THE RAFFLES BULLETIN OF ZOOLOGY 2013 Supplement No. **29**: 49–70
http://zoobank.org/urn:lsid:zoobank.org:pub:87FC5DF3-C00A-4556-BF54-51D82DC803F3
Date of Publication: 30 Nov.2013

BIOLOGY OF THE BAMBOO-INHABITING SEMI-AQUATIC BUGS *LATHRIOVELIA RICKMERSI* KOVAC & YANG AND *L. CAPITATA* ANDERSEN (INSECTA: HETEROPTERA: VELIIDAE) AND HABITAT SPECIALISATION IN THE ORIENTAL *BAPTISTA/ LATHRIOVELIA* COMPLEX

Damir Kovac
Forschungsinstitut Senckenberg, Senckenberganlage 25, D-60325 Frankfurt am Main, Germany
Email: damir.kovac@senckenberg.de

Monika Krocke
Forschungsinstitut Senckenberg, Senckenberganlage 25, D-60325 Frankfurt am Main, Germany

ABSTRACT. — Semi-aquatic bugs of the genus *Lathriovelia* were investigated in Peninsular Malaysia. They inhabited water-filled internode cavities of living (*L. capitata*) or living and decaying (*L. rickmersi*) bamboo culms. They entered the internodes through holes created by other animals or cracks in the bamboo wall. *Lathriovelia* detected its prey by water surface vibrations. In the field the bugs fed on a wide range of live or dead arthropods. Half of the prey items belonged to Collembola and cannibalism was common. The main predators of *L. rickmersi* were mosquito larvae belonging to *Toxorhynchites*, the rove beetle *Acylophorus*, the jumping spider *Paracyrba*, and net-building spiders (mainly Theridiidae). Antipredator strategies observed in *Lathriovelia* included cryptic colouration, hiding, catalepsy, and a special form of “expansion skating”. Grooming occurred after contamination with dirt, after wetting or during intraspecific interactions and also included “bathing”. When wetted, the bugs predominantly groomed their hydrofuge hairs and possibly applied their saliva to their body surface. Migration to new habitats was triggered by rainfall. The mating system of *Lathriovelia* can be characterised as resource defence polygyny. The males of *L. rickmersi* and *L. capitata*, as well as females of *L. capitata*, were territorial. During fighting or mating *Lathriovelia* communicated by generating water surface vibrations. Females deposited their eggs on the bamboo wall close below the water surface in different internodes. The postembryonic development of the five nymphal instars lasted on average 61 days in *L. rickmersi* and 67.5 days in *L. capitata*. A comparison with three *Baptista* species from north Thailand showed that there was a correlation between habitat characteristics, voltinism, and wing polymorphism. *Baptista* species living in stable habitats were predominantly wingless, while species living in unstable patchy habitats were predominantly winged. *Lathriovelia* species have lost their wingless morph. The ancestral habitat of the *Baptista*/*Lathriovelia* complex was probably the margin of streams, which is the present-day habitat of the *Baptista collaris* group (*B. hoedli*, *B. collaris*). Representatives of the *femoralis* group (*B. femoralis*, *B. digitata*) evolved on spring-fed wet ground, and the *B. gestroi* group (*B. gestroi*) in rock or tree pools.

KEY WORDS. — *Lathriovelia*, *Baptista*, life history, territoriality, migration, wing polymorphism

INTRODUCTION

Andersen erected the genus *Lathriovelia* in 1989 and described two species from Peninsular Malaysia: *L. capitata* (habitat unknown at that time) and *L. collaris* (habitat: a hole in a rocky bank of a stream). In 1987 D. Kovac discovered *L. capitata* and a second *Lathriovelia* species in water-filled cavities of bamboo internodes (bamboo phytotelmata) in Ulu Gombak, Peninsular Malaysia (Figs. 3–6). The new *Lathriovelia* species was named *L. rickmersi*, while *L. collaris* was transferred to the closely related genus *Baptista* (Kovac & Yang, 2000).

Lathriovelia rickmersi occurs in Sumatra, Borneo, Peninsular Malaysia, Thailand and South China, and *L. capitata* only in Peninsular Malaysia (Selangor, Pahang, Perak: Kovac & Yang, 2000; own records). Both species are specialised inhabitants of the water surface within bamboo internode cavities. The males of the two *Lathriovelia* species can be easily distinguished by their shape (males of *L. rickmersi* are remarkably slim; Fig. 5) and modifications of their legs and abdominal sternites (Kovac & Yang, 2000). The main focus of the present study is on *L. rickmersi*, which is abundant and easier to observe in the field than *L. capitata* (see Material and Methods).

In the present paper we present our long-term studies on the habitat preferences, feeding biology, predators, defensive behaviour, grooming, mating, agonistic behaviour, migration, development and life cycles of *L. rickmersi* and *L. capitata* from Peninsular Malaysia. Furthermore, we compare *Lathriovelia* with three species of *Baptista* from North Thailand with respect to their habitat preferences, food, voltinism and wing polymorphism. The *Baptista* species inhabited margins of streams, spring-fed wet ground and rock-pools and belonged to all three subgroups of *Baptista*: the *gestroi* group (*B. gestroi*), *femoralis* group (*B. digitata*) and *collaris* group (*B. hoedli*) (see Kovac & Yang, 2000; Zettel, 2004).

MATERIAL AND METHODS

Study areas and general sampling. — The experimental field work dealing with *Lathriovelia* was carried out in Peninsular Malaysia by DK and MK in 1991 (January to November), 1993 (August to November) and 1994–1995 (June to January). The study site was located at the Ulu Gombak Field Study Centre (UFSC) of the University of Malaya (Peninsular Malaysia, Selangor Darul Ehsan). The UFSC is situated about 30 km north of Kuala Lumpur at about 500 m altitude in the foothills on the western flank of the Main Range (Titiwangsa Range), below the Genting Highlands. The rainy season is approximately between September and December, but rainfall can be expected throughout the year and humidity remains high in every month.

The investigation of *Baptista* species was carried out by DK in North Thailand in the Province Mae Hong Son, District Pangmapha between 2001 and present. In Pangmapha the rainy season begins in April/May and ends in October, with the highest amounts of rainfall occurring in July and August. The dry season (usually with no rain at all) can be subdivided into the cold season (December until February) and the hot season (February until April). In the cold season the night temperatures may fall to about 10°C and in the hot season the day temperature may rise to 40°C; humidity is low and fires are frequent.

General collecting was done by DK in Peninsular Malaysia (Selangor Darul Ehsan, Pahang, Perak), East Malaysia (Sabah), Indonesia (West Sumatra), Thailand (Provinces Surat Thani, Kanchanaburi, Tak, Chiangmai, Mae Hong Son), and South China (Yunnan) between 1993 and present. *Lathriovelia* was sampled by opening up internodes of freshly felled or rotting bamboo culms using a saw or a parang (jungle knife).

Breeding. — *L. rickmersi* and *L. capitata* were kept in water-filled containers made of cut bamboo internodes. The containers were sealed with gauze or placed in larger, tightly sealed plastic containers to prevent escape. Breeding internodes were inspected daily. Every two days the specimens were fed with freshly killed *Drosophila* flies collected from rotting fruits. The mean daytime temperature measured in the laboratory was 27.4°C.

In the field we investigated the development of *L. rickmersi* in "experimental internodes", i.e., internodes of felled bamboo culms possessing a lid which could be opened or closed for inspection (Fig. 2). The specimens studied in the field fed on prey occurring naturally in the internodes. The mean daytime temperature measured in the experimental internodes was 23.8°C.

Long-term experiments in the field. — For investigations of the life cycle, migration and feeding biology of *L. rickmersi*, we used experimental internodes (Fig. 2). They were prepared according to the method of Kovac & Streit (1996): bamboo culms were felled and the apical parts cut off. The basal parts of the culms comprising about 15 internodes were stripped of side-shoots and wedged between upright bamboo culms in a horizontal position at a height of ca. 1.5 m off the ground. The lids were created by sawing halfway through each internode near both nodes. The tip of a parang was placed at the end of one of these slits and, using a hammer, driven lengthwise along the internode, thus creating a horizontal slit. Subsequently, the blade was fully inserted into the horizontal slit and carefully tilted, thus breaking open the upper part of the internode and creating a hinged lid (Fig. 2). For the long-term experiments, 10 bamboo culms containing 10 experimental internodes each were set up at different locations in the vicinity of the UFSC.

Long-Term Experiment 1. — In 1991, 100 experimental internodes were checked daily for 7.5 months. We recorded how many *Lathriovelia* individuals occurred in the respective internodes (separate records for males, females and nymphs). Furthermore, the approximate size of the males was recorded (large, medium-sized, or small). Prey items captured by *Lathriovelia*, as well as *Lathriovelia* specimens captured by predators were retrieved with soft forceps and identified in the laboratory.

Long-Term Experiment 2. — In 1994 we inspected 100 internodes daily for 12 weeks.The inspections were conducted in the mornings and in addition immediately after a heavy rainfall. We recorded the amount and time of rainfall and whether any *L. rickmersi* specimens had colonised or left the internodes. The rainfall was measured by setting up a container provided with a funnel (diameter 20 cm) in the clearing in front of the UFSC.

Observation of mating, agonistic and grooming behaviours. — Specimens used for observations of mating and agonistic behaviour were kept isolated in water-filled bamboo containers prior to the experiments. At the beginning of the experiment two specimens were placed in the same bamboo container (diameter of the water surface ca. 7 cm). The bugs were observed using a Zeiss^R prism-head lens and if necessary a torch was applied. If there was no interaction for one hour the experiment was terminated and the specimens were separated. Mating and agonistic behaviour was observed until the specimens stopped interacting.

1

2

3

4

5

6

Figs. 1–6. Habitat, males and females of *Lathriovelia rickmersi* and *L. capitata*. 1. Internode of *Gigantochloa scortechinii* in West Malaysia (diameter ca. 8 cm). The hole in the internode wall (length ca. 6 mm) was created by a larva of the leaf beetle *Lasiochila goryi*. These holes are used by *Lathriovelia* and other arthropods for entering the internode cavities. 2. An experimental internode used for observation and breeding of *Lathriovelia rickmersi*. The hinged lid is opened for inspection. 3. *L. rickmersi* female (length ca. 4 mm) feeds on a collembolan. 4. *L. capitata* male (length ca. 5 mm) resting on the water surface. 5. *L. rickmersi* male (length ca. 5.5 mm) cleans his left antenna with the grooming combs situated at the distal ends of the fore tibiae (lower arrow). The upper arrow points to mites clinging to the rostrum. They are transported by *Lathriovelia* to new habitats. 6. *L. capitata* female (length ca. 5.2 mm) cleaning her forelegs. The arrow points to the extended maxilla.

Different combinations of males and females of both species were used for mating and agonistic behaviour observations: one male and one female of *L. rickmersi*, one male and one female of *L. capitata*, one male of *L. rickmersi* and one female of *L. capitata*, one male of *L. capitata* and one female of *L. rickmersi*; two males of *L. rickmersi*, two females of *L. rickmersi*, two males of *L. capitata*, two females of *L. capitata*, one male of *L. rickmersi* and one male of *L. capitata*, one female of *L. rickmersi* and one female of *L. capitata*.

For quantitative observations of grooming behaviour we briefly submerged the specimens while holding them with forceps. The experiments were terminated about 10 minutes after the last grooming sequence was recorded.

RESULTS

Habitat

Lathriovelia capitata inhabited internodes of upright, living bamboo culms. Occasionally, single individuals were also found in water-filled bamboo stumps or experimental internodes. *L. rickmersi* was abundant in fallen, decaying bamboo culms, but also occurred in older bamboo shoots of *Gigantochloa scortechinii* (6 m and higher) and in older living bamboo culms. Occasionally, *L. rickmersi* was found in water-filled bamboo stumps. However, they did not stay there long, and nymphs were rarely present in this habitat. *L. rickmersi* and *L. capitata* usually did not share the same internodes. In larger bamboo species internodes of upright bamboo culms could exist for about 10 years, while fallen bamboo culms were broken down within one or two years by fungi and detritivorous animals.

In living bamboo culms *Lathriovelia* adults entered the internodes through holes created by insects or woodpeckers. The smallest entrance hole utilised by *Lathriovelia* measured 1.5 × 2.5 mm. It had been bored by a moth larva belonging to the family Crambidae (Lepidoptera). Other holes were created by larvae of the leaf beetle *Lasiochila goryi* (exit hole, ca. 6 × 3 mm, Fig. 1), the longhorn beetle *Abryna regispetri* (round exit hole, ca. 1 cm in diameter) or woodpeckers (hole ca. 10 × 3 mm). The largest hole used by *Lathriovelia* for entering an internode of a living bamboo culm was the entrance of a deserted woodpecker breeding internode: the hole measured about 6 × 4 cm. In living bamboo culms *Lathriovelia* specimens were found up to a height of 21 m.

In fallen bamboo culms *Lathriovelia* entered the internodes through holes created by animals or through narrow slits, which resulted from splitting of the bamboo culms in the dry season. The slits were sometimes almost as long as the internodes and 1–2 mm wide. They were located approximately in the middle of the bamboo culms, thus allowing water to collect at the bottoms of the internodes.

Lathriovelia colonised all large bamboo species possessing internode cavities and holes suitable for entering them. In Malaysia, *Lathriovelia* inhabited *Gigantochloa scortechinii*, *G. latifolia*, *G. levis*, *Dendrocalamus pendulus*, *Schizostachyum grande* and other bamboo species; and in North Thailand *Cephalostachyum pergracile*, *Bambusa polymorpha*, *Dendrocalamus strictus* and other *Bambusa* and *Dendrocalamus* species.

Feeding Biology

Lathriovelia specimens usually did not move or occasionally walked for a short distance on the water surface. If the bugs rested on the internode wall, they usually placed at least two of their legs on the water surface. *Lathriovelia* detected struggling prey by vibrations of the water surface. If collembolans were detected, they were actively chased as long as they stayed on the water surface. Small prey was speared with the proboscis and carried away in order to prevent other *Lathriovelia* specimens snatching the prey away. Large dead insects were sucked dry on the spot, sometimes simultaneously by several *Lathriovelia* individuals.

Lathriovelia preyed on a variety of terrestrial arthropods walking or trapped on the water surface. A small part of the prey items were aquatic insects (Fig. 7). Almost half of the prey items captured by *L. rickmersi* adults and nymphs belonged to Collembola (springtails: Figs. 3, 7). Springtails were common in the humid internode environment and were observed to climb up the bamboo culms during the night. The second largest prey group of *L. rickmersi* were larvae, pupae and adults of aquatic or terrestrial Diptera (flies) developing inside the internodes. They mostly belonged to the Ceratopogonidae (biting midges) and Culicidae (mosquitoes). The bugs fed on dead or living mosquito larvae as well as mosquito eggs (*Toxorhynchites*). The third largest prey group were the larvae or adults of small Staphylinidae or rove beetles (Coleoptera).

Other common prey items belonged to Heteroptera (true bugs), Psocoptera, Hymenoptera (ants, small parasitic wasps) and Acari (mites). The Heteroptera prey items consisted of Ceratocombidae, Miridae and *Lathriovelia* conspecifics. Prey items listed under “Others” (Fig. 7) belonged to Diptera (Psychodidae, Chironomidae, Tipulidae), Coleoptera (aquatic larvae of Scirtidae), Blattodea (small cockroaches, cockroach egg cases, detached leg of a large cockroach specimen), Dermaptera (earwigs), Isoptera (termites) and Pseudoscorpiones (Arachnida).

The nymphs of *L. rickmersi* had the same prey spectrum as the adults, but in general they preferred smaller prey. Thus, springtails comprised 72% of the prey of nymphs and 43% of the prey of adults. Other common prey items collected from nymphs were Psocoptera, various small flies or eggs of *Toxorhynchites*.

The prey spectrum of *L. capitata* was similar to that of *L. rickmersi*. Most prey items of *L. capitata* belonged to Collembola, Hymenoptera (especially ants), Diptera (mosquito larvae) or *Lathriovelia* nymphs.

Lathriovelia rickmersi adults were able to survive without food for a long time: five isolated specimens survived for seven weeks and two specimens survived for nine weeks (all experiments were terminated while the specimens were still alive).

Predators and Defensive Behaviour

Predators occurring in bamboo internodes. — Mosquito larvae belonging to *Toxorhynchites* occasionally hunted close below the water surface. They detected *Lathriovelia* nymphs from a distance of about 1 cm. Subsequently, they slowly approached, swayed their heads and then suddenly snapped at the nymphs. *Toxorhynchites* larvae successfully grabbed *L. rickmersi* nymphs, but we have no records of adults being seized. On one occasion a *Toxorhynchites* larva was observed to snap at a *Lathriovelia* male for 10 consecutive times, but it did not succeed in capturing the bug.

Terrestrial predators found to prey on *Lathriovelia* were the rove beetle *Acylophorus* and the jumping spider *Paracyrba wanlessi*. They hunted *Lathriovelia* from the margin of the water surface. Theridiidae and Pholcidae spiders constructed nets in the upper parts of the internode cavities and captured the largest percentage of *Lathriovelia* specimens. The second largest percentage of captured *Lathriovelia* was seized by *Lathriovelia* conspecifics. In one case a myrmicine ant was observed to feed on a freshly emerged *L. rickmersi* adult.

***Antipredator strategies of* Lathriovelia.** — Anti-predator adaptations in *Lathriovelia* included cryptic coloration and counter-shading obscuring the contours of the bug. The colour of the bug (dark dorsum, pale ventrum) matched the colour of the water surface seen from above (dark) or below (pale). The contour of the bugs was broken by pale or dark areas on the body and the legs. Furthermore, the bugs usually moved slowly or just rested on the water surface, thus presumably avoiding detection. In the daytime *Lathriovelia* was found hiding in darker areas of the internode, at least when staying in bamboo stumps or in internodes possessing large holes. When disturbed, *Lathriovelia* reacted according to the particular circumstances. If the bugs were attacked on the water surface or if the bamboo culm was shaken they fled to the bamboo wall, but if they were attacked by a terrestrial predator they escaped towards the central part of the water surface. When handled, *Lathriovelia* specimens sometimes feigned death, i.e. they tucked up their legs and remained immobile on the water surface, being insensible to stimulation for a while (catalepsy).

A remarkable behaviour exhibited by *Lathriovelia* involved the lowering of the water surface tension when being disturbed. The bugs touched the water surface with their rostrum and subsequently all particles or objects lying on the water surface were violently propelled away (to a radius ca. 1 cm), while *Lathriovelia* remained motionless on the same spot.

Grooming Behaviour

Lathriovelia groomed its legs, antennae and body surface by using grooming combs situated at the inner distal parts of all tibiae. The grooming combs were composed of modified macrotrichia arranged in a row. Grooming occurred after contamination of the body surface with dirt or after wetting. It was also frequent during mating and fighting or occurred spontaneously.

In the following we describe all types of grooming patterns observed in *L. rickmersi*. If not otherwise stated the descriptions also apply to *L. capitata*. Furthermore, we present our data on how often the various parts of the body were groomed after wetting in *L. rickmersi* and *L. capitata*.

Antennae and rostrum. — The right or left antenna was moved forward and both forelegs grasped it several times. Finally, the distal tibial ends (grooming combs) embraced the antenna in the middle of the third segment and then moved downward to the tip (Fig. 5). This movement was repeated several times. Meanwhile, the bug moved the rostrum towards

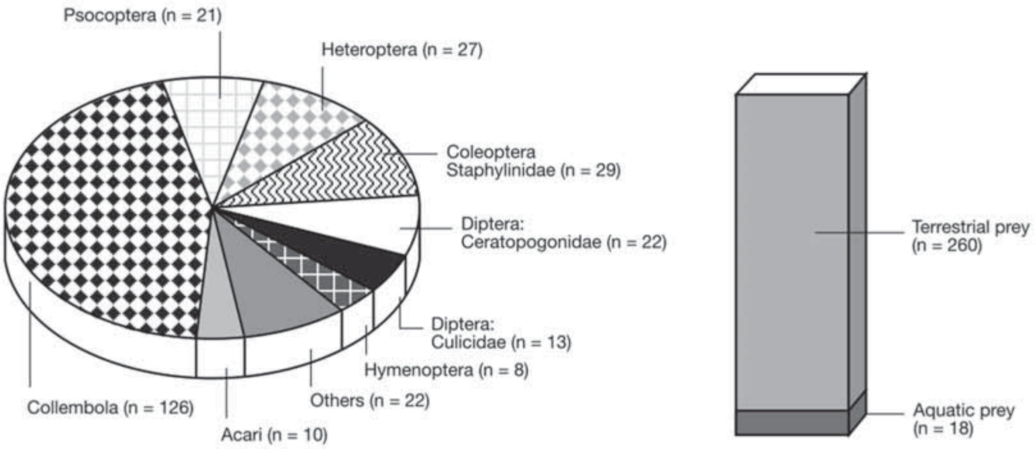

Fig. 7. Prey items of *L. rickmersi* adults and nymphs. Most prey items were terrestrial and belonged to Collembola.

the forelegs and the antenna. Subsequently, the maxilla was extended and swept over the tarsi and the antenna. Occasionally, colourless droplets were seen on the maxilla.

The rostrum was groomed in a similar manner: The grooming combs of the fore tibiae embraced the rostrum and moved downward to the tip of the rostrum. Only the distal third of rostrum was groomed.

Legs. — The forelegs were groomed by rubbing the distal ends of the tibiae and the tarsi against each other. Meanwhile, the rostrum was moved towards the forelegs and the maxilla swept over the distal ends of the fore tibiae and tarsi (Fig. 6). Next, the right or left foreleg was raised and groomed the neighbouring middle leg. The grooming comb of the fore tibia rubbed along the whole middle leg, sometimes also reaching the middle coxa. The middle leg rubbed the fore legs and the tarsi rubbed against each other. In the meantime, the maxilla swept over the tarsi. The middle legs groomed the hind legs in the same manner. The maxilla swept over the middle leg tarsus prior to grooming of the hind leg. An additional type of leg grooming was seen just two times (in *L. rickmersi*): the bug was standing on the three legs of one side thus forming a tripod, while the three legs of the other side groomed each other simultaneously. Alternately, two legs were grooming each other while the third leg simultaneously groomed the abdomen (hind leg) or the head and thorax (foreleg). During this procedure the maxilla swept over the legs.

Body. — The head and the thorax were usually cleaned by the forelegs and the abdomen by the hind legs. Usually only one hind leg was grooming, while the other hind leg remained on the water surface. The hind leg groomed the dorsal, lateral and ventral parts of the abdomen, swept between and under the wings and even reached the thorax and the head. Sometimes, both hind legs were simultaneously raised and rubbed alternately over various parts of the body.

Bathing. — Occasionally, the bugs were seen to quickly lay on the water surface, either on the left or right side of the body or on their backs (Fig. 8), and immediately get up. Sometimes, the antennae were laid on the water surface prior to grooming. This behaviour was more common in *L. capitata*.

Frequency of grooming sequences after wetting. — After wetting *L. rickmersi* groomed the antennae, the legs and the abdomen. The various body parts were treated several times during one grooming session. Grooming usually started with the forelegs, but later on the order of the grooming sequences was not fixed.

The grooming patterns observed after wetting, the use of the maxillae and the frequency of the grooming sequences are presented in Tables 1 and 2. The results show that in both *Lathriovelia* species the frequency of antennal grooming accounted for about 30%, grooming of the legs more than 60%, and grooming of the body less than 10 %.

Migration

All specimens of *L. rickmersi* and *L. capitata* were winged (macropterous), but flying individuals were observed only on three occasions. The specimens slowly flew between the bamboo culms resembling midges or small flying staphylinid beetles. After a while they alighted on bamboo and walked upwards around the culm. Occasionally, adults or older nymphs (4th and 5th stages) colonised neighbouring experimental internodes just by walking.

In 1991 we checked 100 experimental internodes daily for 7.5 months in order to record the internode colonisation by *L. rickmersi* (Long-Term Experiment 1, Fig. 9). After one week 20 internodes were colonised, after four weeks 50 internodes and after eight weeks 68 internodes. In the ensuing weeks the number of colonised internodes continued to increase at a slower rate and reached its peak after 20 weeks (96 colonised internodes). The number of colonised internodes remained at a high level and then slowly decreased (Fig. 9).

During the Long-Term Experiment 2 conducted in 1994 (duration 12 weeks) the results were similar. At the beginning of the observation the number of colonised internodes increased fast and reached 84 internodes after 7–8 weeks. Subsequently, the number of colonised internodes continued to increase slowly and reached 88 internodes after 12 weeks.

The three *L. rickmersi* specimens observed to fly were detected right after rainfall. Therefore, we suspected that colonisation of new internodes was correlated with rainfall. In order to verify this assumption, we recorded the rainfall and the incoming or outgoing individuals in hundred experimental internodes for 12 weeks (Long-Term Experiment 2, see Material and Methods).

The results of the Long-Term Experiment 2 are presented in Fig. 10 and Table 3. In total we have recorded 252 incoming or outgoing individuals after rain and 76 on days without rain. Thus, a correlation between rainfall and migration is

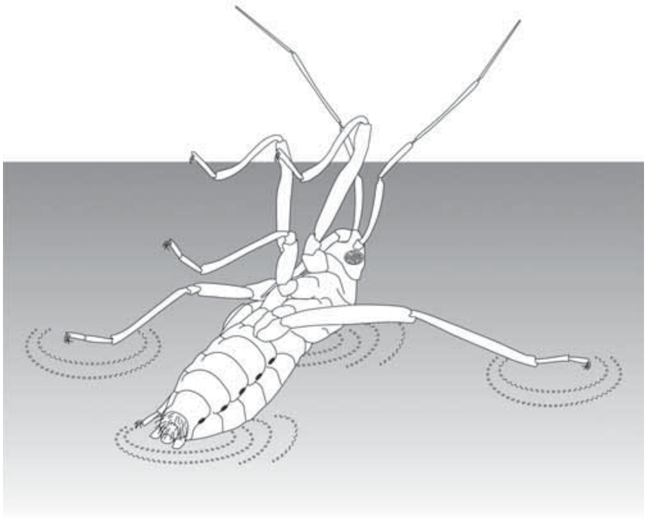

Fig. 8. *L. capitata* female lays on her back ("bathing") and is turning to the right in order to get up.

Table 1. Grooming sequences of *L. rickmersi* caused by wetting of the body surface. The tests were conducted on 10 different days (Test series 1–10), n = number of individual grooming tests. The data stand for how often the various parts of the body were groomed (in percent). A = antenna, AB = abdomen, FL = foreleg, (l) = left, M = maxilla involved in grooming, ML = middle leg, H = head, HL = hind leg, (r) = right, R = rostrum, WS = water surface, FL↔FL = forelegs groom each other, FL→ML = foreleg grooms middle leg. Detailed descriptions of the grooming sequences are given in the text. The total percentage of the grooming sequences of the antennae, legs and body are presented at the bottom of the table.

L. rickmersi Grooming Sequences	1 n=58	2 n=49	3 n=23	4 n=26	5 n=39	6 n=30	7 n=31	8 n=45	9 n=24	10 n=20	Mean
FL(r&l)→A(r)	3.5	16.4	8.7	7.7	2.6	10	16.1	15.9	8.3	10	9.92
FL(r&l)→A(r)+M		4.1						2.2			0.63
FL(r&l)→A(l)	8.6	8.2	13.1	27	2.6	16.7	12.9	15.6	16.6	5	12.63
FL(r&l)→A(l)+M		2		3.8			3.2	2.2			1.12
A(r)→WS						3.3				10	1.33
A(l)→WS						3.3			4.2		0.75
FL↔FL				3.8		10	3.2	4.4			2.14
FL↔FL+M	20.7	20.4	17.4	15.5	15.4	13.3	16.1	22.2	29.1	15	18.51
FL(r)→ML(r)	1.7	10.2	8.7	7.7	2.6	6.7	6.5	6.7	4.2		5.5
FL(r)→ML(r)+M	6.9	4.1	8.7	3.8	15.4	3.3	3.2	2.2	4.2	5	5.68
ML(r)→HL(r)	12	10.2	17.4	7.7	10.2	6.7	3.2	2.2	8.3	5	8.29
ML(r)→HL(r)+M					2.6			2.2			0.48
FL(l)→ML(l)	3.5	8.2	4.3	3.8	5.1	10	6.5	8.9	8.3	5	6.36
FL(l)→ML(l)+M	19	2	4.3	7.7	15.4	6.7	3.2	8.9	4.2	30	10.14
ML(l)↔ M					2.6						0.26
ML(l)→HL(l)	12	2	13.1	3.8	17.8	6.7	6.5	2.2	4.2	5	7.33
ML(l)→HL(l)+M			4.3								0.43
HL(r)→AB	8.6	6.1			2.6		6.5	4.2	4.2		3.22
HL(l)→AB	3.5	4.1		7.7	5.1		12.9		4.2	10	4.75
HL(l)→AB + FL(r)→ML(r)		2									0.2
HL(l)→H						3.3					0.33
Total:											
Antennae	12.1	30.7	21.8	38.5	5.2	33.3	32.2	35.9	29.1	25	26.38
Legs	75.8	57.1	78.2	53.8	87.1	63.4	48.4	59.9	62.5	65	65.12
Body	12.1	12.2	—	7.7	7.7	3.3	19.4	4.2	8.4	10	8.5

highly significant (Chi^2 = 45.5, $p < 0.001$). Most individuals found to migrate on a rainless day flew one day after rainfall (63 out of 76 individuals). On 34 out of 83 days there was no rainfall and no migrations occurred.

During the Long-Term Experiment 2 we have recorded 120 migrating females and 108 males. Our data show, that males usually remained in the internodes for a longer time. If two males were recorded from one internode, one of the

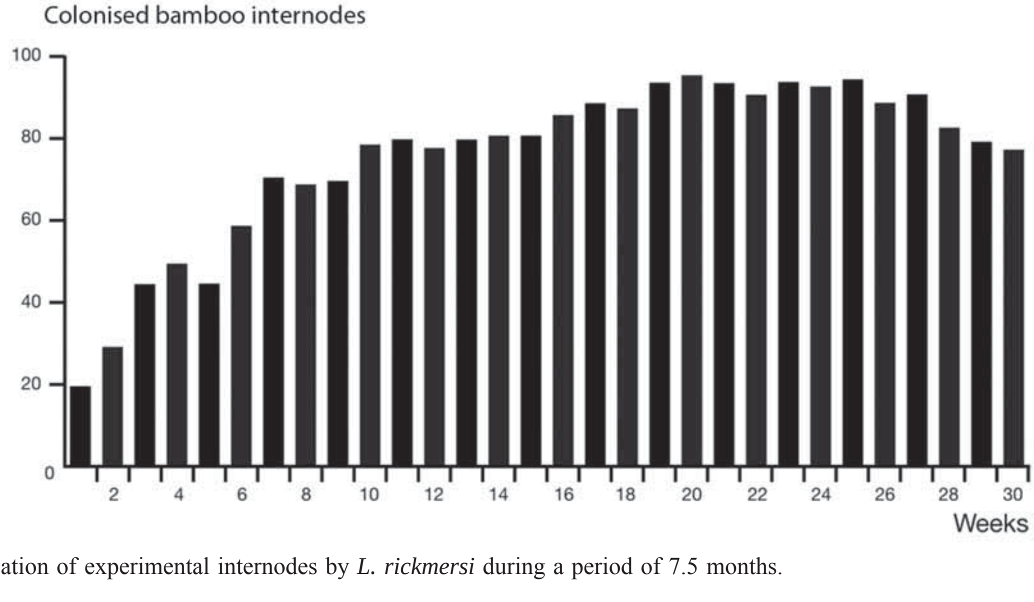

Fig. 9. Colonisation of experimental internodes by *L. rickmersi* during a period of 7.5 months.

Table 2. Grooming sequences of *L. capitata* caused by wetting of the body surface. The tests were conducted on 10 different days (Test series 1–10), n = number of individual grooming tests. The data stand for how often the various parts of the body were groomed (in percent). A = antenna, AB = abdomen, FL = foreleg, (l) = left, M = maxilla involved in grooming, ML = middle leg, H = head, HL = hind leg, (r) = right, R = rostrum, WS = water surface, FL↔FL = forelegs groom each other, FL→ML = foreleg grooms middle leg. Detailed descriptions of the grooming sequences are given in the text. The total percentage of the grooming sequences of the antennae, legs and body are presented at the bottom of the table.

L. capitata Grooming Sequences	1 n=23	2 n=17	3 n=24	4 n=20	5 n=22	6 n=17	7 n=28	8 n=26	9 n=16	10 n=23	Mean
FL(r&l)→A(r)	17.4	5.9	12.5	5	9.3	17.6	17.6	3.6	15.4	12.58.8	10.8
FL(r&l)→A(r)+M					4.5		3.6				0.81
FL(r&l)→A(l)	13	5.9	8.3	5	13.6	5.9	7.1	7.8		13	7.96
FL(r&l)→A(l)+M					4.5			3.8			0.83
A(r)→WS	8.7			5	4.5	5.9	3.6	7.8	6.3		4.18
A(l)→WS	8.7	5.9		5			3.6	3.8			2.7
FL↔FL	4.3	17.6		10			10.8		6.25	17.5	6.645
FL↔FL+M	4.3	17.6	16.7	10	4.5	11.8	10.8	15.4	25	4.3	12.04
FL(r)→ML(r)	4.3	5.9	8.3	5		11.8	7.1	3.8	6.25	13	6.54
FL(r)→ML(r)+M	4.3	5.9	8.3	15		11.8	3.6	3.8	12.5		6.52
ML(r)→HL(r)	4.3	17.6	8.3	5	18.2	5.9	7.1	3.8		13	8.32
ML(r)→HL(r)+M									12.5		1.25
FL(l)→ML(l)	4.3		8.3	5			3.3	15.4	6.2	13	5.555
FL(l)→ML(l)+M	4.3	5.9	4.2	15		5.9	3.6	3.8	6.25		4.895
ML(l)↔ M		5.9	4.2								1.01
ML(l)→HL(l)	8.7		4.2	10	18.2	23.4	14.2	7.8		8.8	9.53
ML(l)→HL(l)+M			8.3	5					6.25		1.955
HL(r)→HB	8.7	5.9	4.2		9.1		10.8	3.8		4.3	4.68
HL(l)→AB	4.7				9.1		3.6	3.8		4.3	2.55
2FL→A(l)+ HL→AB			4.2								0.42
HL(r)→AB+ HL(l)→AB					4.5		3.6				0.81
Total:											
Antennae	47.8	17.7	20.8	20	36.4	29.4	21.5	38.6	18.8	21.8	27.28
Legs	38.8	76.4	70.8	80	40.9	70.6	60.5	53.8	81.2	69.6	64.26
Body	13.4	5.9	8.4	—	22.7	—	18	7.6	—	8.6	8.46

males usually left after a few days (31 out of 34 males). In contrast, females remained in the internodes for a shorter period time. Sometimes, they apparently stayed just for a few hours, because in some internodes we detected eggs, although the females were not present (internodes were checked at least once a day).

Mating Behaviour

Lathriovelia rickmersi. — In *L. rickmersi* the complete mating behaviour was observed 10 times. When a male and a female were placed together, the male usually approached. He revolved around the female or stood behind her and moved the tip of his abdomen up and down, thus causing vibrations of the water surface. These seesaw movements lasted for a few seconds up to six minutes. Occasionally, the male groomed himself, whereas the female did not move at all.

Finally, the male jumped on the female and embraced her thorax with a firm grip of his forelegs (Fig. 11). Sometimes, the distal ends of his tibiae grasped the sides of her thorax, assisted by special grasping combs. The hind legs embraced the female abdomen and also assisted in securing his position on the female's back (Fig. 11). Subsequently, the male inserted his copulatory organ into the genital tract of the female. During copulation the male raised his mid legs, which slightly vibrated. The mid legs were moved forward and backward, touching the female antennae every 4–8 s. The rostrum of the male was raised and the maxilla extended. The copulation lasted between 55 s and 7 min 18 s (n = 10). Usually the female terminated mating (7 out of 10 cases) by raising the frontal part of her body and pushing the male away with her hind legs. Subsequently, the male stood on the water surface and moved his abdomen up and down again. In four cases the males tried to remate, but the females fended them off with their hind legs.

Lathriovelia capitata. — In *L. capitata* mating behaviour was observed 10 times. First, the male moved his body up and down, thus causing vibrations of the water surface. In contrast to *L. rickmersi* males the movements were faster and the body seemed to tremble/vibrate. Subsequently, the male mounted the female and gripped her thorax with his tibiae, assisted by the grasping combs. The hind legs grasped the abdomen of the female. During copulation the mid legs were raised and stretched, but they hardly moved. Sometimes, they were slowly sinking and touched the water surface.

Table 3. Migration in *L. rickmersi*. Rainfall (mm), time of rainfall, and number of *L. rickmersi* males and females colonising or leaving 100 experimental internodes during a 12-week observation period (Long-term Experiment 2) were recorded.

Date	Rainfall (mm)	Time of Rainfall (hours)	Incoming Males	Incoming Females	Outgoing Males	Outgoing Females	Total
4 Jun.	29.9	ca. 0230–0430		4			4
5 Jun.				1			1
6 Jun.	0.8	0615–0715					
7 Jun.	4.46	1730–1800		3			3
8 Jun.	9.4	0130–0430		2			2
9 Jun.	10.8	0600–0730		3			3
10 Jun.							
11 Jun.	12.1	0830–1100	10	10			20
12 Jun.	2.86	1530–1700	4	1	1		6
13 Jun.	20.9	1230–1330	3	4		1	8
14 Jun.	7.48	1700–1800				1	1
15 Jun.			4	5			9
16 Jun.	0.64	0815–0840	2	1		1	4
17 Jun.							
18 Jun.							
19 Jun.							
20 Jun.							
21 Jun.	14.6	1900–2130		1		1	2
22 Jun.			1	2			3
23 Jun.							
24 Jun.							
25 Jun.	85.3	1700–2115	2	3			5
26 Jun.	2.23	1515–1700					
		2200–0200	5	11	2	3	21
27 Jun.	2.32	0000–0200					
		1645–1815	5	3	2	9	19
28 Jun.				2			2
29 Jun.	34.2	0800–1700	22	16	4	7	49
30 Jun.			8	2		1	11
1 Jul.			1		1	2	4
2 Jul.							
3 Jul.	3.18	0400–0800		1		2	3
4 Jul.			1		1	1	3
5 Jul.	1.91	1030–1100	1				1
6 Jul.							
7 Jul.	8.28	0845–0915	3	3	1	2	9
8 Jul.	2.55	1130–1215	1			3	4
9 Jul.	3.18	1530–1615					
10 Jul.	10.4	0200–0600	2	9	3	6	20
11 Jul.	1.27	1730–1800					
12 Jul.				1			1
13 Jul.							
14 Jul.							
15 Jul.							
16 Jul.							
17 Jul.				1	1	1	3
18 Jul.				1			1
19 Jul.							
20 Jul.	3.82	0315–500		3	2	4	9
21 Jul.	0.16	0800–815		1		1	2
22 Jul.							
23 Jul.	1.91	0800–830	2	4			6
24 Jul.							
25 Jul.				1		1	2
26 Jul.						1	1
27 Jul.							
28 Jul.							
29 Jul.							
30 Jul.						1	1
31 Jul.							
1 Aug.							

Table 3. Cont'd.

Date	Rainfall (mm)	Time of Rainfall (hours)	Incoming Males	Incoming Females	Outgoing Males	Outgoing Females	Total
2 Aug.							
3 Aug.	24.4	1545–1930	7	5	1	1	14
4 Aug.			4	1			5
5 Aug.							
6 Aug.							
7 Aug.							
8 Aug.							
9 Aug.							
10 Aug.							
11 Aug.							
12 Aug.	2.55	1400–1600	3	1	1		5
13 Aug.	26.1	1545–1700	8	5	4	7	24
14 Aug.							
15 Aug.							
16 Aug.							
17 Aug.							
18 Aug.	17.69	1615–19150	1		3		4
19 Aug.			9	8	7	4	28
20 Aug.	2.23	1600–1730				3	3
Total			109	119	33	64	325

Meanwhile, the rostrum was also raised, but the maxilla was rarely extended. Furthermore, the male moved his head forward and backward every two seconds. The females did not move during copulation. The mating lasted between 1.40–5.52 min. It was usually terminated by the males (8 out of 10 cases). In four cases the males tried to remate, but the females pushed them away by using their hind legs.

Lathriovelia rickmersi/L. capitata. — The males of *L. capitata* did not interact with the females of *L. rickmersi* (10 tests). However, the males of *L. rickmersi* sometimes interacted with the females of *L. capitata*. When males of *L. rickmersi* were placed in bamboo cups containing *L. capitata* females the results were as follows (n = 15): In four tests there was no reaction. In four other tests the males moved their abdomen up and down and the female generated vibrating movements of the body (like in *L. capitata* males), but there were no further interactions. In three tests the *L. capitata* female approached the *L. rickmersi* male and chased him away. Subsequently, the female produced vibrating body movements or groomed herself. If the male returned to the water surface he was chased away again. Finally, in four tests the *L. rickmersi* male climbed on the *L. capitata* female and tried to copulate. In one case the “copulation” lasted 1 min 15 s, in one case 31 s, and in two cases there were several short copulation attempts. In all cases the female immediately tried to push the male away with one or both hind legs. Sperm transfer was not verified. After separation both individuals groomed themselves. In 10 further experiments *L. capitata* females were place in bamboo cups containing *L. rickmersi* males, but there was no interaction.

Agonistic Behaviour, Territoriality

Males. — Two *L. rickmersi* males (usually different size) were placed in a water-filled bamboo cup. In 34 out of 54 experiments the males remained passive until the end of the observation period (1.5 h). In 20 tests clear interactions could be observed: In eight tests fighting occurred and the larger males expelled the smaller ones from the water surface. In seven tests the attacked male pushed the approaching male away with his hind leg until the attacks ceased. In three cases the larger male climbed up on the smaller male and exhibited behavioural patterns similar to mating behaviour. Finally, in two cases the males approached each other but there were no further interactions.

If the males were fighting, they showed the following behavioural patterns: One male was more active and revolved around the other male. From time to time he stopped and moved his abdomen up and down, thus causing visible vibrations of the water surface. Subsequently, the active male tried to put his forelegs on the back of the other male and climb up or push the other male down. If the attacking male approached from behind the passive male defended himself by raising the rear end of his abdomen. If the fighting was intensive (especially in large males having about the same size) they pushed their bodies against each other, thus gradually rising up until the attacking male was standing on his stilted hind legs and the attacked male did a head stand. Subsequently, they both fell on the water surface and laid on their sides, with the attacking male embracing the abdomen of the other male. If the male attacked from the front, both males gradually raised up facing each other until both were standing on their stilted hind legs and then fell down.

The fighting sequences were usually repeated several times. The succumbed male fled to the bamboo wall and the victorious male remained on the water surface below and moved his abdomen up and down. Sometimes, grooming movements occurred between fighting sequences, but they were most intensive after the fighting was terminated.

In *L. capitata* males we conducted 10 tests on agonistic behaviour. In all cases the males produced signals by trembling movements of their body. Fighting occurred just in two cases and was not as intensive as in *L. rickmersi*. The attacked male defended himself by raising a leg (Fig. 12). After fighting both males remained on the water surface. There was another peculiar movement observed in *L. capitata* males: the body of the bugs moved to the right or left side and the legs were sliding on the water surface following the movements of the body.

Females. — Two females of *L. rickmersi* were placed together in one bamboo container (n = 10), but there was no interaction. When two females of *L. capitata* were placed together (n = 10) their bodies were strongly vibrating like in males. They revolved around each other and sometimes touched the legs or antennae of the opponent, but fighting was not observed. The interactions between the females lasted 15–43 min. After that, both females remained on the water surface and did not move. Like in males, we observed occasional sliding movements of the whole bugs to the left or right.

Interspecific aggressive interactions. — Males of *L. rickmersi* and *L. capitata* were placed in a bamboo cup and observed for 2.5 h (n = 15). In three tests the males did not interact. In nine tests the male of *L. capitata* walked repeatedly towards *L. rickmersi* male. The *L. rickmersi* male stayed near the bamboo wall and did not move. In three tests aggressive encounters were observed, but there was no intensive fighting: the *L. capitata* male just walked towards the *L. rickmersi* male which immediately fled to the bamboo wall.

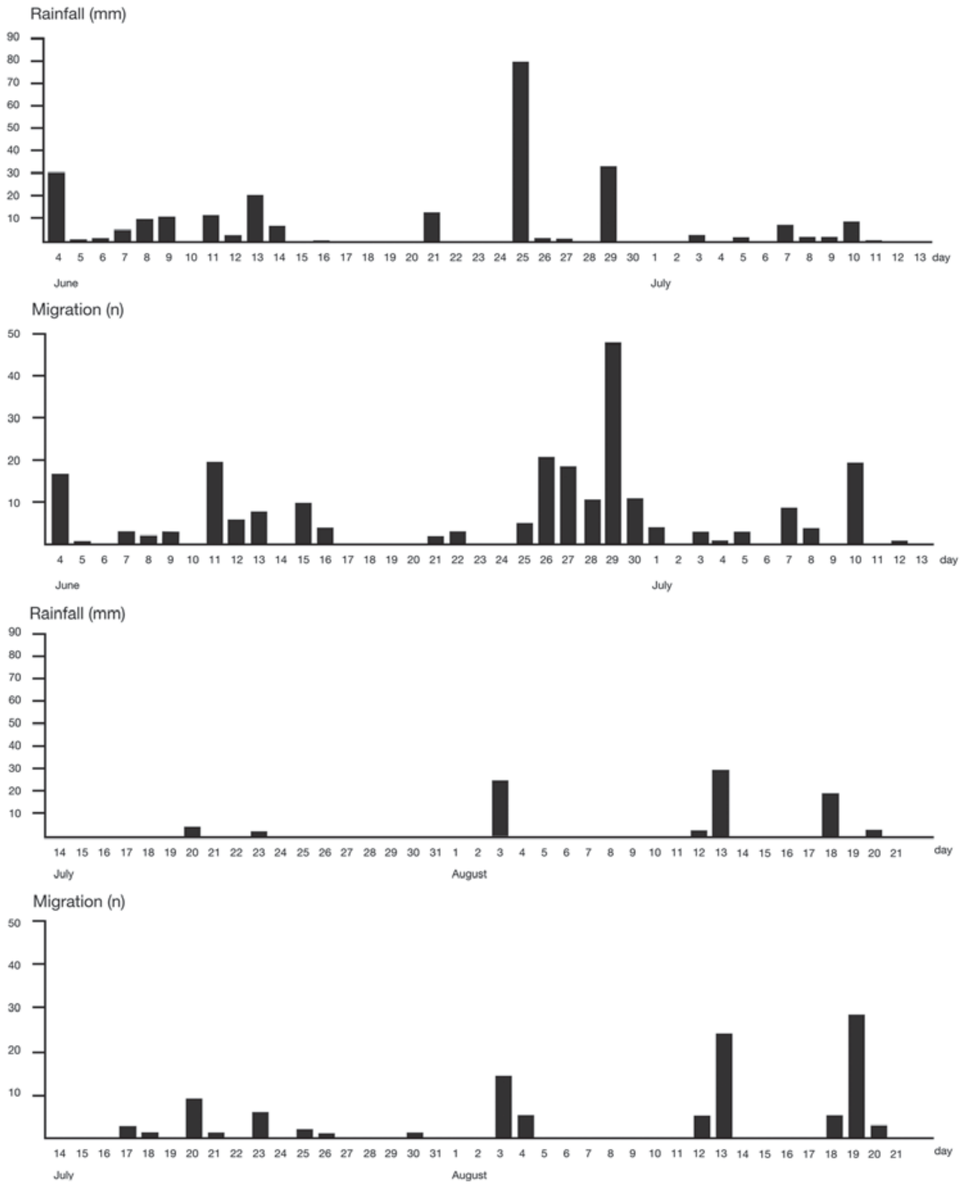

Fig. 10. Number of migrating *L. rickmersi* plotted against rainfall during the Long-Term Experiment 2 (100 internodes observed).

Table 4. Number of eggs deposited by *L. rickmersi* in the experimental internodes during the first four weeks of the Long-term Experiment 2. The 100 observed experimental internodes were consecutively numbered from 1–100. We also recorded whether any males or females were present in the internodes containing the eggs.

Culm No.	Internode No.	Date	Number of Eggs	Adults	Male and Female Together Since
1	1	16 June	2	1 female	
	2	16 June	1	2 females	
	5	16 June	2	2 females	
	6	20 June	1	1 female	
2	20	9 June	1	1 female	
3	25	16 June	1	1 female, 1 male	17 days
4	36	23 June	12	1 female	
	38	25June	2		
	39	19 June	1	1 female	
5	41	23 June	4		
	42	24 June	1	1 female, 1 male	14 days
	43	16 June	5	1 female	
	44	18 June	4		
	47	24 June	2	1 female	
6	60	20 June	7	2 females, 1 male	9 days
7	61	23 June	2	females	
	62	23 June	1	1 female, 1 male	10 days
	63	14 June	1	1 female	
	64	21 June	1	1 female, 1 male	8 days
	70	22 June	3	2 females	
8	71	10 June	1		
	72	27 June	2	1 female	
	73	20 June	2		
	74	25 June	1	1 female	
	75	19 June	1	1 female	
	76	25 June	1	1 male	
	77	19 June	1	1 female	
	78	19 June	1	2 females	
	79	30 June	1	1 female, 1 male	4 days
	80	21 June	1	1 female	
9	84	19 June	3	1 female	
	89	17 June	2	1 female	
10	91	22 June	1	1 female	
	93	26 June	2	1 female	
	95	27 June	1		
	96	25 June	1		

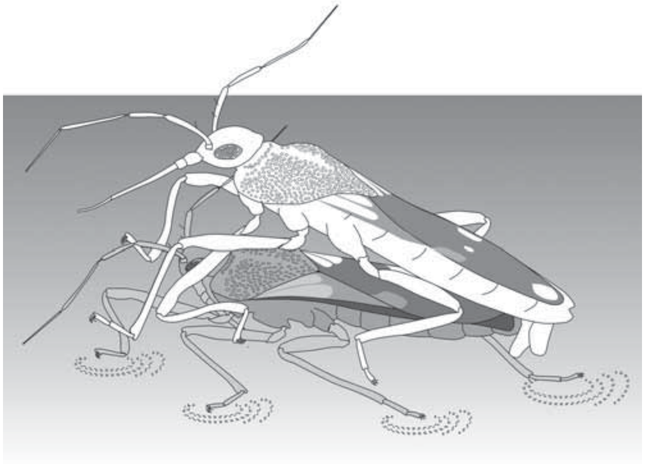

Fig. 11. Copulation in *L. rickmersi*. The forelegs of the male embrace the thorax of the female and the hind legs rest laterally on the abdomen. The middle legs of the male are raised and stretched forward towards the female antennae. The male rostrum is also raised and the maxilla extended.

Interactions of females of *L .rickmersi* and *L. capitata* were tested in 13 experiments. In four tests the females met on the water surface but did not interact. In eight tests *L. capitata* females slowly approached *L. rickmersi* females and then suddenly attacked them with raised forelegs. The *L. rickmersi* females immediately fled and climbed on the bamboo wall. If the females returned to the water surface, they were attacked again. In one test the *L. rickmersi* female approached the *L. capitata* female and touched her body with her forelegs. The *L. capitata* female moved backwards and raised her hind leg for protection. After that both females remained motionless on the water surface for 1 h.

Life cycle: Eggs, nymphs, adults

Eggs. — In both *Lathriovelia* species eggs were laid superficially and lengthwise on the submerged part of the bamboo wall, close below the water surface. They were whitish and oval-elongate. In *L. rickmersi* the median of the egg length was 0.79 × 0.3 mm (n = 10). The eggs were usually laid singly, but sometimes 2–3 eggs were found close to each other. In the laboratory, one *L. rickmersi* female laid 25 eggs. Usually 1–3 eggs were deposited in one internode, but sometimes we recorded up to twelve eggs (Table 4).

Sometimes two or even three females of *L. rickmersi* were found together and probably laid their eggs in the same internode. In *L. rickmersi* the duration of the incubation period in the laboratory was 10–16 days (median = 13, n = 37) and in *L. capitata* 13–14 days (median = 14, n = 10) (Table 5, Figs. 14, 15).

Nymphs. — We have compared the morphological characters of *L. rickmersi* nymphs (Fig. 13) and measured their body segments (Table 5) in order to discriminate the different nymphal stages. The nymphs of *L. rickmersi* and *L. capitata* were difficult to distinguish. In the following we describe the main differences between the five nymphal stages of *L. rickmersi*:

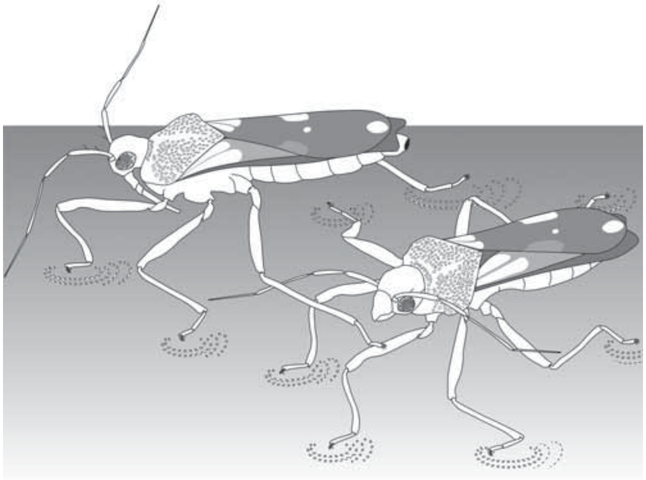

Fig. 12. Agonistic behaviour in *L. capitata*. The upper male has raised his left hind leg and pushes away the attacking male.

The first instar nymph was about 0.69 mm long (median of 5 measurements, see Table 5), the pronotum was short, while the meso- and metanotum were both longer. The second instar nymph was only slightly longer than the first (0.74 mm). However, the proportions of the thorax were different: both the pronotum and mesonotum were longer than the metanotum. The third instar nymph was difficult to discriminate from the preceding stage, but it was distinctly larger than the second nymph (ca. 1.32 mm) and the protruding margins of the abdomen, meso- and metathorax were distinct and appeared darker. The fourth instar nymph was easily distinguishable form the earlier stages by the occurrence of mesothoracic wing pads which did not reach the caudal margin of the metanotum. In the fifth instar nymph the mesothoracic wing pads extended posteriorly as broad lobes which covered the metathoracic wing pads (Fig. 13).

The duration of the nymphal stages of *L. rickmersi* and *L. capitata* is presented in Table 6. In laboratory-bred *L. rickmersi* and *L. capitata*, the second instar nymph was the shortest and the fifth instar nymph the longest. Specimens reared in the field developed slower than specimens in the lab and variation was larger. The development of the males was slightly longer than the development of the females. However, this difference was not significant (U-Test Mann and Whitney). The development from the egg (including incubation period) to the emergence of the adult took on average 61 days in *L. rickmersi* and 67.5 days in *L. capitata* (Figs. 14, 15).

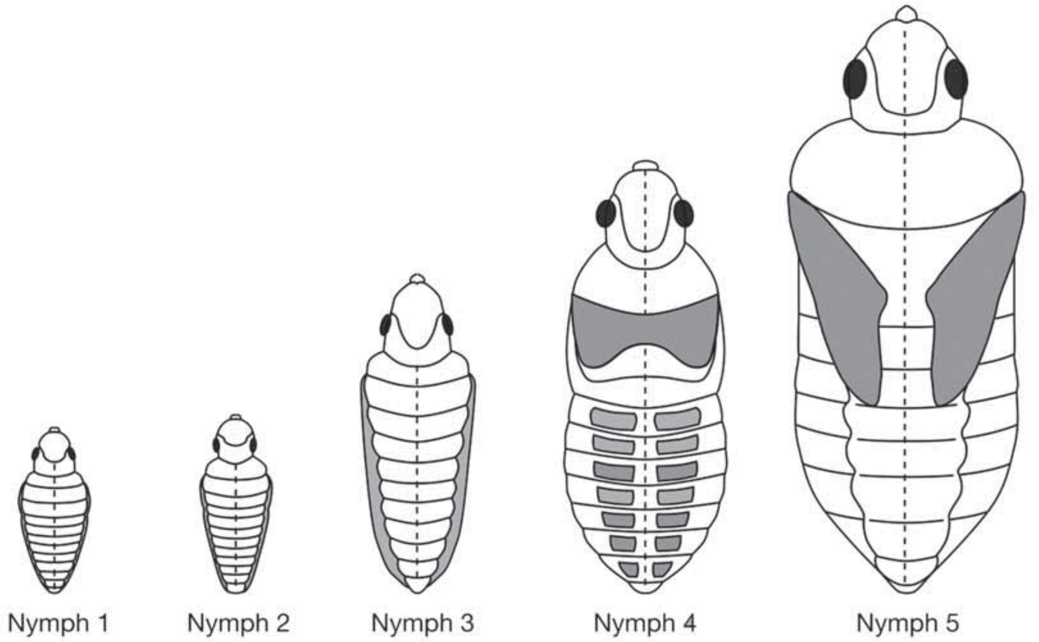

Fig. 13. Nymphs of *L. rickmersi:* comparison of relative sizes and morphological differences.

Table 5. Body measurements of the five nymphal instars of *L. rickmersi* reared in the laboratory. In the table we present the median of five measurements for each nymphal instar in mm.

Lathriovelia rickmersi	**Nymph 1**	**Nymph 2**	**Nymph 3**	**Nymph 4**	**Nymph 5**
Body					
Length	0.69	0.74	1.32	1.81	2.44
Width	0.33	0.36	0.61	0.83	1.03
Head					
Length	0.20	0.22	0.32	0.39	0.42
Width (with eyes)	0.24	0.26	0.39	0.50	0.60
Eye length	0.9	0.9	0.15	0.15	0.22
Proboscis length	0.36	0.47	0.54	0.73	0.95
Antenna					
Antennal distance	0.17	0.19	0.30	0.35	0.42
1st segment	0.13	0.17	0.23	0.29	0.41
2nd segment	0.11	0.16	0.19	0.21	0.32
3rd segment	0.17	0.28	0.34	0.45	0.56
4th segment	0.34	0.40	0.43	0.49	0.54
Total length	0.75	1.01	1.18	1.44	1.83
Foreleg					
Trochanter	0.12	0.16	0.19	0.24	0.26
Femur	0.30	0.41	0.55	0.69	0.91
Tibia	0.25	0.33	0.43	0.57	0.74
Tarsus	0.14	0.18	0.21	0.28	0.35
Total length	0.81	1.08	1.32	1.78	2.26
Middle Leg					
Trochanter	0.12	0.16	0.21	0.24	0.28
Femur	0.32	0.44	0.56	0.74	0.97
Tibia	0.29	0.40	0.50	0.67	0.86
Tarsus	0.16	0.20	0.24	0.32	0.45
Total length	0.89	1.2	1.51	1.97	2.56
Hind Leg					
Trochanter	0.16	0.17	0.22	0.26	0.33
Femur	0.36	0.50	0.64	0.87	1.12
Tibia	0.41	0.53	0.7	0.89	1.15
Tarsus	0.19	0.23	0.28	0.36	0.47
Total length	1.12	1.43	1.84	2.38	3.07

In Malaysia, nymphs of *L. rickmersi* were recorded throughout the year (Table 7), while in North Thailand we did not find nymphs in March and April (hot season). In horizontally placed internodes (larger water surface) there were usually more *L. rickmersi* nymphs per internode than in upright, living internodes.

Adults. — *L. capitata* males were on average slightly smaller than females (males 4.08–5.59 mm, n = 22; females 4.28–5.62 mm, n = 21) and *L. rickmersi* males considerably larger than females (males 4.0–5.81 mm, n = 92; females 3.44–4.56 mm, n = 67). In *L. rickmersi* the sex ratio was always male-biased. During the Long-Term Experiment 1 the ratio of males to females in 100 internodes was as follows: 1 Jul., 36:32; 1 Aug., 40:34; 1 Sep., 67:43; 1 Oct., 77:34; and 1 Nov., 104:53. In the course of the succession the sex ratio shifted towards the males.

We usually recorded one *L. rickmersi* male per internode, but sometimes there were two or occasionally three. During the Long Term Experiment I the ratio of one male: two males: three males per internode was as follows: 1 Jul., 25:5:0; 1 Aug., 25:5:0; 1 Sep., 49:9:0; 1 Oct., 59:6:0; 1 Nov., 57:12:8. If two males were found in one internode, they had usually different sizes (in 32 cases the males had different sizes, in 7 cases they were both large and had about the same size).

Freshly emerged *L. rickmersi* adults stayed in their internodes for a while and then dispersed to other internodes. In four laboratory observations mating was observed 2–3 days after emergence (2; 2; 3; 3 days) and the first eggs were laid 6–8 days after copulation (6; 6; 7; 8 days).

If the internode water evaporated *L. rickmersi* individuals remained in the dry internodes for at least two weeks. However, the debris found at the bottom of the internodes was usually humid for a long time, especially in internodes possessing small entrance holes. In the laboratory, single *L. rickmersi* individuals were kept alive for up to 7 months. Adults of *L. rickmersi* and *L. capitata* did usually not occur in the same bamboo internode.

Baptista: Habitat, Food, Voltinism and Wing Polymorphism

In north Thailand DK observed three *Baptista* species in the field: *Baptista hoedeli* Zettel, *B. digitata* Andersen, and *B. gestroi* Andersen (Fig. 16).

Baptista hoedeli occurred between gravel and rocks at the margins of mountain streams (2–4 m wide, canopy above stream not closed, elevation ca. 900 m). In the daytime the bugs were hiding between stones. In the night time they hunted insects on the water surface in areas of low velocity. The only prey item retrieved in the field was one Collembola specimen.

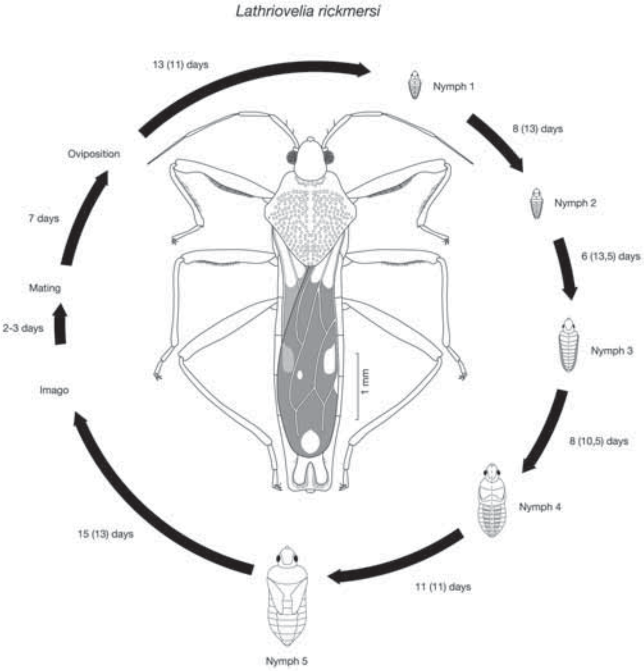

Fig. 14. Life cycle of *L. rickmersi*. Developmental time in the laboratory is given in days (in brackets: developmental time in the field).

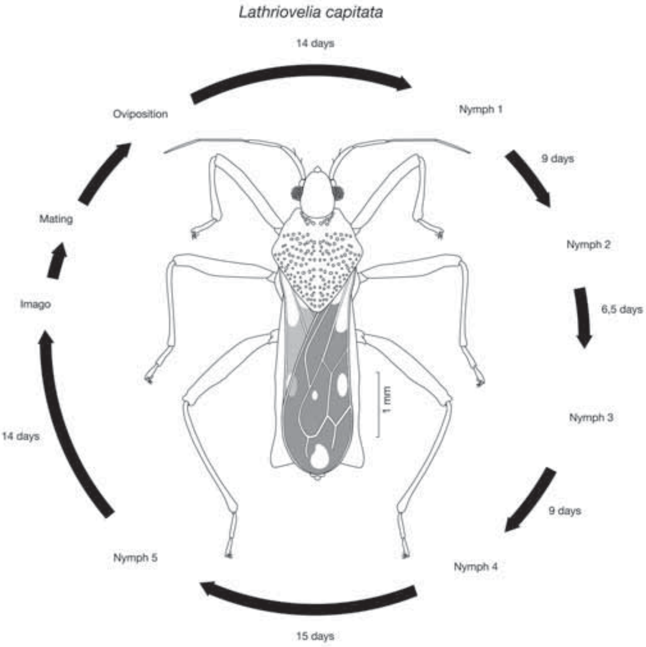

Fig. 15. Life cycle of *L. capitata*. Developmental time in the laboratory is given in days.

B. hoedli specimens were found from the beginning of November until the end of April, i.e., during the cold and hot seasons. In the rainy season, when the water level was high and the water flow fast, *B. hoedli* was not detected. Larvae were collected between 14 Nov. (2nd or 3rd stage) and 22 Apr. (up to the 5th stage) (Table 7). Fifty two adults were winged (31 males and 21 females) and 25 specimens lacked wings (13 males and 12 females) (Table 8).

Baptista digitata inhabited spring-fed wet ground, which gave rise to small streams. The specimens stayed in micro-pools or on the wet ground. In steep valleys the seeps also occurred right beside the margins of streams. In that case *B. digitata* always stayed in the seep area and did not move to neighbouring margins of streams. The wet areas colonised by *B. digitata* covered few to many square meters and often contained rust coloured deposits. The spring habitat was very stable, i.e., the water flow did not change throughout the year. Two prey items were retrieved in the field. They both belonged to Collembola.

B. digitata specimens were found in March, April, June, and September–November, i.e. in the rainy season, as well as in the cold and hot seasons. Larvae were collected in March (small and large sizes up to the last instar), April (middle-sized up to last instar), June (1st stage and middle-sized specimens) and November (small to middle-sized specimens) (Table 7). Most *B. digitata* were apterous (226 specimens). One male and one female were macropterous (Table 8).

Baptista gestroi occurred in rain-fed limestone rock-pools and one record was from a tree pool, i.e., a pool located between buttresses on a very large, fallen tree. All habitats were located far away from streams (several hundred meters or more). The rock-pools and the tree pool were about 1 m long and 50 cm wide. The rock-pools were often partly hidden in the rock. One rock-pool was regularly checked every year and contained *B. gestroi* adults and nymphs in 12 consecutive years. The fallen tree containing the tree-pool pool was checked during three consecutive years, but *B. gestroi* adults and nymphs were only present in the third year (after that the tree was burnt down by locals). We have regularly checked water-filled tree holes of upright trees, but we have never found *B. gestroi* in these small water bodies. Nineteen prey items were retrieved from *B. gestroi* adults and nymphs inhabiting rock-pools: 13 Collembola, 2 Psocoptera, 1 Psychodidae (Diptera), 1 Ceratopogonidae (Diptera), 1 unidentified fly and 1 small Coleoptera.

B. gestroi inhabited rock-pools as long as they contained water, i.e. probably between May (first record at the beginning of June) and November. In November the rock pools dried up and *B. gestroi* specimens left the habitat. The rock-pools remained dry for about 5 months and filled up with water in

Table 6. Incubation period of the embryo and developmental rates of the five nymphal instars of *L. rickmersi* and *L. capitata* in days. In *L. rickmersi* we present separate data for specimens reared in the laboratory (mixed sexes; only males; only females) and in the field (mixed sexes). *L capitata* was only reared in the laboratory (mixed sexes). n = number of specimens investigated.

		Embryo	Nymph 1	Nymph 2	Nymph 3	Nymph 4	Nymph 5	Total
L. rickmersi	**LABORATORY** **Mixed sexes**							
	Days	10–16	6–12	4–8	6–12	8–18	11–25	45–91
	Median (d)	13	8	6	8	11	15	61
	n	37	52	51	50	39	21	250
	Males							
	Days	11–14	6–12	5–8	7–9	9–12	13–20	51–75
	Median (d)	13	8	6	8	11	16	62
	n	7	7	7	7	7	7	42
	Females							
	Days	11–16	6–10	4–7	6–9	8–15	13–25	48–82
	Median (d)	13	7	5	7	9	14	55
	n	12	12	12	12	12	12	72
	FIELD Mixed sexes							
	Days	6–16	6–19	5–16	5–17	8–22	8–34	39–124
	Median (d)	11	13	13.5	10.5	11	13	72
	n	26	11	11	10	14	18	90
L. capitata	**LABORATORY** **Mixed sexes**							
	Days	13–14	6–12	5–7	7–10	9–15	14	54–72
	Median (d)	14	9	6.5	9	15	14	67.5
	n	10	7	6	5	5	1	34

Table 7. Number of *Baptista* nymphs collected throughout the year and their approximate instar stages. S = small nymphs (1st–2nd stage), M = middle–sized nymphs (3rd–4th stage), L = large nymphs (4th–5th stage). In *L. rickmersi* and *L. capitata* from Ulu Gombak only the presence of nymphs is indicated (several hundred nymphs belonging to different stages were observed during the long-term experiments in the field).

Month	*L. rickmersi*	*L. capitata*	*B. gestroi*	*B. digitata*	*B. hoedli*
Jan.	present	no data	habitat dry	no data	no data
Feb.	present	no data	habitat dry	no data	no data
Mar.	present	present	habitat dry	9 × M-L	4 × M-L
Apr.	present	present	habitat dry	30 × M-L	8 × M-L
May	present	present	no data	no data	no data
Jun.	present	present	2 × 1st stage	1 × 1st stage	high water level
Jul.	present	present	no data	no data	high water level
Aug.	present	present	no data	no data	high water level
Sep.	present	present	1 × 1st stage	no data	high water level
Oct.	present	present	4 × M-L	no data	no data
Nov.	present	present	3 × M-L	13 × S-M	2 × M
Dec.	present	present	habitat dry	no data	no data

the next rainy season. Nymphs were found at the beginning of June (1st stage), in September (1st stage), October (small to middle-sized nymphs) and in November (large nymphs) (Table 7). In general, *B. gestroi* adults were macropterous (39 specimens), but one male and one female collected in November were micropterous (Table 8).

DISCUSSION

Habitat. — Our investigations show that *Lathriovelia capitata* and *L. rickmersi* were specialised inhabitants of bamboo. *L. capitata* usually occurred in living bamboo culms, while *L. rickmersi* was found in both living and decaying bamboo culms. The two species did not share the same internodes, probably because of inter-specific competition. In laboratory experiments *L. capitata* males and females always expelled *L. rickmersi* from the water surface. It is not clear why *L. capitata* is confined to Peninsular Malaysia. We suppose that *L. capitata* is more susceptible to drought and therefore prefers living internodes with small holes (less evaporation) and geographic regions with humid climate.

Feeding biology. — *Lathriovelia rickmersi* and *L. capitata* were opportunistic sit-and-wait predators and scavengers. They detected struggling prey by water surface vibrations

Table 8. Number of *Baptista* specimens belonging to different wing morphs. M = macropterous specimens, Mi = micropterous specimens, A = apterous specimens. In *L. rickmersi* and *L. capitata* several hundred individuals were observed during the long-term experiments in the field.

Month	***L. rickmersi*** (Bamboo)	***L. capitata*** (Bamboo)	***B. gestroi*** (Rock-Pool)	***B. digitata*** (Spring Area)	***B. hoedli*** (Stream Margin)
Jan.	M	M	habitat dry	no data	no data
Feb.	M	M	habitat dry	no data	no data
Mar.	M	M	habitat dry	44 A	9 M / 16 A
Apr.	M	M	habitat dry	72 A / 1 M	18 M / 7 A
May	M	M	no data	no data	no data
Jun.	M	M	2 M	25 A	high water level
Jul.	M	M	no data	no data	high water level
Aug.	M	M	no data	no data	high water level
Sep.	M	M	11 M	26 A	high water level
Oct.	M	M	17 M	4 A	no data
Nov.	M	M	9 M / 2 Mi	55 A / 1 M	25 M / 2 A
Dec.	M	M	habitat dry	no data	no data

or walked around and searched for dead insects or insect eggs. In the field springtails were the predominant prey and constituted almost half of the collected prey items (Fig. 7). Springtails were probably also the staple food of the *Baptista* species investigated in the present study. Other semi-aquatic bugs reported to feed on springtails belonged to *Microvelia* (see Pickard, 1978) and *Hydrometra* (see Lanciani, 1991).

Defensive behaviour. — Antipredator strategies observed in *Lathriovelia* involved cryptic coloration, hiding, catalepsy, escape and "expansion skating". Expansion skating is known from *Velia caprai* and some other veliids (Linsenmair & Jander, 1963; Andersen, 1976). The skating is initiated by ejecting saliva from insect's beak onto the water surface. The saliva lowers the surface tension of the water and the bug is sent skimming across the water surfaces at high speed. In contrast to the expansion skating described in other veliids *Lathriovelia* remained on the spot and only the surrounding objects were propelled away, i.e., the saliva was probably ejected centrally underneath the body.

Grooming. **—** Grooming occurred after contamination with dirt, after submergence, during intraspecific interactions or spontaneously. Wetted bugs predominantly groomed their legs, especially the tarsi (more than 60% of the total grooming sequences; Tables 1 and 2). The main function of the grooming was presumably to keep the hydrofuge hair layers of the legs clean and tidily arranged in order to prevent wetting. Some grooming patterns were only seen after feeding (grooming of the rostrum) or mating (intensive grooming of the tip of the abdomen).

During grooming the maxillae were often extended and swept over the tarsi. The maxillae probably smeared saliva over the legs, because we saw occasional colourless liquid droplets on the maxillae. Furthermore, the maxillae first touched the tarsi and then the tarsi groomed other parts of the body, thus implying a distribution of a secretion. We presume that the application of proteolytic saliva may kill microorganisms interfering with the hydrophobe properties of the hairs. An analogous behaviour is known from some water bugs: they use their antibiotic metathoracic secretions in order to kill microorganism growing on their hydrofuge hairs. The contamination of hydrofuge hairs with microorganisms leads to the wetting of the respiratory region, resulting in the loss of the respiratory air bubble, and, finally, drowning of the water bugs (Kovac & Maschwitz, 1989). Another or additional possible function of the saliva may be, that it acts as a detergent by lowering the surface tension (see expansion skating), thereby helping to remove particles attached to the body surface.

A remarkable behaviour observed in *L. rickmersi* and *L. capitata* was the occasional laying of the bugs on their backs or their sides (Fig. 8). Sometimes they also briefly placed their antennae on the water surface. A similar behaviour was observed by Rensing (1962) in *Hydrometra*, *Gerris* and *Velia* and was termed "bathing". Rensing (1962) induced bathing by transferring the bugs from polluted to clean water or by contaminating the bugs with chemicals or smoke. He interpreted bathing as a cleaning behaviour, i.e., during bathing dirt particles are removed from the body by adhering to the water surface.

Migration. — *Lathriovelia* individuals regularly migrated to new internodes. In the Long-Term Experiment 2 the frequency of incoming/outgoing females was larger than in males, although the sex ratio in the internodes was male biased. The females were probably visiting new internodes more often than males in order to lay eggs. In the lab one female laid 25 eggs, while in the field we usually found 1–3 eggs per internode (Table 6), i.e., the females apparently deposited their eggs in several internodes. In contrast, the males were territorial and more stationary, despite of miscellaneous migrating males, which were forced by rivals or other circumstances to leave their internodes.

Most newly arrived or departed specimens were recorded immediately after rainfall (Long-Term Experiment 2; Fig. 10 and Table 3). However, if rain occurred in the night time the bugs moved to new habitats during the next day, i.e., they apparently did not fly in the dark. Heavy and prolonged rainfall appeared to have a stronger effect on the migration than light and brief rainfall (Fig. 10). The benefit of linking migration with rainfall may be that after rain more internodes (including internodes with newly created holes) are filled up with water and available for colonisation.

Migrating individuals of *L. rickmersi and L. capitata* carried mites attached to their rostrum, legs or eyes (Fig. 5). The mites belonged to *Tensiostoma veliaphilum*, a specialised inhabitant of the water surface in bamboo internodes (Wurst & Kovac, 2003).

Mating system. — Detailed studies of mating systems in Gerromorpha are only available for water striders (Gerridae). Water striders exhibit two main types of mating behaviour (see Arnqvist, 1977): Type I mating system is more common and characterised by strong conflicts between the sexes and conspicuous pre- and post copulatory struggles. Type II mating system differs from Type I in that males are territorial, produce ripple signals during courtship and there is much less apparent conflict. Pure Type II matings have been reported from species in the genus *Rhagadotarsus* and *Aquarius* (Wilcox, 1972; Hayashi 1985), but there are also intermediate systems (see Arnqvist, 1977).

The mating system in *Lathriovelia* was similar to the Type II mating system of Gerridae, because the males were territorial, produced vibrational signals and there was not much conflict between males and females. The vibrational signals were probably used to ascertain the sex of the approaching individual (no reaction from the approaching individual meaning: female) and as courtship signals. The males just jumped on the females and dismounted after sperm transfer. During copulation *L. rickmersi* males moved their mid legs repeatedly forward and backward, touching the female antennae. A similar behaviour was observed in copulating *Gerris najas* (Sattler, 1957).

The pre- and post-copulatory struggle between the water strider sexes especially in the Type I matings result from sexual asymmetry in the relative interests in matings (overview Rowe et al., 1994; Arnqvist, 1997). The males are "interested" in frequent matings, because their reproductive success is associated with the number of females they mate. Frequent rematings are also advantageous, because the last male to mate will fertilise the majority of females' eggs. Females are reluctant to mate frequently, because they can store viable sperm and matings involve high costs to females due to energetic expenditure and increased predation risk. On the other hand, resisting mating can also be energetically costly and increase the risk of predation. Furthermore, fleeing from males can displace females from prime foraging areas. Therefore, females act to balance these costs by varying their reluctance to mate.

Remarkably, in *Lathriovelia* there was no pre-copulatory and just occasional post-copulatory struggle between males and females. The lack of pre-copulatory struggle is probably connected to a high cost for females when rejecting a male. Males effectively controlled the egg-laying/feeding sites and the females could not avoid male harassment without leaving the internode. Leaving the internode would mean to fly to a new habitat (after next rainfall), which would be energetically costly. Besides, the new internode would probably be occupied by another male. On the other hand, the males did not try to remate frequently, probably because visits of other males were relatively scarce in the internode habitat (low risk of sperm displacement).

Males of *Lathriovelia* were territorial and defended the water surface of their internodes. They generated vibrational signals, which were produced in the same manner as signals during courtship. In *L. rickmersi* fighting was more intensive than in *L. capitata* and the succumbed male fled to the bamboo wall. He usually left the internode after 1–3 days, if he was repeatedly repelled from the water surface. Smaller males, which resembled females by size and behaviour (i.e., no reaction when the rival produced water surface vibrations) were tolerated in the internodes or treated as females (attempted copulations). The small males had apparently switched to alternative tactics ("sneaking") in order to achieve copulations. The territorial behaviour explains the distribution of males in the experimental internodes. In general, we found only one male per internode, but if an internode contained two males, there was usually one large and one small male.

In Gerromorpha the females are usually larger than males, i.e., there is a pronounced sexual size dimorphism (Andersen, 1982). In contrast, the territorial *L. rickmersi* males were larger than females. In *L. capitata* both sexes were territorial and had about the same size. It is conceivable, that territoriality may affect size on an evolutionary time scale as a consequence of strong competition, as was suggested by Vepsäläinen (1985).

According to the classification of mating systems proposed by Emlen & Oring (1977) and Thornhill & Alcock (1983), *Lathriovelia* exhibits a resource defence polygyny. This type of mating system is supposed to evolve when resources required by females are patchily distributed and relatively limited, the individual males are capable of controlling the access to them and the operational sex ratio is male biased.

The resources controlled by the males of *Lathriovelia* were the oviposition sites (bamboo wall near the water surface), as well as the food sites (water surface). The internodes were patchily distributed and apparently limited, because in our long term experiments almost all experimental internodes were colonised after a few weeks (Fig. 9). The water surface area was small (ca. 7 cm in diameter in upright culms of *G. scotechinii*) and therefore defensible with low energy expenditure by the males. Finally, the sex ratio was always male biased (see Results). The males allowed females to oviposit only after they had mated with them. In this way the males ensured, that the eggs laid in their territory have been inseminated by them. Thus, the mating system of *Lathriovelia* is similar to mating systems found in some terrestrial insects living in patchy habitats, for example in some Diptera (Tephritidae: Kovac et al., 2010).

Life cycle. — The postembryonic development of *L. rickmersi* and *L. capitata* lasted 61 and 67.5 days, respectively (see Figs. 14, 15). That is rather long as compared to the duration of the postembryonic development in some other Veliidae. Andersen (1982) listed between 14.2 and 48 days for *Microvelia*, *Halovelia*, *Rhagovelia*, *Paravelia*, and *Velia*. In the field the development of *L. rickmersi* lasted longer than in the laboratory (72 days), probably due to the lower temperature and less food available in the field. The development of one complete *L. rickmersi* generation probably lasted 2.5–3 months in the field (pre-reproductive period ca. 10 days, see Fig. 14).

***Habitat and voltinism in* Baptista.** — In three *Baptista* species investigated in the present study there was a lack of regular collections throughout the year and the numbers of collected specimens were relatively low. Nevertheless, we think that some conclusions can be drawn by comparing their habitats, voltinism (number of generations occurring in a year) and wing polymorphism (different wing morphs in one generation).

B. hoedli was found along margins of streams between November and April. In the rainy season (May to October) we did not find any specimens due to the high water level. The specimens were probably hiding and did not produce any nymphs during that period of time. The first nymphs of *B. hoedli* were found in November (Table 7). They were mid-sized (3rd larval stage?). In March and April the larvae were mid-sized to large. If we take the duration of *L. rickmersi* development as basis for our calculation (about 3 months, see above), then *B. hoedli* is probably bivoltine.

E. gestroi occurred in water-filled rock pools (and a tree-pool) between June and November, i.e., only in the rainy season. The first nymphs were collected at the beginning of June (1st–2nd stage, Table 7). In September 1st nymphal instars were also present, while in October the nymphs were small to middle-sized and in November large (4th–5th stage). This data suggest that *E. gestroi* is bivoltine during the rainy season. In the dry season *B. gestroi* was not present in the rock-pool habitat. However, Andersen (1989) mentioned a *B. gestroi* specimen collected in North Thailand in a small stream. This indicates that this species survives the dry season in the humid stream environment. The specimen mentioned by Andersen (1989) was found in May, i.e., during the dispersal period when the rock-pools are colonised. Thus, *E. gestroi* is either bivoltine or multivoltine, if there is an additional generation at the margins of streams.

Adults of *B. digitata* were found on spring-fed wet ground at different seasons of the year. They were apparently present in this habitat throughout the year. Different nymphal instars occurred in March/April (hot season), June (rainy season) as well as in November (cold season). This indicates that *B. digitata* is multivoltine.

In summary, *Baptista* species living in habitats which are stable throughout the year were probably multivoltine (*B. digitata*), while species living in temporarily unstable habitats possessed two (*B. hoedli*) or two to three generations (*B. gestroi*). *Lathriovelia* species investigated in the Ulu Gombak area were mulitivoltine (four generations possible), probably because water-filled internodes were available throughout the year and the developmental conditions (temperature, etc.) were always favourable in this tropical environment.

***Wing polymorphism in* Baptista *and* Lathriovelia.** — Most semi-aquatic bugs exhibit a distinct polymorphism of their flight apparatus, which is called wing polymorphism. Some specimens are long-winged (macropterous morph), others lack wings (apterous morph) or possess more or less shortened wings (brachypterous morph: fore wings reaching tergum 3 to 6; micropterous morph: fore wings not surpassing tergum 2; see Andersen, 1982). Wing-length variation is regulated by an interaction of genetic, ontogenetic and environmental effects like temperature, photoperiod, population density, food availability and desiccation of the habitat (overview Spence & Andersen, 1994; Ditrich et al., 2008).

The adaptive significance of wing polymorphism has been discussed by several authors (Brinkhurst, 1959; Andersen, 1973, 1982; Vepsäläinen, 1978; Spence & Andersen, 1994; Ditrich et al., 2008; and others). Long-wingedness is considered as an optimal strategy for species living in unstable habitats, i.e., when frequent colonisations of new habitats are necessary. In stable habitats flight is less important and short-winged individuals prevail. The benefit of short-wingedness is supposed to be, that more energy can be allocated into reproduction (for example, growth of ovaries) rather than building up flight muscles.

One of the better known cases of wing polymorphism is the seasonal dimorphism in bivoltine species of *Gerris* occurring in temperate regions. In the summer generation a large proportion of specimens is apterous, while in the winter generation, which hibernates far away from water, the specimens are always or mostly macropterous. In tropical Gerromorpha detailed data on wing polymorphism are lacking.

Baptista species investigated in the present study were all wing dimorphic (Table 8), but the ratio of macropterous to apterous/micropterous specimens varied considerably:

B. hoedli specimens were either macropterous (52 specimens) or apterous (25 specimens). Their habitat, margins of streams, was an intermediate environment with respect to habitat stability. In the cold and dry seasons there was a low and constant water flow (stable conditions) and the percentage of apterous specimens was relatively high (Table 8). In the rainy season the water level and flow often changed (unstable conditions) and the specimens collected at the beginning and the end of the rainy season (April, October) were predominantly macropterous.

In *B. gestroi*, 37 specimens were macropterous and two were micropterous. It was surprising to find micropterous specimens in the rock-pools, which were just drying up. The micropterous individuals would have hardly been able to reach another aquatic water habitat by walking, since the nearest stream was located several hundred meters from the rock-pool. In the European *Velia caprai* Ditrich & Papáček (2009) found that marked apterous specimens colonised newly established pools and ditches in the vicinity of streams, but only in an area of several tens of metres from the source sites. Therefore, we presume that the micropterous specimens of *B. gestroi* belonged to the first of the two generations possibly inhabiting the rock-pools, which does not migrate.

Finally, in *B. digitata* only two out of 226 specimens were macropterous. Their habitat, spring-fed wet ground, was stable throughout the year.

Our results confirm the correlation between habitat permanence or patchiness, voltinism and wing morph frequency in *Baptista* and *Lathriovelia*. Species living in stable environments (*B. digitata*) were usually apterous, species living in an intermediate habitat (*B. hoedli*) possessed a large proportion of macropterous specimens in the generation occurring during the unstable period (rainy season) and a large proportion of apterous specimens in the generation occurring during the stable period (dry season) and species living in a small and patchy habitat (*B. gestroi*) were predominantly macropterous.

L. capitata and *L. rickmersi* were always macropterous, which is a rare condition in Gerromorpha (Andersen, 1982). The reason for the loss of the apterous morph in *Lathriovelia* is probably, that *Lathrivelia* specimens frequently visit new internodes within every generation. There is no second generation developing in the same habitat like in *B. gestroi*,

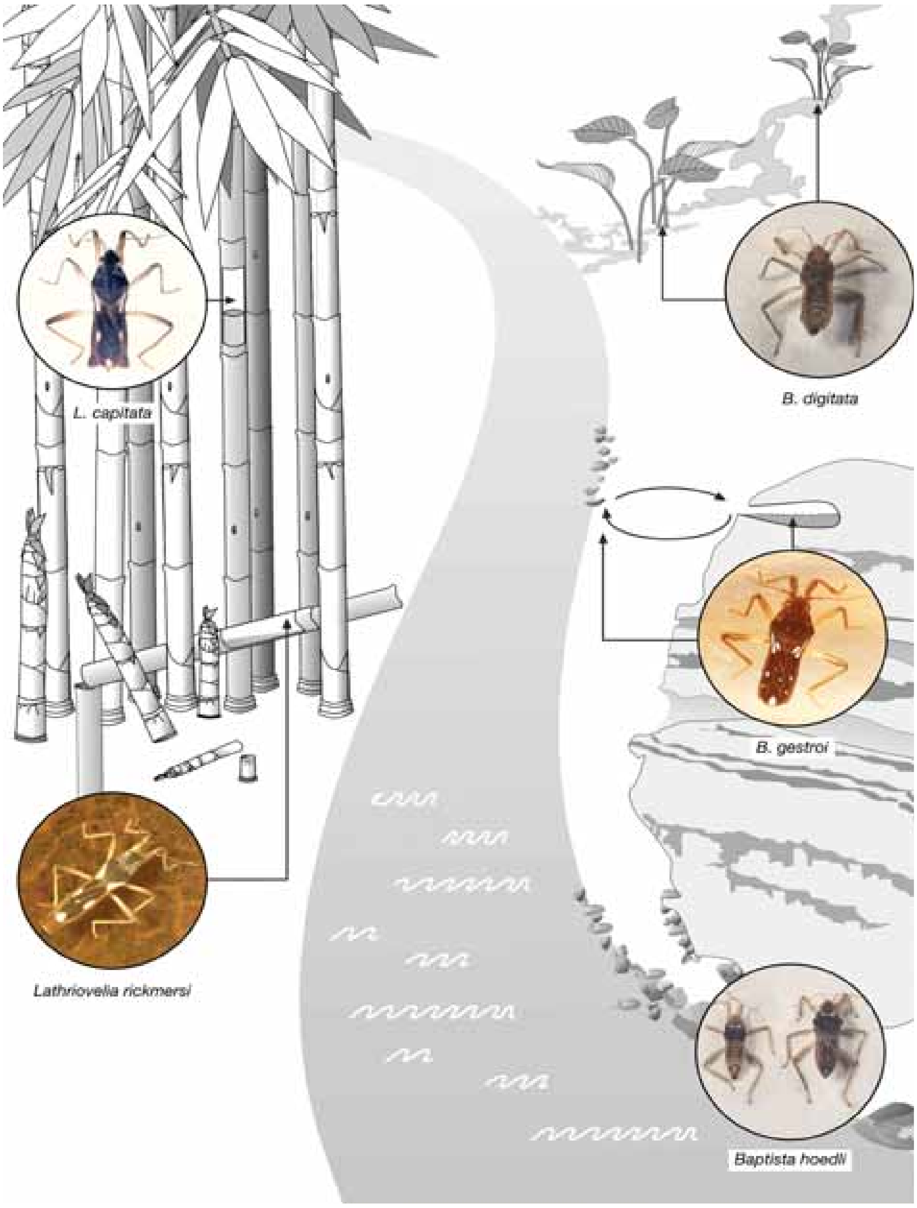

Fig. 16. Habitats of *Baptista* and *Lathriovelia* species: *B. hoedli* inhabits margins of streams; *B. gestroi* alternates between rock/tree-pools and margins of streams; *B. digitata* lives on wet, spring-fed ground; *Lathriovelia capitata* inhabits internodes of upright bamboo culms; and *L. rickmersi* internodes of decaying and living bamboo culms. *Baptista* living in stable habitats usually lacked wings (*B. digitata*), species living in unstable/temporary habitats were usually winged (*B. gestroi*) and species living in intermediate habitats possessed both morphs. All species presented were found in the same study area in north Thailand except of *L. capitata*, which only occurs in Peninsular Malaysia.

because in bamboo internodes the water surface is too small for supplying food for the next generation.

***Evolutionary trends in* Baptista *and* Lathriovelia.** — (See Fig. 16). The ancestral habitat of *Baptista*/*Lathriovelia* was probably the margin of streams, which is inhabited by most species of present-day *Baptista* or genera sharing some primitive characters with them (for example, *Neoalardus*; Zettel, 1998). We presume that the ancestors of *Baptista*/*Lathriovelia* were lacking modifications of the fore femur and abdominal sternites, that they exhibited wing dimorphism and possibly fed on springtails. Springtails may have been an important food source for the ancestors of Gerromorpha in general, because the humid terrestrial and/or marginal aquatic habitats inhabited by springtails are supposed to be the ancestral habitats of most families of Gerromorpha, including Veliidae (Andersen, 1982). The occurrence of springtails may have been one of the selective forces for the colonisation of new habitats by *Baptista*/*Lathriovelia*.

In the ancestral habitat of *Baptista*/*Lathriovelia* (margins of streams) species of the *B. collaris* group evolved and in spring-fed wet areas, which are connected to streams, species of the *B. femoralis* group. Representatives of the *B. femoralis* group became predominantly apterous, but occasional macropterous specimens still occur and facilitate colonisation of distant habitats. The invasion of rock-pools probably began in rock-pools or on fallen trees in the vicinity of streams and resulted in the development of *B. gestroi*. Specimens of *B. gestroi* are predominantly macropterous and have to migrate to their ancestral habitat in the dry season (Fig. 16).

Lathriovelia species have invaded bamboo stands growing along streams. Initially, they probably colonised fallen bamboo culms with large holes and then living, upright bamboo culms. In *Lathriovelia* the short-winged morph has been lost, because frequent visits of different bamboo internodes are obligatory in every generation. *Lathriovelia* became independent of streams, because some internodes contain water throughout the year, at least in tropical areas, and *L. rickmersi* can survive temporary dry conditions.

Lathriovelia species have colonised a unique habitat among Gerromorpha. Some remarkable characteristics, for example, the loss of the wingless morph or the mating system are apparently connected to the properties of the internode habitat. The ability to starve, to survive draught or cannibalism are typical for animals living in small habitats like phytotelms (overview Kitching, 2000). *Baptista* species were regarded as rare, but the present study has revealed that they are in fact common in their special habitats and that *Baptista*/*Lathriovelia* are a suitable model system for comparative studies of various general ecological questions.

ACKNOWLEDGEMENTS

This paper is a contribution to Supplement No. 29 of the Raffles Bulletin of Zoology, marking the eightieth birthday of the Earl of Cranbrook (V). DK and MK gratefully acknowledge the support provided by Rosli Bin Hashim (University of Malaya) during their research stay at the UFSC and DK thanks Decha Wiwatwitaya (Kasetsart University, Bangkok, Thailand) for the support in Thailand. We also acknowledge the help of the UFSC staff, especially Bah Tera, the former main warden. DK thanks the “Deutsche Forschungsgemeinschaft” (DFG) for funding part of the work in Malaysia, and Eveline Junqueira, Frankfurt, for drawing the illustrations.

LITERATURE CITED

Andersen, N. M., 1973. Seasonal polymorphism and developmental changes in organs of flight and reproduction in bivoltine pondskaters (He. Gerridae). *Entomologica Scandinavica*, **4**: 1–20.

Andersen, N. M., 1976. A comparative study of locomotion on the water surface in semiaquatic bugs (Insecta, Hemiptera, Gerromorpha). *Videnskabelige meddelelser fra Dansk Naturhistorisk Forening i Kjobenhavn*, **139**: 337–396.

Andersen, N. M., 1982. *The Semiaquatic Bugs (Hemiptera, Gerromorpha). Phylogeny, Adaptations, Biogeography and Classification*. Entomograph 3, Klampenborg-Denmark. 455 pp.

Andersen, N. M., 1989. The old world Microveliinae (Hemiptera: Veliidae). II. Three new species of *Baptista* Distant and a new genus from the Oriental region. *Entomologica Scandinavica*, **19**: 363–380.

Arnqvist, G., 1997. 8. The evolution of water strider mating systems: causes and consequences of sexual conflicts. In: Choe, J. C. & B. J. Crespi (eds.), *The Evolution of Mating Systems in Insects and Arachnids*. Cambridge University Press. Pp. 146–163.

Brinkhurst, R. O., 1959. Alary polymorphism in the Gerroidea (Hemiptera-Heteroptera). *Journal of Animal Ecology*, **28**: 211–230.

Ditrich, T. & M. Papáček, 2009. Correlated traits for dispersal pattern: Terrestrial movement of the water cricket *Velia caprai* (Heteroptera: Gerromorpha: Veliidae). *European Journal of Entomology*, **106**: 551–555.

Ditrich, D., M. Papáček & T. Broum, 2008. Spatial distribution of semiaquatic bugs (Heteroptera: Gerromorpha) and their wing morphs in a small scale of the Pohořský Potok stream spring area (Novohradské Hory Mts.). *Silva Gabreta*, **14**(3): 173–178.

Emlen, S. T. & L. W. Oring, 1977. Ecology, sexual selection, and the evolution of mating systems. *Science*, **197**: 215–223.

Hayashi, K., 1985. Alternative mating strategies in the water strider *Gerris elongatus* (Heteroptera, Gerridae). *Behavioural Ecology and Sociobiology*, **16**: 301–306.

Kitching, R. L., 2000. *Food Webs and Container Habitats. The Natural History and Ecology of Phytotelmata*. Cambridge University Press. 431 pp.

Kovac, D. & U. Maschwitz, 1989. Secretion-grooming in the water bug *Plea minutissima*: A chemical defense against microorganisms interfering with the hydrofuge properties of the respiratory region. *Ecological Entomology*, **14**: 403–411.

Kovac, D. & B. Streit, 1996. The arthropod community of bamboo internodes in Peninsular Malaysia: Microzonation and trophic structure. In: Edwards, D. S., W. E. Booth & S. C. Choy (eds.), *Tropical Rainforest Research: Current Issues*. Monographiae Biologicae 74. Kluwer Academic Publishers, Dordrecht, Boston, London. Pp. 85–99.

Kovac, D. & C. M. Yang, 2000. Revision of the Oriental bamboo-inhabiting semiaquatic bug genus *Lathriovelia* Andersen, 1989 (Heteroptera: Veliidae) with descriptions of *L. rickmersi*, new species, and notes on the genus *Baptista* Distant, 1903. *Raffles Bulletin of Zoology*, **48**: 153–165.

Kovac, D., P. Dohm & A. Freidberg, 2010. Field observations on the mating behaviour of the Oriental *Rioxa sexmaculata* (van der Wulp) (Diptera: Tephritidae) and a review of the reproductive behaviour patterns in Acanthonevrini. *Biosystematica*, **4**: 5–14.

Lanciani, C. A., 1991. Laboratory rearing of *Hydrometra australis* (Hydrometra: Hydrometridae). *Florida Entomologist*, **74**: 356–357.

Linsenmair, K. E. & R. Jander, 1963. Das "Entspannungsschwimmen" von *Velia* und *Stenus*. *Naturwissenschaften*, **50**: 231.

Pickard, S., 1978. Un prédateur des Collemboles aquatiques Microvelia reticulata (Bur.) Hémiptère Hétéroptère, Veliidae. *Revue d'écologie et de biologie du sol*, **15**: 103–112.

Rensing, L., 1962. Beiträge zur vergleichenden Morphologie, Physiologie und Ethologie der Wasserläufer. *Zoologische Beiträge, N. F.*, **7**: 447–485.

Rowe, L., G. Arnqvist, A. Sih & J. Krupa, 1994. Sexual conflict and the evolutionary ecology of mating patterns: Water striders as a model system. *Trends in Ecology & Evolution*, **9**: 289–293.

Sattler, W., 1957. Beobachtungen zur Fortpflanzung von *Gerris najas* De G. (Heteroptera). *Zeitschrift für Morphologie und Ökologie der Tiere*, **56**: 411–428.

Spence, J. R. & N. M. Andersen, 1994. Biology of water striders: Interactions between systematics and ecology. *Annual Review of Entomology*, **39**: 101–128.

Thornhill, R. & J. Alcock, 1983. *The Evolution of Insect Mating Systems*. Harvard University Press, Cambridge, Massachussets, and London England. 547 pp.

Vepsäläinen, K., 1978. Wing dimorphism and diapause in *Gerris*: Determination and adaptive significance. In: Dingle, H. (ed.), *Evolution of Insect Migration and Diapause*. Springer Verlag, New York. Pp. 218–253.

Vepsäläinen, K., 1985. Exclusive female vs. male territoriality in two waterstrider (Gerridae) species: Hypotheses of function. *Annales Entomologici Fennici*, **51**: 45–49.

Wilcox, R. S., 1972. Communication by surface waves: Mating behaviour of a water strider (Gerridae). *Journal of Comparative Physiology*, **80**: 255–266.

Wurst, E. & D. Kovac, 2003. Description and biology of the mite *Tensiostoma veliaphilum* n. gen. n. sp. from the water surface of bamboo phytotelmata in Southeast Asia (Arachnida, Acari, Astigmata, Histiostomatidae). *Senckenbergiana biologica*, **82**: 63–98.

Zettel, H., 1998. On the Oriental genus *Neoalardus* Distant 1912 (Heteroptera: Veliidae). *Linzer biologische Beiträge*, **30**: 595–599.

Zettel, H., 2004. *Baptista hoedli* sp. n. (Insecta: Heteroptera: Veliidae) from Laos, and definition of the *B. collaris* group. *Annalen des Naturhistorischen Museums in Wien*, **105B**: 441–445.