

Larvae of the water scavenger beetle, *Hydrophilus acuminatus* (Coleoptera: Hydrophilidae) are specialist predators of snails

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Abstract. *Hydrophilus acuminatus* larvae are known to feed on aquatic prey. However, there is no quantitative study of their feeding habits. In order to determine the feeding preferences and essential prey of larvae of *H. acuminatus*, both field and laboratory experiments were carried out. Among the five potential species of prey, *Austropeplea ollula* (Mollusca: Lymnaeidae), *Physa acuta* (Mollusca: Physidae), *Asellus hilgendorfi* (Crustacea: Asellidae), *Palaemon paucidens* (Crustacea: Palaemonidae) and larvae of *Prosilocerus akamusi* (Insecta: Chironomidae), the first instar larvae of *H. acuminatus* strongly preferred the *Austropeplea* and *Physa* snails in both cafeteria and single-prey species experiments. Larvae that were provided with only snails also successfully developed into second instar larvae, while larvae fed *Palaemon*, *Prosilocerus* larvae or *Asellus* died during the first instar. In addition, the size of adult *H. acuminatus* reared from first-instar larvae and fed only snails during their entire development was not different from that of adult *H. acuminatus* collected in the field. This indicates that even though the larvae of *H. acuminatus* can feed on several kinds of invertebrates, they strongly prefer snails and without them cannot complete their development.

INTRODUCTION

Predacious aquatic insects are a diverse group and the top predators in fishless water habitats. Larvae and adults of some species of diving beetles (Dytiscidae), for example, are regarded as effective predators of mosquito larvae (Bay, 1974; Berman et al., 2000; Lundkvist et al., 2003), other insect larvae, amphibian larvae, isopods and fish fry (Blunck, 1923; Balduf, 1935; Wesenberg-Lund, 1943; Jeffries, 1988; Johansson & Nilsson, 1992; Inoda & Kamimura, 2004; Inoda et al., 2009).

Although predatory aquatic insects have been studied for decades, the feeding ecology and behaviour of many taxa are relatively poorly known. In the past, most predatory aquatic insects in standing water were thought to be generalists (Batzer & Wissinger, 1996; Cummins, 1973; Bay, 1974). However, recent laboratory experiments and field studies have shown that they are often specialists rather than generalists (Klečka & Boukal, 2012).

Some predators are known to have adaptations for handling certain types of prey, such as asymmetric feeding structures. For example, some snail-eating specialists have a conspicuous, one-sided asymmetry in their feeding apparatus (Shoup, 1968; Snyder & Snyder, 1969; Ng & Tan, 1985; Hoso et al., 2007). Since snail shells are mainly dextral (i.e., with right-handed coiling of the shell) regardless of habitat (Vermeij, 1975), to specialize on dextral snails would be selectively advantageous for predators of snails (Shoup, 1968; Snyder & Snyder, 1969; Ng & Tan, 1985; Inoda et al., 2003; Shigemiyu, 2003; Hoso et al., 2007). Asymmetrical mandibles that may indicate a specialized feeding apparatus are common in the larvae of various groups of Hydrophilidae, e.g., *Laccobius*, *Berosus* and some Acidocerinae (Archangelsky, 1997; Minoshima &

Hayashi, 2011). While the diet of most of these groups is poorly known, the larvae of *Hydrophilus* are reported to feed on freshwater snails, insect larvae, amphibian larvae, isopods and fish (e.g., Miall, 1895; Kawamura, 1918; Wilson, 1923; Bøwing & Henriksen, 1938; Hosoi, 1939; Tsuda, 1983; Archangelsky, 1997; Inoda et al., 2003). Under laboratory conditions, the larva of *Hydrophilus acuminatus* feed on *Caenestheriella gifuensis*, *Tubifex tubifex*, *Carassius auratus* (Tsuda, 1983) and viviparid snails (Hosoi, 1939). These observations suggest that *Hydrophilus* species are generalist predators.

On the other hand, Inoda et al. (2003) report that the asymmetric mandibles of *H. acuminatus* are more suitable for feeding on right-handed (*Austropeplea ollula*) than left-handed snails (*Physa acuta*). As there is no quantitative analysis of the eating of snails by *H. acuminatus*, the present study provides a brief survey of the acceptability of the potential prey in a natural habitat of *H. acuminatus* and the results of laboratory experiments on the prey preferences, essential prey and ability the first instar larvae to complete their development when fed different types of prey.

MATERIAL AND METHODS

Field observations and identification of potential prey

To identify the potential prey of *H. acuminatus* larvae, an aquatic community in an irrigation ditch of a rice paddy in Tochigi Prefecture (Nasu), Japan was surveyed. Larvae of *H. acuminatus* were also repeatedly found at this site during this study. The ditch was 15 × 1 m, the depth of the static water 30–50 cm and had a muddy bottom, in which grew two species of water plants, *Cabomba caroliniana* and *Sagittaria trifolia*. *Cabomba caroliniana* was the most abundant and dominant plant. This community was surveyed using 60 quadrates (50 × 50 cm) in June of 2005,

2007 and 2009 and the samples from all quadrates were subsequently pooled each year. The animals were collected using a D-type net (45 × 40 × 40 cm with a mesh size of 0.8 mm) by means of a single sweep through the water column and across the bottom as described in Inoda et al., 2009. The animals were counted and identified using the following references: aquatic insects (Tsuda, 1983; Mori & Kitayama, 2002), amphibians (Uchiyama et al., 2002), fish (Nakabo, 2000) and other benthic animals (Ueno, 1973).

Potential prey were kept in an aquarium (74 × 39 × 40 cm; water depth 20 cm) until the experiment started. The mud from the beetles' habitat and some aquatic plants, such as giant elodea (*Elodea densa*), fanwort (*Cabomba caroliniana*) and Japanese parsley (*Oenanthe javanica*), were collected and placed in the same aquarium. The plants, giant elodea, fanwort and Japanese parsley, were planted with vegetation cover rate (VCR; Braun-Blanquet, 1964) of 35%, 35% and 10%, respectively. The VCR for each species in the aquarium was measured as follows. The aquarium was photographed from above with a digital camera (Nikon, CoolPi×990, Tokyo, Japan) and the VCR of each plant species and the open spaces were measured from pixel counts using Photoshop 6.0 (Adobe systems); see (Inoda, 2011) for details. Dechlorinated tap water was supplied every 6 h to keep the water clean (Inoda & Kamimura, 2004).

Breeding of larvae

First instar larvae of *H. acuminatus* (c.a., 20 mm body length) were collected from June to July of 2009 and used in the experiments 1–2 days after hatching. The larvae were not provided with food before the experiments. To obtain the larvae, adult *H. acuminatus* were collected in Tochigi Prefecture (Nasu), Japan. Five pairs were kept in an outdoor aquarium (74 × 39 × 40 cm, with a 20 cm water column) following the method used by Inoda et al. (2003). During oviposition, females laid egg cases each containing approximately 30 eggs. The egg cases were transferred to an artificial breeding system (Inoda et al., 2003; Inoda & Kamimura, 2004) and kept there until the larvae hatched.

Feeding experiments

We conducted a series of individual-level feeding experiments using first-instar larvae of *H. acuminatus*. All these experiments were carried out in small aquaria (12 × 8 × 8 cm; water depth 6 cm, water temperature 25–28°C) placed outdoors. All these experiments were run for eight hours between 22:00 and 6:00 (June 9–16, 2009).

Experiment 1: Screening of potential prey and predators of the first instar larvae

To determine the potential prey to be used in subsequent experiments, we placed one first-instar larva of *H. acuminatus* and one individual animal of each potential prey species in each aquarium (n = 3). At the end of each trial we assessed whether predation had occurred, and if so, who ate whom.

Experiment 2: Prey selectivity in cafeteria experiment

After conducting the screening test, five species were selected as potential prey: *Palaemon paucidens*, *Prosilocerus akamusi* larvae, *Asellus hilgendorfi*, *Austropeplea ollula* and *Physa acuta*. To investigate the feeding preferences of *H. acuminatus* in detail, one beetle larva and three specimens of each potential prey (i.e., one beetle larva with 15 prey items) were placed together in an aquarium. The number of prey consumed and number of beetle larvae that fed on prey were counted at the end of each trial. Percentage predation was calculated as follows:

Percentage predation (%) = 100 × (Number of beetle larvae which fed on at least one prey item) / (Total number of beetle larvae).

In addition to percentage predation, we used Manly's alpha preference index for constant prey populations (Chesson, 1978; Krebs, 1989) to calculate the preference of beetle larvae for different species of prey:

$$\alpha_i = (r_i/n_i) / \left[1 / \sum_{i=1}^m (r_i/n_i) \right]$$

where α_i is the preference index for prey type i , r_i is the proportion of prey item i , n_i is the proportion of prey item i in the environment, and m is the total number of types of prey (in this case, $m = 5$ prey species). If $\alpha_i > 1/m$, prey species i is preferred. Conversely, $\alpha_i < 1/m$ indicates avoidance of prey species i . The number of replicates was 30 and beetle larvae were not used repeatedly.

Experiment 3: Single-prey predation

One beetle larva and three individual specimens of a single-prey (i.e., one beetle larva versus three prey individuals) were placed together in an aquarium in this experiment. A total of 179 beetle larvae were used (38 *Palaemon paucidens*, 39 *Prosilocerus akamusi* larvae, 33 *Asellus hilgendorfi*, 34 *Austropeplea ollula* and 35 *Physa acuta*). Neither predators nor prey individuals were used repeatedly. The number of beetle larvae that consumed prey was counted at the end of the experiment and the percentage predation calculated as outlined above.

Experiment 4: Essential prey and survival of the larvae

To investigate the percentage survival of the first instar larvae when provided with a single species of prey, one beetle larva and three individual specimens of the same species of prey were placed in the aquarium (12 × 8 × 8 cm; water depth 6 cm). A total of 113 beetle larvae were used in this experiment (23 *Palaemon paucidens*, 22 *Prosilocerus akamusi* larvae, 15 *Asellus hilgendorfi*, 24 *Austropeplea ollula* and 29 *Physa acuta*) and they were not used repeatedly. The number of larvae that developed into the second instar was counted and the percentage survival calculated as follows:

Percentage survival (%) = 100 × (Number of larvae that developed into the second instar) / (Total number of larvae).

Prey was provided everyday to keep the number of each type of prey constant. Water in each aquarium was changed with aged tap water daily and the debris of prey carcasses was also removed.

To supplement the feeding experiments described above, we measured body length and width of adult beetles reared from the first instar larvae fed on *Austropeplea* or *Physa* in order to clarify the nutritional suitability of snails for the development of *H. acuminatus*. First, we placed two aquaria (75 × 40 × 35 cm) containing water to a depth of 10–15 cm outdoors. Each aquarium contained *H. acuminatus* larvae and *Austropeplea* or *Physa* as prey. The aquaria were covered with 3-mm mesh plastic lids to reduce the intensity of direct sunlight (corresponding to a 50% reduction in light intensity) and prevent larvae from escaping. The aquatic plants, giant elodea, fanwort and Japanese parsley, with VCRs of 35%, 35% and 10%, respectively were also placed in the aquaria to provide resting places. Eaten prey were regularly replaced to maintain constant numbers of prey in each aquarium. Dechlorinated tap water was supplied every six hours (Inoda & Kamimura, 2004). Third instar larvae, which stopped feeding prior to pupation (body length approximately 60 mm), were transferred to plastic containers filled with moist peat moss (11 × 8 × 7 cm) and kept at 20–25°C until adult emergence. Body size of the adult beetles was measured and compared with that of adults collected in the wild.

TABLE 1. List of candidate prey species found in an irrigation ditch of a rice paddy in Tochigi Prefecture, Japan in June of 2005, 2007, and 2009. *N* = total number of individuals found.

Class	Order	Family	Species	Body size (mm)	<i>N</i>		
					2005	2007	2009
Actinopterygii	Cypriniformes	Cobitidae	<i>Misgurnus anguillicaudatus</i>	40–45	6	8	9
Amphibia	Caudata	Salamandridae	<i>Cynops pyrrhogaster</i>	80–100	10	3	5
Gastropoda	Pulmonata	Lymnaeidae	<i>Austropeplea ollula</i>	*5–7	8	18	7
Gastropoda	Pulmonata	Physidae	<i>Physa acuta</i>	*5–7	13	8	21
Insecta	Coleoptera	Dytiscidae	<i>Cybister brevis</i>	20–23 (15–20)	2 (2)	1 (1)	0 (1)
Insecta	Coleoptera	Dytiscidae	<i>Cybister chinensis</i>	30–35	(1)	0	0
Insecta	Coleoptera	Dytiscidae	<i>Hydaticus bowringii</i>	13–14	4	1	2
Insecta	Coleoptera	Dytiscidae	<i>Rhantus suturalis</i>	11–12	5	8	7
Insecta	Coleoptera	Hydrophilidae	<i>Hydrophilus acuminatus</i>	35–39 (19–21)	5 (2)	5 (1)	2 (4)
Insecta	Hemiptera	Nepidae	<i>Ranatra chinensis</i>	41–45	3	1	1
Insecta	Hemiptera	Belostomatidae	<i>Diplonychus japonicus</i>	18–20	9	8	11
Insecta	Hemiptera	Belostomatidae	<i>Kirkaldyia deyrolli</i>	12–17	(2)	(1)	(0)
Insecta	Diptera	Chironomidae	<i>Prosilocerus akamusi</i>	10	15	8	21
Insecta	Odonata	Libellulidae	**Dragonflies	15–20	(23)	(10)	(8)
Malacostraca	Isopoda	Asellidae	<i>Asellus hilgendorfi</i>	5–8	71	45	82
Malacostraca	Isopoda	Palaemonidae	<i>Palaemon paucidens</i>	5–8	8	4	6
Malacostraca	Decapoda	Cambaridae	<i>Procambarus clarkii</i>	25–30	24	35	15

Parentheses indicate larvae; * – shell length; ** – unidentified species.

Data analysis

Fisher's exact test was first conducted to assess the differences in percentage predation and percentage survival. If there was a statistical difference and all data were non-zero, Ryan's multiple comparisons for proportions (Ryan, 1960) were used to determine differences between groups. Two sets of binary data, feed/not feed and survive/die, were used in the analysis.

Differences in the body sizes of the beetles reared on a diet of *Austropeplea ollula* or *Physa acuta* and collected in the wild, were analyzed using Tukey's multiple comparison test.

Statistical analyses were carried out using R software, version 3.0.1 (R Development Core Team, 2013). Significance level was set at *P* = 0.05 in all tests.

RESULTS

Nineteen taxa were collected at the field site (Table 1). The isopod *Asellus hilgendorfi* was the most abundant taxon uniformly present throughout the habitat and in different years (data not shown), followed by the crayfish *Procambarus clarkii*, chironomid *Prosilocerus akamusi* and two gastropod species, *Austropeplea ollula* and *Physa acuta*. In the first experiment, we established that only five of these taxa, *Palaemon*, *Prosilocerus* larvae, *Asellus* and the two species of snails (*Austropeplea* and *Physa*), were eaten by first-instar larvae of *H. acuminatus* and thus used as potential prey in subsequent experiments (Table 2). Three of the five species of potential prey, *Palaemon*, *Prosilocerus* larvae and *Asellus*, were not eaten by *H. acuminatus* larvae in the cafeteria experiment (Experiment 2). On the other hand, 21 (70%) and 17 (57%) of 30 beetle larvae fed on *Austropeplea* and *Physa*, respectively. Fisher's exact test revealed a marked differences in the feeding preferences of *H. acuminatus* larvae for these five species of prey (*P* < 0.001). Manly's alphas for the three species of prey that were ignored prey were zero, while those for the snails (*Austropeplea* and *Physa*) were 0.58 and 0.43,

respectively, indicating that both of these snails were preferred prey.

When beetle larvae were provided with a single species of prey (Experiment 3) they consumed the other three potential species of prey: *Palaemon* (8 of 38 beetle larvae, percentage predation: 21%), *Prosilocerus* larvae (17 of 39 beetle larvae, 44%) and *Asellus* (13 of 33 beetle larvae, 39%). Nevertheless, the larvae always fed on the two

TABLE 2. Screening of prey candidates of first-instar *H. acuminatus* larvae (*n* = 3). *N*_{prey} = number of individuals eaten by *H. acuminatus* larvae (prey link); *N*_{pred} = number of *H. acuminatus* larvae eaten by the prey candidate (predation link).

Prey candidate species	Body length [mm]	<i>N</i> _{prey}	<i>N</i> _{pred}
<i>Misgurnus anguillicaudatus</i>	40–45	0	2
<i>Cynops pyrrhogaster</i>	80–100	0	1
<i>Austropeplea ollula</i>	*5–7	3	0
<i>Physa acuta</i>	*5–7	3	0
<i>Cybister brevis</i>	20–23	0	0
<i>Cybister brevis</i> larvae	15–20	0	3
<i>Cybister chinensis</i> larvae	30–35	0	3
<i>Hydaticus bowringii</i>	13–14	0	0
<i>Rhantus suturalis</i>	11–12	0	0
<i>Hydrophilus acuminatus</i>	35–39	0	0
<i>Hydrophilus acuminatus</i> larvae	19–21	0	0
<i>Ranatra chinensis</i>	41–45	0	1
<i>Diplonychus japonicus</i>	18–20	0	2
<i>Kirkaldyia deyrolli</i> larvae	12–17	0	3
<i>Prosilocerus akamusi</i> larvae	10	1	0
<i>Asellus hilgendorfi</i>	5–8	1	0
<i>Palaemon paucidens</i>	5–8	1	0
<i>Procambarus clarkii</i>	25–30	0	1
**Dragonfly larvae	15–20	0	1

Body length indicate animal size used in the experiments; * – shell length; ** – unidentified species.

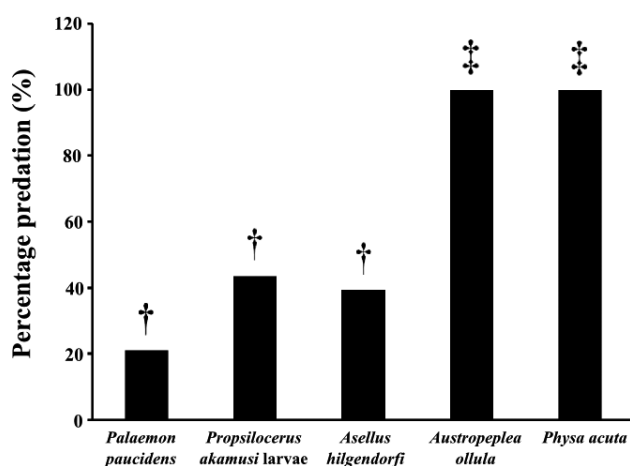


Fig. 1. Percentage predation by larvae of *H. acuminatus* provided with single species of prey. Columns with different symbols indicate significant differences ($P < 0.05$).

snail species: *Austropeplea* (34 of 34 beetle larvae) and *Physa* (35 of 35 beetle larvae) (Fig. 1). This again indicates a stronger preference for feeding on snails than the other species ($P < 0.05$, Ryan's multiple comparisons). When only *Palaemon*, *Propsilocerus* larvae or *Asellus* were provided as prey for the larvae of *H. acuminatus*, all of the larvae (23, 22 and 15, respectively) died during the first instar. On the other hand, the larvae provided with each of the snail species, *Austropeplea* and *Physa*, developed into the second instar. The percentage survival of the first instar larvae was 96% (23 of 24 beetle larvae survived) when provided with *Austropeplea* and 97% (28 of 29 beetle larvae survived) when provided with *Physa*. The survivorship of the larvae provided with each of the five different types of prey differed greatly ($P < 0.001$, Fisher's exact test). As shown in Table 3, there was no significant difference in the body size (body length and width) of *H. acuminatus* adults reared from larvae fed only snails (*Austropeplea* or *Physa*) and those collected in the field ($P > 0.64$, Tukey's multiple comparison t-test). In addition to body size, 100% completed their development. This indicates that snails provide sufficient nutrition for the growth of beetle larvae.

DISCUSSION

Top invertebrate predators substantially affect the biomass, species composition and diversity of fishless pond ecosystems (Turner & Chislock, 2007; Cobbaert et al., 2010). Predators can reduce the numbers of some species of prey. Snail biomass in fishless marshes and ponds is influenced by direct predation by dragonfly nymphs (Turner & Chislock, 2007). In the present study, the larvae of *H. acuminatus* showed a marked preference for feeding on snails, suggesting that larvae may directly affect snail biomass in their habitats. Adult beetles reared from the first-instar larvae on a diet consisting only of snails were of normal size, indicating that snails are an important prey that can support the complete development of *Hydrophilus* larvae. As we used only first-instar larvae in the feeding experiments, a similar study using all instars should be

TABLE 3. Comparison of the body size of bred and wild-caught *H. acuminatus* adults.

	Food	Body length [mm]	Body width [mm]	Statistics
Bred (18)	<i>Austropeplea</i>	39.2 ± 1.6	18.8 ± 0.8	
Female Bred (10)	<i>Physa</i>	39.4 ± 1.0	19.0 ± 0.7	NS
Wild (10)	—	39.3 ± 3.2	19.2 ± 2.2	
Bred (20)	<i>Austropeplea</i>	36.9 ± 2.0	17.6 ± 1.0	
Male Bred (10)	<i>Physa</i>	36.5 ± 2.3	17.5 ± 1.1	NS
Wild (10)	—	37.3 ± 2.2	17.7 ± 1.3	

Number in parentheses indicates sample size. Values are mean ± SD. NS – non-significant difference based on a Tukey's multiple comparison test.

conducted in order to fully quantify their ability to control snail populations.

Many reports have suggested that *Hydrophilus* larvae can feed on many types of prey (Kawamura, 1918; Wilson, 1923; Hosoi, 1939; Tsuda, 1983; Inoda et al., 2003), even snakes (Mori & Ohba, 2004). However, there is no information on what cues larvae use to detect food and which species of prey they need to complete their development. The present study experimentally demonstrates that *H. acuminatus* larvae are specialist predators of snails. It is not clear why the larvae of this species in this study also fed on prey on which they were not able to successfully complete their development. In the case of diving beetles, *Dytiscus verticalis* (Coleoptera: Dytiscidae), the larvae use mechanical stimuli or some chemical cues instead of visual cues to find prey (Formanowicz, 1987). The larvae of *Dytiscus sharpi sharpi* also respond to the scent of prey when hunting (Inoda, 2012), e.g., of the adults of *Kirkaldyia* (Tsuzuki et al., 1999). The larvae of *H. acuminatus* may similarly be able to recognize the smell of prey and are attracted by many species of prey, although some are unsuitable for them to complete their development and may thus serve only as supplementary food.

The results are also important for insect conservation. Predatory invertebrate populations are often limited by their food supply (Lenski, 1984; Pearson & Knisley, 1985; Juliano, 1986) and understanding their trophic ecology can result in the development of more efficient conservation measures. *Hydrophilus* species are endangered taxa in many parts of the world, including, e.g., Great Britain (Beebe, 2007) and Japan (Ministry of the Environment, Government of Japan, 2012). While the larvae of *Hydrophilus* are carnivores, the adults are mainly herbivores or omnivores; thus, they need diverse ecosystems for their development. The habitats of freshwater species, including insects and other invertebrates, are increasingly threatened worldwide (Allan & Flecker, 1993). Decrease in the numbers of suitable aquatic habitats due to the abandonment of rice paddies, water pollution, pesticide use and invasion by non-native species is causing great concern in Japan (Ministry of the Environment, Government of Japan, 2007; Nishihara et al., 2006). The result presented in this paper may help focus the conservation efforts on protecting species of *Hydrophilus* by maintaining appropriate habitats for them

as the association between the occurrence of *Hydrophilus* species and the local snail fauna is largely overlooked and unknown.

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REFERENCES

- ALLAN J.D. & FLECKER A.S. 1993: Biodiversity conservation in running waters. — *Bioscience* **43**: 32–43.
- ARCHANGELSKY M. 1997: Studies on the biology, ecology, and systematics of the immature stages of New World Hydrophiloidea (Coleoptera: Staphyliniformia). — *Bull. Ohio Biol. Surv. (N.S.)* **12**: 207 pp.
- BALDUF W.V. 1935: *The Bionomics of Entomophagous Coleoptera*. E.W. Classey, Hampton, 200 pp.
- BATZER D.P. & WISSINGER S.A. 1996: Ecology of insect communities in nontidal wetlands. — *Annu. Rev. Entomol.* **41**: 75–100.
- BAY E. 1974: Predator-prey relationships among aquatic insects. — *Annu. Rev. Entomol.* **19**: 441–453.
- BEEBEE T.J.C. 2007: Population structure and its implications for conservation of the great silver beetle *Hydrophilus piceus* in Britain. — *Freshw. Biol.* **52**: 2101–2111.
- BERMAN E.H., WRIGHT P. & MASHKE J.E. 2000: Biology of *Agabus disintegratus* (Crotch) (Coleoptera: Dytiscidae) in central Georgia with a description of its mature larva. — *Georgia J. Sci.* **58**: 208–216.
- BLUNCK H. 1923: Die Entwicklung des *Dytiscus marginalis* L. vom Ei bis zur Imago. 2. Teil. Die Metamorphose (B. Das Larven- und das Puppenleben). — *Z. Wiss. Zool.* **121**: 117–391.
- BOWING A.G. & HENRIKSEN K.L. 1938: The developmental stages of the Danish Hydrophilidae. Videnskabelige Meddelelser fra dansk naturhistorisk Forening i Kjobenhavn **102**: 27–162.
- BRAUN-BLANQUET J. 1964: *Pflanzensoziologie. 3. Aufl.* Springer, Wien, xiv + 865 pp. [Japanese translation 1971, by T. Suzuki (as *Shokubutsu Shakaigaku*), Asakura Shoten, Tokyo].
- CHESSON J. 1978: Measuring preference in selective predation. — *Ecology* **59**: 211–215.
- COBBAERT D., BAYLEY S.E. & GRETER J.L. 2010: Effects of a top invertebrate predator (*Dytiscus alaskanus*; Coleoptera: Dytiscidae) on fishless pond ecosystems. — *Hydrobiologia* **644**: 103–114.
- CUMMINS K. 1973: Trophic relations of aquatic insects. — *Annu. Rev. Entomol.* **18**: 183–206.
- FORMANOWICZ D.R. JR. 1987: Foraging tactics of *Dytiscus verticalis* larvae (Coleoptera: Dytiscidae): prey detection, reactive distance and predator. — *J. Kans. Entomol. Soc.* **60**: 92–99.
- HANSEN M. 1999: *World Catalogue of Insects 2: Hydrophiloidea (s. str.) (Coleoptera)*. Apollo Books, Amsterdam, 416 pp.
- HOSO M., ASAMI T. & HORI M. 2007: Right-handed snakes: convergent evolution of asymmetry for functional specialization. — *Biol. Lett.* **3**: 169–173.
- HOSOI M. 1939: The life-history of *Hydrous acuminatus* Motschulsky. — *Bot. Zool.* **7**: 1867–1874 [in Japanese].
- INODA T. 2011: Preference of oviposition plant and hatchability of the diving beetle, *Dytiscus sharpi* (Coleoptera: Dytiscidae) in the laboratory. — *Entomol. Sci.* **14**: 13–19.
- INODA T. 2012: Predaceous diving beetle, *Dytiscus sharpi sharpi* (Coleoptera: Dytiscidae) larvae avoid cannibalism by recognizing prey. — *Zool. Sci.* **29**: 547–552.
- INODA T. & KAMIMURA S. 2004: New open aquarium system to breed larvae of water beetles (Coleoptera: Dytiscidae). — *Coleopt. Bull.* **58**: 37–43.
- INODA T. & KITANO T. 2013: Mass breeding larvae of the critically endangered diving beetles *Dytiscus sharpi sharpi* and *Dytiscus sharpi validus* (Coleoptera: Dytiscidae). — *Appl. Entomol. Zool.* **48**: 397–401.
- INODA T., HIRATA Y. & KAMIMURA S. 2003: Asymmetric mandibles of water-scavenger larvae improve feeding effectiveness on right-handed snails. — *Am. Nat.* **67**: 811–814.
- INODA T., HASEGAWA M., KAMIMURA S. & HORI M. 2009: Dietary program for rearing the larvae of a diving beetle, *Dytiscus sharpi* (Wehncke), in the laboratory (Coleoptera: Dytiscidae). — *Coleopt. Bull.* **63**: 340–350.
- JEFFRIES M. 1988: Individual vulnerability to predation: the effect of alternative prey types. — *Freshw. Biol.* **19**: 49–56.
- JOHANSSON A. & NILSSON A.N. 1992: *Dytiscus latissimus* and *D. circumcinctus* (Coleoptera, Dytiscidae) larvae as predators on three case-making caddis larvae. — *Hydrobiologia* **248**: 201–213.
- JULIANO S.A. 1986: Food limitation of reproduction and survival for populations of *Brachinus* (Coleoptera: Carabidae). — *Ecology* **67**: 1036–1045.
- KAWAMURA T. 1918: *Freshwater Biology in Japan*. Shokabo, Tokyo, 323 pp. [in Japanese].
- KLEČKA J. & BOUKAL D.S. 2012: Who eats whom in a pool? A comparative study of prey selectivity by predatory aquatic insects. — *PLoS ONE* **7**(6): e37741.
- KREBS C.J. 1989: *Ecological Methodology*. Harper Collins, New York, 654 pp.
- LENSKI R.E. 1984: Food limitation and competition: a field experiment with two *Carabus* species. — *J. Anim. Ecol.* **53**: 203–216.
- LUNDKVIST E., LANDIN J., JACKSON M. & SVENSSON C. 2003: Diving beetles (Dytiscidae) as predators of mosquito larvae (Culicidae) in field experiments and in laboratory tests of prey preference. — *Bull. Entomol. Res.* **93**: 219–226.
- MIALL L.C. 1895: *Aquatic Beetles: The Great Water-Beetle (Hydrophilus)*. *The Natural History of Aquatic Insects*, Macmillan, London, 61–87 pp.
- MINISTRY OF THE ENVIRONMENT, GOVERNMENT OF JAPAN 2007: *Red List of Japan*. [in Japanese].
- MINISTRY OF THE ENVIRONMENT, GOVERNMENT OF JAPAN 2012: *Red List of Japan*. [in Japanese].
- MINOSHIMA Y. & HAYASHI M. 2011: Larval morphology of the Japanese species of the tribes Acidocerini, Hydrobiusini and Hydrophilini (Coleoptera: Hydrophilidae). — *Acta Entomol. Mus. Nat. Pragae (Suppl.)* **51**: 118 pp.
- MORI M. & KITAYAMA A. 2002: *Dytiscoidea of Japan. Revised ed.* Bun-ichi Sogo Shuppan, Tokyo, 217 pp. [in Japanese].
- MORI A. & OHBA S. 2004: Field observations of predation on snakes by the giant water bug. — *Bull. Herpetol. Soc. Japan* **2004**: 78–81 [in Japanese].
- NAKABO T. 2000: *Fishes of Japan with Pictorial Keys to the Species. 2nd ed.* Tokai University Press, Kanagawa, 2428 pp. [in Japanese].
- NG P.K.L. & TAN L.W.H. 1985: Right handedness in heterochelous calappoid and xanthoid crabs – suggestion for a functional advantage. — *Crustaceana* **49**: 98–100.
- NISHIHARA S., KARUBE H. & WASHITANI I. 2006: Status and conservation of diving beetles inhabiting rice paddies. — *Jpn. J. Conserv. Ecol.* **11**: 143–157 [in Japanese].

- PEARSON D.L. & KNISLEY C.B. 1985: Evidence for food as a limiting resource in the life cycle of tiger beetles (Coleoptera: Cicindelidae). — *Oikos* **45**: 161–168.
- R DEVELOPMENT CORE TEAM 2013: *R: A Language and Environment for Statistical Computing*. R Foundation for Statistical Computing, Vienna, Austria. Available at <http://www.R-project.org>
- RYAN T.A. 1960: Significance tests for multiple comparison of proportions, variances, and other statistics. — *Psychol. Bull.* **57**: 318–328.
- SHIGEMIYA Y. 2003: Does the handedness of the pebble crab *Eriphia smithii* influence its attack success on two dextral snail species? — *J. Zool.* **260**: 259–265.
- SHOUP J.B. 1968: Shell opening by crabs of the genus *Calappa*. — *Science* **160**: 887–888.
- SHORT A.E.Z. & FIKÁČEK M. 2011: World catalogue of the Hydrophiloidea (Coleoptera): additions and corrections II (2006–2010). — *Acta Entomol. Mus. Nat. Pragae* **51**: 83–122.
- SHORT A.E.Z. & HEBAUER F. 2006: World catalogue of Hydrophiloidea – additions and corrections, 1 (1999–2005) (Coleoptera). — *Koleopt. Rundsch.* **76**: 315–359.
- SNYDER R. & SNYDER R.A. 1969: A comparative study of mollusc predation by limpkins, everglade kites, and boat-tailed grackles. — *The Living Bird* **8**: 177–223.
- TSUDA M. 1983: *Aquatic Entomology*. 7th ed. Hokuryukan, Tokyo, 166 pp. [in Japanese].
- TSUZUKI Y., TANIWAKI A. & INODA T. 1999: *The Perfect Manuals for Breeding of Aquatic Insects*. Data House, Tokyo, 223 pp. [in Japanese].
- TURNER A.M. & CHISLOCK M.F. 2007: Dragonfly predators influence biomass and density of pond snails. — *Oecologia* **153**: 407–415.
- UENO M. 1973: *Kawamura Nihon Tansui Seibutsugaku*. [Freshwater Biology of Japan.] Hokuryukan, Tokyo, 760 pp. [in Japanese].
- UCHIYAMA R., NUMATA K., MAEDA N. & SEKI S. 2002: *A Photograph Guide; Amphibians and Reptiles in Japan*. Heibonsha, Tokyo, 317 pp. [in Japanese].
- VERMEIJ G.J. 1975: Evolution and distribution of left-handed and planispiral coiling in snails. — *Nature* **254**: 419–420.
- WESENBERG-LUND C. 1943: *Biologie der Süßwasserinsekten*. Nordisk Forlag, Copenhagen, 682 pp.
- WILSON C.B. 1923: Life history of the scavenger water beetle, *Hydrous (Hydrophilus) triangularis*, and its economic relation to fish breeding. — *Bull. U.S. Bur. Fish.* **39**: 9–38.

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