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Evolutionary ecology of inducible morphological plasticity in predator-prey interaction: toward the practical links with population ecology

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Abstract

The outcome of species interactions is often strongly influenced by variation in the functional traits of the individuals participating. A rather large body of work demonstrates that inducible morphological plasticity in predators and prey can both influence and be influenced by species interaction strength with important consequences for individual fitness. Much of the past research in this area has focused on the ecological and evolutionary significance of trait plasticity by studying single predator-prey pairs and testing the performance of individuals having induced and non-induced phenotypes. This research has thus been critical in improving our understanding of the adaptive value of trait plasticity and its widespread occurrence across species and community types. More recently, researchers have expanded this foundation by examining how the complexity of organismal design and community-level properties can shape plasticity in functional traits. In addition, researchers have begun to merge evolutionary and ecological perspectives by linking trait plasticity to community dynamics, with particular attention on trait-mediated indirect interactions. Here, we review recent studies on inducible morphological plasticity in predators and their prey with an emphasis on internal and external constraints and how the nature of predator-prey interactions influences the expression of inducible phenotypes. In particular, we focus on multiple-trait plasticity, flexibility and modification of inducible plasticity, and reciprocal plasticity between predator and prey. Based on our arguments on these issues, we propose future research directions that should better integrate evolutionary and population studies and thus improve our understanding of the role of phenotypic plasticity in predator-prey population and community dynamics.

Keywords

Key words: Inducible defense · Inducible offense · Phenotypic plasticity · Polyphenism · Population dynamics · Trait-mediated indirect effect

Introduction

The nature and strength of predator-prey interactions can exert a major influence on the phenotypic design of predators and their prey (Kerfoot and Sih 1987; Tollrian and Harvell 1999; Barbosa and Castellanos 2005). The outcome of predator-prey interactions is often influenced by trait variation that is subject to selection. As a result, many organisms have evolved plasticity in relevant traits that can improve fitness when the intensity of predator-prey interactions is variable or unpredictable in space and time (Tollrian and Harvell 1999). Morphological plasticity in predators and prey has attracted considerable attention from ecologists and evolutionary biologists, in part because such changes are often quite dramatic and conflict with the previously held notion that morphology, unlike behavior, is rather inflexible (West-Eberhard 2003). In particular, inducible defenses, which describe the specific case of plastic changes in prey traits in response to predation risk, appear to be particularly common in natural systems. For example, elongated spines in water fleas (Tollrian 1995) and marine bryozoans (Harvell 1984), deeper bodies in fishes (Brönmark and Miner 1992) and thickened shells in marine snails (Appleton and Palmer 1988; Trussell 1996) have all been suggested to be adaptive plastic responses that reduce prey vulnerability.

Similarly, and more recently, it has become clear that inducible offenses (termed by Padilla 2001) such as enhancement of the capturing organs of crabs (Smith and Palmer1994) and amphibian larvae (Collins and Cheek 1983; Pfennig 1992; Michimae and Wakahara 2002) can also play a key role in predator-prey interactions by countering the inducible defenses expressed by prey.

Much of our current knowledge has been obtained via experiments involving single predator-prey pairs (Collins and Cheek 1983; Pfennig 1992; Tollrian and Harvell 1999; Michimae and Wakahara 2002) by comparing variation in prey morphology in the presence and absence of predators, and then testing the performance of individuals with induced and non-induced phenotypes. This approach has been instrumental in documenting the taxonomic prevalence of inducible defenses (Torllian and Harvell 1999; DeWitt and Scheiner 2004) and has shed considerable light on the adaptive value of trait plasticity (Lively 1986a,b; Kopp and Tollrian 2003a; Kishida and Nishimura 2005; Benard 2006). These insights have been further enhanced by studies of the role of inducible defenses in driving the evolution of geographic variation in prey phenotypes (Lively et al. 2000; Trussell 2000a,b; Trussell and Smith 2000; Relyea 2002a; Trussell and Nicklin 2002; Laurila et al. 2006; Kishida et al. 2007) and the genetic basis of morphological plasticity via quantitative genetic (Relyea 2005a) and molecular genetic (Mori et al. 2005, 2009) approaches. For example, *Rana pirica* frog tadpoles of the populations in the predator-common mainland have higher expression ability of defensive morph when exposed to predation risk from the salamander larvae (*Hynobius retardatus*) than those of a predator-free island population (Kishida et al. 2007). This research suggests that history of predator-prey interaction may shape evolution of prey inducible defense as an adaptive strategy.

Studies of morphological plasticity are now moving to a new phase by increasing attention to the complexity of organismal design and how community-level properties (e.g., trophic complexity) can influence the plasticity of individuals (Agrawal 2001; Relyea 2003, 2005b; Kishida et al. 2009a). In addition ecologists are exploring how morphological plasticity influences population dynamics and community structure via trait-mediated indirect effects (TMIIs) (Werner and Peacor 2003; Miner et al. 2005). It is well known that changes in prey behavior in response to predation risk can cause the emergence of trait-mediated indirect effects (see Werner and Peacor 2003; Schmitz et al. 2004), but the connection between morphological plasticity and these indirect effects has not been adequately studied (Miner et al. 2005).

In this paper, we review studies on inducible morphological defenses and offenses with an emphasis on topics such as multiple-trait plasticity, flexibility and environmental modification of plastic responses, and phenotypic reciprocity between predator and prey. We argue that studying morphological variation from these perspectives is essential to a better understanding of individual adaptation to variation in the nature and strength of predator-prey interactions, and that such an approach will likely lead to new insights for population, community and evolutionary ecology.

Multiple inducible traits in predator-prey interaction

Plasticity in response to environmental change often involves multiple behavioral, life historical or morphological traits (DeWitt et al. 1999; Rundle and Brönmark 2001; Van Buskirk 2002; Teplitsky and Laurila 2007). Although morphology is generally viewed as being less flexible, it is clear that multiple morphological traits can

simultaneously change after exposure to environmental cues, such as those released by predators (Pfennig 1992; Relyea and Auld 2004). Consideration of the developmental and functional relationships among multiple, inducible traits should yield a better understanding of phenotypic design (Steiner 2007; Steiner and Pfeiffer 2007). The fitness consequences of multiple trait induction can be classified in two ways: (1) an inducible traits complex that is fully adaptive (i.e., all changes are adaptive) and (2) an inducible traits complex that involves both adaptive and maladaptive changes.

Adaptive inducible traits complex

In this case, the inducible changes in multiple traits yield additive benefits to individual fitness. Such additive responses are frequently observed in the morphological and behavioral defenses of animal prey when confronted with predation risk (DeWitt et al. 1999; Rundle and Brönmark 2001; Van Buskirk 2002; Teplitsky and Laurila 2007 see also Urban 2007). For example, many species of amphibian larvae increase their tail depth to reduce their vulnerability to predators because an enlarged tail may enhance swimming performance (Dayton et al. 2005) or attract the predator to a less vital part of their body such as the head (Van Buskirk et al. 2003). In addition to this morphological defense, tadpoles also become less active to reduce their encounter rate with the predator (Skelly 1994; Van Buskirk 2002). Thus, both behavioral and morphological changes serve to increase prey fitness by reducing their vulnerability to predators.

Functional additivity of multiple inducible traits may enhance the adaptive value of trait compensation, particularly when the expression of inducible traits depends on

spatial and/or temporal variation in the strength of predator-prey interactions. For example, tadpoles (*Rana pirica)* exhibit inducible behavioral (less activity) and morphological (bulgy body) defenses against salamander larvae (a sit-and-wait and gape-limited predator). However, individuals having the defended morph decrease their behavioral defense compared to individuals having the undefended morph (Kishida et al. 2009b). Thus, the tadpoles that are developing the defended morph after being exposed to the predation risk may compensate for their incomplete morphological defense by enhancing behavioral defense until completing their highly functional morphological defense. Hence, trait compensation can evolve as a general strategy to provide fitness advantages in environments where there is spatio-temporal variation in predation risk, in case, time to development vary among inducible traits (DeWitt et al. 1999; Rundle and Brönmark 2001).

Alternatively, changes in one trait in direct response to a focal inducing agent (e.g., a predator) can indirectly lead to other trait changes that are necessary to cope with the new ecological demands that arise because of the initial trait change. Such situations are expected to arise when responses to one environmental variable (predation risk) require the animal to occupy habitats different from those it occupies in the absence of predation risk. The results of several studies support this hypothesis (Stoks et al. 2005; Vonesh and Bolker 2005; Schmidt et al. 2006; Iwami et al. 2007). For example, in the presence of dragonfly predation risk cues, salamander larvae (*Hynobius retardatus*) develop enlarged external gills to cope with the environmental changes (reduced O_2 levels) that accompany their anti-predator behavior (Iwami et al. 2007). When dragonflies are present, salamanders reduce their surfacing frequency (lung respiration). Although this behavior reduces the likelihood of salamanders being detected by

dragonflies it also increases salamander exposure to hypoxic conditions. External gill enlargement represents a compensatory adaptation to the costs of hypoxia. Indeed, salamanders having enlarged gills are more resistant to hypoxic environments than those with non-induced, typical gills.

We hypothesize that inducible responses causing major transitions in the habitats and life history of individuals may induce other adaptive responses. For example, inducible traits causing significant changes in ontogeny (e.g., changes in metamorphosis timing of animals with complex life history) are likely candidates because matching trait development with seasonal environment and phenology is critical to the individual fitness. In addition, predator habitat shifts in response to resource availability and those by prey in response to predation risk may also be important candidates because such habitat shifts may require individuals to respond to new ecological demands.

Inducible traits by-products or trade-offs of adaptive inducible traits

Inducible trait complexes can involve traits that have negative or neutral fitness consequences and such traits may reflect costs or by-products of adaptive trait plasticity. Developmental constraints or allocation trade-offs among multiple traits likely underlie the maladaptive nature of individual trait responses within the overall inducible trait complex. For example, reduced body mass, shorter intestines, and delayed development of reproductive organs in individual organisms that express inducible defenses in response to predation risk represent maladaptive trait changes that may occur because of allocation trade-offs and developmental constraints (Lively 1986a; Trussell and Nicklin 2002; Relyea and Auld 2004, 2005). In marine snails, predator-induced shell thickening

imposes architectural constraints that slow the production of internal soft tissue, which may affect snail fecundity (Trussell 2000b; Trussell and Nicklin 2002). Natural selection may allow such maladaptive trait subsets to persist simply because the fitness benefits of plasticity in a focal trait outweigh the negative effects of plasticity in other traits within the trait complex.

Correlated responses among different traits with a trait complex might become more apparent in longer-term interactions because of the lasting effects of focal trait change on physiological process (Relyea 2001; Van Buskirk and Saxer 2001). For example, juvenile frogs that deepen their tails during the tadpole stage in response to dragonfly risk cues have shorter but wider legs as juvenile frogs (just after metamorphosis) than individuals that had not been exposed to predation risk during their larval period (Van Buskirk and Saxer 2001). These delayed morphological inductions may thus reflect physiological neutral changes in larval period rather than adaptive or maladaptive responses. In fact, Van Buskirk and Saxer (2001) could not find significant differences among predation risk treatments (presence, absence) in the functional consequences of the inducible traits and individual tadpole performance at juvenile stages.

Correlated morphological trait expressions may also emerge because of adaptive plasticity in response to distinct environmental factors. A good example comes from organisms that adopt both inducible offense and defense. Michimae and Hangui (2007) documented the existence of such trade-offs between inducible offense and defense in *Hynobius retardatus* salamander larvae. Salamanders exhibiting the inducible offensive morph (larger gape) in response to frog tadpole prey during early development did not respond as strongly with their inducible defense (higher tail) against predatory

dragonfly larvae in later larval stages. This limitation on functional traits may affect individual fitness as well as the demography of predators and prey. Demonstrating developmental conflicts among traits is thus key to better understanding trade-offs between multiple inducible traits.

Flexibility and modification in the expression of inducible morphology

The intensity of predator-prey interactions can vary considerably in both space and time within natural food webs. Despite this variation, most experimental studies of inducible morphological plasticity have focused on pairwise predator-prey interactions. Much of this focus can be attributed to experimental convenience that nevertheless has been instrumental in establishing the foundation for phenotypic plasticity research. Recently, however, plasticity studies have taken the necessary steps to better understand more complex plasticity scenarios (e.g., multiple predators) and it has become clear that morphological traits are much more flexible than previously recognized. Here, we discuss gradual responses, repetitive changes as a form of flexibility, and environmental modification of inducible morphological plasticity.

Gradual responses

Although much work has examined how the presence and absence of predator-prey interactions influence prey trait plasticity, such interactions are often continuous rather than discrete because of spatiotemporal variation in predator and prey densities. Evidence of gradual, induced morphological change in predators and prey is

accumulating (Van Buskirk and Arioli 2002; Relyea 2004; Schoeppner and Relyea 2008) and the degree of induction appears to be highly dependent on the strength of a particular predator-prey interaction. For example, inducible defense and offense in the morphology of ciliates and larval amphibians correlate with the density (Van Buskirk and Arioli 2002; Relyea 2004) and individual performance of the interacting species (Wicklow 1988; Kopp and Tollrian 2003b; Kishida et al. 2006). However, there has been little attention to the adaptive value of gradual responses. We need to quantify the costs and benefits of different degrees of inducible response, because only in the case that the extent of inducible traits positively correlates with their functional performance and with induction costs, the gradual expression in response to the interaction intensity could be adaptive strategy. For example, suppose that increased expression of inducible defenses assures higher protection against predation risk. If fitness costs monotonically increase as a function of the degree of induction, organisms should maximize their fitness by matching the degree of inducible defense to actual predation risk to better balance the benefits of increased protection with the costs required to pay for it. In contrast, if fitness costs are constant as a function of inducible defense, then organisms should express the greatest defense possible across a broad range of predation risk. In this case, gradual responses likely have a negative impact on fitness because anything but the greatest level of defense will increase the likelihood of being consumed. Hence, a positive relationship between the degree of defense expression and the costs required to pay for it is a prerequisite for gradual responses to be adaptive. Similarly, an increase in functional performance with increased defense expression is also required for gradual responses to be adaptive. For example, suppose that increased defense expression incurs higher fitness costs. If increased protective function does not accompany

increased defense expression, then organisms should express minimal defense across a range of predation risk because high expression does not increase survivorship despite its higher costs.

Repetitive changes

Another important aspect of inducible responses is temporal variation in interaction intensity at shorter time scales. For example, stochastic demographic processes such as migration of predators and prey into and out of local environments can expose individuals to considerable temporal variation in interaction intensity within an individual's lifetime. Thus, such variation may require the individuals to make adaptive phenotypic changes repetitively. Our recent work has demonstrated flexible, repetitive changes in prey morphological defenses in response to repetitive changes in predation risk (Kishida and Nishimura 2006). In this study, *Rana pirica* tadpoles with the predator-specific defensive morphs were subjected to either the removal or changing of the predator to which they had been exposed. After predator removal, tadpoles with each predator-specific phenotype changed to the non-defensive basic phenotype. In addition, after changing predator identity, tadpoles with each predator-specific phenotype reciprocally shifted their phenotype to one that was more suitable to the new predator. Although reversible responses in inducible morphologies are taxonomically widespread (Hanazato 1990; Brönmark and Pettersson 1994; Chivers et al. 2008), little is known regarding the fitness contributions of repetitive changes. This topic is important to address because repetitively induced phenotypes may have different levels of functional significance compared to initially induced phenotypes. Moreover,

repetitive changes may incur additional costs by being more costly than the initial change. Alternatively, if individuals can resorb and recycle the costs of materials invested in the initial trait induction, then repetitive changes are not so expensive. Indeed, reversible responses of *Rana pirica* tadpoles from the salamander-specific defensive morph (bulgy body with thickened epithelium tissue) to the non-defensive basic morph after removal of predation risk suggests such recycling occurs because tadpoles shrink their thickened tissue as part of their reversible response (Kishida and Nishimura 2004).

Repetitive phenotypic changes also may play an important role in population dynamics. Most mathematical models exploring the effects of inducible responses on population dynamics assume reversibility of focal inducible traits and predict that such flexibility can stabilize the population dynamics of predator and prey (Adler and Grünbaum 1999; Ramos-Jiliberto 2003; Vos et al. 2004a; Kopp and Gabriel 2006; DeAngelis et al. 2007; Ramos-Jiliberto et al. 2007). The effects of reversibility on population dynamics likely depend on the quickness of the response (Padilla and Adolph 1996), the frequency of environmental change, and the balance between the benefits and costs of inducible and non-inducible phenotypes. The effects of reversibility should also depend on type of traits involved. For example, morphological changes typically require more time to emerge than behavioral changes. In addition, developmental constraints often limit repetitive flexibility in morphology whereas behavior is expected to be much more flexible. We suggest that further exploration of qualitative and quantitative differences in the repetitive responses of focal traits will yield much insight into their influence on the population dynamics of interacting species.

Modification by external factors

Ecologists have begun to devote more effort to better understand the ecological significance of trait plasticity in more complex contexts. This is critical because 1) prey must often contend with multiple predators (Sih et al. 1998; Relyea 2003), 2) the interaction between intermediate predators and their prey may be strongly influenced by risk from a top predator (Werner and Peacor 2003; Kishida et al. 2009a), and 3) most prey experience competition in addition to predation risk (Gurevitch et al. 2000; Chase et al. 2002). Several studies have explored how the expression of inducible offenses and defenses in a given predator-prey pair are affected by other community members. For example, competitors negatively influence the expression of induced morphological defenses in *Rana sylvatica* tadpoles (Relyea 2002b; Relyea and Hoverman 2003). Although *Rana sylvatica* tadpoles exhibit less activity, deeper tails and shorter bodies in the presence of the predation risk, the presence of competitors induces changes in these traits in the opposite direction. Because these responses are adaptive if expressed in the appropriate environmental context (i.e., when either predation risk or competition is operating), the tadpoles must balance the trade-offs involved with each plastic response when they are exposed to both predators and competitors.

Modification of trait plasticity by other community members has also been observed for inducible offensive morphologies in predators (Andersson et al. 2007; Kishida et al. 2009a). Kishida et al. (2009a) examined how a top-predator affects antagonistic inducible offense and defense between salamanders and tadpoles, using a dragonfly - salamander - tadpole intraguild predation system. In the presence of the chemical cues from *Aeshna nigroflava* dragonfly larvae (top-predator), the expression

of inducible offensive morphology of *Hynobius retardatus* salamander larvae (intermediate predator) and inducible defensive morphology of *Rana pirica* (bottom prey) were both reduced compared to the trait expression observed in both species in the absence of the dragonfly risk cues. The limited expression of inducible offense (a wide gape that facilitates swallowing of tadpoles) by salamander larvae in response to the dragonfly risk cues is likely adaptive because it balances the cost (increased vulnerability to dragonflies) with the benefit (increased foraging efficiency on tadpoles) of having a large gape. In contrast, the limited expression of inducible defense by tadpoles (a bulgier body) is likely due to a reduction in the cues that induce the defended morphology. Hence, when dragonflies are present, salamanders are less active, which reduces the intensity of the salamander-tadpole interactions that are necessary to induce the tadpole defense. Such modification of predator-specific inducible defenses by presence of another predator have been documented in other predator-prey systems (Teplitsky et al. 2004; Hoverman and Relyea 2007; Lakowitz et al. 2008; Bourdeau 2009).

It has also become well established that abiotic factors can modify the role that morphological plasticity plays in predator-prey interactions (Rundle et al. 2004; Teplitsky et al. 2007; Baldridge and Smith 2008; Mirza and Pyle 2009). Abiotic modification of trait plasticity can be adaptive if abiotic conditions are a reliable indication of future environmental conditions. For example, longer spine and helmet, which are expected to be defensive trait, of a population of *Daphnia lumholtzi* are induced in a certain temperature range (Yurista 2000). If predation risk maximize within the temperature range, such temperature-induced change may be adaptive phenotypic plasticity. However, abiotic factors may have negative effects on fitness if

they modify the physiological mechanisms involved in the production of induced morphological change. For example, low calcium carbonate availability can limit predator-induced changes in the shell morphology of freshwater snails (Rundle et al. 2004). Similarly, in marine systems water temperature influences the availability of calcium carbonate because $CaCO_3$ becomes less saturated and more soluble with decreasing water temperature (Clarke 1983). As a result, water temperature can affect shell thickness plasticity in marine snails (Trussell 2000a) and claw enlargement in predatory crabs (Baldridge and Smith 2008).

Little effort has explored the ecological consequences of abiotic and biotic modification of induced morphological responses. We need to assess how modification of inducible traits affects individual fitness as well as predator-prey population dynamics. Modification of trait plasticity and its consequences for individual fitness may be determined by how strongly such modification is correlated with strength of the interaction (i.e., inducing agent). If modifying factors reduce the degree of trait expression without decreasing interaction strength, individuals may have reduced fitness because such modification may induce maladaptive responses. For example, suppose that a secondary factor (abiotic or biotic) reduces the expression of prey defenses but does not affect predator density and offenses. If prey vulnerability depends on the extent of their defense, then prey with reduced defenses will experience increased predation risk while predators enjoy more efficient consumption. In contrast, when reduced defenses are a product of reduced interactions between a prey and its predator, modification of the inducible response may not reduce prey fitness. Our recent study (Kishida et al. 2009a) illustrates this point. We found that induced morphological defenses in *Rana pirica* tadpoles against predatory salamander larvae were reduced by

the presence of other predator (i.e., dragonfly larvae). However, tadpole mortality caused by salamander predation was not higher in the presence of versus the absence of the dragonfly, because dragonflies also suppressed the predation efficiency of salamanders.

Reciprocity of antagonistic inducible phenotypes

Inducible offenses by predators and inducible defenses by prey are known for a variety of predator-prey interactions, including cannibalistic systems, but usually either the inducible offense or inducible defense in the focal interaction is considered. However, several studies have documented both types of antagonistic phenotypic plasticity within predator-prey pairs involving ciliates (Wicklow 1988; Kopp and Torllian 2003b; Banerji and Morin 2009), marine crabs and snails (Smith and Palmer 1994; Trussell 1996 see also Edgell and Rochette 2007, 2008), and salamander larvae and frog tadpoles (Michimae and Wakahara 2002; Kishida et al. 2006). Our interest here is whether reciprocity in antagonistic phenotypic plasticity is widespread and how it affects the demography of the predator, prey and other community members (Agrawal 2001; Agrawal et al. 2007). To address this issue, one must examine how antagonistic phenotypic plasticity has coevolved and is maintained in a focal predator-prey interaction. Previous theoretical models have focused on either the inducible defense or offense and have concluded that both types of plasticity can stabilize predator-prey population dynamics (Abrams 1984, 1992, 1995; Matsuda et al. 1993, 1994, 1996; Abrams and Matsuda 1997; Bolker et al. 2003; Kondoh 2003, 2007; Ramos-Jiliberto 2003; Vos et al. 2004a,b; Kopp and Gabriel 2006; DeAngelis et al. 2007; Mougi and

Nishimura 2007, 2008a, 2009). However, few studies have specifically focused on reciprocity in plasticity for both the predator and its prey and behavioral reciprocity has received more attention than morphological reciprocity (Abrams 1992; van Baalen and Sabelis 1993; Adler and Grünbaum 1999; Kokko and Ruxton 2000; Abrams 2007; Krivan 2007; Krivan et al. 2008; Mougi and Nishimura 2008b; but see Mougi and Kishida 2009). To our knowledge, only one study (Mougi and Kishida 2009) examined how reciprocity in morphological plasticity for both the predator and its prey affect their population dynamics. According to their model analyses, antagonistic fashion between inducible offense of predator and inducible defense of prey has significant stabilizing effects on their population dynamics. In particular, higher stability is achieved when the prey exhibits a high-performance inducible defense. Thus, this study suggests that antagonism of phenotypic plasticity in predator and prey interaction may be more prevalent in nature than we thought.

We encourage theoreticians to develop models that consider both inducible offenses and defenses to determine when and how reciprocity between these responses can evolve and have stabilizing effects on population dynamics. Based on predictions from such models, empiricists may have a better sense of where such antagonism is likely to operate. And also, we expect that empiricists directly examine whether combination of inducible offense and defense have significant effects on predator-prey population dynamics.

Linking phenotypic plasticity to population ecology

The population and community consequences of phenotypic plasticity are increasingly appreciated (Agrawal 2001; Werner and Peacor 2003; Miner et al. 2005; Agrawal et al. 2007). Theory suggests that such plasticity can promote species coexistence and stabilize population dynamics (Matsuda et al. 1993; Bolker et al. 2003) as well as provide insight into the paradox of enrichment (Vos et al. 2004a,b; Mougi and Nishimura 2007, 2008a, b, 2009) and the complexity-stability debate (Kondoh 2003, 2007). Many empirical studies have documented the importance of trait-mediated indirect effects in three species food chains (see Werner and Peacor 2003; Schmitz et al. 2004) via their influence on trophic cascades (Trussell et al. 2002, 2006a; Schmitz et al. 2004) and ecosystem function (Trussell et al. 2006b, 2008; Schmitz et al. 2008). Many of these empirical works have focused on plasticity in behavioral traits such as prey habitat or diet shifts in response to predation risk and predator diet shifts in response to the prey availability (reviewed in Werner and Peacor 2003). Such behavioral shifts are clearly important but more attention to the ecological importance of morphological plasticity to the demography of predators and prey is needed. Few studies have explored how morphological plasticity affects the population processes of predators and their prey as well as the strength of trophic cascades (Verschoor et al. 2004; Van der Stap et al. 2007; Kishida et al. 2009b). Using ideal experimental systems, Verschoor and his colleague elegantly showed stabilizing effects of inducible defense on population dynamics, in which inducible morphological defense of algae stabilize the dynamics of bi- and tritrophic planktonic food chains in case of eutrophic environment (Verschoor et al. 2004). Recently, using interactions between predatory salamander larvae and frog tadpole prey, we experimentally demonstrated that the defensive morph of tadpoles intensifies cannibalism among salamanders (Kishida et al. 2009b). We

suggest that the indirect effects mediated by the inducible defenses of prey can emerge because of predator diet shifts in response to these defenses and likely play a pivotal role in maintaining predator diet breadth and cannibalism that, in turn, determine how trophic dynamics unfold in natural systems.

Although we have a limited understanding of the demographic effects of inducible, offensive predator morphologies, their trait-mediated effects can have significant impacts on their prey and other community members. If a predator changes its phenotype in response to prey defenses to enhance its foraging efficiency on the defended prey, other prey species may indirectly benefit if this induced phenotype limits the predator's ability to consume them. On the other hand, such offensive morphologies may enhance the predator's impact on other prey species because of functional properties associated with the inducible change. For example, reinforcement of predator capturing organs in the presence of certain defended prey species (e.g., inducible reinforcement of marine crab claws after consuming mollusks with thickened shells) may allow them to consume other prey with similar defenses. Such effects may be particularly important when diet shifts occur after exhaustion of the target prey (i.e., the inducing agent) and the morphological shift lasts a long time (i.e., less reversibility).

It is clear that a better connection between theoretical models and empirical field studies is essential for a more comprehensive understanding of ecological consequences of phenotypic plasticity. We believe that a more effective synthesis of theory and empiricism may be achieved if empiricists focus on:

1. Determining how the expression of plastic traits varies with interaction strength between participating species.
2. Establishing the functional significance of trait plasticity.

3. Better understanding the consequences of time lags to initiate and complete the inducible change, which is especially important for morphological traits.
4. Determining the alternative tactics that may compensate for the lag-time of inducible phenotype and their costs.
5. Better understanding the consequences of emergent trait-mediated indirect effects on predator-prey demography and individual trait development.

We also suggest that theoreticians focus on the following topics (note that empiricists may address these topics using ideal model systems):

1. Examining the consequences of continuous and discontinuous inducible plasticity and reversible and non-reversible plasticity to population dynamics
2. Examining the effects of time-lag for induction and reversibility of phenotypes on population dynamics.
3. Examining the effects of alternative tactics that compensate for the lag-time of inducible phenotype on population dynamics.
4. Examining the conditions that favor the evolution of antagonistic plasticity and its effects on population dynamics.
5. Examining the consequences of cascading effects of inducible traits in complex food webs.

In this paper, we have argued that studies focusing on morphological plasticity can provide significant insights that complement studies on plasticity in other traits such as behavior and life history. Future work involving plasticity in all trait types may allow a more general understanding of whether the ecological consequences of trait plasticity are dependent on the type of trait involved. Indeed, inducible defenses

in prey and inducible offenses in predators are expressed in morphological, behavioral, and life history traits. Hence, the ecological consequences of antagonistic plasticity may be similar across trait types. Although this prediction is intuitive, it is clear that much work is needed if we are to fully understand the importance of plasticity to individual fitness and population and community dynamics in natural systems. We hope that our review has provided more fertile ground for this endeavor.

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