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Enhanced recruitment of larger predators in the presence of large prey

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ABSTRACT

1. Most carnivores undergo diet shift from smaller to larger prey items during ontogeny. The trophic relationship between a growing carnivore and larger prey is representative of a size-structured predator-prey interaction. The strength of this interaction is, in part, determined by the recruitment of individuals from smaller predatory size classes into larger predatory size classes. Therefore, it is interesting to investigate how larger prey alter the recruitment of smaller predator size classes into larger predator size classes, since this can affect their own future predation risk.

2. Past empirical studies have exclusively documented that large prey reduce predator recruitment by decreasing growth and/or survival of the smaller predators. In this study, we provide empirical evidence of the contrasting pattern: large prey enhance the recruitment of smaller predators into larger predators even though they increase cannibalism mortality of the smaller predators. We have done this here by studying the trophic interaction between predatory salamander larvae (*Hynobius retardatus*) and the frog tadpoles (*Rana pirica*) that represent their large prey.

3. In a field experiment in which salamander hatchlings were exposed to the presence or absence of large frog tadpoles, we found that more giant salamanders emerged in the presence of frog tadpoles than in their absence. Re-assignment of frog tadpoles (to both treatments) in the subsequent experimental period showed that the enhanced emergence of giant salamanders in the presence of frog tadpoles leads to the intensification of salamander predation on the frog tadpoles.

4. In an additional laboratory experiment, to better understand the underlying mechanisms, we manipulated both the presence of frog tadpoles and the occurrence of cannibalism between

salamander hatchlings. This experiment revealed that frog tadpoles intensify the cannibalism of salamander larvae during their hatchling stage, thus allowing more salamander larvae to become large-sized predators.

5. Our results suggest that frog tadpoles can inadvertently intensify their own future predation risk by intensifying cannibalistic interactions among predatory salamander hatchlings, thereby enhancing the degree of predator recruitment to a larger size class. Hence, large prey can enhance the recruitment of individuals from small predator size classes into larger predator size classes.

Key-words: cannibalism, gigantism, *Hynobius retardatus*, predator recruitment, *Rana pirica*, size-structured predator-prey interaction

SECOND ABSTRACT

「サイズ構造のある捕食－被食系」の代表的な構造として、「成長する捕食者と大型餌種」の食う－食われるの関係がある。この構造において、捕食者種は成長することで大きな餌種を食べるようになるが、小さなサイズの段階においても大きな餌種と関係がないとは限らない。その成長や生存が大きな餌種によって影響を受ける場合がある。小さいサイズの捕食者個体の生存や成長は、大きなサイズの捕食者個体の加入に反映されるため、大きな餌種はその加入の程度を決めることで将来に被る捕食のリスクを自ら制御するといえる。このような系の性質から、サイズ構造のある捕食－被食系は、個体の特徴に種内変異がないことを前提とした従来の理論では予測できない個体群動態を示すと考えられてきた。このため、サイズ構造のある捕食－被食系の動態を理解するには、①大きな餌種が小さいサイズ段階にある捕食者個体の生存や成長にどのような影響を与えるのか？②それが大きなサイズの捕食者個体の加入の程度を決め、結果的に大きな餌種の捕食リスクの強度にまで反映されるのか？を明らかにすることが重要である。

過去この問題に着目した研究は少なくないが、それらは一貫して、「大きな餌種が、大きなサイズの捕食者の加入を減らし、将来の捕食リスクを抑える」ことを示してきた。これは、大きな餌種と小さな捕食者が資源を巡って競争したり、大きな餌種が小さな捕食者を捕食することによって生じる。従来の研究とは対照的に、今回私たちは、「大きな餌種が大きなサイズの捕食者の加入を増やし、結果として、将来の捕食リスクを高める」場合があることを両生類2種のサイズ構造のある捕食－被食系で確かめた。

エゾサンショウウオ幼生は相手を丸のみにして食うタイプの捕食者種で、捕食できる餌の大きさ

は口の大きさで決まる。エゾサンショウウオ幼生は孵化直後に共食いをすると急激に成長し、大型の餌種であるエゾアカガエル幼生を食うことができる。私たちは、野外実験と室内実験を行い、「エゾアカガエル幼生は、孵化直後のエゾサンショウウオ幼生の共食いを促進することで、大型化するエゾサンショウウオ幼生を増やし、結果的に将来自身が被る捕食圧を高めている」ことを明らかにした。大型の餌種と小さなサイズの捕食者との間に食う－食われる関係や競争関係がなかったとしても、大型餌種は小さなサイズの捕食者の採餌生態に関わることで捕食者の加入に影響するのだ。大きな餌種が捕食者の成長や加入に与える影響は多様であり、系特異的なプロセスとメカニズムに従っていると言えるだろう。

1| INTRODUCTION

Carnivorous animals often change prey items throughout ontogeny (Rudolf & Lafferty, 2011). In most cases, they shift from small prey items to larger prey items as they themselves grow larger (Werner & Gilliam, 1984). The relationship between a growing carnivore and their prey items is a typical example of a size-structured predator-prey interaction, which is prevalent among various communities in nature (Krenek & Rudolf, 2014; Takatsu & Kishida, 2015; Toscano, Rombado, & Rudolf, 2016; see also review by Werner & Gilliam, 1984). Direct and indirect interactions between conspecifics of different size classes make the dynamics of these size-structured populations distinctive from population dynamics predicted by conventional size-unstructured models (De Roos, Persson, & McCauley, 2003; Abrams, 2011; De Roos & Persson, 2013). Therefore, it is necessary to investigate how prey items in size-structured populations affect the growth, survival and reproduction of predatory individuals with different size classes, so that we can better understand the population ecology of a growing predator and its prey.

In a typical size-structured predator-prey system, the prey items of a larger size class of predator (hereafter referred to as large prey), as well as the prey items of a smaller size class of predator (i.e., small prey), can play a key role in determining the size class composition of the predator population. In such systems, while large prey can improve the survival and reproductive performance of predatory individuals in the larger size class (hereafter referred to as large-sized predator), they can also affect the survival and growth of predatory individuals in the smaller size

class (i.e., small-sized predator), through processes such as competition and predation. For example, if small-sized predators and large prey compete for the same resources (i.e., life history intraguild predation), this can lead to a reduction in the survival and/or growth of the small-sized predator (Persson & Greenberg, 1990; Byström, Persson, & Wahlström, 1998; Toscano et al., 2016). Similarly, when large prey are capable of predating on small-sized predators (i.e., predator-prey reversal), the growth and/or survival of the small-sized predator may again be negatively impacted (Montserrat, Magalhães, Sabelis, De Roos, & Janssen, 2012; Nilsson, Flink, & Tibblin, 2019). As a result, large prey are capable of decreasing their own future predation risk by reducing the recruitment of small-sized predators into large-sized predators (Werner & Gilliam, 1984; Polis, Myers, & Holt, 1989). Because past empirical studies have consistently documented a negative effect of large prey on the recruitment of small-sized predators into large-sized predators, this negative relationship has commonly been assumed in theoretical models that describe size-structured predator-prey systems (Abrams, 2011; Hin, Schellekens, Persson, & De Roos, 2011; De Roos & Persson, 2013).

Although evidence suggests that a reduction in predator recruitment may be a typical effect of large prey, it is also possible that the opposite effect is true, i.e., a positive effect of large prey on predator recruitment. Large prey may increase resource availability for small-sized predators through several ways. For example, large prey can increase the abundance of resources for small-sized predators, e.g. when their excretion significantly improves the nutritional condition of a resource (Leibold & Wilbur, 1992; Vanni, 2002). Alternatively, large prey can increase a small-sized predator's access to already existing resources, e.g. if large prey lessen resource competition among small-sized predators via predation (i.e., thinning effects [Brodin & Johansson, 2002; Vonesh & De la Cruz, 2002; Sniegura, Golab, & Johansson, 2019]). Large prey could also change behavioral interactions between small-sized predators and their resources (e.g., disturbance by large prey increasing the rate of encounter between a small-sized predator and its resource [Yamaguchi, Takatsu, & Kishida, 2016]). All this considered, by enhancing the trophic condition of small-sized predators, large prey could also enhance the recruitment of small-sized predators into large-sized predators, thus increasing their own future predation risk. Testing this unconsidered pattern is worthwhile, since it would allow a greater insight into the variable nature of size-structured predator-prey interactions. In this study, using a larval amphibian

predator-prey interaction, we experimentally show that large prey can enhance the recruitment of small-sized predators into large-sized predators by increasing the consumption rate of the small-sized predators, thereby also eventually increasing their own future predation risk.

The trophic relationship between the larval stage of the *Hynobius retardatus* salamander and the *Rana pirica* frog, both of which are distributed throughout Hokkaido, Japan, is an excellent model system to investigate size-structured predator-prey interactions, since the predatory salamander larvae can only consume the frog tadpoles once their gape size is larger than the tadpoles body size (Nosaka, Katayama, & Kishida, 2015; Takatsu & Kishida, 2015; Takatsu, Rudolf, & Kishida, 2017). Although the two amphibian species concurrently lay their eggs in small ponds (1 to several tens m²) in early spring, the *R. pirica* frogs generally hatch 2-4 weeks earlier than the *H. retardatus* salamanders (Nosaka et al., 2015). Due to this difference in hatch timing, the frog tadpoles are generally larger than the newly hatched salamander larvae (i.e., the frog tadpoles are large prey). Because the frog tadpoles continue to grow throughout their larval period, the larval salamanders must exhibit a faster growth rate if they are to successfully achieve a body size that would allow predation on the frog tadpoles. As a typical scenario, *H. retardatus* salamander hatchlings that successfully cannibalize conspecifics generally grow much faster. Moreover, as these cannibalistic conspecifics grow larger, they are more easily able to consume small non-cannibalistic salamanders, due to the size asymmetry. Therefore, this often results in the cannibals growing rapidly and becoming giants (i.e., positive feedback between consumption and growth, Kishida et al., 2011). These giant cannibals of *H. retardatus* salamander larvae then start to consume *R. pirica* frog tadpoles (large prey) once their gape size exceeds the body size of the frog tadpoles (i.e., recruitment to large-sized predators) (Takatsu & Kishida, 2015; Takatsu et al., 2017).

For this study, we hypothesize that *R. pirica* frog tadpoles increase the recruitment of *H. retardatus* salamanders from small-sized predators into large-sized predators, based on the following knowledge. Firstly, the frog tadpoles are neither a competitor nor a predator of the salamander hatchlings. Therefore, the frog tadpoles do not lower the growth and survival of the salamanders through competitive and predatory effects. Secondly, the frog tadpoles can intensify the cannibalistic interaction among salamander hatchlings by affecting behavioral and morphological traits. For example, large tadpoles of *R. pirica* may increase the likelihood of a *H.*

retardatus salamander larva encountering prey by stimulating the movements of prey items (Yamaguchi et al., 2016). The frog tadpoles can also induce the gape enlargement of the salamander larvae when both amphibian larvae coexist in close proximity (i.e., an inducible offense [Michimae, Nishimura, & Wakahara, 2005; Kishida, Trussell, & Nishimura, 2009]), thus allowing them to more effectively consume large prey, including conspecifics (Takatsu & Kishida 2013; Takatsu et al., 2017). By inducing these trait changes in the salamander larvae, frog tadpoles may intensify cannibalistic interaction among salamanders to promote the recruitment of salamanders from small-sized predators into large-sized predators. In the present study, we tested these hypothetical processes by conducting experiments in both the field and laboratory. While the field experiment was intended to test the overall hypothesis about the size-based interaction between the two amphibian species under natural conditions, the laboratory experiment was designed to test the hypothetical mechanisms and processes more thoroughly.

2| MATERIALS AND METHODS

2.1| Field experiment

Objectives of the field experiment

Objectives of the field experiment were to test (1) whether frog tadpoles enhance the recruitment of salamanders from small-sized predators into large-sized predators and (2) whether the prospective enhancement of salamander recruitment by frog tadpoles lead to an intensification of predation pressures on frog tadpoles. To achieve these objectives, we conducted a field-enclosure experiment that was performed in two steps (Fig. 1a). The first and second steps were designed to achieve the first and second objectives, respectively (see below).

Characteristics of the experimental environments

The field experiment was conducted in a field pond (3 m width × 30 m length × 0.6 m depth) in the Tomakomai Experimental Forest of Hokkaido University (42° 42' 8.20" N, 141° 32' 14.11" E) (Fig. 1b). The pond contains spring water, has a canopy cover and a bottom composed of soil and small rocks. We placed 24 cubic enclosures (60 cm × 60 cm × 60 cm) in a line at 50 cm intervals in the pond on 23 June 2016 (Fig. 1b), with each enclosure acting as an experimental unit. The enclosures were made with PVC framing covered by 1 mm nylon mesh

on all sides. Small aquatic insects, such as *Chironomid* larvae, were able to pass through the mesh to provide prey resources for the salamander larvae, while periphyton was able to grow on the mesh as a food resource for the frog tadpoles.

Details of experimental setting

A schematic diagram of the field experiment is shown in Fig. 1a.

(1) First step of the experiment

The first step of the experiment was intended to test whether frog tadpoles enhance the recruitment of salamanders from small-sized predators into large sized predators. On 29 June 2016 (day 1), we haphazardly assigned 50 salamander hatchlings at developmental stage 40-43 (these stages are typically several days after hatching, during which the branching of external gills occurs [Iwasawa & Yamashita, 1991]) into each of the enclosures (20 of the 24 available enclosures, with the remaining four enclosures being used in second step of the experiment). Mean $\pm$ SD ($N = 20$) gape width and snout-vent length (hereafter, body length) of the assigned salamander hatchlings were 3.42 ± 0.56 mm and 13.25 ± 1.08 mm, respectively. By using these 20 enclosures containing 50 salamander hatchlings, we established the following two treatments: Tadpole treatment and No-tadpole treatment. For the Tadpole treatment, we assigned 75 two week old frog tadpoles to 10 of the enclosures (manipulation-A in Fig. 1a). Mean $\pm$ SD body length and body width of the frog tadpoles were 11.51 ± 1.04 mm and 7.30 ± 0.69 mm ($N = 20$), respectively. For the No-tadpole treatment, we did not assign tadpoles into the remaining 10 enclosures. The densities of both frog tadpoles (208 individuals m^2) and salamander hatchlings (139 individuals m^2) were within their natural ranges (Michimae, 2006). A fuller overview of the collection and husbandry methods are described in Appendix A.

At day 23, we counted all surviving frog tadpoles and salamanders to measure their survival. We then photographed the dorsal area of all surviving frog tadpoles and salamanders using a camera (EOS Kiss X3, Canon, Tokyo, Japan). The captured images were then used to measure the body width of 10 frog tadpoles randomly sub-sampled from each enclosure. In addition, we also measured gape width and body length of all surviving salamanders by using the photographic images. All measurements in this study were conducted using Image J (National Institutes of Health, USA). Salamanders can consume frog tadpoles when their gape width is more than 10% larger than the tadpoles body width (Nosaka et al., 2015). Thus, we defined a

salamander individual as having been recruited to large-sized predators when their gape size was 10% larger than the smallest body width of the frog tadpoles. Based on the body width distribution of the frog tadpoles in the Tadpole treatment, we counted the number of salamanders that exceeded this 10% threshold. We used this count variable as an indicator of the degree of salamander recruitment.

(2) Second step of the experiment

The second step of the experiment was designed to test whether the prospective increase in predator recruitment (from small-sized to large-sized) by the initial presence of frog tadpoles lead to an intensification of predation pressure on frog tadpoles in the future. On day 23, all of the salamanders from step 1 remained in the enclosures while the surviving frog tadpoles were removed (manipulation-B in Fig. 1a). We then assigned new tadpoles to each enclosure (for both Tadpole and No-Tadpole treatments). Since almost all frog tadpoles survived during the first step (see Results), we again placed the same number of frog tadpoles (75) into each enclosure (manipulation-C in Fig. 1a). As a control, we placed 75 frog tadpoles into 4 of the enclosures that had not been assigned salamander larvae in step 1 (No-salamander treatment). This No-salamander treatment enabled us to estimate the natural mortality of frog tadpoles in the absence of predation. We were not able to reassign frog tadpoles that had been reared with the salamander larvae in step 1 (i.e., predator-experienced frog tadpoles) since the second step required more than twice the number of frog tadpoles. Therefore, in step 2, we used frog tadpoles which had been previously reared in a no-salamander stock tank (i.e., predator-naïve frog tadpoles). These new predator-naïve frog tadpoles did not differ significantly in body size to the predator-experienced frog tadpoles from step 1 (body length of predator-naïve and predator-experienced frog tadpoles were 12.64 ± 0.78 mm and 13.08 ± 0.96 mm [t -test; $t_{38} = 2.59$, $P = 0.12$], respectively, and body width of predator-naïve and predator-experienced frog tadpoles were 8.00 ± 0.70 mm and 8.24 ± 0.66 mm [t -test; $t_{38} = 1.33$, $P = 0.26$], respectively). Using the predator-naïve tadpoles as a substitute for predator-experienced tadpoles is acceptable, because the difference in defensive performance against salamander larvae between the predator-experienced and -naïve tadpoles is negligible. Further reasoning for this argument is described in Appendix B. Step 2 of the experiment was terminated on day 49; on which we counted all surviving frog tadpoles and salamanders to calculate survivorship.

2.2| Laboratory experiment

Objectives of the laboratory experiment

Objective of the laboratory experiment was to test hypothetical mechanisms underlying the enhancement of predator recruitment by frog tadpoles. In the field experiment, we showed that the initial presence of frog tadpoles lowered the survival of salamander hatchlings and enhanced the recruitment of salamanders from small-sized predators into large-sized predators (see Results). Although we hypothesized that the frog tadpoles intensify cannibalism between salamander hatchlings (thus allowing the salamander hatchlings that successfully cannibalize to rapidly become large-sized predators), this hypothesis was not directly tested in the field experiment. Therefore, in order to properly address this point, we conducted a factorial laboratory experiment in which (1) presence of frog tadpoles and (2) occurrence of salamander cannibalism was multifactorially manipulated (see below).

Characteristics of experimental environments

We used 22 L semi-transparent polypropylene tanks (43.6 cm × 28.4 cm × 14.1 cm high), each filled with 5 L of aged tap water as an experimental unit. Throughout the laboratory experiment, we added one piece of rabbit chow (0.2 g dry weight) and ~ 400 brine shrimps (*Artemia salina*) to all tanks every second day as food for the frog tadpoles and salamanders, respectively. The water in all tanks was exchanged every two days throughout the experiment. Collection and keeping methods of the experimental animals are described in Appendix A.

Details of the experimental setting

A schematic diagram of the laboratory experiment is shown in Fig. 2.

(1) First step of the experiment

The first step of the experiment was intended to test whether frog tadpoles enhance salamander recruitment by intensifying cannibalism among salamander hatchlings. We established six treatments in which we manipulated the presence of frog tadpoles and the occurrence of salamander cannibalism. To control the cannibalism of salamander hatchlings, we followed methods used in Takatsu and Kishida (2015) and Takatsu et al. (2017). In brief, the occurrence of cannibalism in salamander hatchlings depends greatly on size asymmetry between interacting individuals (Kishida, et al., 2011, Kishida, Tezuka, Ikeda, Takatsu, & Michimae, 2015). Thus, to control the occurrence of cannibalism, we manipulated the size structure of the salamander hatchlings (i.e., cannibalistic conditions were established by assigning both early-

and late- salamander hatchlings into experimental tank, while non-cannibalistic conditions were established by assigning either early- or late- salamander hatchlings into the tank) while keeping the salamander density constant across the treatments. The methodological details to obtain the early- and late- salamander hatchlings are the same as those shown in Appendix A in Takatsu and Kishida (2015). In brief, we obtained these early- and late- salamander hatchlings by manipulating the water temperature experienced by embryos. Difference in hatch timing between early- (June 5th) and late- (June 11th) salamander hatchlings was six days. The salamander hatchlings were assigned into the relevant treatments one day after they hatched (i.e., manipulation -A and -B in the first step of the experiment in Fig. 2).

By crossing the cannibalistic and non-cannibalistic conditions with presence and absence of frog tadpoles, we conducted a factorial experiment: (1) “No-tadpole No-cannibalism-early”, (2) “No-tadpole No-cannibalism-late”, (3) “No-tadpole Cannibalism”, (4) “Tadpole No-cannibalism-early”, (5) “Tadpole No-cannibalism-late”, (6) “Tadpole Cannibalism” (Fig. 2). We haphazardly assigned 30 two-weeks-old frog tadpoles to each replicate in the three Tadpole treatments (treatments 4, 5, and 6, manipulation-A in Fig. 2). Mean $\pm$ SD body length and body width of the frog tadpoles were 12.38 ± 1.03 mm and 8.04 ± 0.61 mm ($N = 20$), respectively. We assigned 5 early- and 15 late- salamander hatchlings in the two Cannibalism treatments (treatments 3 and 6, manipulation -A and -B in Fig. 2). We assigned 20 early-salamander hatchlings in the two No-cannibalism-early treatments (treatments 1 and 4, manipulation-A in Fig. 2). We assigned 20 late-salamander hatchlings in the two No-cannibalism-late treatments (treatments 2 and 5, manipulation-B in Fig. 2). We replicated “No-tadpole No-cannibalism (treatments 1 and 2)” 5 times, “No-tadpoles Cannibalism (treatment 3)” and “Tadpole No-cannibalism (treatments 4 and 5)” 10 times, and “Tadpole Cannibalism (treatment 6)” 20 times. In step 1, the number of Tadpole treatment replications were twice that of the No-tadpole treatments, so that they could be used as additional experimental treatments in step 2 (see below). Our previous studies have shown that variance of demographic and trait level consequences were larger in the Cannibalism treatments than No-cannibalism treatments (Takatsu & Kishida, 2015; Takatsu et al., 2017). Therefore, we adopted this unbalanced replication design to avoid excessive use of the animals. Each replicate was randomly assigned to one of the 60 tanks. Densities of the frog tadpoles (242 individuals m²) and salamander hatchlings (162 individuals

m²) were within their natural ranges (Michimae, 2006).

We assigned the early-salamander hatchlings and frog tadpoles into relevant tanks on 6 June 2016 (day 1) (manipulation-A in Fig. 2). We assigned late-salamander hatchlings into the relevant tanks on day 7 (manipulation-B in Fig. 2). Just before the assignment of the late-salamander hatchlings, we scanned the ventral aspect of all surviving salamanders using a scanner (CanoScan 9000F, Canon, Tokyo, Japan). Using these scanned images, we measured gape width, head width and body length of all surviving early-salamander hatchlings to examine whether existence of frog tadpoles affects morphological traits of the early-salamander hatchlings (see *Morphology of salamander hatchlings*). We focused on the morphological traits of early-salamander hatchlings, since their morphology likely influences their cannibalism success on the late-salamander hatchlings (Kishida et al., 2015). Mean $\pm$ SD body length and gape width of the salamander hatchlings at the timing of assignment were 13.38 ± 0.80 mm and 3.44 ± 0.40 mm ($N = 20$), respectively. We counted the surviving salamander hatchlings every day until day 15 to check whether cannibalism occurred.

At day 15, we measured several different traits in the amphibians. First, we counted all surviving animals. Then, by using scanned images of the ventral aspect of the amphibians, we measured body width of 10 frog tadpoles randomly selected from each replicate in the three Tadpole treatments, as well as gape width and body length of all surviving salamanders. As with the field experiment, to estimate the degree of recruitment of salamanders from small-sized predators into large-sized predators, we counted the number of salamanders whose gape size was 10% larger than the smallest frog tadpole body width at day 15.

(2) Second step of the experiment

The second step of the experiment was designed to confirm that a prospective increase in salamander recruitment by intensified cannibalism among salamander hatchlings subsequently also leads to an intensified predation pressures on the frog tadpoles. On day 15, the salamanders from step 1 remained in the tanks while the surviving frog tadpoles were removed. New cohorts of 30 one-month old frog tadpoles were assigned to all of the treatments at day 15 (manipulation C-D in Fig. 2). In addition, to make a no-salamander control treatment (No-salamander treatment), we placed 30 one-month old frog tadpoles into 5 additional experimental tanks. To enable sufficient numbers, these new cohorts of frog tadpoles were made up of both

predator-naïve tadpoles (that had been reared in laboratory stock tanks without salamander, see Appendix A), and predator-experienced tadpoles from the first step of the experiment. The two types of frog tadpoles were similar in their size (body length of predator-naïve and predator-experienced frog tadpoles were 13.27 ± 0.96 mm and 12.93 ± 1.12 mm [t -test; $t_{38} = 1.03$, $P = 0.31$], respectively, and body width of predator-naïve and predator-experienced frog tadpoles were 8.37 ± 0.64 mm and 8.20 ± 0.55 mm [t -test; $t_{38} = 0.89$, $P = 0.38$], respectively). Predator-experienced frog tadpoles were assigned into half of the replicates in each Tadpole treatment, while predator-naïve frog tadpoles were assigned into the other half of replicates in each Tadpole treatment. We also assigned predator-naïve frog tadpoles into each of the experimental replicates in the three No-tadpole treatments and No-salamander treatment. We terminated the experiment on day 20. At the end of the experiment, we counted all surviving frog tadpoles and salamanders. Because no frog tadpoles died in the No-salamander control treatment, we considered mortality of frog tadpoles in the treatments with salamanders in the second step as predation mortality. Although we used the two types of frog tadpoles described above, our preliminary analyses revealed no effect between the types of frog tadpoles in the experimental results (Wilcoxon tests: $P > 0.52$). Thus, we do not consider this in the further analyses and arguments (i.e., we pooled the data of predator-experienced and predator-naïve frog tadpoles in each Tadpole treatment).

Measurements of prospective traits that determine occurrence of cannibalism

We hypothesized that large frog tadpoles affect cannibalistic interactions among salamander hatchlings, thus determining the occurrence of giant salamander larvae by influencing the morphology and/or activity of salamander hatchlings. To test these mechanistic hypotheses, we examined how the initial presence of frog tadpoles affected the morphology and activity of the salamander hatchlings in the Cannibalism treatments (“[3] No-tadpole Cannibalism” and “[6] Tadpole Cannibalism” treatments [Fig. 2]). Because cannibalism should occur just after the assignment of late-salamander hatchlings (i.e., early-salamander hatchlings prey on late-salamander hatchlings), we measured the activity and morphology of early-salamander hatchlings just before assigning the late-salamander hatchlings (day 7 [Fig. 2]).

(1) Activity of salamander hatchlings

We counted the number of salamander hatchlings exhibiting movement at least once

within 30s by observing them. Because all 5 of the early-salamander hatchlings in each tank of the two Cannibalism treatments survived, we used the number of salamanders exhibiting movement (out of 5) as an indicator of their activity level. We conducted the activity survey three times and used the median value in each replicate for the statistical analysis.

(2) Morphology of salamander hatchlings

We scanned the ventral aspect of all surviving salamander hatchlings (i.e., early-salamander hatchlings). Using the scanned images, we measured gape width, head width, and body length. We calculated the ratio between head width and gape width as an index of the salamander's predaceous phenotype (Kishida et al., 2009). We calculated the mean value of each trait in each tank, which was then subsequently used in the statistical analyses.

2.3| Statistical analyses

All statistical analyses described below were conducted using JMP pro version 12 (SAS institute, Tokyo, Japan). In order to analyze 1) the mortality of salamander hatchlings, 2) the mortality of frog tadpoles, and 3) the degree of salamander recruitment, we used traditional non-parametric tests (i.e., Kruskal-Wallis test and Wilcoxon test) instead of analyses using generalized linear models. This was due to the nature of the data, which resulted in a substantial number of the data points being zero, e.g., in the four No-cannibalism treatments in the laboratory experiments (see Fig. 4a-c). Kruskal-Wallis test was used to test whether variation among all treatments was significant. If a significant difference was detected among treatments in Kruskal-Wallis test, we performed post hoc pairwise comparisons using Wilcoxon test with adjusted significance levels. We used step-up false discovery rate correction method for significance adjustment (Benjamini & Hochberg, 1995).

In the laboratory experiment, we compared the number of active salamander at day 7 between "Tadpole Cannibalism" and "No-tadpole Cannibalism" by using a Wilcoxon test. We compared the morphological traits of early-salamander hatchlings at day 7 (i.e., gape width, head width, predaceous phenotype index, and body length) between the two Cannibalism treatments using a *t*-test.

3| RESULTS

3.1| Field experiment

Mortality and recruitment of salamanders and survival of frog tadpoles in the first step

At the end of step 1, salamander mortality in the Tadpole treatment ($45.0 \pm 9.5\%$ [mean $\pm$ SD]) was 2.2 times higher than that in the No-tadpole treatment ($20.6 \pm 6.6\%$) (Wilcoxon test, $\chi^2_1 = 13.27$, $P = 0.0003$ [Fig. 3a]), suggesting that more salamander cannibalism occurred in the presence of frog tadpoles. The number of salamanders with a gape size larger than the smallest body width of a frog tadpole (i.e., the degree of recruitment of salamanders from small-sized predators into large sized predators) in the Tadpole treatment (4.8 ± 1.2 individuals [mean $\pm$ SD]) was 2.7 times greater than that of the No-tadpole treatment (1.8 ± 0.8) (Wilcoxon test, $\chi^2_1 = 13.68$, $P = 0.0002$ [Fig. 3b]). This result shows that the initial presence of frog tadpoles enhanced salamander recruitment to the larger size class.

Up until the end of the first step, almost all of the frog tadpoles survived in the Tadpole treatment (mean $\pm$ SD survival of tadpoles = $97.7 \pm 3.9\%$, $N = 10$). This showed that salamanders generally did not consume tadpoles during step 1 and assured us that frog tadpoles were large prey for the salamander larvae.

Mortality of tadpoles and salamanders in the second step

Mortality of the newly assigned frog tadpoles in step 2 differed among the three treatments (Kruskal-Wallis test, $\chi^2_2 = 16.73$, $P = 0.0002$) (Fig. 3c). Although almost all frog tadpoles survived in the No-salamander treatment ($96.3 \pm 0.7\%$), more than a quarter of the frog tadpoles died in the two salamander treatments (Fig. 3c). Therefore, we considered tadpole mortality in the treatments containing salamanders as predation mortality. Frog tadpole mortality in the Tadpole treatment ($59.6 \pm 13.3\%$) was 1.5 times greater than the No-tadpole treatment ($39.2 \pm 8.7\%$) (Wilcoxon test, $\chi^2_1 = 10.13$, $P = 0.0015$). These results show that the existence of frog tadpoles during step 1 of the experiment subsequently intensified the predation mortality of the frog tadpoles. In step 2, the mortality of salamanders in the Tadpole treatment ($20.0 \pm 8.3\%$) was marginally higher than that in the No-tadpole treatment ($8.8 \pm 2.8\%$) (Wilcoxon test, $\chi^2_1 = 3.71$, $P = 0.054$).

3.2| Laboratory experiment

The hatch timing of salamanders had no effect on any of the measured traits of the salamanders and frog tadpoles (Appendix C) same as our previous results (Takatsu & Kishida, 2015; Takatsu, Rudolf, & Kishida, 2017). Therefore, we pooled the data of the two

No-cannibalism treatments (i.e., No-cannibalism-early and No-cannibalism-late treatments) in each of the Tadpole and No-tadpole treatments. Thus, hereafter, we used “Tadpole No-cannibalism” and “No-tadpole No-cannibalism” treatments in the further statistical analyses.

Mortality and recruitment of salamanders and survival of frog tadpoles in the first step

Details of the statistical analysis are presented in Appendix D. There were significant differences in salamander mortality during step 1 (Kruskal-Wallis test, $\chi^2_3 = 48.81$, $P < 0.0001$), and the degree of recruitment of salamanders from small-sized predators into large-sized predators (Kruskal-Wallis test, $\chi^2_3 = 31.62$, $P < 0.0001$) among the four treatments (i.e., “Tadpole Cannibalism”, “No-tadpole Cannibalism”, “Tadpole No-cannibalism”, and “No-tadpole No-cannibalism” treatments) (Fig. 4a, b). In the two No-cannibalism treatments, almost all salamanders survived; however, recruitment of the salamanders to the larger size class was rarely observed. In contrast, many salamanders died and recruitment of the salamanders to the larger size class was frequently observed in the two Cannibalism treatments. Importantly, both salamander mortality and the degree of salamander recruitment to the larger size class differed between the two Cannibalism treatments. Salamander mortality during step 1 in the “Tadpole Cannibalism” treatment ($58.0 \pm 14.9\%$) was 1.6 times higher than that in the “No-tadpole Cannibalism” treatment ($36.0 \pm 17.1\%$) (Wilcoxon test, $\chi^2_1 = 9.66$, $P = 0.0019$). The degree of salamander recruitment to the larger size class in the “Tadpole Cannibalism” treatment (3.5 ± 1.7 individuals) was 1.8 times greater than that in the “No-tadpole Cannibalism” treatment (1.9 ± 1.5 individuals) (Wilcoxon test, $\chi^2_1 = 5.57$, $P = 0.018$). These results clearly show that the initial presence of frog tadpoles enhanced the recruitment of salamanders to the larger size class by intensifying cannibalism between salamander hatchlings.

Almost all of the frog tadpoles in the three Tadpole treatments survived until the end of the first step (i.e., mean $\pm$ SD survivorship of tadpoles in “Tadpole Cannibalism”, “Tadpole No-cannibalism” were $98.5 \pm 2.3\%$, $98.7 \pm 4.1\%$, respectively). This showed that salamanders generally did not consume tadpoles during step 1 and assured us that frog tadpoles were large prey for the salamander larvae.

Mortality of frog tadpoles and salamanders in the second step

There were significant differences in mortality of the newly assigned frog tadpoles (Kruskal-Wallis test, $\chi^2_3 = 37.67$, $P < 0.0001$) among the four treatments (i.e., “Tadpole

Cannibalism”, “No-tadpole Cannibalism”, “Tadpole No-cannibalism”, and “No-tadpole No-cannibalism” treatments) (Fig. 4c). Almost all frog tadpoles in the two No-cannibalism treatments survived. In contrast, many frog tadpoles in the two Cannibalism treatments died. Mortality of the frog tadpoles depended on the presence of frog tadpoles in step 1. Frog tadpoles in the “Tadpole Cannibalism” treatment ($33.9 \pm 14.9\%$) suffered 1.5 times greater predation mortality than those in the “No-tadpole Cannibalism” treatment ($22.0 \pm 17.7\%$), although the difference was marginally non-significant (Wilcoxon test, $\chi^2_1 = 3.20$, $P = 0.074$). These results show that the existence of frog tadpoles during the first step of the experiment intensified predation mortality during the second step of the experiment only when cannibalism occurred between the salamanders.

In step 2, the mortality of salamanders significantly differed among the four treatments (Kruskal-Wallis test, $\chi^2_3 = 11.74$, $P = 0.0083$). Salamander mortality during the second step (mean $\pm$ SD%) in “No-tadpole No-cannibalism”, “No-tadpole Cannibalism”, “Tadpole No-cannibalism”, and “Tadpole Cannibalism” treatments were 2.5 ± 2.6 , 18.2 ± 13.1 , 2.0 ± 3.0 , and 10.1 ± 10.9 , respectively. Except for pairwise comparisons between “No-tadpole Cannibalism” and “Tadpole No-cannibalism” treatments (Wilcoxon test, $\chi^2_1 = 10.12$, $P = 0.0015$) and between “No-tadpole Cannibalism” and “No-tadpole No-cannibalism” treatments (Wilcoxon test, $\chi^2_1 = 6.54$, $P = 0.011$), we found no significant difference in all post hoc pairwise comparisons using step-up false discovery rate correction ($P > 0.034$ [see Table D2 in Appendix D]).

Activity and morphology of salamander hatchlings

Just before the assignment of the late-salamander hatchlings (i.e., day 7), we found a significant difference in the activity of early-salamander hatchlings between the “No-tadpole Cannibalism” and “Tadpole Cannibalism” treatments (Wilcoxon test, $\chi^2_1 = 19.07$, $P < 0.0001$). While we did not find active salamander hatchlings in the “No-tadpole Cannibalism” treatment, about half of the salamander hatchlings were active in the “Tadpole Cannibalism” treatment (Fig. 5a). There was no significant difference in the measured morphological traits (i.e., gape width, head width, index of predaceous phenotype, and body length) of the hatchlings between the “Tadpole Cannibalism” and “No-tadpole Cannibalism” treatments (t -test, $df = 28$, $P > 0.11$ [see Table D3 in Appendix D]) (Fig. 5b-e).

4| DISCUSSION

To better understand the population ecology of size-structured predator-prey systems, it is important to investigate how a prey species mediates indirect interactions between smaller and larger size classes of their predators (De Roos et al., 2003; De Roos & Persson, 2013; Toscano et al., 2016; Nilsson et al., 2019). Here, we investigated how prey species can affect the demographic traits of predators that exhibit different size classes, e.g. by changing early-life cannibalistic interactions among the predators. More specifically, in this study, by using a larval amphibian predator-prey interaction, we tested the hypothesis that prey items of a larger size class of predator (large prey) can improve the individual growth of predators in the smaller size class by intensifying cannibalism among these small predators, thus enhancing recruitment to the larger predatory size class. In the field experiment, we showed that *Rana pirica* frog tadpoles increased the initial mortality of *Hynobius retardatus* salamander larvae but enhanced the recruitment of small-sized salamanders into large-sized salamanders (Fig. 3a, b). We then showed that this increased degree of recruitment to the large predatory class resulted in an increased predation pressure on the frog tadpoles (Fig. 3c).

Furthermore, in our associated laboratory experiment, we tested the hypothetical processes that underlie this predator-prey interaction, by directly manipulating the cannibalistic interactions between the salamander hatchlings. In the first step of the laboratory experiment, mortality of the salamander larvae was low and almost none of the individuals were recruited to the large predatory class in our non-cannibalistic treatment, regardless of the presence of frog tadpoles (Fig. 4a, b). In contrast, salamander larvae suffered significant mortality and were often recruited to the large predatory class in the cannibalistic treatment, with the degree of both mortality and recruitment being larger in the presence of frog tadpoles (Fig. 4a, b). These results showed that the intensification of cannibalistic interactions among salamanders during their early life stage (caused by the presence of the frog tadpoles) is a key mechanism that enhances the recruitment of salamanders to the large predatory class. We then showed that by enhancing the recruitment of the predatory salamanders, the frog tadpoles subsequently experienced an increase in mortality (Fig. 4c). Considering our field and laboratory results combined, we have demonstrated that *R. pirica* frog tadpoles increase their future predation risk by enhancing the

recruitment of predatory *H. retardatus* salamanders because of intensified cannibalistic interactions among salamanders during their early life stages.

The degree of which small-sized individuals are recruited into the large size class is determined by the growth and/or survival of the small-sized individuals (Werner & Gilliam, 1984). Therefore, factors that affect the growth and/or survival of the small-sized individuals can, in turn, influence the degree of recruitment to the larger size classes. In contrast to our study, past empirical studies on size-structured predator-prey systems have exclusively reported large prey reducing the recruitment of small-sized predators into larger size classes (Persson & Greenberg, 1990; Byström et al., 1998; Montserrat et al., 2012; Toscano et al., 2016; Nilsson et al., 2019; see also review by Polis et al., 1989). In many of these former studies that found large prey to negatively affect the survival of small-sized predators (Byström et al., 1998; Toscano et al., 2016), recruitment of small-sized predators into large-size predators is also reduced. Similar to these former studies, we also found the large prey frog tadpoles to negatively affect the survival of small-sized salamanders. However, in contrast with these former studies, we found that the large prey frog tadpoles enhanced the recruitment of salamanders to large-sized predators. This is partly due to the frog tadpoles increasing the growth rate of the small-sized salamander cannibals, which was significantly associated with the enhanced recruitment of large-sized salamanders.

The contrasting pattern between past and present studies suggests that the relationship between growth and survival of small-sized predators is a key factor in predicting the impact of large prey on predator recruitment to a large-sized class. In the previous studies, survival and growth of the small-sized predators were either independent of each other or positively correlated. As a result, any negative impacts of the large prey on the small-sized predator's survival and/or growth led to a reduction in predator recruitment (Byström et al., 1998; Toscano et al., 2016). On the contrary, like with our system, if growth and survival of the small-sized predators are negatively correlated, due to intraspecific interactions such as cannibalism and competition (Van Buskirk & Yurewicz, 1988; Brodin & Johansson, 2002; Vonesh & De la Cruz, 2002; Craig, Burke, Crowder, & Rice, 2006; Davenport & Chalcraft, 2012; Sniegura et al., 2019), large prey can increase predator recruitment by negatively affecting survival of the small-sized predators. For example, in cannibalistic species like our model, predation between conspecific individuals can decrease the population survival rate, while increasing the growth rate of

surviving individuals (i.e., those that are cannibalizing) (Sniegura et al., 2019). Likewise, in species that suffer from severe intraspecific competition, lower population survival can increase individual growth rate by reducing resource competition (i.e., thinning effects) (Brodin & Johansson, 2002; Vonesh & De la Cruz, 2002). Under these intraspecific interactions, a reduced survival rate of small-sized individuals may therefore lead to an increase in the recruitment of small-sized individuals into larger size classes.

In our study system, cannibalism between *Hynobius retardatus* salamander larvae is a common behavior that allows the larvae to achieve a large enough body size to consume frog tadpoles (Takatsu & Kishida, 2015). Importantly, our present study has shown that frog tadpoles can intensify the rate of cannibalism between salamander larvae (when salamander larvae are too small to consume frog tadpoles), thereby increasing their own future predation risk. A predator can achieve an accelerated growth rate by consuming particular prey items (i.e., prey species with high nutrition and/or with high assimilation efficiency for their predators), which has been commonly observed in carnivorous fish and amphibians (Post, 2003; Galarowicz, Adams, & Wahl, 2006; Hardie & Hutchings, 2014; Kishida et al., 2011; Sánchez-Hernández, Eloranta, Finstad, & Amundsen, 2017). Theoretically, if particular prey items (e.g., with high nutrition) that allow small-sized predators to achieve an accelerated growth rate are included in the system, it's possible that their large prey could alter their future predation risk by affecting the foraging ecology of their predators during its earlier life stages. For example, in situations where large prey can predate on the earlier life stages of their predators (i.e., predator-prey reversal system [Polis et al., 1989]), small-sized predators should less actively forage in their presence of the current predator (i.e., large prey) to reduce the likelihood of being predated upon. The reduced foraging of small-sized predators could then reduce recruitment to the larger predatory stage and result in a reduced predation risk for the large prey. To deepen our understanding of the dynamic and complicated nature of size structured predator-prey interactions, further studies are needed to investigate how large prey may modify the foraging ecology of small-sized predators in other systems.

There are several possible explanations for the higher rate of cannibalism between salamander hatchlings in the presence of frog tadpoles. Firstly, large prey may increase the abundance of food items for the small-sized predators. This could be expected if the large prey

improve nutrient condition of food items (e.g., nutrient provision through excretion; Leibold & Wilbur, 1992; Vanni, 2002) or weaken the mortality effects on food items (e.g., competitive and predatory effects on the food items; Chase et al., 2002). Secondly, large prey may induce trait changes in both small-sized predator and/or their food items, which could enable small-sized predators to consume their food items more efficiently (e.g., inducible offence; Kishida et al., 2009). In our case, the former mechanism is unlikely to be involved because food items of the salamander hatchlings were conspecifics that did not increase in the number of hatchlings during the experiment and our experimental system did not contain heterospecific competitors and/or predators for the salamander hatchlings. We therefore consider the latter mechanism to be more likely. To test the hypothetical trait changes of salamander hatchlings, we compared morphological and behavioral traits of the salamander hatchlings between the presence and absence of frog tadpoles (i.e., “Tadpole Cannibalism” and “No-tadpole Cannibalism” treatments) in the first step of the laboratory experiment. The results showed a large difference in behavioral activity (Fig. 5a), but with no difference in the morphological traits (Fig. 5b-e). While very few salamander hatchlings moved in the absence of frog tadpoles, 49% of salamander hatchlings moved at least once (within a 30-second observation) in the presence of frog tadpoles (Fig. 5a). In general, higher activity of predator and/or prey individuals leads to an increased likelihood of a predation event, because it raises the encounter rate between predator and prey (Biro, Abrahams, Post, & Parkinson, 2006; Yamaguchi et al., 2016). Therefore, it is reasonable to conclude that frog tadpoles intensify cannibalism of salamander hatchlings by increasing the movement of the salamander hatchlings. The frequent movement of salamander hatchlings in the presence of frog tadpoles was perhaps caused by the disturbance effects of the frog tadpoles. Our previous study has shown that frog tadpoles induce the movement of salamander larvae prey via direct contact with them, thus increasing the foraging opportunity of the salamanders (Yamaguchi et al., 2016). Therefore, in small pond systems, disturbance by frog tadpoles may be a trigger of the dynamic trophic interactions among amphibians.

However, it is worth noting that potential disturbance effects by frog tadpoles on the intensity of salamander cannibalism might be context dependent. For example, the density of both larvae (frog and salamander) could alter the strength of disturbance effects. In natural ponds, the density of both *H. retardatus* and *R. pirica* larvae can vary widely (ranging from a few to

thousands of individuals per square meter) and is often higher than the density we used in our experiments (Michimae, 2006). When the density of salamander hatchlings is very high, the frequency of encounters among salamander hatchlings (and thus cannibalistic interactions) might also be high, regardless of the presence and absence of frog tadpoles. In a similar way, when the density of tadpoles is high, this may increase the movement of the salamander hatchlings, thus also increasing the direct contact (and likelihood of cannibalism) among individuals. Presuming that there is a frog tadpole density effect on the level of cannibalism among the salamander larvae, we might expect this to reduce with the density of the salamander larvae, but increase with the density of the frog tadpoles. In addition, environmental factors such as habitat structure complexity and temperature may alter the strength of the frog tadpole effects. In the present study, we used enclosures and tanks that were relatively lacking in structural objects and the water temperature was relatively low ($\sim 14^{\circ}\text{C}$); however, both species of amphibian larvae can also inhabit ponds that are more structurally complex (e.g., leaf litter, tree trunks, aquatic plants, and rocks) and that contain warmer water. In general, the activity level of both predator and prey is often reduced in habitats that are more structurally complex, thus also reducing direct contact between the two (Savino & Stein, 1989; Michel & Adams, 2009), which could also potentially reduce the strength of frog tadpole effects on salamander cannibalism. In contrast, warm temperature condition can increase activity level of both predator and prey (Lang, Rall, & Brose, 2012; Stoks, Swillen, & De Block, 2012; Start, Kirk, Shea, & Gilbert, 2017), thus likely increasing the rate of contact between the two. However, the context dependency of such effects remains to be tested.

In size-structured predator-prey interactions, the effect of a predator or prey on the growth of its opponent can strongly dictate population dynamics by altering the structure of interactions (Abrams, 2011; De Roos & Persson, 2013; Toscano et al., 2016). There have been previous reports of large prey eventually weakening their future predation risk by limiting the growth of their small-sized predator (e.g., Werner & Gilliam, 1984). However, in this study, we have shown that the opposite pattern is also possible. The discrepancy of reported patterns among studies emphasizes the diversity and complexity of processes in size-structured predator-prey interactions. Identifying the life stages at which both predator and prey interact with each other, determining how they interact, as well as determining how these interactions

vary among systems will be important next steps in furthering our understanding of the variable nature of population dynamics among animal species.

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AUTHORS' CONTRIBUTIONS

K.T. and O.K. conceived the ideas and methodology; K.T. carried out the experiments; K.T. and O.K. analyzed data; K.T. led the writing of the manuscript. All authors contributed critically to drafts and gave final approval for publication.

DATA ACCESSIBILITY

Data available from the Dryad Digital Repository:
<https://doi.org/10.5061/dryad.dv41ns1v4> (Takatsu & Kishida, 2020).

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SUPPLEMENTARY MATERIALS

APPENDIX A: Methods of animal collection and husbandry

APPENDIX B: Justification for using predator-naïve tadpoles in the field experiment

APPENDIX C: Summary of statistical analyses comparing “No-cannibalism-early” and “No-cannibalism-late” treatments in each of “No-tadpole” and “Tadpole” treatments in the laboratory experiment

APPENDIX D: Summary of statistical analyses relating to the laboratory experiment

FIGURE LEGENDS

Figure 1. (a) Schematic diagram of the field experiment. “No-tad”, “Tad”, and “No-sal” are abbreviations of “No-tadpole”, “Tadpole”, and “No-salamander” treatments, respectively. In the figure, outlines of experimental design and result processes are depicted. For simplification, the numbers of individuals depicted in this figure are relative – please refer to materials & methods for true sample sizes. (b) Photograph of the 24 enclosures in an outdoor pond in Tomakomai Experimental Forest of Hokkaido University.

Figure 2. Schematic diagram of the laboratory experiment. In the first step of the experiment, we established six treatments in which we manipulated both the presence of frog tadpoles and the occurrence of salamander cannibalism (i.e., [1] “No-tadpole No-cannibalism-early”, [2] “No-tadpole No-cannibalism-late”, [3] “No-tadpole Cannibalism”, [4] “Tadpole No-cannibalism-early”, [5] “Tadpole No-cannibalism-late”, and [6] “Tadpole Cannibalism”). “No-tad” and “Tad” represent absence and presence of frog tadpoles, respectively. “No-can”, and “Can” represent absence and presence of cannibalism of salamander hatchlings, respectively. “E” and “L” are abbreviations of “early-salamander hatchlings” and “late-salamander hatchlings”, respectively.

Figure 3. Results of field experiment. (a) Mortality of salamander larvae in the first step of the experiment, (b) number of salamander larvae whose gape size was 10 % larger than the frog tadpole with the smallest body width at day 23 (i.e., degree of salamander recruitment to the large size class), and (c) mortality of frog tadpoles in the second step of the experiment. “No-tad”, “Tad”, and “No-sal” are abbreviations of “No-tadpole”, “Tadpole”, and “No-salamander” treatments, respectively. The thick horizontal bars represent the median, the box contains 50 % of the data and the whiskers indicate the range. Asterisks indicate significant differences between Tadpole and No-tadpole treatments in pairwise comparisons ($P < 0.05$). Treatments not sharing

the same lowercase letter had significantly different means at the $P < 0.05$ level following step-up false discovery rate correction method.

Figure 4. Results of the laboratory experiment. (a) Mortality of salamander larvae in the first step of the experiment, (b) number of salamander larvae whose gape size was 10 % larger than the frog tadpole with the smallest body width at day 15 (i.e., degree of salamander recruitment to the large size class), and (c) mortality of frog tadpoles in the second step of the experiment. “NoTad-NoCan”, NoTad-Can”, “Tad-NoCan”, and “Tad-Can” are abbreviations of “No-tadpole No-cannibalism”, “No-tadpole Cannibalism”, “Tadpole No-cannibalism”, and “Tadpole Cannibalism” treatments, respectively. The thick horizontal bars represent the median, the box contains 50 % of the data and the whiskers indicate the range. Treatments not sharing the same lowercase letter had significantly different means at the $P < 0.05$ level following step-up false discovery rate correction method.

Figure 5. Overview of the behavioural and morphological traits of salamander hatchlings measured at day 7 of the laboratory experiment in the “Tadpole Cannibalism” and “No-tadpole Cannibalism” treatments. (a) Proportion of active salamanders, (b) gape width, (c) head width, (d) ratio of head width to gape width (i.e., index of the salamander larvae predaceous phenotype), and (e) body length of salamander larvae at day 7. See Fig. 4 for abbreviations. The thick horizontal bars represent the median, the box contains 50 % of the data and the whiskers indicate the range. An asterisk indicates a significant difference between “Tadpole Cannibalism” and “No-tadpole Cannibalism” treatments ($P < 0.05$).

Figure. 1

(a)

v

First step

■

Day 1**Manipulation-A**

Assignment of
amphibian larvae

■

Day 23

Measure survival of
frog tadpoles and
survival and morphology
of salamanders

v

Second step

■

Day 23**Manipulation-B**

Removal of
frog tadpoles

■

■

Manipulation-C

Reassignment of
frog tadpoles

■

Day 49

Measure survival of
salamanders and
frog tadpoles

859 Figure. 2

Figure. 5