

Effects of head shape variation on growth, metamorphosis and survivorship in larval salamanders (*Hynobius retardatus*)

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The effects of head shape variation on growth and metamorphosis in larval salamander (*Hynobius retardatus*) were examined by a laboratory experiment and a field experiment. In the laboratory experiment, each larva was fed equal amounts and was prevented from accessing others in both the solitary and group treatments, although chemical cues could be transmitted through water in the group treatment. The relative head width of larvae became larger in the group treatment during the early periods but having a large head width did not finally influence growth rate and days for metamorphosis. In the field experiment, larvae were allowed to contact each other directly in two density conditions. The enlarged relative head width was linked to high growth rate in the high-density treatment but not in the low-density treatment. The larval body size distribution in the high-density condition tended to be smaller, and there was a small proportion of large-sized individuals with a broad head width. Moreover, the small number of large larvae metamorphosed much earlier than the others. The mortality of larvae in high-density conditions was much higher than that in the low-density treatments. This would be a consequence of cannibalism in the high-density condition. From the experimental results obtained, it is argued that for the larvae of *H. retardatus* having a large head is an adaptive tactic that maximizes fitness, particularly in temporary ponds with an unpredictable environment and in crowded conditions.

Key words: cannibalism; cannibalistic morph; density effect; growth rate; head width; *Hynobius retardatus* metamorphosis; salamander.

INTRODUCTION

The role of phenotypic plasticity in achieving an adaptive compromise under various environmental conditions has received attention for a long time (Schlichting 1986; Stearns 1989; Newman 1992; Scheiner 1993). Such adaptive plasticity has been reported to be generally associated with several costs and limits, including trade-offs in behavior, morphology and life-history traits (see review in DeWitt *et al.* 1998). Plasticity in trophic or resource-based polymorphism, in which different morphs often exhibit very different use of food resources even in sympatric conditions, have been discovered in a number of animals (Crump 1992;

Schluter 1995; Skulasson & Smith 1995). For instance, development or maintenance costs of expressing a certain trophic morph following an environmental condition may result in an increasing energy cost to the organism as well as an efficient energy intake rate (Black & Dodson 1990; McCollum & Buskirk 1996; Pettersson & Brönmark 1997).

Cannibalistic polyphenism is the occurrence in a population of alternative phenotypes (discrete cannibal and non-cannibal form) that are produced from a single genotype in response to different environmental stimuli (Polis 1981; West-Eberhard 1989). In particular, cannibalistic polyphenism has been reported in the larvae of several amphibian species (see review in Crump 1992). Such cannibalistic morphs, which are often flexibly induced by environmental stimuli after hatching (Rose & Armentrout 1976; Crump 1992), differ from typical morphs in having a greater head size and mouth width, and

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elongated vomerine teeth (Powers 1903; Rose & Armentrout 1976; Lannoo & Bachmann 1984). Previous studies have suggested that cannibalistic polyphenism is an adaptive trait, particularly in ponds that are small and short of food (Polis 1981; Crump 1983, 1992; Sadler & Elgar 1994). Because the prey size of larval salamanders is generally gape-limited (Kusano *et al.* 1985; Ohdachi 1994; Nishihara-Takahashi 1999), cannibalistic morphs, having a wider mouth, can achieve advantageous foraging over typical morphs in the same population under such pond environments (Reilly *et al.* 1992). However, few studies have addressed the trade-off between the direct costs that are accompanied by the morphological change and the consequent benefit gained by cannibalism. If the development of cannibalistic morph increases physiological cost (e.g. decline in growth rate and/or metamorphosis success), the fitness of the morph would be lower than that of a typical one when the former fails in eating conspecifics.

The flexible development of cannibalistic morph has been reported for *Hynobius retardatus* (Wakahara 1995), which breeds in small, temporary ponds in northern Japan (Sato 1989). In *H. retardatus*, the head width of larvae were found to enlarge when they perceived conspecific cues under high-density conditions even without any actual cannibalism or direct contact among larvae (Nishihara 1996a,b). In addition, a previous study pointed out that larvae with cannibalism achieved a relatively high growth rate compared to ones without cannibalism (Wakahara 1995). However, to date, no studies have attempted to address the effects of morphological change on the growth and metamorphosis of this species. Cannibalistic morph could have advantages in energy intake, growth rate and, consequently, metamorphosis over typical morph under high-density conditions where the former can eat conspecifics. However, larvae of *H. retardatus* may decrease growth rate so as to have the larger head when food resource is limited. Moreover, larvae having a large head may not achieve a higher growth than typical larvae under low-density conditions where the encounter rate with conspecifics and thus cannibalistic success is likely to be low. In the present study, we first examine the cost of the development of a large head width to growth and metamorphosis by a laboratory experiment in which larvae were prevented

from accessing conspecific prey. Second, we explore the developmental effects of large head width on growth, metamorphosis and survival by a field experiment that involves two density conditions in which larvae are allowed direct contact.

METHODS

Laboratory experiment

The laboratory experiment was performed from 24 May to 15 August 1997. Six egg sacs (i.e. six different clutches) of *H. retardatus* were collected from a pond (1.6 m² surface area, 60 cm deep) in Sapporo, southwest of Hokkaido, Japan (42°9'N, 141°17'E), and transferred to the laboratory on 11 May 1997. Individual eggs ($n=96$) obtained from the sacs were kept individually in plastic cups (3 cm diameter, 2.5 cm height) with 3 ml groundwater under a 14 h light/10 h dark regime at room temperature (17–20°C) until hatching. All such larvae were randomly assigned to one of the following experimental treatments within a day of their synchronized hatching.

Each larva was kept separately in a clear plastic cup (6 cm diameter, 5 cm height), which was held in a container (18 cm × 12 cm area, 5 cm height) to prevent physical interaction from one another. The cups were perforated by 15 holes (1 mm diameter each) of 10 rows. Two density treatments, six (hereafter to be called group treatment) or a single individual (solitary treatment) per container, were established so as to produce a variation in head width by controlling conspecific cues (Nishihara 1996a). Each treatment was replicated, using eight and 48 containers, respectively, with a total of 48 larvae being tested for each treatment (i.e. group and solitary). The group and solitary treatments corresponded, respectively, to about 300 and 50 individuals per m² density, which were within the range observed in natural habitats in Hokkaido (Y. Kohmatsu, unpubl. data, 1999). Both the cups and containers were filled with groundwater (4 cm deep). In the group treatment, in order to equalize sibship effects among the containers, each of the six cups in the same container was stocked with a larva from each of the six clutches. In the laboratory, a 14 h light/10 h dark regime and room temperatures of 17–20°C were maintained over

the experimental period. On day 7 of the experiment, larval feeding with equal quantities (10 mg wet mass) of frozen Chironomid larvae was initiated, and continued three times a week thereafter. Each container was cleaned three times a week and refilled with fresh groundwater.

To assess the treatment effects on the relative head width, snout–vent length (SVL, distance from anterior tip of snout to posterior margin of vent) and head width (HW, maximum width across dorsal surface of head) were measured by a digital vernier caliper to the nearest 0.01 mm every 15 days from the start to day 45 of the experiment. Larvae were not anesthetized before being measured to prevent them from being damaged. They were also measured at the final larval stage (i.e. just before metamorphosis; stage 68 in Iwasawa & Yamashita 1991). The relative HW of larval *H. retardatus* shows continuous variation within a population (Wakahara 1995; Nishihara 1996a), and to assess the degree of development of large head width, the residuals of a simple linear regression of HW to SVL were examined. The HW of larvae correlated significantly with SVL on the day of hatching ($r^2=0.797$, $P<0.001$), day 15 ($r^2=0.360$, $P<0.001$), day 30 ($r^2=0.459$, $P<0.001$), day 45 ($r^2=0.457$, $P<0.001$), and on the day of metamorphosis ($r^2=0.363$, $P<0.001$: for \log_{10} transformed data), when all the individuals were pooled (Fig. 1). Note that one individual in the group and two in the solitary treatments died during the experiment.

Field experiment

The 50 egg clutches of *H. retardatus* were collected from a pond (330 m² surface area, 75 cm deep) in Tomakomai Experimental Forest of Hokkaido University (TOEF) and transferred to the laboratory on 29 April 1997. Individual eggs ($n=1188$) were kept separately in plastic cups (3 cm diameter, 2.5 cm height) with 3 ml groundwater under a 14 h light/10 h dark regime at room temperature (17–20°C) until hatching.

We used 36 plastic tanks (90 cm × 60 cm area, 18 cm deep) as artificial ponds, which were within the size range of temporary ponds where *H. retardatus* breed naturally. Tanks, which were placed in two rows in TOEF, were filled with groundwater (40 l) and mud (6 l) collected from the bottom of a

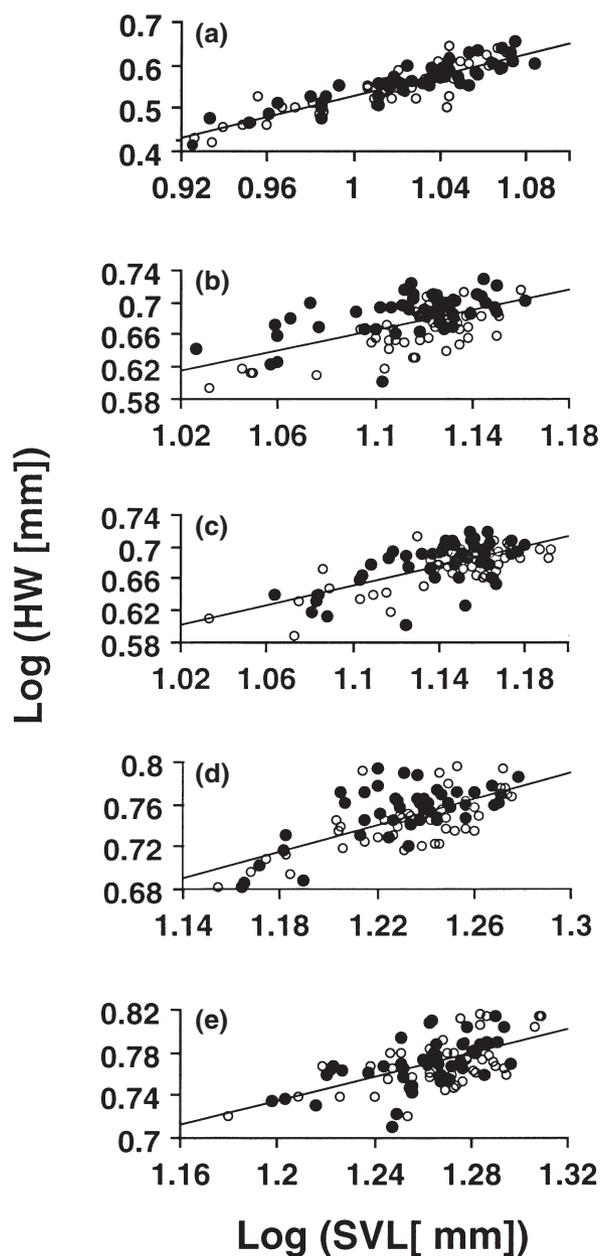


Fig. 1. Relationship between snout–vent length (SVL) and head width (HW) of larvae in (●) group and (○) solitary treatments in the laboratory experiment. (a) Hatch; (b) day 15; (c) day 30; (d) day 45; (e) metamorphosis.

natural pond on 3 May 1997, three months before the experiment. This allowed aquatic invertebrate assemblages to develop in the artificial ponds, from which predators of *H. retardatus* larvae (e.g. dragonfly, water beetle) were completely excluded. The two rows of tanks were surrounded by a 1 mm mesh black net to prevent predators from invading and

sunshine causing a drastic rise in water temperature. All tanks were exposed to natural changes in light cycles and air temperature.

The larvae were immediately assigned to one of the following experimental treatments within a day of simultaneous hatching on 1 June 1997. The tanks were stocked with either 50 (hereafter to be called high-density treatment) or 16 larvae (low-density treatment), in which each treatment corresponded to 93 and 30 individuals per m². Each treatment was replicated using 18 tanks, with a total of 900 and 288 larvae being used for the high- and low-density treatments, respectively. To equalize sibship effects between the treatments, each tank was stocked with larvae, each of which was derived from each of the different clutches.

To assess the effects of the treatments on the development of large head width, the SVL and HW of larvae in each tank were measured every 15 days during the initial 45 days and at metamorphosis. The HW of larvae correlated significantly with SVL on hatching day ($r^2=0.597$, $P<0.001$), day 15 ($r^2=0.800$, $P<0.001$), day 30 ($r^2=0.809$, $P<0.001$), day 45 ($r^2=0.857$, $P<0.001$) and at metamorphosis day ($r^2=0.724$, $P<0.001$: for \log_{10} transformed data), when all the individuals were pooled (Fig. 2).

Statistical analysis

For both laboratory and field experiments, we compared the HW residual between the two treatments using a *t*-test for each measuring day. In the laboratory experiment, specific growth rate (SGR) was calculated using the following formula (Ricker 1979):

$$SGR = 100 \times (\ln L_2 - \ln L_1) / (t_2 - t_1),$$

where L_2 and L_1 are the SVL (mm) at times t_2 and t_1 , respectively, t being expressed in days. The effects of HW residual on the SGR, days for metamorphosis and SVL at metamorphosis of larvae were examined by simple linear regression analyses. As most larvae survived until metamorphosis in both treatments of the laboratory experiment, we did not examine statistically the treatment effects on larval survivorship.

For the field experiment, the SVL for each measuring day was compared between the high- and low-density treatments using Mann–Whitney's *U*-test.

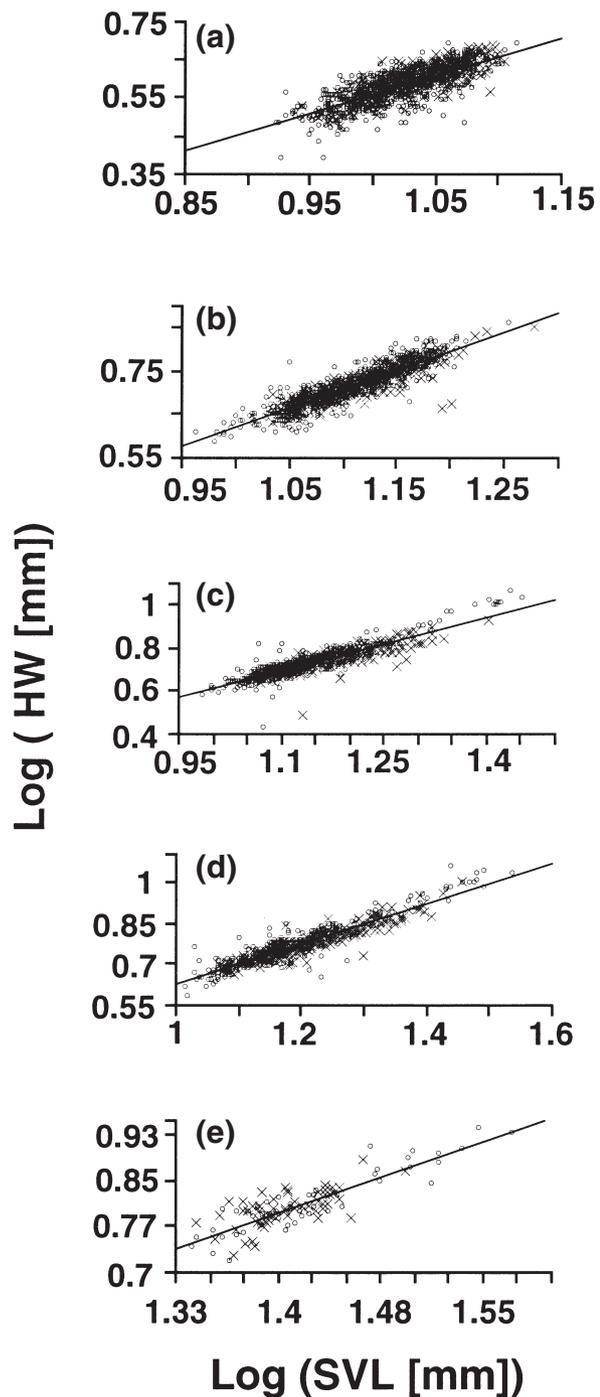


Fig. 2. Relationship between snout–vent length (SVL) and head width (HW) of larvae in (O) high and (X) low density treatments in the field experiment. (a) Hatching; (b) day 15; (c) day 30; (d) day 45; (e) metamorphosis.

Distributions of SVL in two density treatments were compared with the normal distribution using the Kolmogorov–Smirnov test for each measuring day. All the larvae were classified as either large- or small-headed according to the HW residuals on SVL (plus or minus value, respectively) for each measuring day (Fig. 2). We subsequently compared the SVL of larvae between the two groups using Mann–Whitney’s U -test. The non-parametric Mantel–Cox log rank test was used to test for differences in survival curves obtained by the Kaplan–Meier method between the two treatments (Abacus 1994). The relationship between SVL and day for metamorphosis was examined by simple linear regression analyses in each treatment.

\log_{10} transformations were made for exact values in order to standardize variances and improve normality, if necessary, to satisfy the assumptions of parametric tests. However, non-parametric tests were used when the normality was violated, even after the data transformations. All statistical tests were two-tailed. For all statistical tests, the alpha value of 0.05 was used for statistical significance. All analyses were conducted using the statistical package STATVIEW (ver. J5.0, SAS Institute Inc., Berkeley, CA, USA).

RESULTS

Laboratory experiment

The relative HW differed between the group and solitary treatments (Figs 1, 3). The HW residual for the group was significantly larger than that for the solitary treatments on day 15 ($t_{[94]}=5.47$, $P<0.001$), day 30 ($t_{[94]}=2.63$, $P=0.009$), and day 45 of the experiment ($t_{[92]}=3.17$, $P=0.002$), with such differences disappearing at metamorphosis stage although ($t_{[91]}=0.50$, $P=0.622$).

The relative HW, however, did not finally influence days for and body size at metamorphosis in larval *H. retardatus*, when reared without any direct contact among conspecifics. No significant correlation was found between HW residual and SGR on days 30–45 ($r^2=0.001$, $P<0.806$) and during the day 45 to metamorphosis period ($r^2=0.02$, $P=0.207$), although the greater the HW residual value, the lower the SGR was for both hatching to

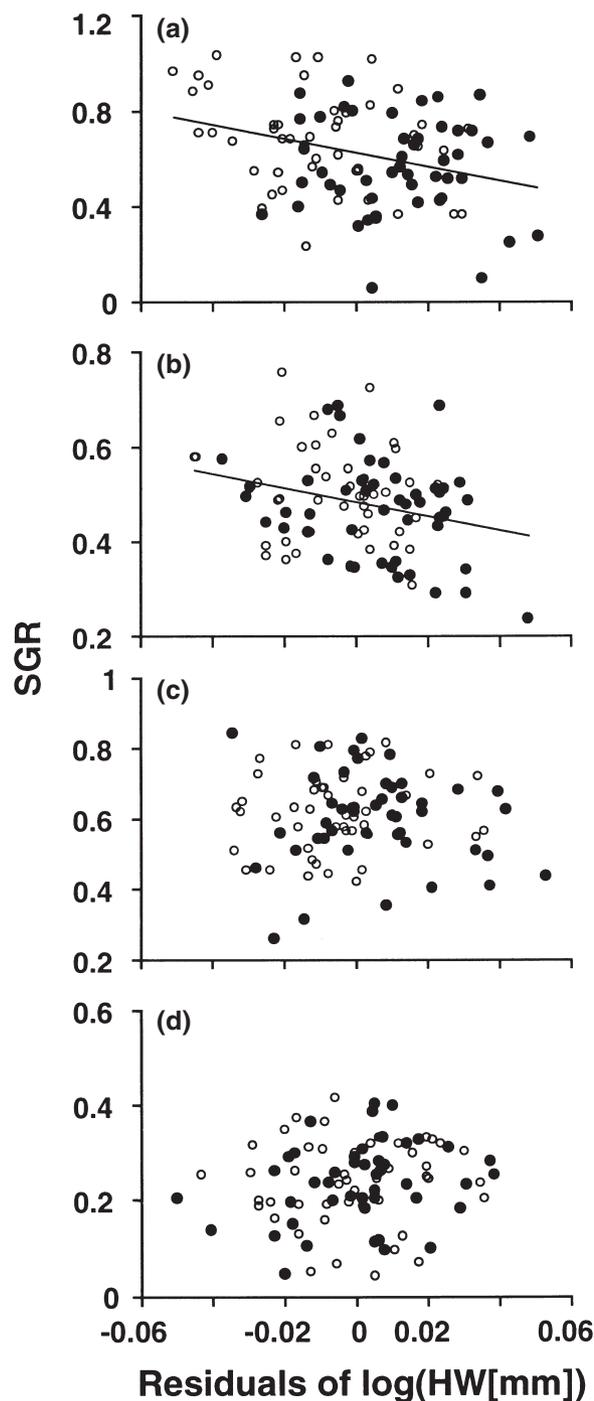


Fig. 3. Relationship between the residual head width (HW) of larvae and specific growth rate (SGR) in (●) group and (○) solitary treatments in the laboratory experiment. (a) Hatch to day 15; (b) day 15–30; (c) day 30–45; (d) day 45 to metamorphosis.

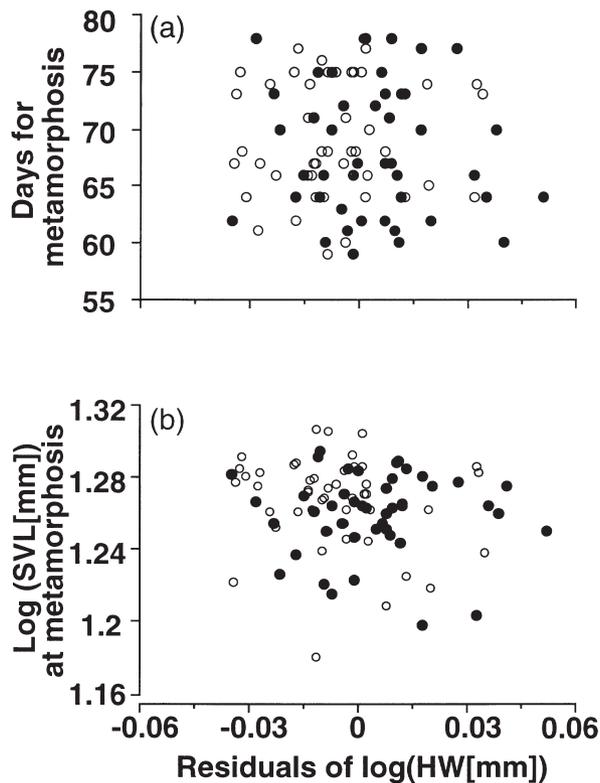


Fig. 4. The relationship between the (a) residual head width (HW) and (b) days for metamorphosis and snout-vent length (SVL) at metamorphosis of larvae in (●) group and (○) solitary treatments in the laboratory experiment.

day 15 ($r^2=0.099$, $P=0.002$) and days 15–30 ($r^2=0.07$, $P=0.009$). The residual of HW at day 45, however, did not correlate significantly with either the day at metamorphosis ($r^2=0.01$, $P=0.806$; Fig. 4a) nor SVL for metamorphosis ($r^2=0.01$, $P=0.207$; Fig. 4b).

Field experiment

A contrast in larval density resulted in differences between treatments for relative HW and survival (Figs 5, 6). The HW residual for the high-density conditions was significantly larger than that for the low-density treatments on day 30 ($t_{[34]}=5.00$, $P<0.001$) and day 45 ($t_{[34]}=4.01$, $P<0.001$), but not on day 15 ($t_{[94]}=2.06$, $P=0.101$) and at the metamorphosis stage ($t_{[34]}=3.11$, $P=0.753$) of the experiment. Meanwhile, survival under low-density conditions was better than for the high-density treatments (Mantel–Cox log rank test; $\chi^2=189.09$, $P<0.001$).

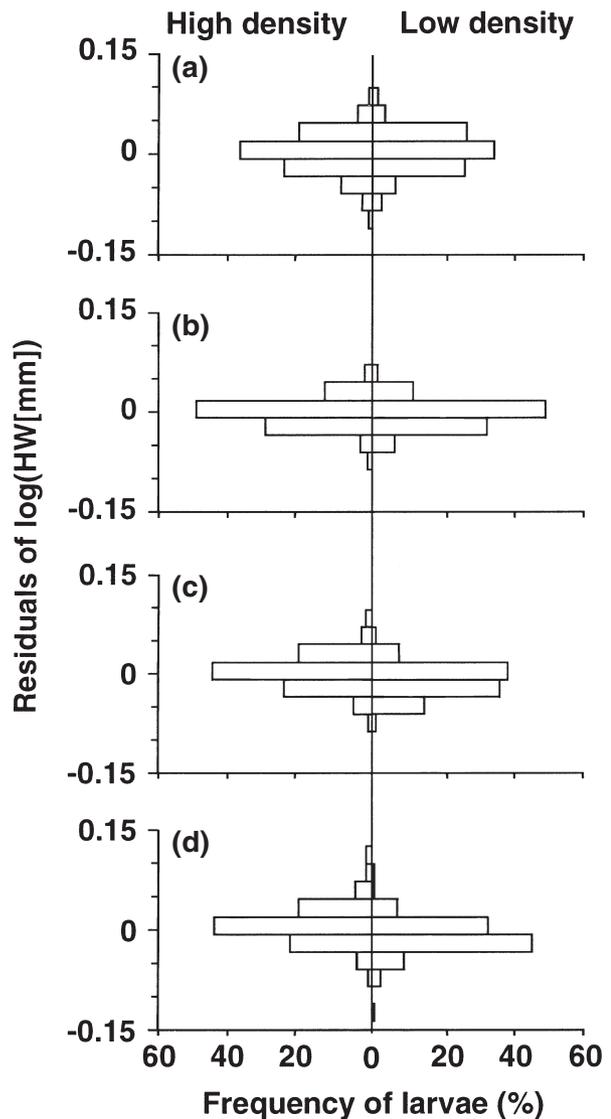


Fig. 5. Frequency distribution of the residual head width (HW) in high- and low-density treatments in the field experiment. (a) Hatch; (b) day 15; (c) day 30; (d) day 45.

The relative HW was closely linked with growth variation in the high-density treatments but not in the low-density treatments (Fig. 7). The SVL of larvae in the high-density treatments was significantly lower than the low-density treatments on day 15 ($U=18.0$, $P<0.001$ by Mann–Whitney U -test), day 30 ($U=29.0$, $P<0.001$), day 45 ($U=40.0$, $P<0.001$) of the experiment and at metamorphosis ($U=91.5$, $P=0.026$). The SVL of larvae formed a normal distribution from the hatching day ($\chi^2=2.28$, $P=0.641$ by Kolmogorov–Smirnov test) to day 15 ($\chi^2=3.36$, $P=0.373$). However, it

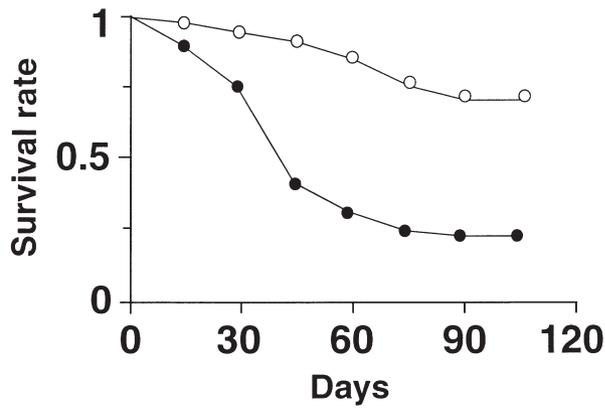


Fig. 6. Survival curves drawn using the Kaplan–Meier method based on larval survival over the experimental period. Mortality of an individual of a larva in (●) high and (○) low densities in the field experiment.

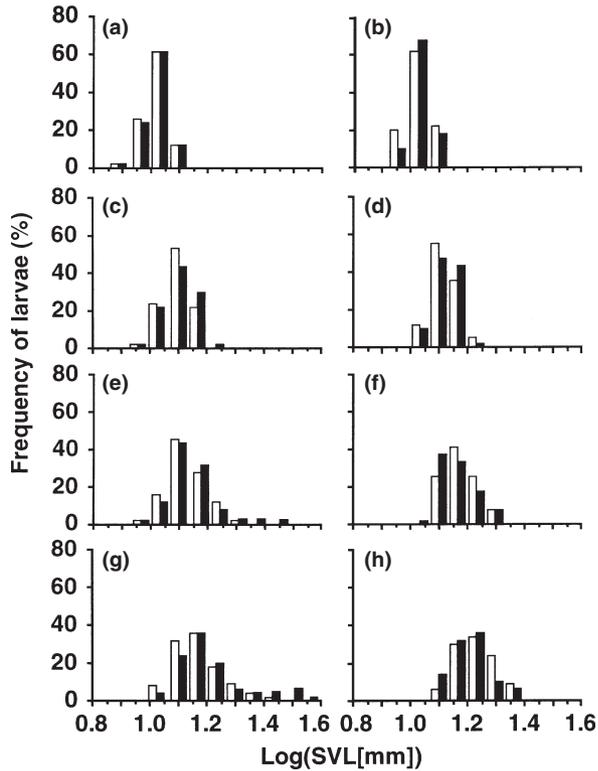


Fig. 7. Frequency distribution of snout–vent length (SVL) for (■) large head and (□) small head larvae in (a,c,e,g) high- and (b,d,f,h) low-density treatments in the field experiment. (a,b) Hatch; (c,d) day 15; (e,f) day 30; (g,h) day 45.

did not form a normal distribution but was skewed to the smaller measurements on day 30 ($\chi^2 = 8.36$, $P = 0.031$) and day 45 ($\chi^2 = 8.42$, $P = 0.030$) of the experiment for the high-density treatment (Fig. 7).

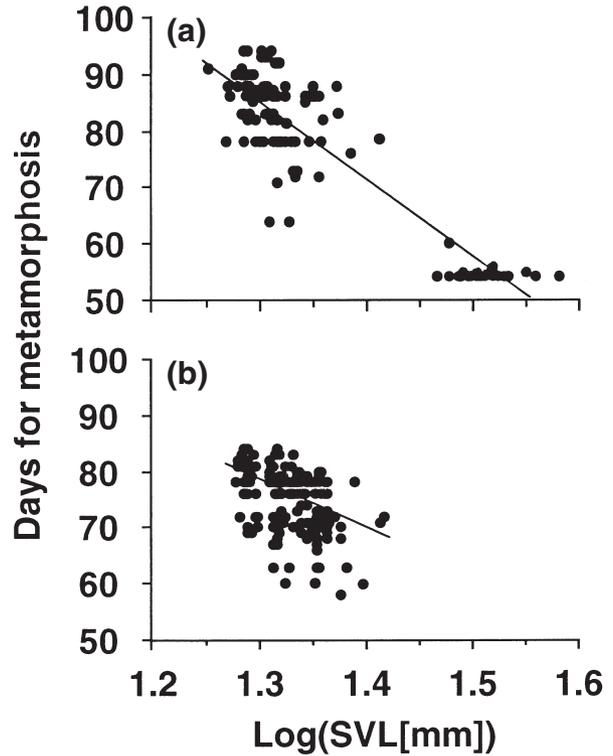


Fig. 8. Relationship of snout–vent length (SVL) and day of metamorphosis in (a) high- and (b) low-density treatments in the field experiment.

In contrast, the SVL distribution was normal over all the experimental periods of the low-density treatment ($\chi^2 = 0.70–22.25$, $P > 0.64$). To assess the effect of HW residual on growth, the SVL was compared between the large- and small-headed groups for each treatment and each measuring day (Fig. 7). For the high-density treatment, the SVL of larvae with large heads was significantly larger than that of the small-headed group on day 45 of the experiment ($U = 99.0$, $P < 0.044$ by Mann–Whitney U -test), but not on day 15 ($U = 113.0$, $P = 0.121$) and day 30 ($U = 115$, $P = 0.137$ for both; Fig. 5). In contrast, the SVL did not differ significantly between the groups on day 15 ($U = 152.0$, $P = 0.752$), day 30 ($U = 114.0$, $P = 0.129$) and day 45 ($U = 137.0$, $P = 0.597$) in the low-density treatment.

Days for and body size at metamorphosis were strongly influenced by growth variation (Fig. 8). The days for metamorphosis was negatively correlated to the SVL of larvae in both high- ($r^2 = 0.765$, $P < 0.001$) and low-density treatments ($r^2 = 0.209$, $P < 0.001$). There was no significant difference in days for metamorphosis between the two

treatments ($U=102.0$, $P=0.058$ by Mann–Whitney's U -test). However, the high-density treatment included two distinct groups, one of which (17/123 larvae (13.8%)) was characterized as having an exceedingly large body size and a short larval period for metamorphosis. These individuals metamorphosed at a larger body size and much earlier than any of the individuals in the low-density treatment.

DISCUSSION

In the laboratory experiment, the larvae of *H. retardatus* of the group treatment had a relatively larger head width, with head width becoming equal at metamorphosis when the two treatments are compared (Fig. 3). The development of a larger head width can be induced by conspecific cues even without any direct contact, as studied previously by Nishihara (1996a). Even though the groups were fed equal amounts, it was found that increasing head width was proportional to reduced growth rate during the early developmental stages (i.e. from hatching to day 30). It is likely that the decrease in larval growth rate is caused by energy being re-allocated to the development of the larger head. The larvae with larger heads and mouths are at an advantage to cannibalize and are prevented from being caught and swallowed by conspecific larvae because the larval prey size is gape-limited (Kusano *et al.* 1985; Ohdachi 1994). Moreover, in the field observation, conspecifics fed more heavily on *H. retardatus* larvae that were at the prefeeding stage compared to at feeding stage (Nishihara-Takahashi 1999). Therefore, in high-density conditions, increased head width is a positive adaptive tactic for decreasing mortality and increasing growth rate, particularly in the early larval period. The negative effect of an enlarged head on growth rate, however, disappeared from day 45 onwards. Consequently, such flexible polyphenism in head morphology resulted in no differences in either the day or body size for metamorphosis (Fig. 4), both of which can be closely related with fitness (Werner 1986). Therefore, we can conclude that *H. retardatus* larvae changed their growth process by developing a large head width, which is associated neither with a notable

investment of energy nor as an advantage when food intake rate is equal.

Similarly to the laboratory experiment, the relative head width of larvae in high-density conditions was enlarged compared with low-density conditions also in the field experiment (Fig. 5). Overall mean growth of the experimental population was suppressed by high-density conditions during the early developmental stage, as found for many amphibian species (Wilbur & Collins 1973; Semlitsch & Caldwell 1982; Scott 1990). However, in high-density conditions, size tended to be smaller, with a small proportion of individuals being much larger than others (Fig. 7). In addition, the body size of large-headed larvae became larger than that of small-headed larvae on day 45 of the experiment in the high-density treatment. It is likely that such large larvae exist in the population as a consequence of cannibalism. Cannibalism, which was found to occur under crowding conditions (Crump 1992; Wakahara 1995), has been known to generally facilitate the growth of salamander larvae (Crump 1992; Sadler & Elgar 1994). In fact, the mortality of *H. retardatus* larvae in high-density treatments was much higher than that in low-density treatments (Fig. 6). In the experiment, the growth, death and behavior of unidentified larvae were not recorded individually. Such mortality, however, could be primarily caused by cannibalism, because larvae in the group treatment did not have a high mortality when, during the laboratory experiment, the larvae were prevented from any direct contact. Moreover, larval body size did not differ between the large- and small-headed groups in the low-density treatment. Therefore, the large-headed larvae were considered to attain advantageous growth by eating conspecifics under high-density conditions, which is consistent with earlier findings for other salamander species (Lannoo *et al.* 1989; Pfennig 1990; Pfennig *et al.* 1991b).

Days for and body size at metamorphosis were strongly influenced by larval growth. The earlier the metamorphosis of larvae occurred, the larger their resulting body size in both treatments of the field experiment (Fig. 8). Moreover, in the high-density treatment, a relatively small number of larvae metamorphosed much earlier and attained a larger body size compared to the others in the same

treatment and compared to any individual in the low-density treatment. This is likely to be a consequence of cannibalism in the high-density condition, because even large-headed larvae did not achieve any advantageous growth in the low-density treatment. Therefore, we can conclude that *H. retardatus* larvae with a large head width are associated with a higher growth compared to typical larvae under high-density conditions where the encounter rate with conspecifics and thus cannibalistic success is high. For amphibian metamorphosis, Werner (1986) theoretically predicted that a large metamorphosis size increases post-metamorphic (i.e. subadults) growth and survival. Age at maturity was also demonstrated to increase with body size at metamorphosis (Scott 1994). In general, a higher growth rate is known to result in a shorter larval period in many amphibians (Wilbur & Collins 1973; Wilbur 1980; Smith 1983; Newman 1987; Alford & Harris 1988). Cannibalism, which enables individuals to rapidly grow and consequently shorten the larval period, may increase the probability of survival allowing the larvae to metamorphose before the pond dries (Wilbur & Collins 1973; Crump 1992). Indeed, the occurrence of cannibalistic morphs in amphibians was pointed out to be usually associated with the use of temporary ponds (Lannoo *et al.* 1989; Pfennig 1990; Pfennig *et al.* 1991b), although, this has not been reported for *H. retardatus*. Present experimental results argue that *H. retardatus* larvae with a large head width is an adaptive tactic that maximizes fitness components during both the larval and adult periods, particularly under crowded conditions. In the field experiment, small-headed larvae also occurred in the high-density treatment. This result suggests that the larvae with a large head width do not always utilize this advantage. For instance, the cost of cannibalism includes risk of injury or death, risk of eating a relative (reviewed in Crump 1992), or risk of consuming pathogens from victims (Pfennig *et al.* 1991a). In fact, most larvae develop a large head width only in high-density conditions, even though notable physiological costs are not detected (Figs 3,4). In future studies, we should clarify the cost of morphological change and address the adaptive significance of plasticity of larval morphology in *H. retardatus*.

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