzugten Wassertemperaturen liegen sehr wahrscheinlich zwischen +6 und +9 °C. Die Populationsgröße im Untersuchungsgebiet wurde auf 291 ± 81 geschlechtsreife Individuen geschätzt. Das Geschlechterverhältnis betrug 1:1. Als Freßfeinde wurden *Salvenius malma, Cottus poecilopus, Agkistrodon blomhoffii, Meles meles* und *Ursus tibetanus* festgestellt. Der Einfluß von Fischen auf die Verbreitung dieser Salamanderart wird diskutiert.

ABSTRACT

Population ecology of *Onychodactylus fischeri* (BOULENGER, 1886) was studied. Data on spatial distribution, diurnal and seasonal activity, population size, reproduction, site fidelity, and natural enemies are presented. The mean distance of diurnal migrations is 0.52 m (maximum 2.5 m), and of annual migrations 154 m (maximum 280 m). Preferred water temperatures are very likely from +6 to +9 °C. Population size (291 ± 81 mature specimens) was estimated. Sex ratio was found to be 1: 1. The newts are devoured by *Salvenius malma, Cottus poecilopus, Agkistrodon blomhoffii, Meles meles* and *Ursus tibetanus*. The influence of fishes on the newts' distribution is discussed.

KEYWORDS

Onychodactylus fischeri, activity, distribution, enemies, ecology, Russia

INTRODUCTION

The salamander *Onychodactylus fischeri* (BOULENGER, 1886) was first described more than a century ago. However, its biology is still poorly known.

The most diverse ecological informations can be found in the work of EMELIANOV (1947). Later, some papers were published concerning feeding (KOROTKOV 1977; KUZMIN 1990), reproduction (REGEL & EPSTEIN 1975, 1977), and conservation (BORKIN & KOROTKOV 1989). The authors emphasize the importance of long-term stationary ecological studies of this species.

MATERIALS AND METHODS

Fieldwork was performed in the northern part of the species' range (Olginsky District of Primorie, Far East Russia) in summer 1989 and from April to November 1990. The studied population inhabits the upper Levaya Mysovka River (right tributary of Mineralnaya River; see fig. 5). About half a century ago a vast fire destructed the taiga of the river basin. But the areas along the upper parts of the streams Gimalai, Mutnyi, Zapovednyi and Kitaiskii remained intact. They provide suited habitats for the salamander which is present there until now. Since this fire the territory was not further influenced by economic activities; roads and paths are absent, human visits are rare.

Water supply of the streams is incontinuous and restricted to isolated sections of about 1000 m. The banks are steep, abrupt, and overgrown by a forest of *Pinus sibirica*, intermixed with *Abies*. Maximum daily fluctuations of the water level were 18 cm.

The extension of the salamanders' territories were determined by night excursions. A population inhabiting the stream Kitaĭskii (monitoring plot 300 m in length) was selected as a model. Animals of this population were not collected. Investigations that could have led to habitat destruction were not done there but at the streams Mutnyi and Zapovednyi.

Nocturnal observations were successful only during the seasonal activity period of the species. The plot was examined twice to three times a night. The precise locality of each newt record was mapped. Substrate type, the animal's position relative to the water current, sex and behavior were recorded. The animals were marked individually by toe clipping (according to GARANIN & SZCZERBAK 1989). Developmental stage of oocytes and extent of the webs (male secondary sex character) were registered. Sympatric animal species and traces of their activities were noted. The salamanders' potential enemies were observed more detailed and dissected when necessary. Water temperature was determined twice to three times a night, as well as fluctuations of the water level.

In total 285 salamanders were registered. 56 males, 43 females, and 36 subadults were marked. The number of reproductive salamanders was determined by means of PETERSON's method and BAILEY's correction (CAUGHLEY 1977).

RESULTS

Spatial distribution of adults

Selected characters of 11 sites in the studied plot are listed in table 1. The most preferred parts of the stream are characterized by minimum sunlight exposure, maximum thickness of the pebble layer, presence of single or aggregated logs, unfrozen permanent stream pools, and discharging underground springs. The absence of at least one of these parameters apparently diminishes the attractability of the site to the newt.

Table 1: Selected characters of 11 sites in the studied plot.
Tab. 1: Ausgewählte Merkmale von 11 Fundstellen im Unteruchungsgebiet.

Site No.	Sunlight exposure (h/day)	Pebble layer (cm)	permanent Pools	Blocks and Snags	under water Spring	Individuals marked
1	7	10	-	-	-	2
2	5	10	-	-	-	3
3	5	15	-	2	-	5
4	6	15-20	1	-	-	7
5	5	10	-	1	-	9
6	5	20	1	1	-	8
7	3	30	-	-	-	10
8	-	40-50	2	3	1	9
9	-	60	-	1	1	16
10	0.5	50	1	1	1	24
11	5	10	-	-	-	3

Salamanders were found almost exclusively during their diurnal activity period (sites 8 ,9 and 10). Analysis of recaptures of marked animals (n = 16) did not reveal absolute site fidelity of any specimen. The mean distance of diurnal movement (monitored for one night each) was 0.52 m (maximum 2.5 m), the mean distance of the annual movements was 154 m (maximum 280 m).

Diurnal activity

Diurnal activity (fig. 1) seems to be restricted to three hours. Its pattern is similar in different months. Activity peaks are found in the evening twilight time,

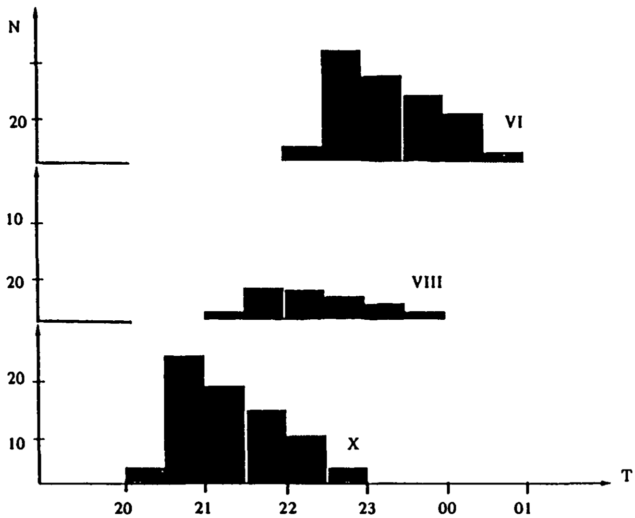

Fig. 1: Diurnal activity dynamics in *Onychodactylus fischeri*. N - number of specimens registered; T - daytime; VI - June, VIII - August, X - October.

Abb. 1: Tagesgang der Aktivität von *Onychodactylus fischeri*. N - Anzahl beobachteter Exemplare; T - Tageszeit; VI - Juni, VIII - August, X - Oktober.

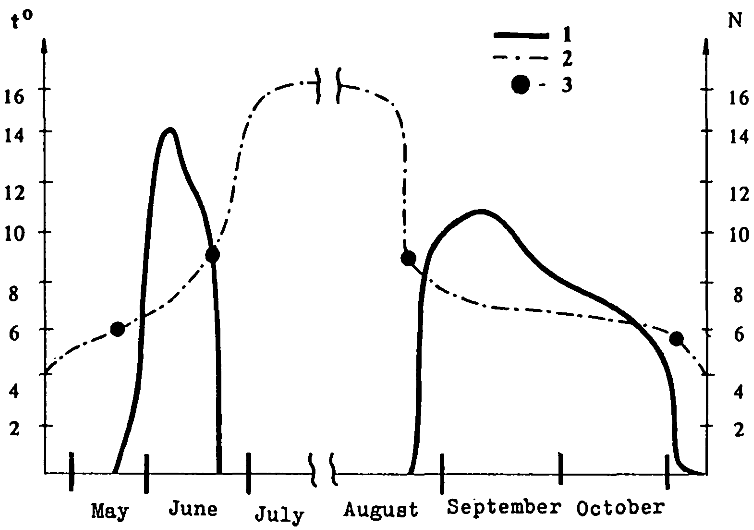

Fig. 2: Seasonal activity dynamics in *Onychodactylus fischeri*, and its dependence on water temperature at night. 1 (N) - Number of specimens marked at night; 2 (t°C) - mean night water temperature; 3 (t°C) - mean water temperature when activity ceased.

Abb. 2: Jahreszeitliche Schwankungen in der Aktivität von *Onychodactylus fischeri* und ihre Abhängigkeit von den nächtlichen Wassertemperaturen. 1 (N) - Anzahl während der Nacht markierter Exemplare; 2 (t°C) - Mittlere Wassertemperatur bei Nacht; 3 (t°C) - Mittlere Wassertemperatur beim Rückgang der Aktivität.

whereas activity ceases at total darkness. The seasonal shift of the beginning of diurnal activity (from 10 pm in June to 8 pm in October) corresponds with the time of sunset. In spite of rather negative phototaxis, some salamanders were active even at daytime (n = 8). E. g., the salamanders' successfull hunt for caterpillars of *Papilio maackii* L. was twice observed in the open sunlight.

Seasonal activity

Salamanders were not found before April 28th. At this time the specimens living in the upper Zapovednyi stream were restricted to a section which was approx. 50 m long. They formed aggregations of 8 - 11 individuals per m² and were covered by a pebble layer 20 - 25 cm deep. Water temperature minimum was +5.6 °C . At the monitoring plot (Kitaiskii stream) salamanders did not appear before May 20th (water temperature +6.2 °C).

Comparison of the salamanders' diurnal activity dynamics with the seasonal temperature dynamics (fig. 2) indicates that the salamander's appearance in spring and its disappearance in autumn coincide with water temperatures of +6 °C.

When water temperature increased to more than +9 °C, the salamanders' nocturnal activities ceised. Beginning of July water temperatures at night started to exceed +9.8 °C and continued to increase (up to +14.9 °C) until the last third of August. During this warm period active salamanders were not found. Excavations at the bottom of Zapovednyi stream indicated that mature specimens dwelled in depths of ca. 70 cm within the pebble layer at the base of waterfalls. In these places substrate and water temperatures were between +9.2 and +9.5 °C.

In July and August water level decreased by 15 cm and the streams transformed into a disrupted chain of pools. In August, the typhoon "Robin" raised the water level for 18 cm. However, active salamanders were not found at this time.

They re-appeared (n = 8) within 24 hours in the night before August 26th, when water temperature decreased from +11 °C to +8.9 °C. This second peak of activity lasted until November. Specimens that emerged from the pebble layer looked emaciated. However, one week later, only corpulent individuals were observed.

Between July 25th and August 18th, during the summerly interruption of adult activity described above, nocturnal mass appearance of juveniles (n = 54; 27 specimens were marked) at the stream banks was observed. In the light of a lamp, the juveniles made no attempts to hide in the water, but ran away towards dry stones. At this time we saw juveniles on insolated stones even by day. The size of these specimens was relatively constant: Snout-vent length = 99 - 115 mm (x = 102.3 ±0.2 mm). Seasonal dynamics of activity in subadults are shown in fig. 3.

Population size

Maximum number of salamanders observed simultaneously was three in sites 4, 6, and 10. However, the total number of specimens marked in these sites was 9, 8, and 20, respectively. So there was every indication (comp. BORKIN & KOROTKOV 1989) to estimate population size. Frequency of occurence was one criterion to estimate the salamanders' abundance. According to estimations based on recaptures of marked salamanders (modified PETERSON's method) 291 ±88 mature specimens inhabited the plot at Kitaiskii stream. Long term studies using the mark-recapture method may ascertain this estimation and permit calculation of demographic parameters of this population.

Marked specimens from Kitaiskii stream (n = 59) were never found among the salamanders collected in Zapovednyi stream.

Reproduction

Sex ratio in the studied sample was close to 1. Monthly counts of *O. fischeri* in reproductive condition (determined by external characters) are shown in fig. 4.

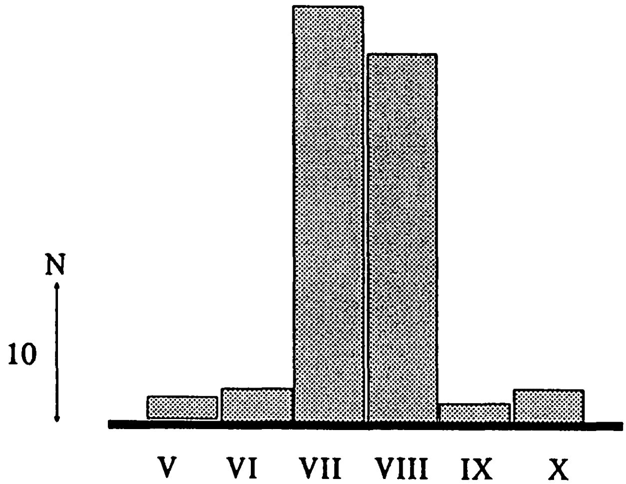

Fig. 3: Seasonal dynamics of occurrence in juvenile *Onychodactylus fischeri* on land. N - Number of records; V - X - May trough October.

Abb. 3: Jahreszeitliche Schwankungen in der Zahl an Land gefundener Jungtiere von *Onychodactylus fischeri*. N - Anzahl der Beobachtungen; V - X - Mai bis Oktober.

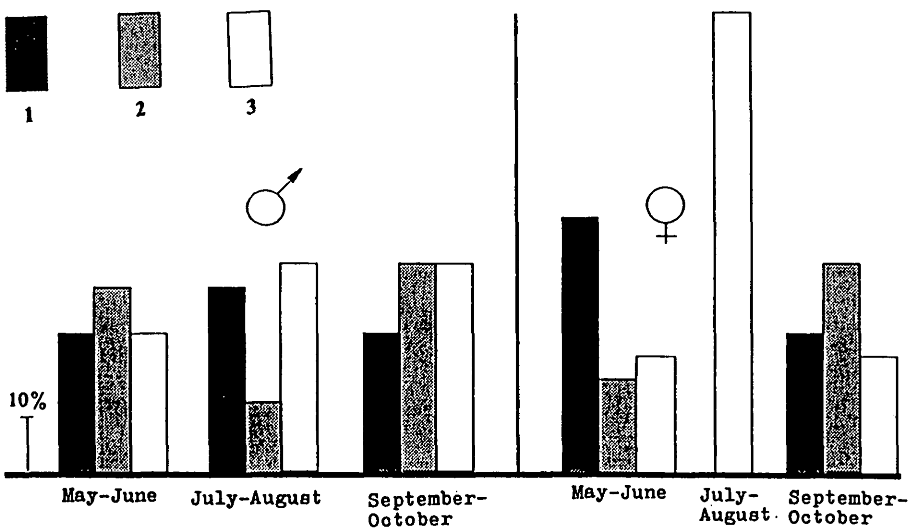

Fig. 4. Relative frequencies (%) of three developmental stages of male hindleg webs, and of female oocytes (as far as visible from external) in *Onychodactylus fischeri*. 1 - well developed; 2 - moderately developed; 3 - not developed.

Abb. 4: Die relative Häufigkeit (%) dreier Stadien der Schwimmhautentwicklung an den Hinterbeinen (Männchen) sowie äußerlich erkennbarer Eientwicklung (Weibchen) bei *Onychodactylus fischeri*. 1 - wohl entwickelt; 2 - mäßig entwickelt; 3 - nicht entwickelt.

Percentage of males with well developed webs is high during the whole reproductive period. But not all females observed between beginning of July and end of August contained oocytes. Maximum diameter of oocytes was the same (ca. 6 mm) in May/June and August/September. However, the aspect of females is different in June and September. In June the skin of females bearing well developed oocytes is slightly pigmented, stretched and transparent. The animal appears "fluorescent" in the light of a lamp and, thus, is well visible from a distance of 5 - 6 m. In September/October female skin is thick, well pigmented, and non-transparent. The light of a lamp does not induce the effect mentioned above.

These data from recaptures do also permit conclusions on the timing of the reproductive cycle (table 2). E. g., both growth and reduction of the male webs takes longer than two months. The new generation of oocytes becomes externally visible one month after spawning.

In July (when the activity period is usually interrupted) 2 males with well developed hindleg webs were caught. They were found 70 cm deep in the water among pebbles at the base of a waterfall in Zapovednyi stream. The specimens had leaf-like webs descending 5 mm below the tips of the toes. These animals did not use their hindlegs but crawled only with their forelegs.

Table 2: Seasonal dynamics of male hindleg web and female egg development in *Onychodactylus fischeri*, shown by comparison of captured and recaptured salamanders.

Tab. 2: Jahreszeitliche Veränderungen an den Schwimmhäuten der Männchen sowie im Trächtigkeitsgrad der Weibchen von *Onychodactylus fischeri*, dargestellt anhand von Vergleichen bei Fang und Wiederfang

Sex	No.	Date of record	Developmental degree
Males (webs)			
	3	June, 16	not developed
		September, 5	moderately developed
	7	June, 16	weakly developed
		October, 11	well developed
	10	June, 16	well developed
		September, 27	moderately developed
	16	June, 18	moderately developed
		September, 25	not developed
	30	July, 20	well developed
		September, 24	moderately developed
Females (oocytes)			
	9	June, 19	well developed
		September, 29	weakly developed
	10	June, 20	absent
		October, 20	well developed
	21	June, 27	well developed
		October, 1	weakly developed

Enemies

In the upper Mineralnaya river *Salvenius malma* WALB. occurs. At high water level this fish ascends and is then occasionally caught in the pools of the drying stream. Another fish, *Cottus poecilopus* HECKEL lives there permanently. Local fishermen use the larvae of *O. fischeri* as a bait for fishing *S. malma* (oral communication).

In laboratory tanks *S. malma* (n = 4) preyed on *O. fischeri* larvae (n = 10) of all developmental stages, and also attacked adult newts (n = 10). We therefore conclude that in drying pools newts are regularly eaten by these fishes. In the puddles of the drying stream we observed *C. poecilopus* successfully hunting for *O. fischeri* larvae. E. g., in a stream pool containing ca. 1 m^3 of water, only one larva out of twelve (probably drifted there from the upper course) survived after two weeks of coexistence with this fish. In another pool, all larvae were devoured by *C. poecilopus* within 2 weeks. We found larvae of *O. fischeri* in 6 out of 22 *C. poecilopus* stomachs dissected, and in one case even an adult salamander.

Mapping of the local distribution of *O. fischeri*, *S. malma* and *C. poecilopus* revealed stable presence of the salamander only in the upper courses, which are inaccessible to *C. poecilopus*.

The number of salamanders clearly decreases where they occur sympatric with one of the fish species. In sites inhabited

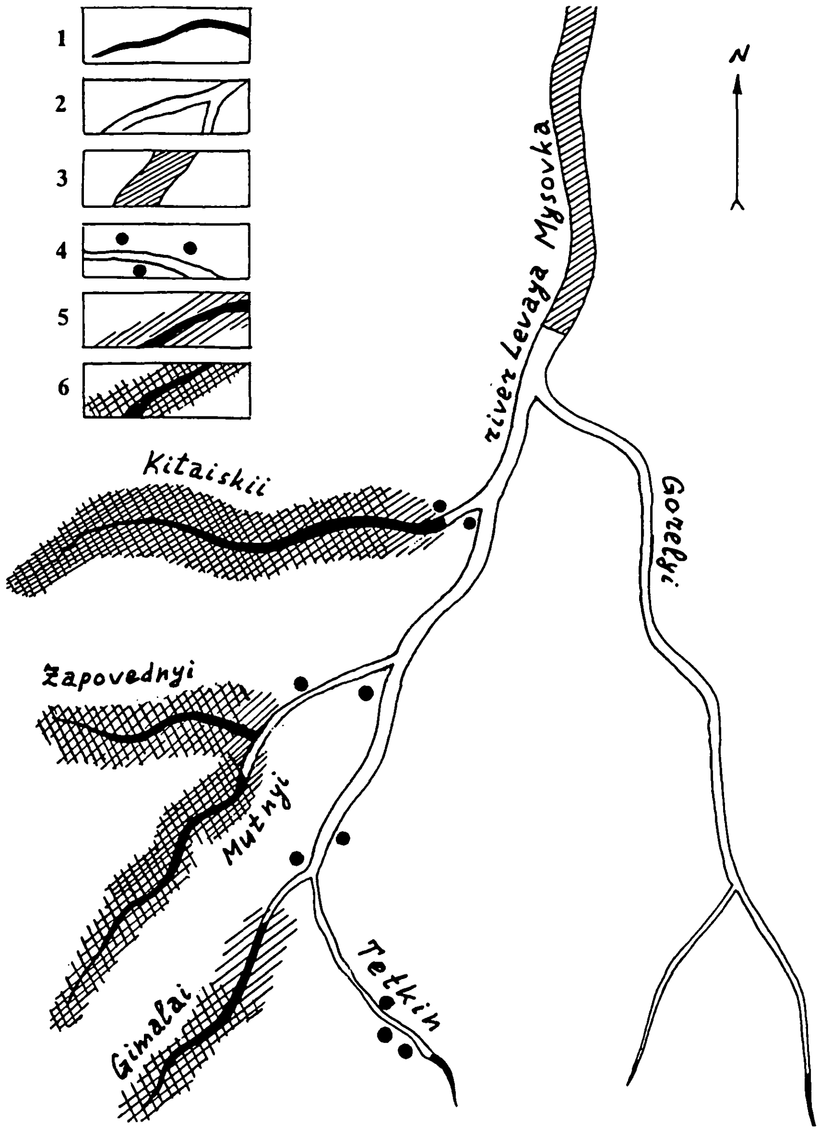

Fig. 5: Distribution of *Onychodactylus fischeri* in the streams of the study area and its relation to the presence of predatory fishes. 1 - fishless sections; 2 - *Cottus poecilopus* present; 3 - *C. poecilopus* and *Salvelinus malma* present; 4 - sections with singular records of postmetamorphic *O. fischeri*; 5 - sections with postmetamorphic *O. fischeri* (abundance less than 1 specimen per 10 m of streambed); 6 - sections with postmetamorphic *O. fischeri* (abundance more than 1 specimen per 10 m of streambed).

Abb. 5: Die Verbreitung von *Onychodactylus fischeri* in den Flußläufen des Untersuchungsgebietes und ihre Beziehung zum Vorhandensein bestimmter Raubfische. 1 - fischfreie Zonen; 2 - Vorkommen von *Cottus poecilopus*; 3 - Vorkommen von *C. poecilopus* und *Salvelinus malma*; 4 - Abschnitte mit vereinzelten Vorkommen metamorphosierter *O. fischeri*; 5 - Abschnitte mit metamorphosierten *O. fischeri* (Häufigkeit weniger als 1 Exemplar auf 10 m Flußlänge); 6 - Abschnitte mit metamorphosierten *O. fischeri* (Häufigkeit über 1 Exemplar auf 10 m Flußlänge).

by both fish species, adult *O. fischeri* are completely absent, because larvae that may drift into this region are totally eliminated. Besides that, we found *Agkistrodon blomhoffii* (BOIE, 1826) (n = 4), *Meles meles* L. (n = 3), and *Ursus tibetanus* CUVIER (n = 3) to be predators of *O. fischeri*.

DISCUSSION

Stenothermy seems to be an important factor of habitat requirement in this salamander.

Our data confirm previous observations (EMELIANOV 1947; REGEL & EPSTEIN 1975) on optimum water temperatures between +6 °C and +9 °C for *O. fischeri*. Nevertheless, some individuals (n = 3) were active at lower and higher temperatures.

Just below +6 °C streambank invertebrates withdrew from the surface of the water. Cessation of the salamander's surface activity may be caused by lack of food, but could also be due to temperature-dependent decline of metabolic rate and mobility.

Surface water temperatures above +9 °C are not absolutely limiting the salamander's distribution. However, warming of the upper zones of the water leads to changes in the salamander's habits. The animals move down into the pebble layer where water and substrate temperatures constantly are around +9 °C.

REGEL & EPSTEIN (1975, 1977) supposed that specimens ready for reproduction would move into the ground of the streams. This assumption is supported by our observations on the cessation of adult surface activity at this time. Nevertheless, the detailed timing mechanism of reproduction in *O. fischeri* remains obscure.

The presence of hindleg webs in males and of oocyte masses in females may well indicate that specimens are ready to reproduce. However, these characters cannot be used as indicators without detailed knowledge on their annual developmental cycle. In this respect lack of externally recognizable oocytes in adult females appears to be the only significant criterion. This character cannot be interpreted ambiguously. It clearly designates the end of the specimen's reproduction period (July in the year 1990).

ACKNOWLEDGEMENTS

We are indebted to I. A. SERBINOVA (Moscow Zoological Garden) and V. V. ARAMILEV (Pacific Institute of Geography) for their effective assistance in our studies.

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DATE OF SUBMISSION: December 12th, 1992

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