

The role of amphibian prey in the diet and growth of giant water bug nymphs in Japanese rice fields

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Abstract Predatory insects that depend upon particular prey animals are commonly regulated by the prey animal's abundance. Nymphs of the giant water bug *Kirkaldyia* (= *Lethocerus*) *deyrolli* (Heteroptera: Belostomatidae) are predators regarded as specialists in feeding on tadpoles. We studied the ontogenetic diet shift of aquatic nymphs by quantifying instar abundance and by analyzing captured prey and prey relative abundance during the period of rice irrigation in three localities. We also evaluated the contribution of major prey items (tadpoles, frogs, and Odonata nymphs) on specific growth rates of each nymphal stage in a rearing experiment. First to third-instar nymphs of *K. deyrolli* fed mainly on tadpoles, regardless of differences in prey availability. Nymphs of subsequent fourth and fifth instar stages shifted from tadpoles to other prey animals within each rice field. A rearing experiment demonstrated that giant water bug nymphs provided with tadpoles had greater specific growth rates at all nymphal stages, except for the final stage, than nymphs fed other prey (frogs and Odonata nymphs). The emergence of young *K. deyrolli* nymphs seemed to coincide with the period during which tadpoles became abundant in the rice fields. Consumption of tadpoles seems important to allow the nymph to complete its larval development in an unstable temporary habitat.

Keywords Belostomatidae · *Kirkaldyia deyrolli* · Life history · Temporary water · Tadpole · Frog

Introduction

The quantity and quality of prey animals are important factors determining a predator's life history and abundance. This fact has been documented for many predacious arthropods, for example predacious mites (Riverd 1962), spiders (Anderson 1974; Wise 1979), predaceous beetles (Dixon 1959; Lenki 1984; Pearson and Knisley 1985; Juliano 1986), predaceous stink bugs (Mukerji and LeRoux 1969), damselflies (Lawton 1971), backswimmers (Fox 1975), and mantids (Matsura et al. 1975). Among predacious insects, a predatory species depending upon a particular prey animal, i.e., specialists, adapt their life history to that of their prey animal—specialists breed when their prey animal is abundant (Hagen 1962; Evans 1982; Sota 1985; Albuquerque et al. 1997). Especially during the nymphal period, specialists' development must coincide with the appearance of specific prey animals (reviewed by Elkinton 2003). Some studies have examined terrestrial insect predators, but few have addressed aquatic ones, possibly because most aquatic insect predators are recognized as generalists (reviewed by Sih 1987). Very few studies have investigated the life history and dietary changes of aquatic specialist insect predators that breed in unstable habitats, e.g., temporary water environments.

In a shallow temporary aquatic habitat, giant water bugs (aquatic Heteroptera), e.g., Belostomatidae, have raptorial forelegs that are used to prey upon a variety of aquatic animals, for example insects, cladocerans, amphibians, and small fish (Cullen 1969; Smith 1997; Hirai and Hidaka 2002; Toledo 2005). The subgenus *Lethocerinae*, which

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has the largest body size among Belostomatidae, is known to be a vertebrate specialist (Smith 1997; Swart et al. 2006). In fact, dietary items of sympatric Belostomatidae, *Kirkaldyia* (= *Lethocerus*) *deyrolli* Vuillefroy and *Appasus japonicus* Vuillefroy species differ in rice fields (Ohba and Nakasuji 2006). Nymphs of *A. japonicus* feed on a wide range of animal species, whereas nymphs of *K. deyrolli* prey upon tadpoles more than other kinds of prey in rice fields. For that reason, *K. deyrolli* nymphs have been regarded as predators mostly specialized for tadpoles (Ohba and Nakasuji 2006). Why *K. deyrolli* nymph is a specialist for tadpoles is not well understood.

In this study, we examined dietary changes along the development of giant water bug nymphs during the period of irrigation of rice fields. Field surveys were conducted at three locations during the life cycle of the *K. deyrolli*. A rearing experiment was also conducted in a laboratory to determine optimum prey animals for enhancing growth rates of *K. deyrolli*. Finally, ecological aspects of tadpole-feeding by *K. deyrolli* in nymphal stages are discussed.

Materials and methods

Study sites and animals

Field surveys were conducted in water paths connecting rice fields (“ditches”) at three study sites in Japan: at Fukusawa (35°1′N, 134°21′E) from 14 June to 6 August 2003, at Uekidani (35°1′N, 134°19′E) from 1 June to 6 August 2004, and at Chuo (34°58′N, 133°58′E) from 2 June to 11 August 2004 (Table 1). Rice fields in Japan provide major habitats for lentic aquatic insects including the giant water bug *Kirkaldyia deyrolli* (Vuillefroy) (Hasizume 1994; Mukai et al. 2005). One or three ditches at each study site were set up as census plots in which to investigate the diet of *K. deyrolli* and the frequencies of occurrence of *K. deyrolli* and potential prey. Rice fields

were surrounded by a ridge covered with weeds, making a small convenient footpath that reduced site disturbance between adjoining rice fields. The water temperature in the ditches was 22–30°C during the study period. Before transplanting rice, the rice fields are ploughed and irrigated; the muddy bottoms of the rice fields are then leveled. Subsequently, the rice fields are filled with water to depths of 5–15 cm. Water in all rice fields in the three study sites was maintained from mid-May to the end of June (irrigation period). In early July, the water was drained from the field and the rice field continued draining for a few weeks, eventually becoming fully drained, with the ground exposed to the sun (drainage period). Nevertheless, the ditch water remains at 3–5 cm depth, even during the drainage period.

In central Japan, the giant water bug is a univoltine species with a reproductive period between late May and early August, after overwintering, with the new generation reaching adulthood between early July and September (Hasizume 1994; Hasizume and Numata 1997; Mukai et al. 2005). Egg masses of *K. deyrolli* were laid on the stems of plants on the ridge or on the rice plants. Hatched nymphs molt five times, and adults emerge approximately 50 days later (Hasizume 1994). Finally, the adults disperse to hibernation places.

Frequency of occurrence of *K. deyrolli*, and diet

To measure the number of *K. deyrolli* in ditches, we conducted censuses at intervals of 2–7 days—a total of 21 times in Fukusawa, 13 in Uekidani, and 20 in Chuo during the study period. Censuses were conducted along the ridges around rice fields. They were performed by visual observation of *K. deyrolli* at night in the ditches using a flashlight (11,000 lx) from 2000 to 0100 hours. Primarily a nocturnal animal, *K. deyrolli* ambushes prey on the water surface after sunset. It is much easier to observe at night than in the daytime (Ohba and Nakasuji 2006). Flashlight illumination did not interfere with foraging behavior of *K. deyrolli*, because they do not stop feeding and ambushing prey, even in strong light (S. Ohba, unpubl. data). For direct observation, one observer maintained a constant distance from the water surface (0.3 m), and a constant pace (3 m min⁻¹ walking speed). To maintain sampling consistency, sampling was not conducted during periods of rain. We caught *K. deyrolli* nymphs using a 500 µm mesh dipnet (0.15 m × 0.10 m mouth opening) and measured their body length with calipers. The nymphs were assigned to instars based on data obtained from rearing experiments (S. Ohba, unpubl. data) as follows: first instar, 10–12 mm; second instar, 14–17 mm; third instar, 21–25 mm; fourth instar, 31–35 mm; and fifth instar, 42–51 mm. After capture and

Table 1 General descriptions of the three study sites

	Fukusawa	Uekidani	Chuo
Mean temperature during the study periods (mean ± SE)	22.4 ± 0.3	23.9 ± 0.3	24.8 ± 0.3
Altitude (m)	140	270	220
Irrigation periods (day)	76	60	79
Number of rice fields investigated	1	3	3
Research area: ditch length (m) × width (m)	130 × 0.5	35.4 × 0.3 37.8 × 0.3 44.4 × 0.4	99.8 × 0.3 62.3 × 0.3 89.3 × 0.5

measurement, nymphs were released carefully at their point of capture. At each study site, we summed the total number of *K. deyrolli* from all ditches. Because different water management among the rice fields affected the phenology of aquatic dwellers, we were unable to calculate mean and variance values of the number of individuals at each site.

We carefully observed whether or not the proboscis was inserted into the prey when we found *K. deyrolli* holding prey with their raptorial legs. Prey into which the proboscis had been inserted were recorded as dietary items and were preserved in 80% ethanol until identification. From the preliminary survey, diets were classified as including five categories of prey: tadpoles, Odonata nymphs, frogs, fish (loach, *Misgurnus anguillicaudatus* and rice fish, *Oryzias latipes*), and miscellaneous prey.

Frequency of occurrence of prey animals

To evaluate availability of food to *K. deyrolli* nymphs, we calculated the relative abundance of prey, except frogs, during the daytime (1200–1700 hours). A 3-mm-mesh D-frame dipnet (28 cm wide) was pulled 20 times for 50 cm along the bottom of the rice field at each site. Captured animals with >5 mm body length were classified using the five prey categories given above. After classification, we immediately released prey back into the ditch. A census of frogs was performed differently because they were very difficult to collect for counting and measurement. We counted frogs as we walked carefully. Censuses were performed on each ditch and the surrounding area (50 cm from the edge of the water) from 2000 to 0100 hours. Two censuses were conducted weekly on the same day, eight times in Fukusawa, nine times in Uekidani, and nine times in Chuo.

Rearing experiment

To examine the effects of different prey on the growth stages of *K. deyrolli* nymphs, a rearing experiment was conducted in containers (10 cm × 10 cm mouth opening, 20 cm height) maintained at 29.0°C water temperature and 16L:8D light. First, we collected egg masses of *K. deyrolli* from a fringe of a study rice field in 2004. Hatched nymphs were reared individually in containers filled with water to a depth of 15 cm; the tops were covered with plastic netting (3 mm mesh). We selected three prey diets—tadpoles, tadpoles–frogs, and Odonata nymphs—as representative dominant food resources and commonly available prey at the three study sites. In this experiment, fish were excluded as prey because they were not found at the Fukusawa site. In the tadpole–frog treatment, first and second-instar nymphs, which cannot prey effectively on frogs, were supplied with

tadpoles whereas third–fifth-instar nymphs were supplied with frogs. The tadpole, tadpole–frog, and Odonata nymph treatments were replicated, respectively, 21, 21 and 10 times. Prey were collected from the study sites and stocked separately in an aquarium under identical experimental conditions. In the Odonata nymph treatment, the first and second instars were fed smaller Odonata nymphs (damselfly nymphs—Platycnemididae: *Copera annulata* Selys; Lestidae: *Lestes* spp., all 10–20 mm in length). The third–fifth instars were fed larger Odonata nymphs (dragonfly nymphs—Libellulidae: *Orthetrum albistylum speciosum* Uhler, *Sympetrum frequens* Selys and *S. infuscatum* Selys; Aeshnidae: *Anax parthenope julius* Brauer, *A. nigrofasciatus nigrofasciatus* Oguma and *Gynacantha japonica* Bartenev, 20–40 mm). The tadpole treatment used tadpoles at Gosner stages 35–42 (Gosner 1960) of the tree frog, *Hyla japonica* Günther, a dominant species in Japanese rice fields. The prey density in each container was maintained at a constant level (six individuals per container for the first and second instars, and ten individuals per container for the third–fifth instars). We counted the prey animals daily to maintain the same prey density throughout each nymphal stage. Dead prey animals were removed from the containers.

Specific growth rates (SGR) (Ricker 1979) were calculated and compared among the three prey treatments to examine the effects of different prey diets on *K. deyrolli* nymphal development. The nymphal periods between instars N_i and N_{i+1} were recorded. The body lengths of all nymphal instars were then measured. The SGR was calculated as:

$$\text{SGR} = 100 (\ln L_{i+1} - \ln L_i) / (N_{i+1} - N_i),$$

where L_i and L_{i+1} denote the body lengths on days N_i and N_{i+1} , respectively.

Statistical analysis

To examine diet shifts that occur with growth, along with differences in diet among study sites at each nymphal stage of *K. deyrolli*, the four dominant prey categories were compared using χ^2 -contingency table tests with sequential Bonferroni tests (Rice 1989).

The SGR of *K. deyrolli* in three prey treatments were compared using a repeated-measures one-way ANOVA, with diet (tadpole, tadpole–frog, or Odonata nymph) as the between-subject factor and nymphal stage (first–fifth instar) as the within-subject factor. Because Mauchly's test indicated a significant violation of the assumption of sphericity ($P < 0.001$), significance levels for within-subject effects were calculated using Greenhouse–Geisser for the degrees of freedom (Quinn and Keough 2002). Separate one-way ANOVA tests were applied to the differences among prey in

each nymphal stage when a significant interaction effect was encountered between-subject and within-subject. Scheffe's tests with sequential Bonferroni corrections were performed to assess differences among prey when significant effects were detected in the separate one-way ANOVA. Statistical significance was set at 0.05. All statistical tests were conducted using computer software (SPSS for Windows ver. 11.0; SPSS).

Results

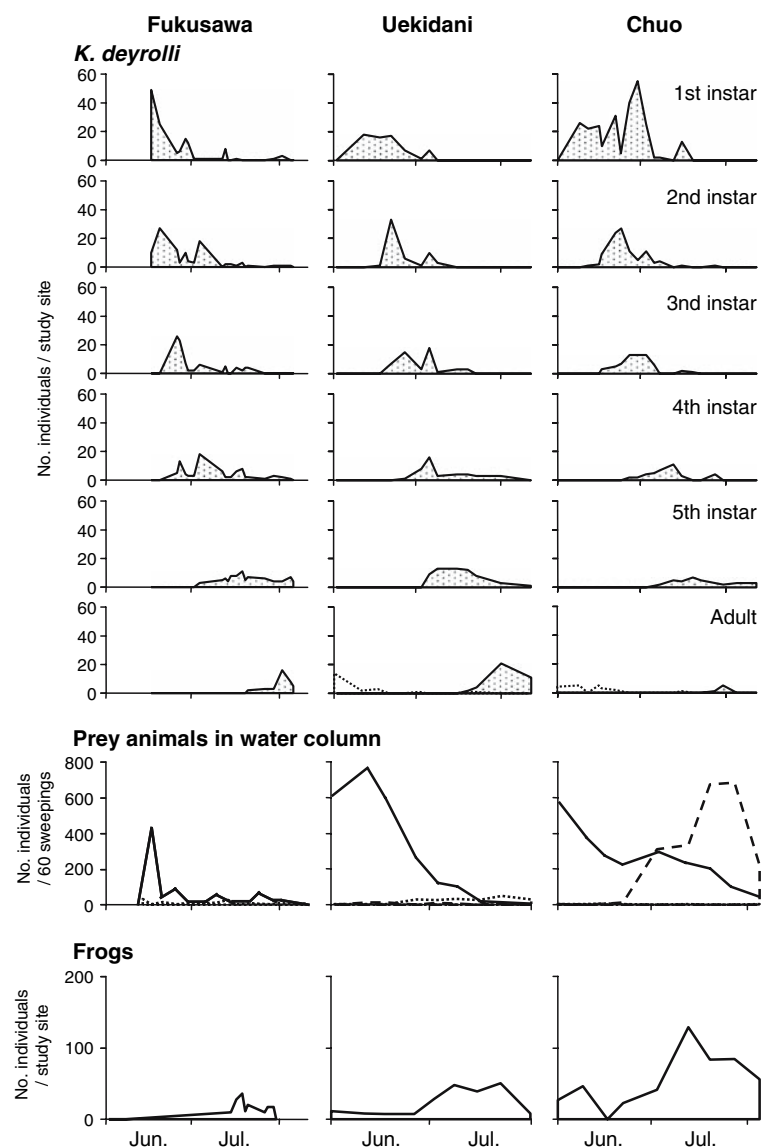
Frequency of occurrence of *K. deyrolli* nymphs and prey animals

Frequency of occurrence of *K. deyrolli* nymphs and prey animals are shown in Fig. 1. First-instar nymphs appeared

at all study sites from June to mid-July. From June to July, second and third-instar nymphs appeared and developed at all study sites as the season progressed. From late June to August, fourth and fifth-instar nymphs appeared. Newly emerged adults appeared from mid-July to August. The *K. deyrolli* nymphal periods from the first to final occurrence in Fukusawa, Uekidani, and Chuo were, respectively, 50, 61, and 57 days.

Tadpoles were abundant in June at the three study sites; as the season progressed, they became frogs and their numbers declined. Their density was extremely low during mid-July to August when older-instar nymphs and adults of *K. deyrolli* appeared. The Odonata nymphs at the three study sites were present with low density throughout the season. Few fish were found at Uekidani throughout the seasons. No fish were observed at Fukusawa. In contrast, fish present in June gradually increased in July at Chuo.

Fig. 1 Seasonal changes in the frequency of *K. deyrolli* and four prey categories at the three study sites. For *K. deyrolli*, broken lines indicate overwintered adults, and solid lines denote newly emerged adults. For prey animals in the water column, solid, broken, and dotted lines indicate tadpoles, fish, and Odonata nymphs, respectively



Most fish in Chuo were rice fish, *Oryzias latipes*, and most were abundant at Chuo among the study sites. Hereafter, we will regard Fukusawa, Uekidani, and Chuo, respectively, as little tadpole–frog, large tadpole–frog, and tadpole–fish sites.

Composition of prey of *K. deyrolli* nymphs

As *K. deyrolli* nymphs grew, their diets changed significantly at each study site (Fukusawa $\chi^2_{12} = 61.50$, Uekidani $\chi^2_{16} = 42.95$, Chuo $\chi^2_{12} = 60.34$; $P < 0.001$ for all; Fig. 2).

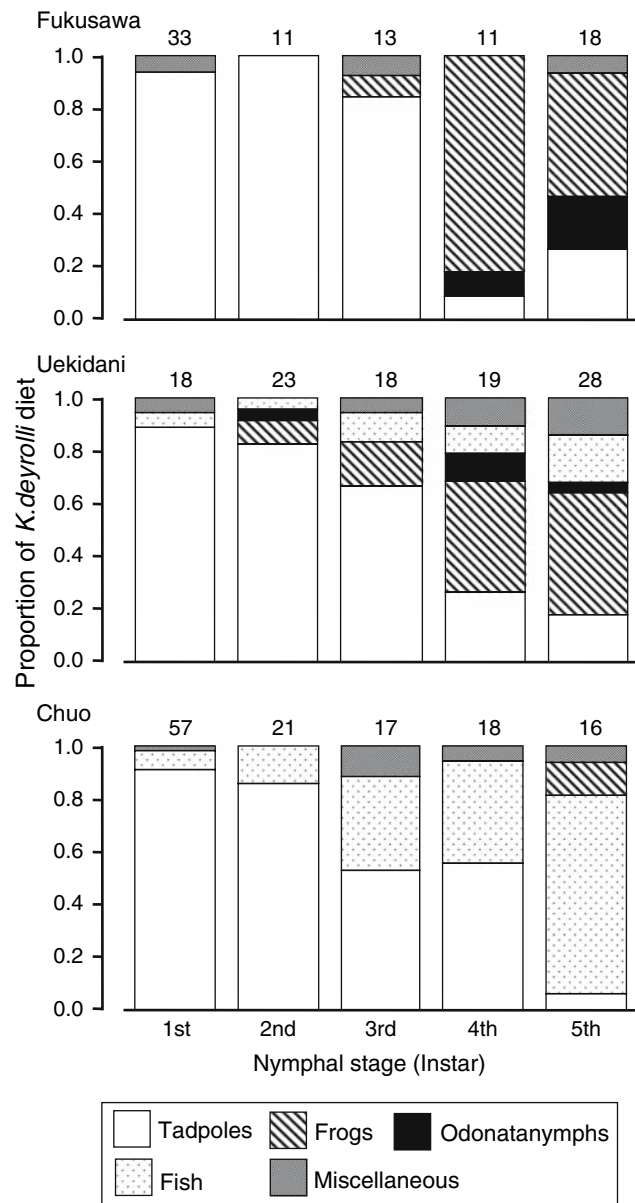


Fig. 2 Five prey groups in the diet of *K. deyrolli* nymphs at Fukusawa in 2003 (top), Uekidani in 2004 (middle), and Chuo in 2004 (bottom). Numerals show sample sizes

First to third-instar nymphs fed primarily on tadpoles, with no statistically significant difference observed among study sites ($P > 0.05$ for all). However, diets of fourth and fifth-instar nymphs differed significantly (fourth $\chi^2_8 = 27.91$, fifth $\chi^2_8 = 29.15$; $P < 0.001$ for both). At the Chuo (tadpole–fish site) site, fourth-instar nymphs also fed predominantly on tadpoles. The proportion of older nymphs’ diets at the three study sites tended toward reduced tadpole frequency. Instead of tadpoles, a large proportion of the diets of fourth and fifth-instar nymphs were frogs at Fukusawa (little tadpole–frog site) and Uekidani (large tadpole–frog site). In contrast, the fifth-instar nymphs at Chuo (tadpole–fish site) fed mainly on fish, primarily rice fish.

Specific growth rates (SGR) of *K. deyrolli*

From the rearing experiment, the effects of three prey diets, tadpoles, tadpoles–frogs, and Odonata nymphs, on the development of *K. deyrolli* nymphs were evaluated in terms of the SGR (Table 2). The SGR of first to third-instar nymphs, especially those of the second instar, tended to be higher than those of the fourth and fifth instars, irrespective of diet treatment. The SGR decreased as nymphs grew. A repeated-measures one-way ANOVA revealed that diet in between-subject, and in nymphal stage and nymphal stage-by-diet interaction effects were all significant factors affecting the SGR of *K. deyrolli* (Table 2).

The SGR differed significantly among diet treatments for the first (one-way ANOVA, $F_{1,34} = 101.32$, $P < 0.001$, Fig. 3), second ($F_{1,34} = 40.04$, $P < 0.001$), third ($F_{2,33} = 14.63$, $P < 0.001$), and fourth instars ($F_{2,33} = 7.54$, $P = 0.002$). However, the SGR in the fifth instar did not differ among diet treatments ($P = 0.08$). For third-instar nymphs, the SGR in the tadpole treatments was significantly higher than that in either the Odonata nymph or tadpole–frog treatment (Scheffe’s test, $P < 0.05$), but it did not differ significantly between the Odonata nymph and

Table 2 Results from repeated-measures one-way ANOVA of the specific growth rate (SGR) of *K. deyrolli* nymphs in the rearing experiment

Source	df	Mean squares	F	P
Between-subject				
Diet	2	38.45	111.20	<0.001
Error	33	0.35		
Within-subject				
Nymphal stage	2.024	210.78	210.78	<0.001*
Nymphal stage × diet	4.049	12.80	12.80	<0.001*
Error	82.45	1.23		

* Corrected P, Greenhouse-Geisser $\epsilon = 0.506$

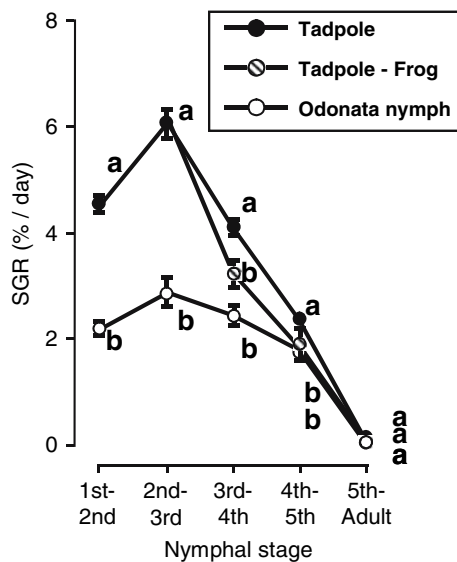


Fig. 3 Comparison of the specific growth rates (SGR) (mean \pm SE) among the different diets in the rearing experiment. Different letters among each instar denote significant differences ($P < 0.05$, 1st–2nd and 2nd–3rd: One-way ANOVA, 3rd–4th, 4th–5th, and 5th–Adult: Scheffe’s test)

tadpole–frog treatments ($P = 0.157$). Similarly, for fourth-instar nymphs, the SGR of the tadpole treatment was significantly greater than that of Odonata nymph or tadpole–frog treatment (Scheffe’s test, $P < 0.017$), but it was not significantly different between the Odonata nymph and tadpole–frog ($P = 0.863$). Demonstrably, the first to fourth-instar nymphs in the tadpole treatment had higher growth rates than those in other treatments.

Discussion

Relationship between ontogenetic diet shift and specific growth rates of *K. deyrolli*

As *K. deyrolli* nymphs grew, their diets changed at each study site. First to third-instar nymphs fed primarily on tadpoles (55–100%) whereas diets of fourth and fifth-instar nymphs were more diverse (Fig. 2). The main diet of fourth and fifth-instar nymphs at the Fukusawa (little tadpole–frog site) and Uekidani (large tadpole–frog site) was frogs (46–62%), but the diet of nymphs in Chuo (tadpole–fish site) primarily included fish (56%). During June, when first to third-instar nymphs were present at the sites, tadpoles were abundant at all study sites. As the season progressed, their numbers declined. The ontogenetic dietary shift is explainable by various factors, for example predator body size and raptorial-trait size (Cloarec 1992; Perez Goodwyn 2001), and prey availability (Charnov 1976; Sherratt and Harvey 1993). In theory, diet choice is

determined by prey availability, that is, the density of preferred food items. Thus, results of this study illustrate the dietary shift of *K. deyrolli* nymphs based on the prey availability.

The first–third (tadpole specialist) and fourth and fifth-instar nymphs (generalist) were classified respectively into younger and older nymphs on the basis of the ontogenetic diet shift (Fig. 2). For younger nymphs, growth rates differed among supplied diets. Younger nymphs supplied with tadpoles achieved the highest growth rates among nymphs supported by all food combinations (Fig. 3). In contrast, growth rates of older nymphs did not differ if they ate either tadpole or other prey. For younger nymphs, tadpole-feeding might be an important prerequisite for survival through their entire life history. In other words, the existence of tadpoles when *K. deyrolli* are younger nymphs is an important life history trait of *K. deyrolli* in respect not only to their abundance, but also their quality.

Younger nymphs fed primarily on tadpoles, irrespective of the study site, and developed more rapidly by eating tadpoles. In addition, appearance of *K. deyrolli* younger nymphs when tadpoles are abundant is expected to moderate cannibalism attributable to food shortage, as with other predatory insects (mantis: Matsura and Nakamura 1981; ladybird: Takahashi 1989; Osawa 1992; Agarwala and Dixon 1992; Hironori and Katsuhiko 1997). The frequency of cannibalism among *K. deyrolli* nymphs is lower than that among *A. japonicus* nymphs in the field (Ohba and Nakasuji 2006). The presence of younger nymphs of *K. deyrolli*, coincident with the appearance of tadpoles, is evolutionarily reasonable as an adaptive strategy.

Prey selection by a carnivorous predator in a temporary habitat

Temporary aquatic habitats, which have unstable and unpredictable features, exhibit amplitudes in both physical and chemical conditions that are more protracted than those of more permanent aquatic habitats. Organisms surviving in temporary aquatic habitats depend largely on exceptional physiological tolerance or effective immigration and emigration (Williams 1987, 2006). In our study, we observed that *K. deyrolli* nymphs grew to adults in approximately two months (56 ± 3 days, mean \pm SE, $n = 3$) within the ditches of all three study sites (Fig. 1). The *K. deyrolli* nymphs reached adulthood with time to spare during the irrigation period (72 ± 6 days at all sites). In this study, we recognized that *K. deyrolli* finished their nymphal stage by the time that water in the ditches lessened (3–5 cm in depth). In fact, *K. deyrolli* is the largest carnivorous insect (45–65 mm in all length) in the rice fields of Japan; they might therefore be regarded as

requiring a rapid rate of growth to reach adulthood during limited irrigation periods.

Aquatic hemipterans breeding in temporary aquatic habitats must complete their immature stage as soon as possible to disperse by flight, which is only possible in the adult stage (Williams 1987, 2006). For adaptive significance in the life history of *K. deyrolli* using temporary aquatic habitats, tadpole-feeding by *K. deyrolli* in early nymphal stages achieves higher growth rates and might be an important ecological adaptation. We suggest that tadpole-feeding by *K. deyrolli* in early nymphal stages not only represents prey selection in response to the environment—it is a necessary means of survival in temporary aquatic habitats. Higher growth rates in tadpole-feeding instars also indicate they are in better physiological condition, which ultimately can support increased survival and fitness, even though the enhanced fitness is not limited to attainment of a higher growth rate.

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References

- Agarwala BK, Dixon AFG (1992) Laboratory study of cannibalism and interspecific predation in ladybird. *Ecol Entomol* 17:303–309
- Albuquerque GS, Tauber MJ, Tauber CA (1997) Life-history adaptations and reproductive costs associated with specialization in predacious insects. *J Anim Ecol* 66:307–317
- Anderson JF (1974) Responses to starvation in the spiders *Lycosa lenta* (Hentz) and *Flistata hibernalis* (Hentz). *Ecology* 55:576–585
- Charnov EL (1976) Optimal foraging: attack strategy of a mantid. *Am Nat* 110:141–151
- Cloarec A (1992) The influence of feeding on predatory tactics in a water bug. *Physiol Entomol* 17:25–32
- Cullen MJ (1969) The biology of giant water bugs (Hemiptera: Belostomatidae) in Trinidad. *Proc R Entomol Soc Lond A* 44:123–137
- Dixon AFG (1959) An experimental study of the searching behaviour of the predatory coccinellid beetle *Adalia decempunctata* (L.). *J Anim Ecol* 28:259–281
- Elkinton JS (2003) Population ecology. In: Resh VH, Cardé RT (eds) *Encyclopedia of insects*. Academic, Massachusetts, pp 933–944
- Evans EW (1982) Timing of reproduction by predatory stinkbugs (Hemiptera: Pentatomidae): patterns and consequences for a generalist and a specialist. *Ecology* 63:147–158
- Fox LR (1975) Some demographic consequences of food shortage for the predator, *Notonecta hoffmanni*. *Ecology* 56:868–880
- Gosner N (1960) A simplified table for staging anuran embryos and larvae with notes on identification. *Herpetologica* 16:183–190
- Hagen KS (1962) Biology and ecology of predaceous Coccinellidae. *Annu Rev Entomol* 7:289–326
- Hasizume H (1994) All about the giant water bugs—wishes for symbiosis with aquatic animals (in Japanese). Tombo Publishing, Osaka
- Hasizume H, Numata H (1997) Effects of temperature and photoperiod on reproduction in the giant water bug, *Lethocerus deyrolli* (Vuillefroy) (Heteroptera: Belostomatidae). *Jpn J Entomol* 65:55–61
- Hirai T, Hidaka K (2002) Anuran-dependent predation by the giant water bug, *Lethocerus deyrolli* (Hemiptera: Belostomatidae). *Ecol Res* 17:655–661
- Hironori Y, Katsunori S (1997) Cannibalism and interspecific predation in two predatory ladybirds in relation to prey abundance in the field. *Entomophaga* 42:153–163
- Juliano SA (1986) Food limitation of reproduction and survival for *Brachinus* (Coleoptera: Carabidae). *Ecology* 67:1036–1045
- Lawton JH (1971) Maximum and actual field feeding-rates in larvae of the damselfly *Pyrhosoma nymphula* (Sulzer) (Odonata: Zygoptera). *Freshwater Biol* 1:99–101
- Lenki RE (1984) Food limitation and competition—a field experiment with two *Carabus* species. *J Anim Ecol* 53:203–216
- Matsura T, Inoue T, Hosomi Y (1975) Ecological studies of a mantid, *Paratenodera angustipennis* De Saussure I. Evaluation of the feeding condition in natural habitats. *Res Popul Ecol* 17:64–76
- Matsura T, Nakamura K (1981) Effects of prey density on mutual interferences among nymphs of a mantis, *Paratenodera angustipennis* (s.) (in Japanese with English Abstract). *Jpn J Ecol* 31:221–223
- Mukai Y, Baba N, Ishii M (2005) The water system of traditional rice paddies as an important habitat of the giant water bug, *Lethocerus deyrolli* (Heteroptera: Belostomatidae). *J Insect Conserv* 9:121–129
- Mukerji MK, LeRoux EJ (1969) A quantitative study of food consumption and growth of *Podisus maculiventris* (Hemiptera: Pentatomidae). *Can Entomol* 101:387–403
- Ohba S, Nakasuji F (2006) Dietary items of predacious aquatic bug *Nepoidea* (Heteroptera) in Japanese wetlands. *Limnology* 7:41–43
- Osawa N (1992) A life table of the ladybird beetle *Harmonia axyridis* Pallas (Coleoptera, Coccinellidae) in relation to the aphid abundance. *Jpn J Entomol* 60:575–579
- Pearson DL, Knisley CB (1985) Evidence for food as a limiting resource in the life cycle of tiger beetles (Coleoptera: Cicindelidae). *Oikos* 45:161–168
- Perez Goodwyn PJ (2001) Size selective predation by *Belostoma oxyrurum* (Heteroptera: Belostomatidae) on *Aedes aegypti* (Diptera: Culicidae) larvae. *Rev Soc Entomol Argent* 60:139–146
- Quinn GP, Keough MJ (2002) *Experimental design and data analysis for biologists*. Cambridge University Press, Cambridge
- Ricker WE (1979) Growth Rates and Models. In: Hoar WS, Randall DJ, Brett JR (eds) *Fish physiology*, vol. VIII. Academic, London, pp 677–743
- Rice WR (1989) Analyzing tables of statistical tests. *Evolution* 43:223–225
- Riverd I (1962) Some effects of prey density on survival, speed of development, and fecundity of the predaceous mite *Melichaeres dentriticus* (Berl.) (Acarina: Acarosejidae). *Can J Zool* 40:1233–1236
- Sherratt TN, Harvey IF (1993) Frequency-dependent food selection by arthropods: a review. *Biol J Linnean Soc* 48:167–186
- Sih A (1987) Nutritional ecology of aquatic insect predators. In: Slansky F, Rodriguez JG (eds) *Nutritional ecology of insects, mites, spiders, and related invertebrates*. Wiley, New York, pp 579–607
- Smith RL (1997) Evolution of parental care in the giant water bugs (Heteroptera: Belostomatidae). In: Choe JC, Crespi BJ (eds) *The*

- evolution of social behavior in insects and Arachnids. II. Evolution of sociality. Cambridge University Press, Cambridge, pp 116–149
- Sota T (1985) Activity patterns, diets and interspecific interactions of coexisting spring and autumn breeding carabids: *Carabus yaconinus* and *Leptocarabus kumagaii* (Coleoptera: Carabidae). *Ecol Entomol* 10:315–324
- Swart CC, Deaton LE, Felgenhauer BE (2006) The salivary gland and salivary enzymes of the giant waterbugs (Heteroptera: Belostomatidae). *Comp Biochem Phys A* 145:114–122
- Takahashi K (1989) Intra- and interspecific predations of lady beetles in spring alfalfa fields. *Jpn J Entomol* 57:199–203
- Toledo LF (2005) Predation of juvenile and adult anurans by invertebrates: current knowledge and perspectives. *Herpetol Rev* 36:395–400
- Williams DD (1987) The ecology of temporary waters. Timber Press, Portland
- Williams DD (2006) The biology of temporary waters. Oxford University Press, New York
- Wise DH (1979) Effects of an experimental increase in prey abundance upon reproductive rates of two orb-weaving spider species (Araneae: Araneidae). *Oecologia* 41:289–300