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Cannibalism and the Resulting Dimorphism in Larvae of a Salamander *Hynobius retardatus*, Inhabited in Hokkaido, Japan

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ABSTRACT—A cannibalism in the larvae of a salamander (*Hynobius retardatus*) and a resultant dimorphism were firstly described in laboratory-raised population. The cannibalistic larva develops to a "broad-headed" morph which has a wider head and grows faster compared with a non-cannibalistic "typical" morph. Laboratory experiments were conducted to examine a possible relationship between the dimorphism and cannibalism. Level of food supply and kinship of larvae affected the frequency of cannibalism. Low level of the food supply resulted in higher incidence of the cannibalism. The frequency of cannibalism in siblings was significantly lower than in the mixed-sibling groups. Possible biological significance of the cannibalism in this species was discussed.

INTRODUCTION

Many populations contain multiple, functionally distinctive morphs. Some of the polymorphism depend on sex (sexual dimorphism) and are genetically controlled. Others are considered to be controlled by environmental or trophic conditions, such as in "worker" and "queen" morphs in social insects, crested and noncrested *Daphnia*, sedentary and migratory forms of locusts, pupal color in various Papilionidae, and "major" and "minor" morphs in dynastine beetles. These polymorphisms have been studied on the view points of evolutionary ecology (see [23]).

The most conspicuous polymorphism in amphibians involves the occurrence of sexually mature metamorphosed (ordinary) and gilled (neotenic) morphs in many species of salamanders [5, 9]. In spadefoot toad tadpoles (*Scaphiopus multiplicatus*) which inhabits desert ponds, a large, rapidly developing carnivorous morph and a smaller, more slowly developing omnivorous morph have been reported [13, 14]. A subspecies of *Ambystoma tigrinum, A. t. nebulosum* (Arizona tiger salamander) has been reported to show a different polymorphism other than the neoteny; a typical larval and so-called cannibalistic or "broad-headed" larval morphs [2, 3, 15, 16].

Hynobius retardatus living in Hokkaido, Japan has interesting characteristics: 1) This species has been reported to show neotenic reproduction in a specific environment of Lake Kuttara, a small volcanic lake [17, 18], and can produce morphologically mature spermatozoa even in larval forms when metamorphosis is arrested by goitrogens [24]. 2) A transition of hemoglobin subunits from larval to adult types occurs on the same time schedule in both normally metamorphosing animals and metamorphosis-arrested larvae [1, 25], like in the axolotl [4]. 3) It has been reported to show two dimorphisms: "large" and "common" types in adult forms have been reported in Obihiro, eastern Hokkaido [10, 19], and "broad tail" larvae are living in the resting water and "narrower tail" type are living in the running water [21]. 4) A cannibalism is frequently observed in the larval stages among the laboratory-raised larvae [12] as well as even in the natural habitats, like in the Arizona tiger salamanders.

It has long been known to experimenters of *H. retardatus* that the number of larvae per aquarium gradually decreases after cannibalism when a large number of the larvae were reared in one aquarium. It has also been noticed that extraordinarily large larvae eventually appear among the larvae after cannibalism. In the present study, possible factors affecting the frequency of cannibalism in the larvae of *H. retardatus* were examined, and relationship between cannibalism and the dimorphism (extraordinarily large and ordinary larvae) observed in the larval population was analyzed.

MATERIALS AND METHODS

Animals

Fertilized eggs of *H. retardatus* were collected from several ponds or small streams of three localities in the vicinity of Sapporo; Bankei, Nopporo and Okusawa. After hatching, the larvae were reared in plastic tanks (22×15×13 cm) filled with 2 *l* of dechlorinated tap water supplemented with antibiotics (100 IU/ml penicillin G and 100 μg/ml stretpomycin). They were fed with live freshwater oligochaete (*Tubifex*) or with commercially available frog feed pellets (Oriental Kobo Co., No. 2 for frogs). The rearing water was exchanged every two days when the larvae were fed with live *Tubifex* or everyday when fed with artificial pellets. Developmental stages were determined according to the normal table for *H. nigrescens* [6].

Experimental design

Three experiments were conducted to evaluate possible rela-

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tionship between the kinship of larvae and the frequency of cannibalism (Experiment I), between levels of food supply and the frequency of cannibalism (Experiment II), and between the density of larvae and the frequency of cannibalism (Experiment III). Each was done in a laboratory with a natural light/dark schedule at a room temperature.

Experiment I: Twenty to forty larvae developed from one egg sac (siblings) or developed from two egg sacs (mixed-siblings) were grown in each plastic tank. In mixed-sibling groups, larvae of the same size developed from two egg sacs collected in either the same place or different places were mixed (see Table 1). Seventeen tanks of sibling groups (total number of larvae used was 465) and 12 mixed-sibling groups (total number of larvae used was 317) were prepared. They were fed once a day with a medium level of food supply (described later). The dead larvae were removed from tanks and the number of larvae in each tank was recorded everyday. The duration of observations was 3 to 4 weeks, until the cannibalism basically ceased (see Fig. 1). The reduced number of larvae except dead ones were considered to be the number of victims by cannibalism.

Experiment II. In order to analyze the effects of the food level on cannibalism, three different levels of food supply were prepared: 20 to 25 larvae of mixed-siblings were placed in tanks with 2 *l* of rearing water and fed with high (approximately 4–8 *Tubifex* or 3 pellets of artificial frog food per larva per day), medium (2–3 *Tubifex* or 1 pellet per larva per day) and low (less than 1 *Tubifex* or 0.5 pellets per larva per day) levels of food. Five to eight tanks were prepared in each experimental group. The number of larvae in each tank was recorded everyday.

Experiment III. Five to ten larvae (low density), 20 to 25 larvae (medium density) and 30 to 40 larvae (high density) of the mixed-siblings were placed in tanks filled with 2 *l* of rearing water respectively, and fed with *Tubifex* of medium level. Six to eight tanks were prepared in each experimental group. The number of larvae in each tank was recorded everyday.

Measurements of larvae

The body length (snout-vent length; SVL) and the width of head at the level of eyes were measured by slide calipers to the nearest 0.05 mm for each individual, on every 10 days during the course of experiments.

RESULTS

Cannibalism in Hynobius retardatus

Figure 1 shows several patterns of the increase of the victims by cannibalism (i.e., the decrease of survivors) in each tank observed in various rearing conditions. For instances, numbers of larvae decreased rapidly by cannibalism in Tank A+C and Tank D+E, in each of which larvae developed from two different egg sacs had been mixed. On average, 2 victims were eaten per tank per day during the first 2 weeks. Contrary to these, no cannibalism was occurred in Tank A where larvae developed from the same egg sac (in detail, described later).

The cannibalism began at the stage of the beginning of feeding (Stage 44), just after hatching, and continued during larval stages. During and after metamorphic stages, however, no cannibalisms were occurred. Thus, the cannibalism in *H. retardatusis* just limited to the larval stages. Cannibalistic larvae were not always one per tank, in contrast to the famous case of cannibalism in *Ambystoma tigrinum nebulosum*, in which only one cannibalistic larva appeared per aquarium [3, 15].

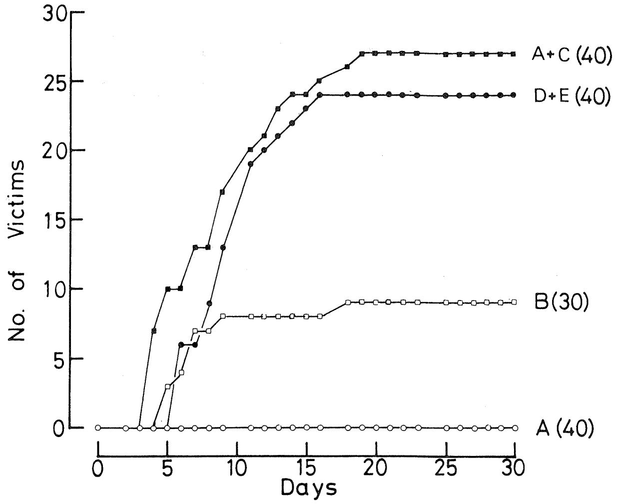

FIG. 1. Several patterns of increase of victims by cannibalisms in larval *Hynobius retardatus*. Larvae hatched from 5 different egg sacs (A to E) were reared in various combinations in 4 different plastic tanks as indicated in right side of the graph. When 30 (B) or 40 (A) larvae which had been hatched from the same egg sacs were placed in each tank, respectively (sibling groups), number of victims by cannibalisms was 0 (A) or relatively small (B). When 20 larvae each from two different egg sacs were mixed (A+C, D+E; non-sibling groups), number of victims by cannibalisms rapidly increased. After about 3 weeks from hatching, victims by cannibalisms no longer increased.

Cannibalism is suppressed in sibling group

In order to test whether the kinship of larvae influenced the frequency of cannibalism, larvae of similar size were reared in mixed-brood groups or in sibling groups (Table 1). In 4 out of 17 tanks of siblings, no cannibalism occurred at all. Contrary to this, cannibalisms was observed in all tanks of mixed-brood groups. Approximately one-fifth of larvae (96 larvae out of 465; 21.5%) were eaten in sibling groups. Average number of victims by cannibalism was 5.7 larvae per tank. In mixed-sibling groups, however, about half of larvae (155 larvae out of 317; 44.7%) were sacrificed by cannibalism. Average number of victims was 12.0 per tank. Both of the differences in the per cent reduction (total number of victims/initial number of larvae) and in the number of victims per tank were statistically siginificant between the sibling and mixed-sibling groups (Mann-Whitney's $U=42.5$, $0.005<P<0.01$).

Effects of food supply and density on cannibalism

Levels of food supply: When the larvae were fed with low level of food, 67% of larvae were eaten (Fig. 2A). Contrary to this, in the groups of high level of food, 15% of

TABLE 1. Frequency of cannibalism in larvae of *Hynobius retardatus* among siblings and mixed-siblings

Siblings						Non-siblings					
Tank No.	Collection site*	No. of larvae		No. of victims**	% Reduction	Thank No.	Collection site	No. of larvae		No. of victims	% Reduction
		Initial	Final					Initial	Final		
1	B	40	40	0	0	1	B-B	30	18	11	33.0
2	B	35	25	10	28.6	2	B-B	30	9	21	70.0
3	B	25	25	0	0	3	B-N	20	16	4	20.0
4	B	30	30	0	0	4	B-O	20	6	14	70.0
5	B	30	17	13	43.3	5	N-N	30	18	11	36.7
7	N	20	8	12	60.0	7	N-N	25	15	10	40.0
8	N	20	13	7	35.0	8	N-O	32	12	20	62.5
8	N	20	13	7	35.0	8	N-O	32	12	20	62.5
9	N	30	19	10	33.3	9	O-O	25	19	4	24.0
10	N	30	20	10	33.3	10	O-O	25	14	11	44.0
11	N	25	15	10	40.0	11	O-O	25	23	2	8.0
12	N	25	25	0	0	12	O-O	25	13	12	48.0
13	O	25	18	7	28.0						
14	O	25	24	1	4.0	Average		26.4	13.3	12.0***	44.7***
15	O	25	23	2	8.0						
16	O	25	18	7	28.0						
17	O	25	23	2	8.0						
Average		27.4	21.5	5.7	21.5						

* B, Bankei; N, Nopporo; O, Okusawa

** Initial number-(final number+dead larvae)

*** Statistically significant ($P<0.01$) to the sibling groups by Mann-Whitney's U-test

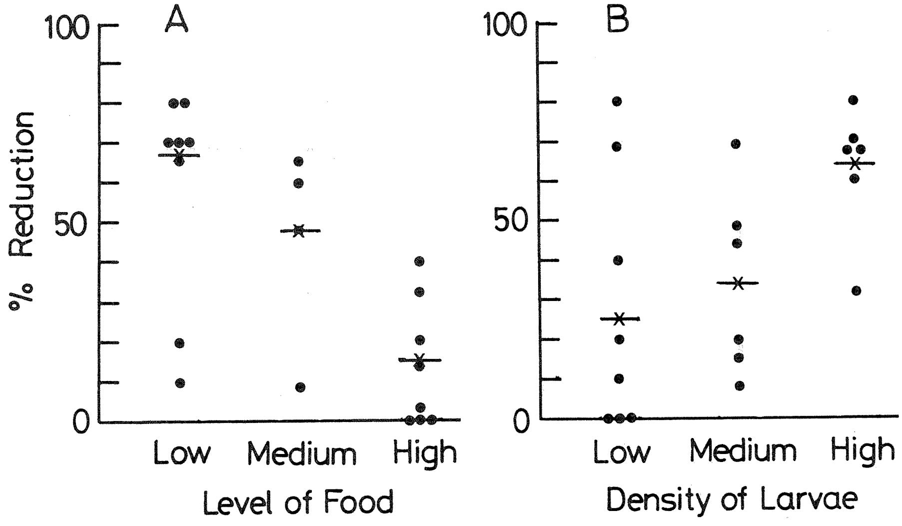

FIG. 2. Effects of levels of food supply (A) and densities of larvae (B) on the frequency of cannibalism in the larvae of *Hynobius retardatus*. Each point shows per cent reduction of larvae in each tank. Cross on bar, an average in each experimental group. A: Results of Experiment II. In the larvae fed with low level of food, cannibalism was observed more frequently. The difference in per cent reduction among the three different levels of food supply was statistically significant (Kruskal-Wallis' H test, $0.005<P<0.01$). B: Results of Experiment III. High density of larvae resulted in higher incidence of cannibalism, and low density resulted in lower incidence of cannibalism. But, the difference in the per cent reduction among the three density groups was not so high (Kruskal-Wallis' H test, $0.1>P>0.05$).

larvae were sacrificed by cannibalism. In 3 out of 8 tanks of larvae fed with high level of food, no cannibalism was observed. The frequency of the cannibalism in the larvae fed with medium level of food was in between the two. The difference in the per cent reduction among the three groups was statistically significant (Kruskal-Wallis' $H=10.23$, 0.005

$<P<0.01$). Thus, the frequency of cannibalism in *H. retardatus* larvae was affected by the level of food supply.

Densities of larvae: In the low density group, about 25% of initial larvae were eaten, whereas 55% of larvae were sacrificed in the high density group (Fig. 2B). In 3 out of 8 tanks, no cannibalism was observed in the low density groups. The frequency of cannibalism in the larvae of medium density group was in between the two. Whereas the difference in the per cent reduction among the three density groups was not significant (Kruskal-Wallis' $H=4.91$, $0.1>P>0.05$), frequency of the cannibalism seemed to be affected by the density of conspecifics.

Dimorphism in Hynobius retardatus

Cannibalistic larvae may grow faster and larger than the non-cannibalistics. We noticed two types of larvae: many small (ordinary) larvae and a few large ones in aquaria where cannibalism had frequently happened (Fig. 3). Thus, the large larvae should be cannibalistic one and the small should be non-cannibalistic. Non-cannibalistic larvae had a relatively slender snout and small head. The extra-large larvae had a wider snout and larger head. Among the larvae captured from the natural habitats, we could also find many ordinary larvae with a slender snout and a few extraordinarily large ones with a large head. In order to elucidate this size difference quantitatively, the snout-vent length (SVL) and the width of head at the level of eyes were measured in two different groups. The first group contained only non-cannibalistic larvae which were exclusively observed in the sibling groups. The second contained both cannibalistic and non-cannibalistic larvae in the same tanks.

Figure 4 shows the frequency desitribution of larvae from the populations showing cannibalism (Fig 4B) and the ones not showing cannibalism at al (Fig. 4A). Head width was measured individually on 30 days after hatching. Larvae of no cannibalism group showed a single peak of head width (Fig. 4A). These larvae having a slender snout and narrower head were designated to "typical" morphs. Contrary to this, head widths of larvae from the population showing the cannibalism (Fig. 4B) were very diverse: whereas a majority of larvae had a slender snout and narrower head, some ones had extraordinarily large head. Solid columns in Fig. 4B indicate the cannibalistic larvae whose cannibalism was witnessed once or more. These larvae with extra-large head were designated to "broad-headed" morphs.

Figure 5 shows the allometry of the head to the snout-vent length (SVL) during larval development. In the population of non-canniblistic larvae or of "typical" morphs (Fig. 5A), it was demonstrated that the width of head grew proportionally to body size (SVL) from very small to relatively large larvae. This indicates that the proportion of head region to entire body size remains constant in this group. In the tanks where cannibalism was observed frequently (Fig.

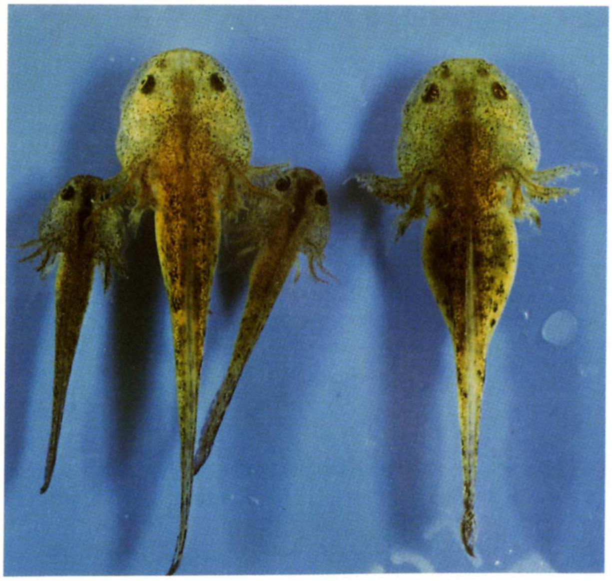

Fig. 3. External views of "typical" and "broad-headed" morphs. Smaller larvae, "typical" morphs are non-cannibalistic and have a slender snout and narrower head. Larger ones, "broad-headed" morphs grow larger than the "typical" morphs and have a wider head. These 4 larvae developed from the same egg sac, and thus of the same age (30 days after hatching). They were reared under the high density condition and fed with a medium level of food.

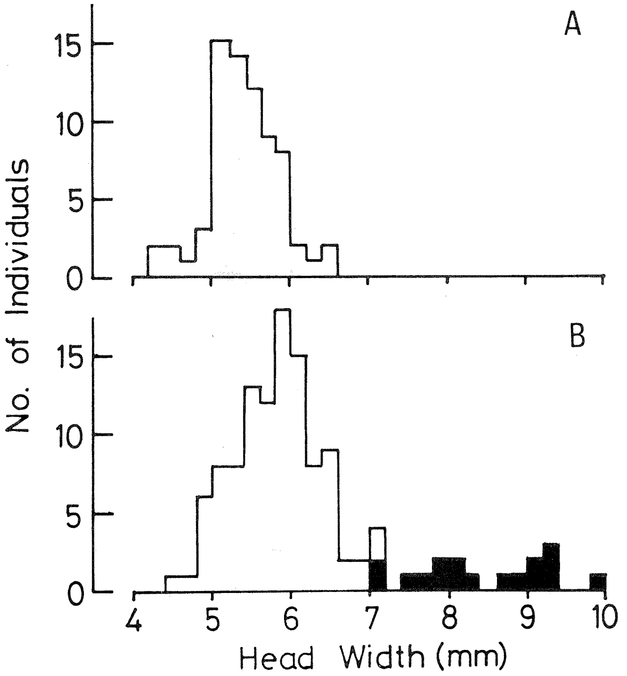

Fig. 4. Frequency distribution of larvae from the tanks where cannibalism was not observed at all (A) and were frequently observed (B). Head width of each larva was measured on 30 days after hatching. A: Larvae of non-cannibalism group showed a single peak of head width (5.42 mm in average of 70 larvae). These larvae having a slender snout and narrower head were designated to "typical" morphs. B: Seventeen larvae (solids) out of 119 larvae were cannibalistic and had an extra-ordinarily large head, whereas the others (non-cannibalistic) had a slender snout and narrower head (5.75 mm in average of 102 larvae). The larvae with the extra-large head were designated to "broad-headed" morphs.

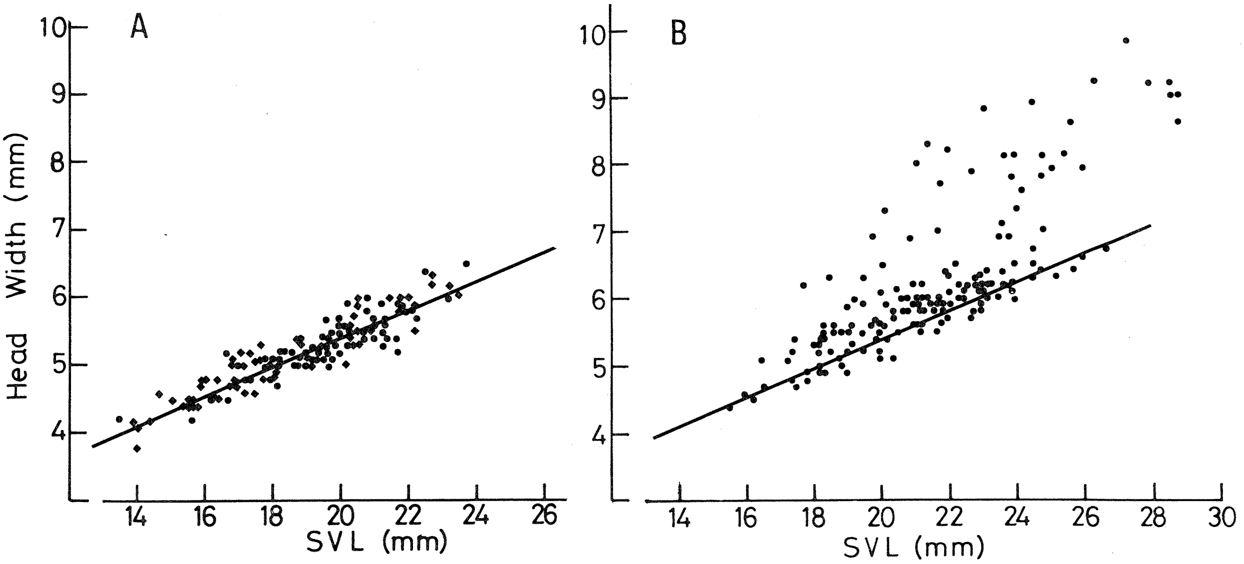

Fig. 5. Proportion of the head to the snout-vent length (SVL) during larval development in *Hynobius retardatus*. These are combined from two measurements on the same populations on 20 and 30 days after hatching. A: Head width of larvae of non-cannibalism group ("typical" morphs) developed proportionally to entire body size (SVL) irrespectively of localities (closed circle, Asari; closed square, Nopporo). The regression line was drawn by the least square method ($Y=0.209X+1.24$, $r=0.9154$). B, In the tanks where cannibalism happened frequently, majority of larvae showed the same proportion as the "typical" morphs, whereas some ones showed considerable deviations from the "typical" morph to develop a wider head. These larvae, "broad-headed" morphs, showed different allometry of head to body size. The regression line obtained in Fig. 5A was superimposed on Fig. 5B.

5B), a majority of larvae showed the same proportion as the "typical" morphs as indicated in Fig. 5A. However, several larvae showed considerable deviation from the regression line of the "typical" morphs. The proportion of the width of head to SVL was significantly larger than that of the "typical" morph. This means the proportion of head to the entire body size in "broad-headed" morphs is different from the "typical" ones.

DISCUSSION

Cannibalism in Hynobius

Although cannibalism in *Hynobius retardatus* has been recognized by many experimenters using larvae of this salamander, this is the first description of dimorphism resulting from the cannibalism in *H. retardatus*. In the Arizona tiger salamanders, *Ambystoma tigrinum nebulosum*, cannibalism is reported even in adult forms, as well as in the larval forms [2]. In *Hynobius*, however, the cannibalism is restricted to the larval stages.

Results of this study indicate that the level of food supply and kinship have significant effects on the frequency of the cannibalism: low level of food supply resulted in higher incidence of the cannibalism (Fig. 2A), and the frequency of cannibalism in the sibling groups was significantly lower than in the mixed-blood groups (Table 1). The density of larvae also affects the occurrence of the cannibalism. These factors affecting cannibalism are similar to those reported in *Ambystoma tigrinum nebulosum* [3, 15].

It has recently been reported that larvae of *H. retardatus* reared in group have shorter larval period and also smaller size at metamorphosis than those reared individually and that smaller larvae are more vulnerable to cannibalism and mutilation than larger ones [12]. When larvae at different developmental stages or of different size in *H. retardatus* were reared in one aquarium, the larger one exclusively ate the younger or smaller conspecifics (umpublished data). Because it is generally accepted in amphibians that larger larvae developed from larger eggs, the larvae developed from the larger eggs may be less vulnerable to cannibalism, and thus have a higher survival rate than the ones developed from smaller eggs. Similarly to this, the larvae developed from eggs which are spawned earlier in breeding season will have an advantage to eat conspecifics which developed from the eggs spawned later. Thus, an evolutional pressure has been acting to make *H. retardatus* to spawn larger eggs and to oviposit earlier in the breeding season. This assumption is consistent with the fact that females oviposit very early in spring when the ponds and small streams are almost covered with ice and snow [7, 8] and oviposit extra-large eggs (2.3–3.07 mm [17] or 2.5–3.0 mm [7] in diameter) of very small egg clucth size (55–138 eggs [8] or 44–102 [20] per female).

Kinship and cannibalism

The results that the cannibalism in the larvae of *H. retardatus* has a tendency to be suppressed in sibling groups (Table 1) are basically identical to earlier observations reported in the Arizona tiger salamander [15]. Cannibalistic morph of the latter avoided killing siblings when given a choice between siblings, cousins and non-kin, and preferentially ate unrelated larvae when presented with cousins and unrelated individuals [16], suggesting that the salamander recognizes its kin. These kin-recognition mechanism effectively remove the potential loss of inclusive fitness that arises by cannibalizing close kin [16]. Similar mechanism to this may control the kinship-limited cannibalism in *H. retardaus*.

Because the eggs spawned by a female of *H. retardatus* are usually fertilized with spermatozoa released by more than one male in the natural habitats [17], the larvae developed from one egg sac does not always mean pure sibship. Thus, the larvae developed from the same egg sacs are probably subgrouped genetically into two categories: pure siblings (eggs fertilized by one male) and half blooded siblings (eggs fertilized by two or more different males). This may explain the variation in the occurrence of cannibalism among the larvae developed from one egg sac (Table 1). Provided that the cannibalism is suppressed among the pure siblings and is inducible among the half blooded siblings, it is expected that only the larvae in the 4 tanks in which no cannibalism was observed at all (tank no. 1, 3, 4 and 12 of sibling groups) might be pure siblings. Further analyses using pure sibship larvae developed from artificially inseminated eggs are necessary to elucidate more accurate relationship between the occurrence of cannibalism and kinship.

Kinship recognition in amphibians has hardly been studied except for a few species such as in a chorus frog *Pseudacris triseriata* [22], spadefoot toads *Scaphiopus couchii* [11] or *S. multiplicatus* [13, 14], and the tiger salamander *Ambystoma tigrinum* [15]. Cannibalism in *H. retardatus* may provide a new material for investigation of the kinship recognition in amphibians.

Dimorphism in Hynobius

Polymorphism in larval and adult *Hynobius* has already been reported [19, 21]: electrophoretic analyses have shown that the genetic distance between "large" and "common" types which have been known in the adult forms inhabiting very close regions in Obihiro, Tokachi Plain is much smaller than between the "common" types inhabiting different regions [10]. Thus, the dimorphism in the adult forms does not seem to be attributable directly to their genetic differentiation, but to the ecological divergence [10].

Contrary to this, the dirmorphism in the larval forms reported here is induced facultatively under some environmental and ecological conditions. Presumably, the cannibalism may be induced under conditions of food shortage: the risk of starvation becomes more important than the cost of eating a relative [16]. However, all larvae that are food-deprived do not become cannibalistic: only a few members of larvae reared in one aquarium become cannibalistic and grow to the "broad-headed" morphs (Fig. 4B). Thus, the occurrence of the "broad-headed" morphs will be limited by some factors such as a balance of the benefit of cannibalism and cost of eating relative [16]. At present, however, what factors infuence individual morphogenesis to the cannibalistic is entirely unknown. Once the "broad-headed" morphs are expressed in specific larvae, they can utilize larger prey which the "typical" morphs cannot eat, such as older tadpoles of *Rana pyrica*, which are food resources for larvae of this salamander [12].

REFERENCES

1 Arai T, Wakahara M (1993) Hemoglobin transition from larval to adult types in normally metamorphosing, metamorphosed and metamorphosis-arrested *Hynobius retardatus*. Zool Sci 10: 637–644

2 Collins JP, Holomuzki JR (1983) Intraspecific variation in diet within and between trophic morphs in larval tiger salamanders (*Ambystoma tigrinum nebulosum*). Can J Zool 62: 168–174

3 Collins JP, Cheek, JE (1983) Effect of food and density on development of typical and cannibalistic salamander larvae in *Ambystoma tigrinum nebulosum*. Am Zool 23: 77–84

4 Ducibella T (1974) The occurrence of biochemical metamorphic events without anatomical metamorphosis in the axolotl. Devel Biol 38: 175–186

5 Larris-Regaud E (1985) Hormonal determination of neoteny in facultative neotenic Urodeles. In "Metamorphosis", Ed by M Balls, M Bownes, Clarendon Press, Oxford, pp. 294–312

6 Iwasawa H, Yamashita K (1991) Normal stages of development of a hynobiid salamander, *Hynobius nigrescens* Stejneger. Jpn J Herpetol 14: 39–62 (in Japanese with English abstract)

7 Makino S (1933) Some oecological observations on Hynobius retardatus Dunn. Bot Zool 1: 1136–1142 (in Japanese)

8 Makino S (1934) A cytological study on the maturation and fertilization of the egg of *Hynobius retardatus* (an urodelan amphibian). J Fac Sci Hokkaido Imp Univ Ser IV Zool 3: 117–167

9 Malacinski GM (1978) The Mexican axolotl, *Ambystoma mexicanum*: its biology and developmental genetics, and its autonomous cell lethal genes. Am Zool 18: 195–206

10 Matsui M, Sato T, Tanabe S, Hayashi T (1992) Local population differentiation in *Hynobius retardatus* from Hokkaido: an electrophoretic analysis (Caudata: Hynobiidae). Zool Sci 9: 193–198

11 Newman AR (1988) Adaptive plasticity in development of *Scaphiopus couchii* tadpoles in desert ponds. Evolution 42: 774–783

12 Ohdachi S (1994) Growth, metamorphosis, and gape-limited cannibalism and predation on tadpoles in larvae of salamanders *Hynobius retardatus*. Zool Sci 11: 127–131

13 Pfennig DW (1990) "Kin recognition" among spadefoot tadpoles: A side effect of habitat selection? Evolution 44: 785–798

14 Pfennig DW (1992) Polyphenism in spadefoot toad tadpoles as a locally adjusted evolutionarily stable strategy. Evolution 46: 1408–1420

15 Pfennig DW, Collins JP (1993) Kinship affects morphogenesis in cannibalistic salamanders. Nature 362: 836–838

16 Sadler LM, Elgar MA (1994) Cannibalism among amphibian larvae: a case of good taste. Trend Ecol Evol 9: 5–6

17 Sasaki M (1924) On a Japanese salamander, in Lake Kuttarush, which propagate like the axolotl. J Coll Agr Hokkaido Imp Univ 15: 1–36

18 Sasaki M, Nakamura H (1937) Relation of endocrine system to neoteny and skin pigmentation in a salamander, *Hynobius lichenatus* Boulder. Annot Zool Japon 16: 81–97

19 Sato T (1987) External characteristics of *Hynobius retardatus* from Tokachi district, Hokkaido, in the breeding season. Jpn J Herpetol 12: 80 (in Japanese)

20 Sato T (1989) Breeding environment and spawning of a salamander, *Hynobius retardatus*, at the foot of Hidaka Mountains, Hokkaido. In "Current Herpetology in East Asia". Ed by M

Matsui, Hikida T, Goris RC, Herpetol Soc Jpn, Kyoto, 7 pp. 292–304

21 Sato T, Nakabayashi S (1987) Distribution and habitat of salamander (*Hynobius retardatus*) in Tokachi district, Hokkaido. I. Central Tokachi. Bull Obihiro Centennial City Mus 5: 17–28 (In Japanese)

22 Smith DC (1990) Population structure and competition among kin in the chorus frog (Pseudacris triseriata). Evolution 44: 1529–1541

23 Trivers R (1985) Social Evolution. Benjamin/Cummings Publ Co, New York, p. 53.

24 Wakahara M (1994) Spermatogenesis is extraordinarily accelerated in metamorphosis-arrested larvae of a salamander, *Hynobius retardatus*. Experientia 50: 94–98

25 Wakahara M, Miyashita N, Sakamoto A, Arai T (1994) Several biochemical alterations from larval to adult types are independent on morphological metamorphosis in a salamander, *Hynobius retardatus*. Zool Sci 11: 583–588.