

RECIPROCAL PHENOTYPIC PLASTICITY IN A PREDATOR–PREY INTERACTION BETWEEN LARVAL AMPHIBIANS

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Abstract. In biological interactions, phenotypic change in interacting organisms induced by their interaction partners causes a substantial shift in some environmental factor of the partners, which may subsequently change their phenotype in response to that modified environmental factor. Few examples of such arms-race-like plastic responses, known as reciprocal phenotypic plasticity, have been identified in predator–prey interactions. We experimentally identified a reciprocal defensive plastic response of a prey species against a predator with a predaceous phenotype using a model system of close predator–prey interaction. *Rana pirica* tadpoles (the prey species) were reared with larvae of the salamander *Hynobius retardatus* (the predator species) having either a predaceous or a typical, nonpredaceous phenotype. The *H. retardatus* larvae with the predaceous phenotype, which is known to be induced by the presence of *R. pirica* tadpoles, induced a more defensive phenotype in the tadpoles than did larvae with the typical phenotype. The result suggests that the reciprocal phenotypic plasticity of *R. pirica* tadpoles is in response to a phenotype-specific signal under a close-signal recognition process.

Key words: arms race; bulgy phenotype; coevolution; *Hynobius retardatus*; inducible defense; inducible offense; predator-induced plasticity; *Rana pirica*.

INTRODUCTION

Organisms are exposed to various biotic and abiotic environmental selective agents that are spatially and temporally variable. Phenotypic plasticity, the environmentally sensitive production of alternative phenotypes by given genotypes (defined by Stearns 1989), is a powerful means of adaptation to changing environments that is both prevalent among many taxa and occurs in various traits (Tollrian and Harvell 1999, Pigliucci 2001, DeWitt and Scheiner 2004). As the number of investigations of phenotypic plasticity by evolutionary biologists and ecologists increases, there is a growing recognition of the importance of phenotypic plasticity at the organismal level (Schlichting and Pigliucci 1998, DeWitt and Scheiner 2004) and, because of its ecological consequences, at the level of community assemblages (Trussell et al. 2002, Werner and Peacor 2003, Miner et al. 2005).

Biological interactions such as mutualism, competition, or predation are temporally and spatially variable ecological processes, and it is commonly observed that

the interacting individuals plastically respond to the environmental regimes created by their interaction partners. Numerous studies have reported phenotypic plasticity in species interactions and have identified the adaptive functions of the induced phenotypes (Tollrian and Harvell 1999, Pigliucci 2001, DeWitt and Scheiner 2004). The induction of adaptive phenotypes in interacting organisms implies that the phenotypic change induced in one of the interacting partners by the other results in a substantial shift of some environmental factor for the inducing partner (Agrawal 2001). The modified environmental factor caused by the phenotypic change may lead the partner to respond with a phenotypic change of its own. That is, a reciprocal phenotypic plasticity, termed by Kopp and Tollrian (2003), can be expected to be induced by the opposing environmental shift in the biological interaction. For example, in a mutualistic interaction, an organism may increase its rewards in response to increased services from its mutualistic partner. On the other hand, in an antagonistic interaction, an organism may take countermeasures against the strengthened antagonistic phenotype of its counterpart. Agrawal (2001) suggested that reciprocal phenotypic plasticity may be a result of the long-term evolution of a variable biological interaction and that it

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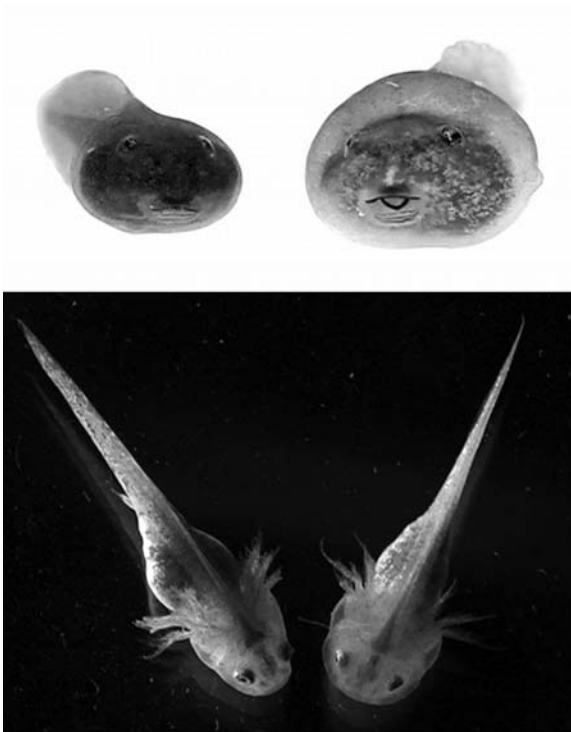


FIGURE 1. Phenotypes of larvae of the two amphibian species: *Rana pirica* tadpoles with the typical phenotype (upper left) and with the bulgy phenotype (upper right), and *Hynobius retardatus* with the typical phenotype (lower left) and with the predaceous phenotype (lower right).

may be common in biological interactions and a primary determinant of an organism's phenotype in nature.

A predator-prey system is a major antagonistic interaction system that sometimes occurs stochastically at both micro- and mesoscales. Morphological plasticity is pervasive in predator-prey interactions; that is, numerous prey species are induced by predators to exhibit defensive morphological phenotypes (inducible defense; reviewed by Tollrian and Harvell 1999), and several predator species develop predatory morphological phenotypes in the presence of certain prey species (inducible offense; e.g., Smith and Palmer 1994, Frankino and Pfennig 2001, Aubret et al. 2004). Because both kinds of phenotypic plasticity alter predator-prey interactions, arms-race-like reciprocal phenotypic plasticity can be expected to be common in predator-prey interactions (Agrawal 2001). There are very few studies on reciprocal phenotypic plasticity in predator-prey systems. The known examples are limited taxonomically to Protozoa (Wicklow 1988, Kopp and Tollrian 2003).

Empirical evidence of a relevant trait would enable us to consider its mechanism from both ecological and evolutionary perspectives, and thus would lead to an understanding of phenotypic diversity in nature and offer deeper insight into the evolution and ecological

consequences of the phenotypic design. In the present study, we sought to identify experimentally a reciprocal plastic defensive response in a prey species against a predator with an offensive phenotype in a model system of an intimate predator-prey interaction.

Amphibian larvae are an excellent model system for studying phenotypic plasticity in biological interactions (Van Buskirk and Relyea 1998, Relyea 2002a, b, Benard 2004). Larvae of many amphibian species can be induced to exhibit morphological defenses (Kishida and Nishimura 2004, Teplitsky et al. 2005, Wilson et al. 2005) when threatened by various predators, and larvae of several species exhibit predaceous morphological changes when the density of conspecifics (Hoffman and Pfennig 1999, Michimae and Wakahara 2001) or of certain prey species (Frankino and Pfennig 2001, Michimae and Wakahara 2002) is high in their environment.

Predator-prey interactions between *Hynobius retardatus* larvae and *Rana pirica* tadpoles are an ideal model system for identifying reciprocal phenotypic plasticity because the predator-prey relationships in their natural pond habitats are temporally and spatially variable and the larvae of both amphibian species reciprocally exhibit antagonistic morphological changes in each other's presence (Fig. 1). *R. pirica* tadpoles are induced to develop bulgy bodies when they are in close proximity to larval *H. retardatus*, which is a swallowing-type predator (Kishida and Nishimura 2004; see Plate 1). This is true, regardless of the phenotype of the *H. retardatus* larvae (O. Kishida, unpublished data). Conversely, when the density of *R. pirica* tadpoles is high, *H. retardatus* larvae are induced to develop a highly predaceous morphology, called the predaceous phenotype, which is characterized by a large gape size and effectively allows them to swallow large prey (Michimae and Wakahara 2002). These two phenotypic plasticities have antagonistic functions, because predation success depends greatly on the balance between the gape size of the *H. retardatus* larvae and the body size of *R. pirica* tadpoles (Ohdachi 1994, Kishida and Nishimura 2004).

R. pirica tadpoles in ponds in which *H. retardatus* larvae with the predaceous phenotype dominate are subject to an intensified predation risk compared with those in ponds in which *H. retardatus* with the typical, nonpredaceous phenotype dominate. Natural selection might favor *R. pirica* tadpoles that can develop a bulgier phenotype in the presence of *H. retardatus* larvae with the predaceous phenotype. We performed an experiment designed to determine whether predaceous *H. retardatus* larvae are more likely than typical larvae to induce the bulgier body in *R. pirica* tadpoles.

MATERIALS AND METHODS

Eggs of *R. pirica* and *H. retardatus* were collected from ponds in Hokkaido, Japan, and each species was

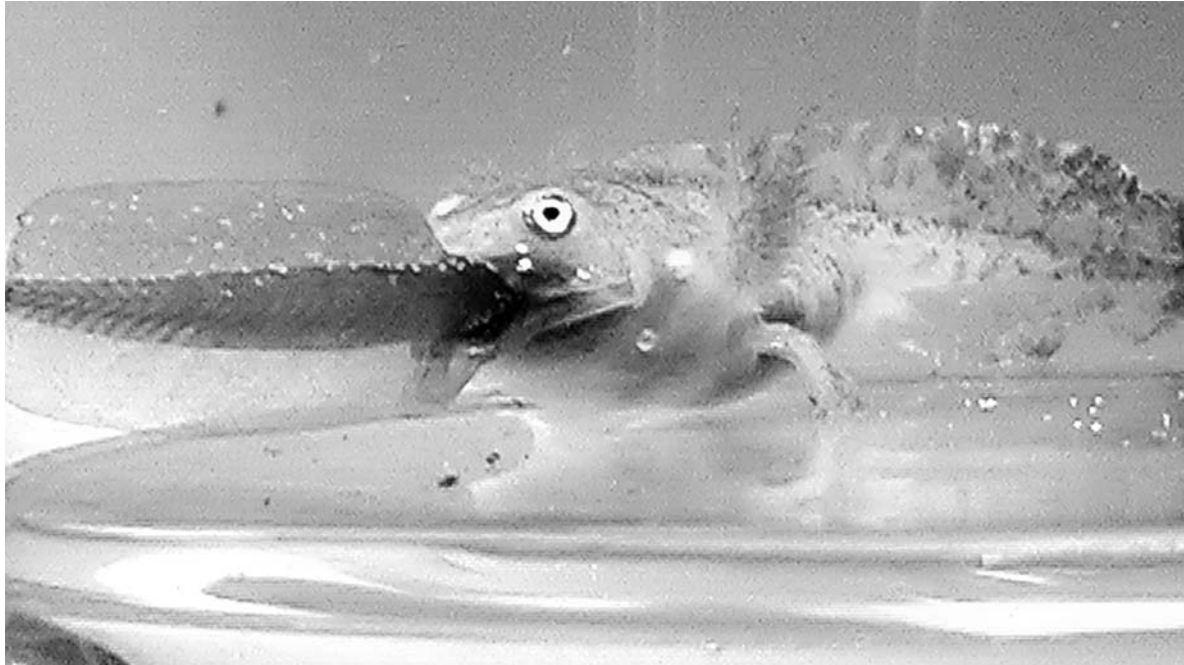


PLATE 1. Gape-limited predatory salamander larva (*Hynobius retardatus*) consuming a *Rana pirica* tadpole. Photo credit: O. Kishida.

placed separately in 12-L stock aquaria. Hatchlings of *R. pirica* were fed rabbit chow ad libitum.

Predaceous and typical *H. retardatus* larvae were obtained by rearing the hatchlings on two different types of food. To induce the predaceous phenotype, the hatchlings were individually reared in 4.5-L aquaria filled with 2-L of aged tap water, in which many small *R. pirica* tadpoles were daily placed as inducing prey agents. To obtain typical *H. retardatus* larvae, the hatchlings were reared individually in 0.35-L plastic cups and fed chironomid larvae ad libitum mornings and evenings. After three weeks, we selected eight similar-sized larvae from each of the two types (snout–vent lengths of the predaceous and typical *H. retardatus* larvae were 18.86 ± 0.28 mm and 19.15 ± 0.34 mm, respectively, mean \pm SD, $n = 8$), using the phenotypic criteria of Michimae and Wakahara (2001): ratio of the head width at the level of the eyes to the largest head width. We defined larvae with a ratio >0.86 as having the predaceous phenotype and those with a ratio <0.78 as having the typical phenotype, and we adopted as the inducing agents individuals that were representative of the two phenotypes, as shown in Fig. 1. To make the morphometric measurements, each individual was placed in a small glass chamber and a photograph in ventral view was taken. Then the photographic image was projected onto a computer monitor and digitized. Preliminary experiments had shown that typical *H. retardatus* larvae of the size given previously are able to

induce the bulgy phenotype in *R. pirica* tadpoles (O. Kishida, unpublished data). The selected *H. retardatus* larvae of each phenotype were starved for three days before the experiment.

For the experiment, *R. pirica* tadpoles were reared with either predaceous or typical *H. retardatus* larvae for a week to determine whether induction of the bulgy morph in the tadpoles depended on the phenotype of the *H. retardatus* larvae. Induction of the bulgy morph in *R. pirica* tadpoles requires that they be in close proximity to *H. retardatus* larvae (Kishida and Nishimura 2004), suggesting that *R. pirica* tadpoles recognize the phenotypes of the *H. retardatus* larvae by a signal that can be detected only when they are close together. Therefore, in the following experiment, we focused on the close-signal recognition process. The experiment was conducted in eight 12-L plastic aquaria (36.5×25.0 cm in surface area and 13.5 cm in height), each filled with 5 L of aged tap water. Each aquarium was divided by a mesh partition (mesh size of 1 mm) into two, equal-sized arenas, each of which was an experimental unit. We randomly assigned 60 similarly sized, 10-d-old *R. pirica* tadpoles (snout–vent length = 7.94 ± 0.88 mm, mean \pm SD, $n = 20$) to each arena of each aquarium. Because there are large variations in sizes of larvae of the two amphibian species in natural pond habitats, the size relationship between the focal *R. pirica* tadpoles and the inducing agents used in the experiment is appropriate. One *H. retardatus* larva with the predaceous phenotype was placed in one arena

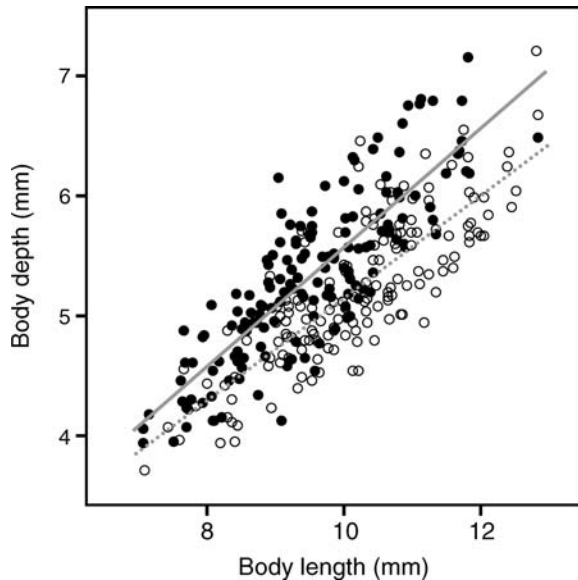


FIG. 2. The relationship between body depth and body length of the *R. pirica* tadpoles in the two treatments (typical treatment, open circles; predaceous treatment, solid circles) as an indicator of the extent of induction of the bulgy phenotype. Each point represents an individual tadpole. The regression lines of body depth (y) on body length (x) show typical treatment, dotted line ($y = 0.875 + 0.426x$, $r^2 = 0.67$); and predaceous treatment, solid line ($y = 0.551 + 0.500x$, $r^2 = 0.70$).

(predaceous treatment) of each aquarium, and one *H. retardatus* larva with the typical phenotype was placed in the other arena (typical treatment) of the same aquarium. The two *H. retardatus* larvae in the same aquarium were chosen to be of similar length, the difference in snout–vent length between the two phenotypes was no more than 0.5 mm. Therefore, although the *R. pirica* tadpoles subjected to the different treatments shared the same water, potentially containing chemicals produced by both salamanders (the inducing agents), they were closely exposed only to one inducing agent with either the predaceous or typical phenotype. The *H. retardatus* larvae in the arenas were free to eat the *R. pirica* tadpoles throughout the experiment. We counted the surviving *R. pirica* tadpoles every two days and determined whether the number of tadpoles differed between treatments and among aquaria. Then, in order to keep the density of tadpoles equal, we equalized the numbers of tadpoles in all arenas by random deletion until all had the same number of tadpoles as the arena with the minimum number.

R. pirica tadpoles were fed rabbit chow ad libitum during the experiment. Rearing water was completely changed every two days. The experiment was conducted in a laboratory at 16°C with a natural day : night (14:10) cycle. After one week, the experiment was terminated, and 20 *R. pirica* tadpoles were randomly selected from each arena for morphological measurement. The

selected tadpoles were killed in 10% ethanol. They were placed in a small glass chamber, and photographs in lateral view were taken. Then the photographic images were projected onto a computer monitor, and the following two traits were digitized: maximum body depth and body length (from the tip of the snout to the tail joint).

Kishida and Nishimura (2004) previously showed that body depth is an appropriate indicator of the morphological trait of bulginess. We adopted body length as the canonical size measurement because it is stable, whereas most other measurable traits (e.g., body width, tail length, and total length) are changed by the induction of the bulgy phenotype (i.e., neither a composite variable of various morphological traits such as the first principal component in a principal components analysis nor mass is an appropriate canonical size measurement; see Kishida and Nishimura 2005). Thus, the data of body depth were corrected for variation in the size measurement. That is, separate regressions of body depth on body length were calculated from the data of each treatment. Then, the residuals were calculated from the regression results to evaluate the extent of induction of the bulgy phenotype. Arena means of the size-corrected variables were used in the statistical analysis.

RESULTS

The number of preyed-upon tadpoles did not differ between the two treatments: 19.62 ± 3.58 ($n = 8$) in the predaceous treatment, 20.38 ± 2.62 ($n = 8$) in the typical treatment (paired t test, $t_7 = 0.386$, $P = 0.71$). To test our main hypothesis that induction of the bulgy morph in the tadpoles depends on the phenotype of the *H. retardatus* larvae, we used a paired t test to compare the means of size-corrected body depth of the tadpoles in the two arenas of each aquarium. (The arena means of the residuals in the predaceous and typical treatments were 0.198 ± 0.074 mm and -0.198 ± 0.079 mm, respectively; mean \pm SE, $n = 8$.) This test found a significant difference between the two treatments ($t_7 = 3.579$, $P = 0.009$; Fig. 2).

DISCUSSION

Our experimental results indicated that the predaceous *H. retardatus* larvae induced *R. pirica* tadpoles to acquire bulgier bodies than did the typical larvae (Fig. 2).

That the number of tadpoles preyed upon was the same between the two treatments is not considered to imply that there was no difference in the predation ability between the two phenotypes of the *H. retardatus* larvae. Rather, we hypothesized that, because the arenas were small, the inducing agents, the *H. retardatus* larvae, regardless of their phenotype, were able to gorge themselves on *R. pirica* tadpoles (in fact, we observed that the abdomens of both larval phenotypes were fully distended with swallowed *R. pirica* larvae at the time of

water exchange and feeding during the experimental period).

Reciprocal phenotypic plasticity may be a primary determinant of morphology in *R. pirica* tadpoles in natural pond habitats and a key ecological factor in the community assemblage. In predator–prey interactions, predation success depends greatly on the balance between the gape size of *H. retardatus* larvae and the body size of *R. pirica* tadpoles (i.e., the broader the head that an *H. retardatus* larva has, the larger the range of body size of *R. pirica* tadpoles that it can swallow) (Ohdachi 1994, Kishida and Nishimura 2004). The increased expression of the bulgy phenotype in *R. pirica* tadpoles would be adaptive when they are exposed to predation risk from the more dangerous predator, the predaceous *H. retardatus* larvae.

The modified phenotypic design would alter the predator–prey interaction and affect the fitness not only of the *R. pirica* tadpoles themselves but potentially also that of their predator, the *H. retardatus* larvae. The altered predator–prey interaction resulting from the reciprocal phenotypic plasticity of the *R. pirica* tadpoles might affect ecological processes in the natural community assemblage at various levels via direct or indirect effects on other members of the assemblage. Identification of reciprocal phenotypic plasticity in natural systems and examination of its influences on the ecological patterns in community assemblages are needed to understand the ecological consequences of phenotypic plasticity (Miner et al. 2005).

What signals did the *R. pirica* tadpoles utilize to recognize the phenotype of the inducing agent during the induction process, resulting in the differences in the degree of the bulgy response between the treatments in the experiment? The tadpoles subjected to the two treatments in each aquarium shared the same water, suggesting that the *R. pirica* tadpoles recognized the phenotype of the inducing agent by means of qualitatively or quantitatively different nondiffusible signals during close interaction, perhaps even by direct contact. The number of tadpoles preyed upon did not differ between the treatments throughout the experiment, indicating that the difference in the extent of the bulgy response did not reflect the number of preyed-upon tadpoles.

The proximate signal recognition of the inducible defense leads us to hypothesize that the result may reflect more frequent direct contact via predaceous attack by the inducing agent (i.e., the tadpoles exposed to the predaceous *H. retardatus* larvae experienced more persistent attacks than those exposed to the typical *H. retardatus* larvae, resulting in a difference in signal perception). However, this hypothesis is likely excluded by the fact that the number of the tadpoles preyed upon between the treatments did not differ. The inducing agents in both treatments reached satiety during the

experiment, suggesting that tadpoles with typical larvae would have experienced more frequent attacks than those with predaceous larvae, since the predation success of the typical larvae would be lower than that of the predaceous larvae.

It is more likely that the *R. pirica* tadpoles utilized phenotype-specific signals to distinguish between the predator phenotypes. During the preliminary induction of the predator phenotype, before the experiment, the *H. retardatus* larvae destined to have the predaceous phenotype were fed *R. pirica* tadpoles to induce the predaceous phenotype, whereas those larvae intended to have the typical phenotype were fed chironomid larvae so that they would retain that morph. Of course, in natural systems, *H. retardatus* larvae with the predaceous phenotype would have preyed on *R. pirica* tadpoles during their development, because a high density of *R. pirica* tadpoles is required to induce the predaceous phenotype (i.e., a past history of predation on *R. pirica* tadpoles is intimately related to the predaceous phenotype). In general, prey organisms, including anuran tadpoles, are sensitive to originating from injured or preyed-upon conspecifics (i.e., alarm substances; e.g., Schoepner and Relyea 2005). *R. pirica* tadpoles may adjust their development of the bulgy morph according to the phenotype of *H. retardatus* larvae to which they are exposed by utilizing memories of alarm substances which have been stored in the nondiffusible signals.

The reciprocal plastic response of the bulgy phenotype of *R. pirica* tadpoles may have evolved in the course of an arms race of the two phenotypic plasticities between the two larval amphibians (i.e., the inducible bulgy phenotype of *R. pirica* tadpoles and the inducible predaceous phenotype of *H. retardatus* larvae). Previous studies have reported some evidence supporting the coevolution of reciprocal phenotypic plasticities. For example, our recent study showed that the signal recognition system for induction of the bulgy phenotype and the morph's adaptive function in *R. pirica* tadpoles are specific to *H. retardatus* larvae (Kishida and Nishimura 2005). In addition, geographical differences in the ability of tadpoles to adaptively express the bulgy phenotype correspond to differences in the geographical distribution of *H. retardatus* (O. Kishida and K. Nishimura, *unpublished manuscript*). *R. pirica* tadpoles from the mainland, where the salamanders are common, express the bulgy phenotype more than tadpoles from an island without the predators. Thus, the bulgy plastic phenotype has been selected for by predation pressure from larval *H. retardatus*. Conversely, induction of the predaceous phenotype in *H. retardatus* larvae seems to be specific to *R. pirica* tadpoles. *R. pirica* tadpoles are the only other amphibians with which *H. retardatus* larvae interact. Although *H. retardatus* larvae with the predaceous phenotype occur not only where the density

of *R. pirica* tadpoles is high but also where the density of conspecific larvae is high, the induction rate is higher in the former environment than in the latter (Michimae and Wakahara 2002). The specificity suggests that this plastic phenotype has evolved during intimate interaction with *R. pirica* tadpoles. *R. pirica* tadpoles might have evolved reciprocal phenotypic plasticity as a survival strategy in their highly antagonistic interaction with *H. retardatus* larvae.

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