



Developmental Plasticity: Preparing for Life in a Complex World

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1. INTRODUCTION

1.1 Developmental Plasticity

Phenotypic plasticity plays a key role for the ability of organisms to survive in heterogeneous environments. The benefits of plasticity ensue from the ability to produce a phenotype–environment match across a wider range of environments than it would be possible if traits were fixed. As plastic responses can take effect faster than evolutionary change, plasticity may rescue populations before a strategy to cope with a stressor can evolve (Chevin & Lande, 2010). Therefore, plasticity may prevent extinction of populations facing rapid environmental change. Plasticity may also act as a potent driver of diversification and innovation (reviewed in Moczek et al., 2011). Plasticity itself is considered an evolving property under selection (reviewed in Pigliucci, 2005; West-Eberhard, 2003). One way to conceptualize plastic responses is reaction norms, that is, the change of trait values in response to an environmental gradient (Stearns, 1992). The shapes of reaction norms are under selection (Nussey, Postma, Gienapp, & Visser, 2005) and can differ between genotypes (e.g., Herman, Sultan, Horgan-Kobelski, & Riggs, 2012). Plasticity is generally expected to be favored by selection when the environment is sufficiently variable, but future conditions are predictable at least to some degree (Burgess & Marshall, 2014; Marshall & Burgess, 2015).

Developmental plasticity is a form of phenotypic plasticity and denotes the ability of organisms to adjust their phenotype to environmental conditions experienced during ontogeny. It is ubiquitous in nature, and it is central for our understanding of phenotypic diversity and adaptation (West-Eberhard, 2003). Morphologic, physiologic, and behavioral traits and the expression of genes are all shaped by interactions between the environment and the developing phenotype (Aubin-Horth & Renn, 2009; Tollrian & Harvell, 1999; West-Eberhard, 2003). Developmental plasticity can have large phenotypic effects because phenotypic changes are made

relatively early in life and are often (Piersma & Drent, 2003) but not always (Champagne & Meaney, 2007; Fischer, Bessert-Nettelbeck, Kotschal, & Taborsky, 2015; Sachser, Kaiser, & Hennessy, 2013) irreversible. Plastic adjustments toward environmental cues made early in life can influence entire suites of later life traits including survival (Birkhead, Fletcher, & Pellatt, 1999) and reproductive rates (Naguib, Nemitz, & Gil, 2006). Developmentally plastic responses are often triggered by cues perceived by the developing individual from the ambient environment experienced during early stages of ontogeny. However, the influences inducing developmental plasticity can also originate from previous generations (“transgenerational plasticity,” reviewed in Burton & Metcalfe, 2014; Herman et al., 2012; Uller, 2008). The nongenetic transmission of information between generations occurs through different mechanisms, ranging from de novo establishing of an effect in each generation through parental effects, e.g., by the quality of provided parental care, to epigenetic inheritance via the germ line (reviewed in Szyf, 2015).

Although in principle, unlimited developmental plasticity would allow organisms to continually track any changes of the environmental conditions during ontogeny, plasticity is assumed to come with certain costs and limitations preventing a repeated restructuring and rebuilding of the body (Auld, Agrawal, & Relyea, 2010; DeWitt, Sih, & Wilson, 1998; Murren et al., 2015). Costs of plasticity may first arise from the necessity to maintain a machinery to sense environmental cues and respond to them developmentally. However, attempts to measure these costs empirically were often unsuccessful (Van Buskirk & Steiner, 2009), and overall these costs may be small because this machinery is part of the normal functioning of cells and therefore comes with no additional costs (Herman, Spencer, Donohue, & Sultan, 2014). Second, costs arise from the actual phenotypic change that is made in response to a cue, for instance, the building of a defensive structure or reorganization of physiologic processes. Third, long-term fitness costs may ensue if phenotypic adjustments are inappropriate or incomplete or their beneficial effect is restricted only to a limited time window in life (see Section 3.2.2).

1.2 Adaptive Value of Developmental Plasticity

The fact that developmental plasticity can affect an organism’s phenotype lifelong with significant fitness consequences gave rise to a vivid discussion about the environmental conditions under which this form of plasticity is adaptive. We tend to propose plausible adaptive explanations whenever we report a case of developmental plasticity. Proposed explanations often

center around the temporal and spatial heterogeneity and assumed autocorrelation properties of the environment and the potential ensuing benefits from anticipatory plasticity of the lack thereof (Krause & Naguib, 2014), despite the fact that these environmental parameters are rarely known or measured (see Uller, Nakagawa, & English, 2013). However, plasticity can as well be harmful and reduce fitness under certain circumstances. For instance, exposure to stressors for a limited period of life, such as during the embryonic stage, may prime an organism to cope better with stressful situations later in life (Sheriff & Love, 2013). In contrast, chronic stress can have quite detrimental effects. It may impair the immune function (e.g., induce autoimmunity, Harpaz et al., 2013) and induce lifelong cognitive and behavioral malfunction (Lupien, McEwen, Gunnar, & Heim, 2009). To be favored by selection, the average net benefits of a plastic phenotype across possible environments must outweigh the benefits of a fixed phenotype across the same range of environments. Thus, to confirm a proposed adaptive value of plasticity, we would have to evaluate its fitness effects across all relevant environments and weigh these values by the likelihood to be in a given environment. This is obviously a challenging and daunting task.

Benefits of developmental plasticity can be reaped along a continuum of time scales. On the one end of this continuum, long delays may occur between the time a plastic adjustment is made and when its benefits become apparent. These delays can span different life history stages or even generations, if a phenotypic change is induced in parents that affects offspring (Burton & Metcalfe, 2014). Mechanisms that may have long delays include anticipatory plasticity, priming, and consolidation effects (Box 1). These adjustments are based on early environmental cues from parents or own experience, and they may prepare a developing individual to cope better with future conditions if these were correctly forecasted. If the current environment is a poor predictor of the future, an individual may be bound to live with a maladapted phenotype, however. Consequently, such life-long effects will only be selected for, if the future can be predicted with some reliability (Burgess & Marshall, 2014).

At the other end of the continuum, the current environment can favor the development of a certain phenotype that can cope well with the current, prevailing conditions early in life. If delays between a phenotypic change and its effect are immediate or short, benefits can be reaped with high certainty, as conditions are more likely to remain stable over short time periods. However, if the plastic changes become irreversible, a short period during which a

Box 1 Phenology of Long-Term Effects of Developmental Plasticity

Long-term effects of developmental plasticity refer to cases in which phenotypic changes are environmentally induced at some stage during ontogeny and the effects of this change persist into later life stages, sometimes lifelong.

Unconditional Effects

Current environment effects: the current or very recent environment induces an immediate phenotypic change, the effects of which remain present in later life.

Fitness: benefits take effect immediately or after short delay and are independent of later conditions; later in life fitness may be affected negatively, neutral or positively.

Example: invest in growth now, pay the cost for the investment in later life (Metcalf & Monaghan, 2001).

Carryover effects or silver-spoon effects: The quality of the parental or early environment carries over to the offspring or later-life environment, regardless of the quality of the latter.

Fitness: benefits take effect with long delay (across generations or life stages), which are independent of later-life conditions.

Example: Improved singing performance of grasshoppers when parents had been reared on high-quality diet (Franzke & Reinhold, 2013).

Maternal buffering, maternal capital hypothesis: Mothers may buffer offspring development from potentially inaccurate or harmful environmental influences; they may do this flexibly, by adjusting their behavior or because they can stabilize conditions because of a superior, long-term physiologic condition (Wells, 2012).

Fitness: Benefits depend on maternal phenotype and are independent of future conditions.

Example: Live-bearing, gravid females of the skink *Niveoscincus ocellatus* maintain higher body temperatures even when provided with shortened basking opportunities, thereby buffering their embryos from detrimental influences of reduced basking opportunities (Cadby, Jones, & Wapstra, 2014).

Conditional Delayed Effects

In all conditional delayed effects, benefits take effect with long delay (across generations or life stages), which do depend on later-life conditions.

Consolidation or cumulative information gathering: the information gained during an earlier developmental stage is only consolidated when in a later developmental stage a similar experience is made.

Fitness: Benefits take effect only if early and late environments are similar.

Example: early development and later consolidation of sexual preferences in zebra finches (Kruijt & Meeuwissen, 1993)

Priming or "conditioning hormesis": exposure to a low level of a stressor enables an individual to cope better with higher levels of the same stressor later in life (Costantini, Metcalfe, & Monaghan, 2010)

(Continued)

Box 1 Phenology of Long-Term Effects of Developmental Plasticity (*cont'd*)

Fitness: Benefits take effect only if early and late environments are similar.

Example: *Drosophila* exposed to small amounts of ethanol in early life survive better when consuming food with higher ethanol concentrations (e.g., from fermenting fruit) later in life (Holmes, Moxon, & Parsons, 1980)

Compensation: Later experience such as social support or high resource abundance may reduce the negative effects of early adverse experiences such as early stressors or resource shortage.

Fitness: Benefits take effect only if early and late environments differ and improve in quality.

Example: Compensatory growth (Mortensen & Damsgard, 1993)

Adaptive developmental plasticity

Environmental matching, External or Informational Predictive Adaptive Response (PAR): Information about the parental or early life conditions act as predictors for the offspring or later-life environment. If the prediction is correct, a phenotype matches its future environment. If the prediction is wrong, there will be a phenotypic mismatch

Fitness: Benefits take effect only if early and late environments are similar; fitness reduction, if early and late environments are dissimilar.

Example: Earwigs (*Forficula auricularia*) have a higher survival to adulthood if mothers and offspring receive the same good or poor diets than do corresponding offspring from mismatched feeding regimens (Raveh et al. 2016).

Internal or Somatic State-based PAR: The environmental input induces a change in state of the developing individual, which then develops a phenotype that can cope best with the altered state.

Fitness: Benefits depend on maternal or early phenotype, independent of future conditions.

Example: Bulb mites develop smaller bodies when growing up on low-food conditions and remain small as adults. Small individuals pursue alternative, nonaggressive behavioral tactics (scrambler) when competing for access to females (Smallegange, 2011)

Note that examples may belong to more than one of these forms of developmental plasticity. For instance, compensatory growth is a form of compensation, and as such, it is conditional on improving later-life conditions: If later conditions are rich, growth reduction can be compensated. However, growth compensation has negative consequences even later in life. From this perspective, a rapid compensatory growth rate in response to increased ambient food conditions can be viewed as current environment effect with negative long-term consequences.

phenotypic change is beneficial may be followed by a long period, during which the change is rather maladaptive (Ruuskanen et al., 2013). In this case, the short beneficial period of plasticity must outweigh all potential negative effects later in life to be selected for. Thus, regardless of whether we look at fitness effects of long or short time delays of plastic changes, we will have to consider all life stages of an individual.

The phenology of possible long-term effects of developmental plasticity is rather complex (see Box 1). Rigorous empirical tests for the adaptive value of most of the long-term effects reviewed in Box 1 are still scarce. Most research has focused on demonstrating the fitness benefits from anticipatory plasticity through environmental matching. Convincing examples for positive fitness effects of environmental matching do indeed exist. For instance, if seeds of the flower *Campanulastrum americana* germinate in the same habitat as their mother plant, they contribute to a higher population growth than do seeds germinating in a mismatching habitat (Galloway & Etterson, 2007). Earwigs (*Forficula auricularia*) survive more likely to adulthood if mothers and offspring were kept at matching good or poor diets than do the corresponding offspring from mismatched treatments (Raveh, Vogt, & Kölliker, 2016). Yet, a considerable number of experiments testing for environmental matching failed to detect evidence for anticipatory plasticity, but rather found support for silver-spoon effects (e.g., Franzke & Reinhold, 2013; Krause & Naguib, 2014), priming by poor conditions for an improved later performance (Giordano, Groothuis, & Tschirren, 2014), or effects of the current, but not the early condition (see Uller et al., 2013). A meta-analysis compiling 58 studies that performed full-factorial experiments by reciprocally varying maternal and offspring conditions found no overall significant adaptive effect of environmental matching (Uller et al., 2013). Interestingly, the same was true for silver-spoon effects (see Box 1), which are often assumed to be common. This gave rise to an intensive debate about the conditions favoring or limiting beneficial effects of developmental plasticity (Bateson, Gluckman, & Hanson, 2014; Hayward, Rickard, & Lummaa, 2013; Nettle & Bateson, 2015).

Why do experiments, on average (see Uller et al., 2013), fail to demonstrate fitness benefits from developmental plasticity? Failure may not necessarily reflect an absence of such benefits. It may rather result from inadequate study systems or approaches. First, most studies are performed in the laboratory, where fitness is notoriously hard to measure, because it is difficult to mimic the selective environment organisms are exposed to in nature. Second, there is a chronic lack of data about the

temporal dynamics of environmental parameters in natural habitats, such as the variability in space and time and predictability of selective forces of most of our model species (Burgess & Marshall, 2014; Uller et al., 2013). Third, for most model species, we lack a detailed understanding of the critical life stages and when and which combination of environmental triggers must be present to elicit an adaptive response. Thus, before we make claims about the possible adaptive value of a particular plastic change, it may be advisable to move one step backward and try first to get a better understanding of how organisms interact with the complexities of their environment during ontogeny.

1.3 An Overlooked Problem: Complexity of Natural Environments

Most experimental studies deliberately reduce the complexity of natural environments and of the considered life stages of their study organisms radically in favor of a tractable experimental design. This holds in particular for experiments with vertebrates, possibly because they have usually much higher space requirements than many invertebrates, which makes it logistically more demanding to provide seminatural conditions in the laboratory. Moreover, vertebrates often have very long generation times. Probably because of these constraints, the vast majority of controlled experiments with vertebrates to date varied only a single environmental factor and rarely observed effects of plasticity over the entire life time. Typically, a two-stage design is chosen. The environment is manipulated at a single early life stage such as the postnatal stage, parts or all of the juvenile stage, or the adolescent stage. Then, at a second, later stage the effect of this manipulation is measured in another set of experimentally controlled environments (see Groothuis & Taborsky, 2015 for review of designs). Single environmental factors that have been successfully manipulated with this approach in vertebrates include, among others, the early resource quality (Birkhead et al., 1999) or quantity (Barrett, Hunt, Moore, & Moore, 2009; Taborsky, 2006a,b), sibling competition (Bashey, 2008; Naguib, Riebel, Marzal, & Gil, 2004), hatching order (Gilby, Sorato, & Griffith, 2012), prenatal acoustic cues (Mariette & Buchanan, 2016), predation risk (Giesing, Suski, Warner, & Bell, 2011; McGhee, Pintor, Suhr, & Bell, 2012), prenatal (Guenther & Trillmich, 2013) and postnatal photoperiod (Finkemeier, Trillmich, & Guenther, 2016), social group size (Arnold & Taborsky, 2010; Fischer et al., 2015), the stability of the social environment (Kaiser, Kruijver, Swaab, & Sachser, 2003; Kaiser & Sachser, 2001), or a single prenatal hormone or

other egg components (McCormick, 1998; reviewed in Williams & Groothuis, 2015).

However, natural environments are multidimensional and complex. Multiple environmental factors can influence development either simultaneously or successively during multiple developmental periods. These phenotypic changes then can take effect at all following life stages in life (Fig. 1). Thus, in nature, organisms grow up under the influence of a multitude of environmental influences, which may act synergistically or antagonistically on phenotypic development (Chevin & Lande, 2015). If we aim to understand the development of integrated adult phenotypes, it seems only natural that we must take the complexity of all these influences into account (Kasumovic, 2013). Ignoring natural complexity in previous research occurred not necessarily, because researchers were unaware of its existence or importance, but rather for the sake of simplicity and tractability of experimental design and interpretation of results. The more environmental factors and life stages we consider, the more complex is the network of dependencies (Fig. 1), which will often result in highly complex reaction norms. Reaction norms with three-way or even higher-order interactions can hardly be understood intuitively. Nevertheless, it is essential that we aim to understand how organisms use and integrate multivariate cues of their environment (Dall, McNamara, & Leimar, 2015), as cue integration has a bearing on fitness (Leimar & McNamara, 2015; McNamara, Dall, Hammerstein, & Leimar, 2016).

Each of the environmental components can interact differently with the genetic background of individuals (gene-by-environment or $G \times E$

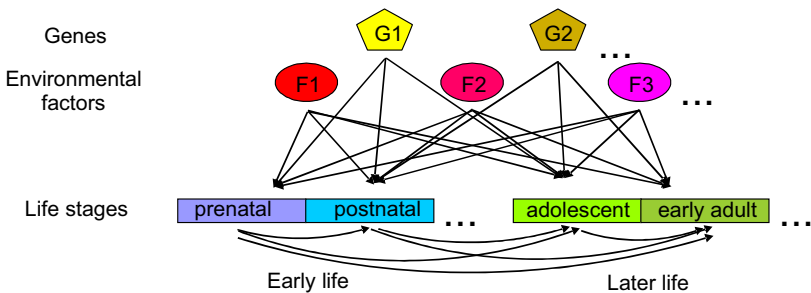


Figure 1 Simplified scheme of the interactions between genes, environment, and developing organisms. Genes and environmental factors interactively shape the development of the phenotype in all stages of ontogeny. Furthermore, plastic changes made in early life stages can influence the phenotype in all later stages.

interactions; Fig. 1). For instance, in the plant *Polygonum persicaria*, different genotypes exhibited different reaction norms in response to own and parental experiences of soil dryness. In different genotypes, evidence for adaptive matching, silver spoon effects, or a combination of both occurred (Herman et al., 2012). In moor frogs (*Rana arvalis*) the investment in anti-predator defenses depended on a match or mismatch of the water acidity level between the habitat of origin and the current environment. Moreover, when the conditions deviated from the population of origin, tadpoles suffered from developmental costs (Teplitsky, Rasanen, & Laurila, 2007). In the biomedical literature, several allelic polymorphisms have been identified, in which one of the genetic variants is linked to a disposition for certain mental diseases (“vulnerability genes” with “risk alleles”). Prominent examples include monoamine oxidase-A, 5-hydroxytryptamine-linked polymorphic region, and the dopamine receptor D4. More recently, it turned out that human carriers of the “vulnerable” mutant variant may express a disease or impaired behavioral performance only if an individual experienced adverse early life conditions. However, if the same genotype experienced supportive early conditions, they could even outperform the “normal” variants in some tasks (Belsky et al., 2009). Similar effects were also reported in 5-HTT knockout mice, which showed reduced anxiety compared with wild-type mice after experiencing positive social stimulation (Kästner et al., 2015). These reports led to a paradigm shift from viewing the former “vulnerability genes” as putative plasticity genes, which may explain why these gene variants were maintained over evolutionary times.

Finally, the understanding of the adaptive value of plasticity is further complicated if several parties with conflicting interests are involved. Nongenetic parental effects are part of the early environmental conditions experienced by young, but they may also represent a strategic decision by parents. Interests of parents and offspring, for instance, over provisioning, may very well diverge and give rise to conflict between these parties (Marshall & Uller, 2007). Maladaptive effects from the viewpoint of offspring may still maximize the fitness of parents. Parents may not have the full control of how offspring deal with the “program” imposed on them through parental provisioning, however. Thus, offspring may be able to overturn parental effects based on own experience made during their development (e.g., Fischer et al., 2015).

To date, developmental experiments allowing for more complex rearing environments have been mostly performed in nonvertebrates with a rather short generation time (e.g., Bryozoans, planktonic crustaceans, mites, certain

insects, plants, or bacteria). In these species, the delay between an environmental cue and its phenotypic effect is usually short, and therefore, the reliability of a cue is often high (e.g., [Burgess et al., 2011](#)). In contrast, in long-lived vertebrates with long generation times the value of environmental cues to predict the future is less trivial. In the past decade, we have studied plastic changes induced during multiple life stages and by multiple ecological variables in a group of long-lived vertebrates, the cichlid fish of Lake Tanganyika. During the same time, there was a surge of theoretical models incorporating features of natural complexity into models of developmental plasticity such as time patterns of repeated sampling, information updating, and phenotypic adjustment (reviewed in [Stamps & Frankenhuis, 2016](#)) or the integration of multiple cues into developmental decisions ([Leimar, Hammerstein, & Van Dooren, 2006](#); [Leimar & McNamara, 2015](#); [McNamara et al., 2016](#)). Here I review the main theoretical insights from these models and contrast them with insights from the work on cichlid fish and other long-lived vertebrates, to illustrate how incorporating natural levels of complexity can improve our understanding of the development of integrated phenotypes. After a general introduction into theoretical and experimental approaches to the study of developmental plasticity, I shall deal with two main questions: (1) When should environmental information influencing development be obtained and when is this information beneficial? (2) How is information obtained during multiple life stages or from multiple environmental parameters integrated during phenotypic development?



2. APPROACHES TO THE STUDY OF DEVELOPMENTAL PLASTICITY

2.1 Theoretical Approaches

Models of the evolution of developmental plasticity require at least three ingredients; a sensitive phase, during which organisms are exposed to environmental cues, a period where a plastic response can occur, and a phase when the produced phenotype is evaluated by selection. As highlighted by [Frankenhuis and Panchanathan \(2011\)](#), most previous models on adaptive plasticity assumed that these ingredients occur only once in a lifetime. Thus, many earlier theoretical studies on developmental plasticity suffered from a similarly simplified approach than do many experimental studies. More realistic evolutionary models of developmental plasticity should allow for repeated sampling of the environment at different stages

of ontogeny (e.g., prenatal, early postnatal, and adolescent stages) with the possibility to receive conflicting information at these stages and to adjust the phenotype repeatedly allowing organisms to partly or fully reverse previous decisions and the possibility to sample and integrate information from a variety of different cues. Moreover, they should explicitly include the dynamics of environmental heterogeneity and autocorrelation.

As a first step toward this aim, [Fischer, Taborsky, and Kokko \(2011\)](#) modeled the evolution of maternal effects on egg size in stochastically fluctuating environments (transgenerational plasticity). Juvenile and adult environments were assumed to be autocorrelated, and the influence of the degree of autocorrelation was investigated. The optimal degree of egg size plasticity in this model turned out to be a function of the quality of available information: The more reliable the information about the environment was, the more plastic egg size, and consequently, offspring quality was. Conversely, if information about future conditions was absent, females produced a fixed, average egg size.

Another step toward more biological realism was taken by a model by [Gabriel, Luttbeg, Sih, and Tollrian \(2005\)](#), which considered the option of reversible plasticity in fluctuating environments. A plastic response was modeled that allowed previously induced predator-defense structures to be reduced again, with some time lag, after predation risk had vanished. In addition to the reliability of environmental information, the model investigated explicitly the role of response lags of different lengths, which helped organisms to avoid overly quick responses toward incomplete or unreliable environmental information. If response lags were short or the environmental information was reliable, reversible phenotypic plasticity readily evolved and the phenotypes closely tracked the state of the environment. However, if environmental information was incomplete or time lags were long, model organisms adopted a canalized generalist strategy that could cope with a broad range of environmental states, thereby avoiding costs of plasticity.

A more recent modeling approach investigates how developing individuals should integrate information from multiple sources when building an adapted phenotype ([English, Fawcett, Higginson, Trimmer, & Uller, 2016](#); [Leimar et al., 2006](#); [Leimar & McNamara, 2015](#); [McNamara et al., 2016](#)). A first model considered the decision to use cues obtained either from observing the ambient environment (detection-based effects) or from the own genes (selection-based effects; cf. [Shea, Pen, & Uller, 2011](#)); as in spatially heterogeneous environments allele frequencies vary between sites because of local adaptation, genes can act as cues informing about the selective conditions

experienced by past generations (Leimar et al., 2006). This approach was extended to the integration of own juvenile and adult, maternal, grand-maternal, and genetic cues (Leimar & McNamara, 2015; McNamara et al., 2016). It assumes that after collecting cues from all available information sources, a developmental system integrates these cues by assigning different, evolving weights to these cues. The developmental system decides about the phenotype at a single time point by combining the information from all cues according to their weights.

Finally, a set of models was developed, which aims to capture the incremental process by which organisms sample the environment and make phenotypic decisions during development. In these models, individuals can sample their environment repeatedly at a number of given time steps, update their information state, and adapt their phenotype stepwise to the obtained information (English et al., 2016; Fischer, van Doorn, Dieckmann, & Taborsky, 2014; Frankenhuis & Panchanathan, 2011; Panchanathan & Frankenhuis, 2016; Stamps & Krishnan, 2014). These recent models use Bayesian updating to model optimal, incremental developmental trajectories, as Bayes theorem provides a “logically consistent way to combine probabilistic information from different sources at different times” (Stamps & Frankenhuis, 2016).

2.2 Experimental Approaches

The body of experimental research studying the function of long-term developmental effects induced by own early experience or the maternal or paternal phenotype (nongenetic parental effects) has grown dramatically over the past decades. This research effort was not the least spawned by the seminal book of Mary-Jane West-Eberhard (2003) raising interest in the reciprocal relationship between evolution and development and the book by Mousseau and Fox (1998) on the adaptive value of maternal effects. Adaptive explanations of maternal effects focus mainly on maternal programming of offspring to cope with future conditions (anticipatory maternal effects, Marshall & Uller, 2007) and to a lesser extent, on “selfish maternal effects” (Marshall & Uller, 2007), which compromise offspring fitness to the benefit of maternal fitness. More recently the interest in paternal effects and their potential role for causing intersexual conflict is rising rapidly (Crean & Bonduriansky, 2014).

2.2.1 Experimental Designs

The strongest inference on the form of developmental plasticity we see in a given trait can be drawn from full-factorial experiments, where

early and late environments are manipulated reciprocally (Fig. 2A, reviewed in Monaghan, 2008; Uller et al., 2013). Ideally, early (or parental) and late (or offspring) environments are varied such that half of the experimental individuals are kept under identical conditions early and later in life, and the other half is switched to the opposite, nonmatching environments for the later-life treatment. This design allows distinguishing between environmental matching with interacting effects of early and late environments from additive effects such as carryover or silver spoon effects.

For the study of behavioral traits, a different reciprocal design is often used. With this design we can test whether in different early environments animals develop different behavioral skills, from which they benefit when early and later-life conditions match. The potential benefits from these skills can be detected by setting up environmental contexts during later life that resemble the rearing contexts and elicit the expression of the focal behaviors (Fig. 2B, see also Groothuis & Taborsky, 2015). In this design, after being reared in different early environments, animals are typically kept under identical, “neutral” conditions until testing. For example, context-dependent benefits of the expression of social behavior in matching social contexts were demonstrated in zebra finches (*Taeniopygia guttata*; Ruploh, Bischof, & von Engelhardt, 2013, 2014). In this study, male birds were kept either in pairs or in groups during adolescence (early environment) and were exposed as adults (late environment) either to females only (pair-context) or to mixed-sex groups (group context).

Finally, a third design which is often used in behavioral and biomedical research has rather limited inferential power to distinguish the forms of

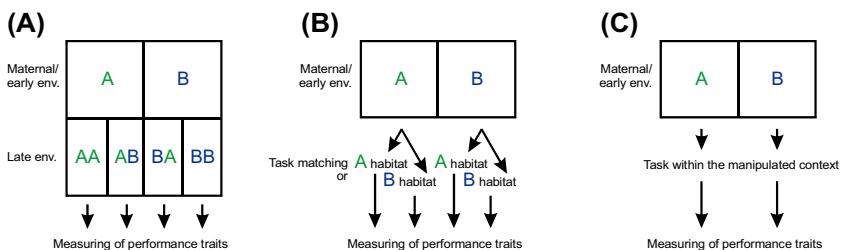


Figure 2 (A) Full-factorial developmental experiment, in which early and late environments are manipulated reciprocally. (B) The early environment is manipulated, and later in life experimental animals are tested in context-specific performance tasks. (C) The early environment is manipulated, but later in life animals are tested only in performance tasks specific for one environmental condition.

plasticity. It is particularly suited, however, to “ask” test animals, which specific abilities they have acquired during early life. As in the designs above, animals are first reared under two divergent early (or parental) conditions, but in later life they are tested in contexts that are either independent of the rearing environments or relate only to one of the rearing contexts (Fig. 2C). In these designs, during the later-life test phase, animals are often exposed to an entire series of different challenges, each asking to reveal a specific skill (reviewed in [B. Taborsky, 2016](#) for the social context).

Full-factorial experiments seem imperative if we aim to understand how animals integrate cues from multiple sources to make plastic decisions, as they allow us to detect the precise contribution of each factor to a plastic change. The classical approach of such factorial experiments varies only two levels per factor. This approach prevents the detection of nonlinear reaction norms, however (e.g., see [Herczeg, Ab Ghani, & Merila, 2016](#) for an example with three levels of social conditions). Limits to the full-factorial approach are set, however, by the number of treatments we can handle and maintain in the laboratory (for instance, three factors varied by two levels result in eight treatments, and if varied by three levels it would be already 27 treatments) and the complexity of resulting reaction norms, which become increasingly difficult to interpret (e.g., [Alekssev & Lampert, 2001](#); [Hopwood, Moore, & Royle, 2014](#)).

2.2.2 Fitness

Most experiments on developmental plasticity require keeping animals from beginning of life to the later-life target stage under fully controlled conditions and therefore the great majority of these experiments are done in the laboratory. This highlights a potential problem: If environmental conditions simulated in laboratory experiments are not biologically relevant, we cannot study evolutionary-relevant reaction norms. Therefore, the traits of interest and the conditions in which they are studied must reflect the action of selection in nature, which means the traits should be relevant for fitness in nature and the environmental manipulations should be performed within a natural range of environmental variation ([Groothuis & Taborsky, 2015](#)). This means that we have to select the traits serving as fitness proxies with the utmost care. One way to pursue is to first confirm that our focal fitness correlate we want to measure in the laboratory significantly affects the fitness of our study species in its natural environment. For instance, fast growth is often a priori assumed to be beneficial. However, the optimal solution to the trade-off between growth and other costly traits, such as

increased mortality rates or reduced reproductive rates, may even favor growth reduction (Arendt, 1997; Gotthard, 2000).

As in experiments we usually measure an array of different traits, we will often encounter a situation where several, potentially fitness-relevant traits change in response to variation of the early environment. In principle, all these, some or none might be the ones driving differences in fitness. To illustrate this by an example, manipulation of the incubation temperature in the skink *Bassiana duperreyi* influenced its size, speed, and learning ability (Amiel, Lindstrom, & Shine, 2014), three performance traits with a potential strong link to fitness. Which of these traits, if any, is responsible for effects of incubation temperature on survival? A suitable, albeit work-intensive, solution to this question is to manipulate each of these “candidate traits” in separate experiments and to test which of them is a strong predictor of survival (B. Taborsky, 2016).

2.3 Constraints of Developmental Plasticity

To achieve a comprehensive understanding about the evolution of developmental plasticity, we must also understand how the machinery works that produces plastic responses. Only by knowing about the functioning of this machinery and its limits and degrees of freedom we can start to predict avenues evolution of plasticity can take. This means, we should aim to understand the role of “constraints” of developmental plasticity. Constraints are usually equaled with what is *not* possible. However, in turn they should rather be viewed as the set of possibilities for evolution and for developmental plasticity.

For instance, hormonal control systems have been suspected to represent important evolutionary inertia (Adkins-Regan, 2008), because hormones pleiotropically affect different tissues. However, when considering entire hormonal regulatory systems including ligands *and* receptors, it becomes clear that hormone systems can act in highly specific ways and therefore pleiotropy does not necessarily represent a constraint. For instance, hormone receptors are expressed in tissue-specific and context-specific densities and therefore can simultaneously affect different tissues, in which they can kick off different molecular cascades. Moreover, many hormones, such as cortisol, bind to different receptors with different binding efficiency even in the same tissue. For instance, during a mammalian stress response a surge of corticosteroids (CORT) is elicited which binds to two receptors in the brain. The mineralocorticoid receptor, which is highly sensitive to corticosterone, is involved in the onset of the stress response. The glucocorticoid

receptor (GR), which is only activated by larger amounts of CORT, feeds back negatively on further CORT release and thereby aids to terminate the stress response and facilitates recovery. Hormonal control systems are important for our understanding of developmental plasticity as they are permanently modulated by interactions with extrinsic factors (e.g., Dawson, 2008).

Another important potential source of evolutionary inertia that may limit the evolution of plasticity is genetic architecture. Genetic costs may potentially emerge from linkage, pleiotropy, or epistasis (Auld et al., 2010; DeWitt et al., 1998). Plasticity of a trait is often positively or negatively correlated to the trait mean (reviewed in Auld et al., 2010). If these correlations are genetic, plasticity of a trait cannot evolve independently of the trait itself.

Finally, the evolution of plasticity can be constrained by phylogenetic history. For instance, many hormone receptors and their ligands are deeply conserved among vertebrates (O'Connell & Hofmann, 2011, 2012). Nevertheless, the distribution of neuroendocrine ligands in different vertebrate brain regions is more flexible than that of their receptors, suggesting that some brain regions underwent different selection pressures (O'Connell & Hofmann, 2012). Despite considerable advances in the current “omics” era in uncovering some aspects of particular developmental control mechanisms in great detail, we are far from understanding the developmental machinery comprehensively, let alone the processes involved in producing plastic responses.

2.4 Lake Tanganyika Cichlids as Model System

A suitable model organism for the study of developmental plasticity in an ecologically relevant framework should fulfill at least two major requirements: (1) It must be possible to study its ecology in sufficient detail. (2) The organism can be experimentally manipulated in the field. (3) The organisms can be kept, bred, and manipulated under controlled laboratory conditions, where it displays its natural behavior and reproductive activities. Among long-lived vertebrates, cichlid fish fulfill these conditions in an almost ideal way. Many cichlid fish are territorial or have stable home ranges and can therefore be followed individually over years in their natural habitat (Jungwirth & Taborsky, 2015). They can be easily observed and experimentally manipulated in the field (e.g., Fischer, Zoetl, Groenewoud, & Taborsky, 2014; Jungwirth, Josi, Walker, & Taborsky, 2015; Taborsky, Guyer, & Demus, 2014). Small cichlid species can be easily brought to the laboratory and bred successfully. They also readily tolerate and habituate to handling

and manipulations, and they show the full range of natural social and reproductive behaviors in the laboratory. This makes them highly suited for life history and behavioral research, involving experiments both in the laboratory and in the field.

With the current rise of integrative approaches to the study of behavior, genomic resources also become increasingly available. The genomes of five cichlids were now published (Brawand et al., 2014), among them the genome of *Neolamprologus pulcher*, which has turned into an important model species for the study of developmental plasticity (see Section 2.4.2). Efficient methods for physiologic monitoring have been developed for cichlids, including hormone sampling (Mileva et al., 2009; Scott et al., 2008), energy expenditure (Grantner & Taborsky, 1998), noninvasive measurement of body reserves (Kotrschal, Fischer, & Taborsky, 2011), and digestive efficiency (Kotrschal, Szidat, & Taborsky, 2014).

We have used two main cichlid models endemic to the East-African Lake Tanganyika to study developmental plasticity: In mouthbrooding cichlids (*Simochromis pleurospilus* and *Eretmodus cyanostictus*), early-life effects on life history strategies and predator evasion abilities were studied. In the highly social, cooperatively breeding cichlid *N. pulcher* the effects of early experience on social behavior, the specialization for social trajectories, and underlying molecular mechanisms of these effects were targeted.

2.4.1 Mouthbrooding Cichlids

Mouthbrooders have a number of highly convenient features for studying early-life effects on life history strategies. As in most mouthbrooding cichlids, females of *S. pleurospilus* breed year-round and perform all parental care. The contribution of males to reproductive effort is restricted to the defense of small courtship territories contributing to the nutrition of females shortly before spawning (Kotrschal & Taborsky, 2010a). Females invest heavily in each brood. They produce up to 30 large, energy-rich eggs, and they carry the brood for about 2 weeks continuously in their buccal cavity during which they do not feed. During the next 2 weeks, juveniles are periodically released allowing offspring and mother to take up some food. All major components of reproductive investment, such as reproductive rates, energy investment per single offspring, offspring number and investment in brood care, and the central life history trade-offs between reproduction and growth and between offspring size versus number are well quantifiable. Thus, *S. pleurospilus* offer the opportunity to study entire life histories of a long-lived vertebrate in a reasonable time in the laboratory.

Their generation time is about 1 year, and their reproductive life span is 2–3 years (Taborsky, 2006a).

Importantly, for the evolution of developmental plasticity in this species, the habitat of *S. pleurospilus* is characterized by high temporal stability over the year, but spatial heterogeneity within and between populations (Kotschal, Heckel, Bonfils, & Taborsky, 2012). Adults live in deeper water than juveniles and in a broader depth range (mostly 1.0–4.0 m) of the lake. Juveniles are almost exclusively found in shallow water in the uppermost depth meter. Most likely, juveniles are released by their mothers at independence of care in deep water and move actively to the shallow habitat by themselves.

2.4.2 Substrate Brooding, Cooperative Cichlids

Several species of the only substrate-brooding lineage of Lake Tanganyika cichlids, the lamprologine cichlids, exhibit an extraordinary degree of sociality and cooperative breeding (Heg & Bachar, 2006; Taborsky, 1994). Within this cichlid subfamily, the social system and ecology of *N. pulcher*, the “Princess of Lake Tangayika,” has been studied most intensively (M. Taborsky, 2016; Wong & Balshine, 2011). It shares certain features with cooperatively breeding mammalian societies, including humans, such as alloparental care, division of labor, kin recognition, help among kin and nonkin, individualized relationships, and a graded repertoire of aggressive, submissive, and affiliative social behaviors. *N. pulcher* defend group territories holding social groups consisting of a breeder pair and 1–25 subordinate group members. Helpers participate in territory defense against predators and space competitors, territory maintenance, and direct alloparental brood care of eggs and larvae (Taborsky & Limberger, 1981).

The evolution of the complex social system of *N. pulcher* is driven by an extraordinarily strong predation pressure (e.g., Brouwer, Heg, & Taborsky, 2005; Groenewoud et al., 2016), requiring elaborate social and predator avoidance competences (Hess, Fischer, & Taborsky, 2016; Fischer, 2014; Taborsky, Arnold, Junker, & Tschopp, 2012). All juveniles first stay at the natal territory and act as brood care helpers (Taborsky, 1984). After maturation they may disperse (Stiver, Dierkes, Taborsky, & Balshine, 2004). Many subordinates delay dispersal, however, and stay at the natal territory long after maturation (Dierkes, Heg, Taborsky, Skubic, & Achmann, 2005; Taborsky, 1984) to benefit from the protection from predators provided by the group. Helpers may be related or unrelated to the current breeders and the latter’s offspring (Stiver, Dierkes, Taborsky, Gibbs, & Balshine, 2005), as breeders are frequently exchanged because of predation (Dierkes et al., 2005). To

avoid eviction from the territory, all group members contribute to alloparental care and territory defense at least to some degree (Balshine-Earn, Neat, Reid, & Taborsky, 1998; S. Fischer et al., 2014).

The social and ecological environment of *N. pulcher* is temporally and spatially stable as long as the fish stay in their natal territory (i.e., before dispersal). Group sizes are highly auto-correlated across years (Heg, Brouwer, Bachar, & Taborsky, 2005). Predation risk differs between populations (Groenewoud et al., 2016), but is most likely stable within populations.



3. WHEN SHOULD INFORMATION BE SAMPLED AND WHEN DOES IT TAKE EFFECT?

3.1 Theory

In Bayesian models, two processes are modeled: individuals repeatedly perceive and update information from their environment and they stepwise build their phenotypes. Sampling and phenotypic change (1) were modeled as independent processes (B. Fischer et al., 2014; Panchanathan & Frankenhuis, 2016), where at each time point the environment is sampled and a phenotypic adjustment can optionally be made at the same time; (2) they were assumed to be coupled, e.g., when finding food both provides information about resources availability at a location and enhances growth (English et al., 2016); or (3) they were explicitly assumed to exclude each other so that time needed for sampling and time needed for phenotypic change have to be traded off against each other (Frankenhuis & Panchanathan, 2011). Under all three scenarios, the models identified periods of higher or lower plasticity during ontogeny, referred to as “sensitive periods.”

The models differ in their outcome depending on whether they consider stable or fluctuating environments, however. Models assuming stable environments predict that plasticity declines monotonously with age. By repeatedly sampling stable environments, the degree of certainty about the real state of the environment steadily increases, and thereby, the value of collecting further information by sampling decreases (Stamps & Krishnan, 2014; Frankenhuis & Panchanathan, 2011; Fawcett & Frankenhuis, 2015) even in the absence of any plasticity costs (English et al., 2016; Panchanathan & Frankenhuis, 2016). Therefore plasticity should decline with age, and it should do so even faster the more informative the cues are.

The only model to date exploring age-dependent plasticity in stochastically fluctuating, autocorrelated environments predicted that in a large part of the parameter space plasticity changes in a nonmonotonous way over life time (B. Fischer et al., 2014). In most model environments, plasticity had a first peak early in life after individuals had accumulated sufficiently sampled the environment to make an informed phenotypic change. Then, after a period of reduced plasticity, a second, broader peak of plasticity followed in response to the environmental changes encountered later in life. Toward the end of life, plastic changes occurred rarely, as the costs for such phenotypic rearrangements are unlikely to pay off before death. The possibility of organisms to update their belief about the environmental state after sampling seems to be a critical condition for optimal plasticity to vary with age. Models allowing repeated, optimal resource allocation during life time in stochastic, autocorrelated environments, but were lacking the possibility to update the belief about the environmental state, produced reaction norms of optimal plasticity, which depended on environmental variability and predictability but not on age (Fischer, Dieckmann, & Taborsky, 2011; Fischer, Taborsky, & Dieckmann, 2009).

3.2 Experimental Studies

In the modeling work described above, the information from previous generations is treated as prior information present before the first updating occurs, that is, before juveniles make their first own observation. In experiments involving two generations, sampling of the environment (by parents) and phenotypic construction (by offspring) are two separate processes. Therefore, in empirical studies we can explicitly study the temporal relationship between the parental “prior” and its effect in offspring. The timing *when* parents should sample the environment and when this parental information is actually *beneficial* for the offspring should depend on the predictive power of environmental cues.

3.2.1 When Should Parents Sample the Environment?

The reliability of environmental cues to predict future conditions is central in the discussion about the function of parental and early-environment effects. As the predictive power of such cues often decreases steadily over time, most parental and early-environment effects take effect after short time delays, and they may vanish entirely after a limited time window (Lindholm, Hunt, & Brooks, 2006). Frequently, maternal effects are induced

by the prevailing conditions during egg maturation (Giesing et al., 2011; Fox, Thakar, & Mousseau, 1997; Taborsky, Skubic, & Bruintjes, 2007; Tschirren, Richner, & Schwabl, 2004). Also after birth, offspring development is influenced by cues from the ambient environment often with immediate effect on their behavior (reviewed for social behavior in B. Taborsky 2016). Therefore, it may appear counterintuitive that in a number of species, environmental information, which was obtained by parents when they were still juveniles (i.e., long before they started to produce offspring), shaped adaptive parental effects on their eggs or embryos (reviewed in Burton & Metcalfe, 2014). If at all one should expect that a transmission of effects from the parental early-life to offspring early-life occurs only in short-lived organisms, in which the probability that parental early-life cues may reliably predict offspring conditions is still reasonably high. For instance, fruit fly offspring raised on poor food underwent a shorter development only when their parents also had been raised on poor food during the larval stage (Vijendravarma, Narasimha, & Kawecki, 2010). Nevertheless, environmental manipulations performed during the ontogeny of the parental generations affects the phenotype of the F1 generation via parental effects in a number of long-lived fish, birds, and mammals (reviewed in Burton & Metcalfe, 2014).

Even in long-lived species, effects of the parental developmental environment on the next generation may be adaptive, if environments are temporally stable. If in addition the habitat is spatially heterogeneous, and juveniles and adults inhabit different spatial niches, parental effects informed by the parental developmental environment may predict the conditions offspring will face better than do the conditions parents experience *during* egg production (Kotrschal et al., 2012). In the mouthbrooder *S. pleurospilus*, adults and juveniles occupy different niches in the depth gradient of Lake Tanganyika (Taborsky, 1999). In the laboratory, females raised as juveniles in low-food conditions produced larger offspring than females raised without food limitations, irrespective of the feeding conditions females experienced during adulthood (Taborsky, 2006b). These results suggest that females give their offspring a head start to endow them for similar environmental conditions as they had encountered themselves during early development. As the feeding ecologies of juveniles and adults differ in this species (Kotrschal et al., 2012), the feeding conditions mothers experienced as juveniles may better predict their offspring's environment than does food availability to adult females during egg production. If this explanation of cross-generational early-life effects holds for *S. pleurospilus*, three conditions

must be fulfilled: (1) the adult ecology should not predict the juvenile ecology of offspring, but (2) the environmental conditions are correlated, and hence predictable, across successive juvenile generations. Moreover, (3) juvenile habitats of different quality must exist, to which offspring may potentially disperse after reaching independence of maternal care. If all juveniles would always end up in exactly the same conditions, a parental strategy of a genetically fixed egg size should fare better than egg size plasticity. Size-structured population counts combined with ecological surveys and a genetic analysis of population structure revealed that all three conditions hold in *S. pleurospilus* (Kotrschal et al., 2012).

When juveniles and adults share the same, temporally stable habitat, the potential benefit of a cross-generational transmission of early-life effects is less intuitive. Nevertheless, this is what happens in another mouthbrooding cichlid, *E. cyanostictus*. When young of this species were repeatedly confronted with an offspring predator during the first months of their juvenile period, these fish produced larger eggs as adults than did fish which were not exposed to an offspring predator (Segers & Taborsky, 2012a). This increase in egg size cannot result from an immediate stress response (Giesing et al., 2011), because the offspring predator presented to the juveniles was too small to pose life-threatening risk to the focal fish and because egg-laying occurred 6 months after the predator treatment had ended. Egg mass is a good predictor of offspring size in cichlids (Segers & Taborsky, 2011), and larger cichlid offspring perform better in predator escape responses (Schürch & Taborsky, 2005). Thus, producing larger eggs after exposure to an offspring predator may represent an adaptive response. However, in contrast to *S. pleurospilus*, in *E. cyanostictus* no habitat shift occurs from the juvenile to the adult stage. Instead, juveniles and adults share the same habitat of the upper 0.5 to 4 depth meters of Lake Tanganyika (Sturmbauer et al., 2008). Therefore, there is no straightforward reason to assume fitness benefits arising from this parental early-environment effect. Because the environment is stable over time, it is possible that females collect the first cues of predator presence already as juveniles. They may then update and adapt and possibly even reverse the effects of early experience, if their adult environment provides conflicting cues.

3.2.2 When do Parental Effects Take Effect?

To understand the fitness benefits gained by offspring from adaptive parental effects, we need to know when during ontogeny a parental effect is beneficial for offspring, and when it is potentially harmful. Individuals can benefit

from a parental effect, if the conditions forecasted by parents still apply when offspring are born (Bateson et al., 2004; Nettle, Frankenhuys, & Rickard, 2013).

In cichlids, which have indeterminate growth like most fish, many behavioral and life history decisions depend on body size. In particular, predation risk is negatively size dependent, as their most important predators, piscivorous fish, are gape-size limited (Sogard, 1997). Thus, predation risk is by far the greatest right after birth. Theory predicts that in a size-structured predator community, even smallest size increments may result in largely enhanced survival chances (Taborsky, Dieckmann, & Heino, 2003; Taborsky, Heino, & Dieckmann, 2012), which is supported empirically by escape performance tests (Schürch & Taborsky, 2005). In *S. pleurospilus*, it seems that an early size advantage of offspring is maintained only during a short period after birth (Stratmann & Taborsky, 2014). When parents of this species were kept together either with a natural offspring predator or similar-sized benign, herbivorous cichlid until spawning, offspring of predator-exposed parents grew faster during the first month of life than did offspring of herbivore-exposed parents. During the first 4 weeks, young are most vulnerable to predation, in particular during periods when mothers release their young from the mouth for external foraging, so that any size advantage during this period should be highly beneficial. After achieving a size when young cannot be predated easily anymore, maintaining accelerated growth rates should no longer be beneficial. Indeed, during the second month of life, offspring of predator-exposed parents grew significantly slower than did offspring from the herbivore-exposed parents, possibly to compensate for the higher costs they had to pay for accelerating growth in the first months. After achieving full compensation, all juvenile offspring grew at the same rate (Fig. 3).

In the above example, eggs were “hand-reared” in an incubator, and they did not differ in size between parental treatments. Therefore, the initial growth spurt of young from predator-exposed parents must be because of some change in egg composition. Alternatively, mouthbrooding cichlids can also employ behavioral mechanisms to prepare their offspring for increased mortality risk after independence. For instance, the cichlid *Ctenochromis horei* prolonged its mouthbrooding care period in the presence of a dangerous offspring predator resulting in larger offspring sizes at the time of independence from care (Taborsky & Foerster, 2004). The cichlid *Tropheus moori* achieves a larger offspring size by feeding its young in the buccal cavity while mouthbrooding (Schürch & Taborsky, 2005).

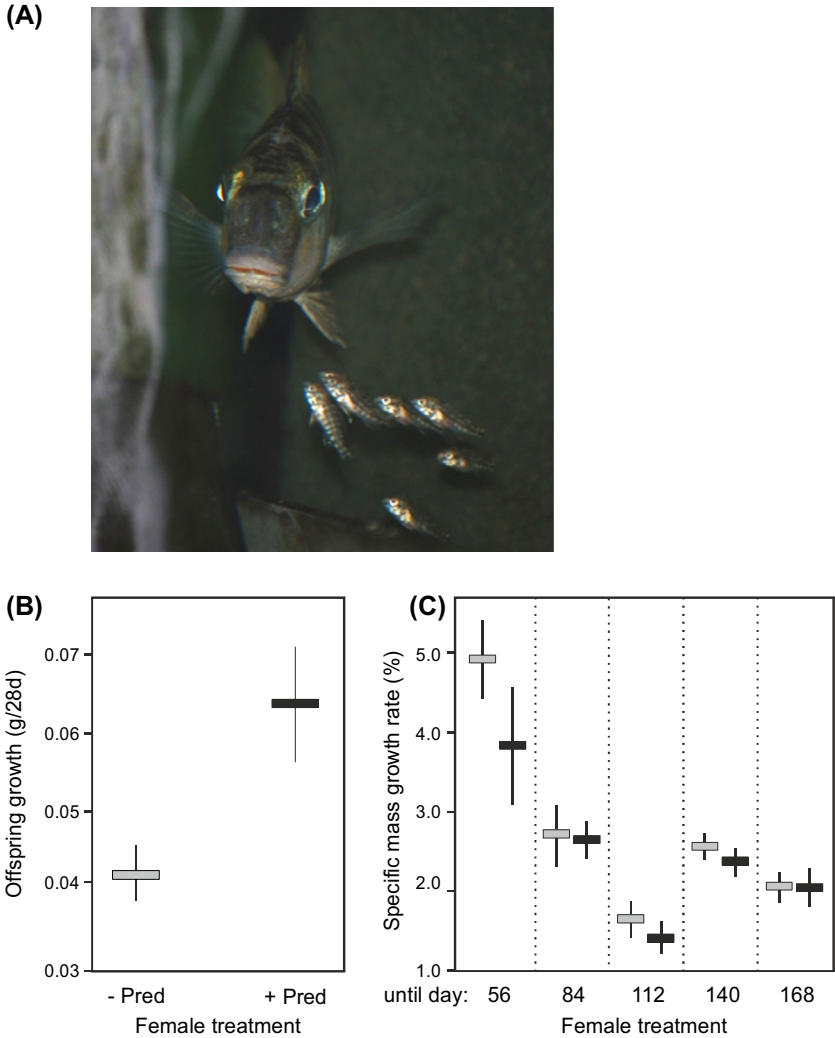


Figure 3 (A) Female *Simochromis pleurospilus* shortly before taking up her brood into the buccal cavity after a disturbance; (B) individual larval mass increase (weight at an age of 28 days minus egg weight) when the mother was exposed to an offspring predator (black bar) or to a harmless herbivore (gray bar) before spawning; (C) specific growth rate of juveniles after day 28 [bars as in (B); means and SE shown]. Modified after Stratmann, A., & Taborsky, B. (2014). Antipredator defences of young are independently determined by genetic inheritance, maternal effects and own early experience in mouthbrooding cichlids. *Functional Ecology*, 28, 944–953.

When parental effects, which have only a limited, early beneficial period, cannot be compensated for, long-term costs of these effects may arise. This was documented in a long-term laboratory and field experiment on pied flycatchers (*Ficedula hypoleuca*) by Ruuskanen and colleagues. A maternal effect on egg yolk composition was mimicked by injecting eggs with androgens. Enhanced yolk androgen is known to enhance the competitive abilities of bird chicks during the nestling period (Groothuis, Muller, von Engelhardt, Carere, & Eising, 2005). Indeed, flycatcher nestlings from the androgen treatment had higher begging rates and an improved digestive efficiency (Ruuskanen & Laaksonen, 2013) compared with a control group. However, they paid substantial later-life costs for this early competitive advantage. They were smaller, males had lower return rates from the first migration (Ruuskanen, Doligez, Pitala, Gustafsson, & Laaksonen, 2012), and adults had higher basal metabolic rates (Ruuskanen et al., 2013), which is known to increase daily energy expenditure. Recently, an experimental study in rock pigeons (*Columba livia livia*) demonstrated suppressive effects of egg androgen supplementation in adults even beyond the first year of life. Pigeons of all age classes between 1 and 3 years laid lighter eggs when they had hatched from androgen-supplemented eggs. Interestingly, adult male pigeons were less aggressive, which runs opposite to the naive expectation that higher early androgen levels should enhance aggressiveness (Hsu, Dijkstra, & Groothuis, 2016). These studies clearly demonstrate that it is not sufficient to demonstrate fitness benefits during a short, early period of a parental or early-environment effect, but that we need to show that a particular effect has net fitness benefits over the entire life span.

Enhanced androgen levels may also be produced by offspring, independent of egg yolk hormone provisioning, in response to selfish maternal effects that increase maternal fitness at the cost offspring performance (Marshall & Uller, 2007). Mothers producing enlarged clutch sizes impose higher levels of among-sibling competition for food on their offspring. This maternal effect was mimicked by experimental clutch size manipulation in zebra finches. Naguib et al. (2004) compared the performance of nestlings raised in experimentally composed small, medium, or large broods. Experimental clutch size was positively associated with plasma androgen levels of chicks, which is assumed to be an adaptation to high competition (see above). However, a suite of morphologic, physiologic, and life history traits was negatively related to increasing clutch size, with carryover effect even to the next generation. Offspring from large broods grew more slowly, attained smaller adults sizes and had an impaired immune function and a lower body

condition (Naguib et al., 2004). Daughters of mothers from large broods were also smaller and suffered from a reduced reproductive success (Naguib et al., 2006). These results suggest that mothers producing large clutches in nature would compromise the fitness of their offspring and grand-offspring, at least in the absence of any further, egg-mediated maternal effect, which were excluded by experimental design in this study.



4. INTEGRATION OF ENVIRONMENTAL INFORMATION

4.1 Theory

The modeling approach developed by Leimar et al. (2006), Leimar and McNamara (2015), and McNamara et al. (2016) assumes that a developmental “switch” exists, which integrates cues obtained from different information sources by assigning them different weights. Cues can be obtained from previous generations (parental, grandparental cues), direct own experience during the juveniles or adult stage, and from own genes, which reflect the selection pressures previous generations were exposed to during their evolutionary history. The conditions, under which a certain information source is given a high weight by the developmental system, depend on the accuracy of a cue, the accuracy of its transmission across generations, the degree of environmental autocorrelation, and the strength of selection.

McNamara et al. (2016) provide a general, analytically tractable analysis of cue integration. A key finding of this model is a positive synergy between maternal cues and own experience. A developmental system integrating information from maternal phenotypes and cues from the own juvenile environment produces phenotypes with higher fitness across a broad range of environmental autocorrelation values compared with the use of only a single cue. In contrast, combining own experience with genetic cues does not always result in positive synergy. Furthermore, the model predicts that a developmental system should strongly rely on cues from the maternal phenotype, rather than on other information sources, if both the environmental autocorrelation is high and the accuracy of transgenerational information transfer is high. However, the latter may not always be true in real organisms.

4.2 Experimental Studies

4.2.1 Information From Multiple Life Stages

The simplest approach to test for the integration of environmental cues obtained during multiple life stages is to manipulate the environmental

information during two different life stages and to test for their joint or separate effect(s) in a third, later life stage. In a factorial experiment in *S. pleurospilus* varying perceived predation risk by an offspring predator both for parents during the period of egg maturation and for offspring in the early postnatal phase, we did not find evidence for cue integration of maternal and own offspring cues predicted by theoretical models. Instead, *S. pleurospilus* young used cues from genes, parents, and own experience independently and at different life stages (Stratmann & Taborsky, 2014). A signal of the innate ability of fish to distinguish dangerous from benign odor cues was detected most prominently in the first week of life: the more dangerous the cue giving species was, the more strongly larvae reduced their breathing rate, which represents a form of freezing behavior. Parental effects induced by exposure to offspring predators influenced growth patterns (see Fig. 3), whereas larval exposure to offspring predator cues did not. Own experience, but not maternal exposure, affected predator avoidance behavior later in the juvenile period. *S. pleurospilus* live in spatially heterogeneous but temporally stable and thus predictable habitats with limited gene flow (Kotrschal et al., 2012). Theory predicts cues integration particularly for this type habitat. One possible reason for the deviation from theoretical predictions may be the oversimplified model assumption of a developmental switch that decides about the phenotype at a single time point. The results obtained in *S. pleurospilus* suggest that at least in these fish genetic, parental, and own experiential cues are not only sampled at but may also act at different life stages.

In contrast to these findings, there are also cases indicative of an integration of prenatal or early life and postnatal or later life cues, which influence jointly certain traits of adult vertebrates. Some studies support the environmental matching hypothesis (see Box 1). For instance, Japanese quail treated prenatally with cortisol, a manipulation mimicking maternal CORT provisioning in yolk, had an attenuated stress response compared with control birds (Zimmer, Boogert, & Spencer, 2013). The treatment was further related to an increased brain gene expression of glucocorticoid receptor and/or mineralocorticoid receptor in the hippocampus, hypothalamus, and pituitary (Zimmer & Spencer, 2014). Quails were then exposed to postnatal stress by providing them with an unpredictable food source or to ad libitum food in a full-factorial experiment. Quails experiencing stressful conditions both pre- and postnatally outperformed birds of the other three treatment groups by using food more efficiently in novel environment because of reduced neophobia (Zimmer et al., 2013). Likewise, consistent

environmental experience during the early and late stages of juvenile life can be important to develop physiologic function. Zebra finches reared under a poor or rich, but consistent, diet during their entire juvenile period had built up a functional total antioxidant capacity (TAC) by the time they reached the subadult stage. In contrast, when they received a switch toward a poor or rich diet in the middle of the juvenile period, further building up of TAC was inhibited, resulting in a reduced TAC of subadults (Noguera, Monaghan, & Metcalfe, 2015). Both, the results of quail and of the zebra finches indicate early canalization for a certain physiologic trajectory, which yields benefits only if later environments match the “programmed,” early conditions.

In contrast to these findings, the challenge of being exposed to changeable conditions may also enhance certain functions, for instance, the ability of organisms to respond plastically to environmental stimuli. Learning is among the most important forms of plasticity. In *S. pleurospilus*, individuals that had experienced an early change of their food ration outperformed fish kept on constant rations in their associative learning ability (Kotrschal & Taborsky, 2010b). This effect was irrespective of the direction of the implemented ration change or the average ration fish received. These results indicate that also the exposure to *changeable* conditions can be beneficial, because they may induce higher levels of neuronal plasticity allowing organisms to cope better with fluctuating environmental conditions.

Changeable conditions can also be beneficial when they allow animals to compensate for early adversity (Box 1). This was demonstrated in female laboratory rats. When kept in standard housing conditions together with same-sex siblings, rat pups developed reduced stress responsiveness when they experienced high-quality maternal care, i.e., high rates of licking and grooming, compared with pups reared by low-quality mothers. As adults, offspring that had received high-quality care became mothers providing themselves high rates of licking and grooming to their pups, and conversely, offspring that had been reared by mothers with poor maternal care became poor carers themselves. These results have become a classic example for transgenerational plasticity (reviewed in Meaney & Szyf, 2005). Interestingly, it turned out that the caring style of rats, which had received poor maternal care, can be “rescued” by providing high-quality environments *after* weaning (Champagne & Meaney, 2007). Female rats kept in spatially enriched cages allowing also for more diverse social interactions became high-quality mothers, regardless of the caring style experienced as pups. In impoverished postweaning conditions, the opposite occurred: when kept alone in small cages, all rats became poor carers.

With respect to life history traits, one might expect lower degrees of trait flexibility, because many life history traits are linked by trade-offs across life stages. Indeed, evidence suggests that reproductive parameters show little flexibility. When *S. pleurospilus* reared either on high or low food availability encountered a ration switch around maturation, the reproductive rate, offspring size, and the allocation trade-offs between growth versus reproduction and egg number versus egg size were all determined only by juvenile food conditions, irrespective of the ration they received as adults (Taborsky, 2006a). Only the growth rates of juvenile and adult *S. pleurospilus* were determined by current food levels, regardless of whether they encountered the ration switch at maturation (Taborsky, 2006a) or already during the juvenile period (Kotrschal et al., 2014; Kotrschal & Taborsky, 2010b). The limited flexibility of early-induced reproductive traits and trade-offs confirms model predictions from B. Fischer et al. (2014) predicting that when changes of conditions are rare relative to life span, plasticity late in life occurs only to a very limited degree.

4.2.2 Information From Multiple Environmental Parameters

In nature, a multitude of environmental influences are present, which may jointly shape phenotypic development (Groothuis & Taborsky, 2015). Full-factorial experiments aiming to disentangle the possible combined effects often found independent (Schrijver, Bahr, Weiss, & Würbel, 2002) or additive effects (Krause & Liesenjohann, 2012) of the two manipulated variables, or only one of the factors had a significant effect (Kasumovic, Hall, & Brooks, 2012; Krause & Liesenjohann, 2012). However, cues from multiple environmental parameters may also combine nonlinearly (Alekseev & Lampert, 2001; Herczeg et al., 2016; Honarmand, Riebel, & Naguib, 2015), and organisms may not be able to express adequate plastic responses if they do not get the combined information of several parameters (Chevin & Lande, 2015; Kasumovic, 2013). A striking example is the control of reproductive decisions in *Daphnia magna*. This species requires combined information on current resource availability, photoperiod, and population density to successfully induce the switch from clonal to sexual reproduction (Kleiven, Larsson, & Hobaek, 1992).

An interactive response toward multiple selective forces can even lead to life-long specialization into alternative life history trajectories. In the cooperative cichlid *N. pulcher*, subordinate group members pursue two alternative social tactics by which they can appease dominant breeders and thereby reduce the risk of eviction from the territory (S. Fischer et al., 2014).

They can show helping behaviors, such as alloparental care or territory defense, or they can increase their readiness to show submissive displays (Bergmüller & Taborsky, 2005). Interestingly, these tactics are not expressed fully flexibly across social interactions. All *N. pulcher* show submissive and helping behavior, but they do so to different degrees. For instance, helpers related to breeders show more submissive displays, whereas unrelated helpers invest more in alloparental care (Zöttl, Heg, Chervet, & Taborsky, 2013).

A developmental experiment revealed that these fish also permanently specialize into a more submissive or a more cooperative type, contingent on the conditions experienced during early life (Fischer, 2014). When the two key selective forces of *N. pulcher*, predation risk and social environment, were manipulated in a full-factorial rearing experiment, they interactively induced the development of alternative social trajectories and life history strategies. When reared in the presence of older family members, but without cues of predation risk, fish developed a submissive, less helpful behavioral type, which delayed dispersal from the group. Conversely, when reared in the absence of parents and helpers, they became better helpers later in life, but dispersed early to breed independently. Remarkably, when in addition to the social manipulation of the rearing environment cues of predation risk were also presented during early life, the opposite reaction norms were observed in the two social conditions later in life.

There are two lessons to learn from such interacting reaction norms. First, if we consider only one environmental factor and perform only one type of performance test in later life, we may understand only half of the real picture. This becomes particularly evident when the absence of an environmental trigger has masking effects. Tadpoles of various anurans are known to respond readily to predator cues by increasing tail depth (Relyea, 2002; Van Buskirk, 2002). In tree frog tadpoles (*Hyla femoralis*), in which population density is negatively correlated to predation risk, reducing density should therefore induce deeper tails. However, when the population density of tree frog tadpoles was varied, no plastic response in tail morphology was observed. Only when chemical predation cues were also added, tail morphology responded to population density in the expected direction (McCoy, 2007). Second, the results found in *N. pulcher* and in *Daphnia magna* (Kleiven et al., 1992) indicate that our perception of separate environmental “units,” such as light, temperature, or predation risk, influencing phenotypic development may not match the way how animals

perceive their environment. Rather, organisms may evaluate complex combinations of environmental components as a composite factor.

Studying the molecular and neurohormonal mechanisms underlying behavioral specialization helped to shed light on the way how young *N. pulcher* may perceive their environment. Analyzing brain gene expression revealed that the differences between fish of the two behavioral types are related to differences in the programming of the hypothalamic–pituitary–interrenal axis (Taborsky, Tschirren, Meunier, & Aubin-Horth, 2013), i.e., the stress axis of fish. When comparing fish reared with or without older family members in the absence of perceived predation risk, fish reared with family were able to use submissive behavior more appropriately across a range of social contexts (Taborsky, Arnold et al., 2012). In these fish, also the gene coding for the glucocorticoid receptor gene GR1 was higher expressed in the telencephalon as compared with fish reared without older family members (Wikström et al., in revision). GR1 is involved in the negative feedback of stress responses contributing to the termination of cortisol production after a stressor was received (e.g., Meaney & Szyf, 2005). This suggests that the presence of older family members reduced the stress levels of offspring. Arnold and Taborsky (2010) argued that the presence of guarding parents and helpers signal to offspring that they live in a safe environment. In this “safe haven,” offspring engaged more often in social interactions with their sibling peers (Arnold & Taborsky, 2010), probably helping them to develop a better competence in the use of social behavior (a.k.a. “social competence”; Taborsky & Oliveira, 2012). A pharmacologic experiment, in which the GR1 receptor was blocked, confirmed its causal role in the shaping of social competence (Wikström, Fischer, Aubin-Horth, & Taborsky, in preparation). These results, taken together with the interactive effects of social and predator environment (Fischer, 2014), suggest that *N. pulcher* offspring combine different indicators of predation risk early in life to a single “predation risk variable,” which decides about behavioral specialization.



5. PARENT–OFFSPRING CONFLICT

5.1 Theory

Although individuals are expected to use environmental experiences made during their ontogeny to improve their fitness, information or programs obtained from the parents may not always be in the interest of

offspring. Parental effects benefitting parents but not offspring (“selfish parental effects”, [Marshall et al., 2007](#); [Uller, 2008](#)) may evolve if parents can enhance their long-term reproductive output by reducing the quality of their current brood. This may occur when any increment of investment in the quality of the current brood disproportionately reduces the future reproductive potential of parents or if the consequences of parental effects bear immediate high costs for parents. For instance, larger offspring hatching from well-provisioned eggs may require more parental care after hatching also. Finally, parents may be limited in their ability to provide favorable starting conditions for the current brood. For example, if high-quality oviposition sites are limited, this renders a continued search for these sites inefficient (reviewed in [Marshall et al., 2007](#)). There are at least three possibilities how offspring may deal with negative parental effects. (1) If offspring cannot counter negative parental effects, as it may be the case for yolk hormone-mediated maternal effects (e.g., [Groothuis et al., 2005](#)) or maternal decisions about clutch size ([Naguib et al., 2004](#)), and if the effects persistently affect the somatic state of offspring, they should develop an adult phenotype that maximizes their ability to cope with this poor state ([Nettle & Bateson, 2015](#)). For instance, a large male body size is often critically important to win aggressive contests about access to mates. If small-born individuals will remain small as adults, they may never be able to gain access for females by fighting. Therefore, they may instead adopt a nonaggressive, alternative behavioral strategy by becoming “scramblers” instead of fighters ([Smallegange, 2011](#)) or they may develop into a female-mimic phenotype and act as sneakers (reviewed in [Taborsky, 1994](#)). Alternatively, if the affected somatic trait is sufficiently plastic, offspring may disagree with the parental information or program and (2) try to compensate for a negative parental effect or (3) even to reverse parental effects and behave opposite to the parental program.

Results from a theoretical model of the evolution of maternal effects under parent-offspring conflict ([Uller & Pen, 2011](#)) indicate that if maternal signals to offspring are cost-free and offspring are able to respond plastically to the maternal strategy, then the offspring’s behavioral strategies evolve to the offspring’s optima. If offspring are constrained to counter the maternal strategy, their behavior evolves toward the maternal optimum. If costs of signaling (for mothers) or responding (for offspring) were introduced, the resulting behavioral strategies deviated from both maternal and offspring’s optima depending on the extent of the assumed costs.

5.2 Experimental Studies

Mouthbrooders exhibit energetically costly brood care, usually coupled with a high investment in individual eggs. Many mouthbrooding parents barely can feed during several weeks of brood care, leading to a strong reduction of the carer's body condition (Grüter & Taborsky, 2004). The high investment in the current brood most likely impacts the future reproductive potential of carers. Caring parents thus have to trade-off the performance of their current brood against their own future reproductive value. In biparental species, this conflict can be solved between the partners by negotiating over the amount each partner cares (Grüter & Taborsky, 2005; Steinegger & Taborsky, 2007). In female-only mouthbrooders, however, optimal maternal decisions about reproductive investment may result in compromising growth and survival of the current brood. For instance, in *S. pleurospilus*, females with experimentally reduced body reserves shortened the phase of continuous mouthbrooding, that is, the period during which the offspring are safe but females cannot feed (Segers, Gerber, & Taborsky, 2011) thereby exposing their offspring to increased predation risk.

There are ample examples suggesting that offspring hatched from small eggs into favorable conditions do not face reduced fitness from their poor initial phenotype (Einum & Fleming, 1999; Fox & Mousseau, 1996; Hutchings, 1991; Kaplan, 1992; Rotem, Agrawal, & Kott, 2003; see Engqvist & Reinhold, 2016), at least not with respect to juvenile survival. Thus, no conflict of interests may exist in benign environments between parents and offspring about egg size. For instance, in *S. pleurospilus*, offspring starting at a small size can fully compensate their size disadvantage by fast growth if they live in conditions with only mild competition for food, which is not possible for small offspring living in high competition conditions (Segers & Taborsky, 2012b). However, if this early phase of catch-up growth has costs to be paid toward the end of life (e.g., Criscuolo, Monaghan, Nasir, & Metcalfe, 2008; Lee, Monaghan, & Metcalfe, 2013; reviewed in Metcalfe & Monaghan, 2001), there might still be potential for conflict even in benign environments.

5.2.1 Offspring Make the Best Out of a Poor Phenotype

In *S. pleurospilus*, egg size varies enormously, ranging from weights between 10 and 21 mg, which translates into significant body size differences once independent of maternal care (Segers & Taborsky, 2011). When comparing growth of juveniles hatched from large versus small eggs, the size advantage

of large-born individuals persists during the juvenile period when they live in environments with poor food availability. When confronted with the opportunity to feed in a risky environment, these juveniles dealt with initial size differences in a context-dependent way. Small-born fish spent more time foraging in a risky environment than did large-born fish. Risk-prone feeding of small-born fish enabled them to grow at the same rate than large-born fish, even if they did not manage to catch up in size with them. When plenty of food was available, however, juveniles behaved similarly careful irrespective of initial body size (Segers & Taborsky, 2011).

5.2.2 Offspring Compensate for Negative Parental Effects

Compensatory growth spurts are likely to be under control of the somatotropic axis, which promotes embryonic and postnatal growth in vertebrates. In *S. pleurospilus*, young hatched from small eggs had a higher expression of the gene coding for the growth hormone receptor (GHR) compared with young hatched from large eggs (Segers, Berishvili, & Taborsky, 2012). GHR is an important receptor of the somatotrophic axis promoting growth by binding growth hormone. Furthermore, when kept under favorable food conditions, fish hatched at a small size were fully able to catch up with large-born fish (Segers & Taborsky, 2011, 2012b; Segers et al., 2012). There are two alternative mechanisms that may explain these growth spurts: small-born offspring may have used the constrained energy availability in small eggs as cue for their own size disadvantage at hatching and, when encountering favorable feeding conditions after hatching, may have used the combination of internal and external cues as signal to kick off accelerated growth. Alternatively, growth compensation may have been a response to maternal GHR transcripts that may have been deposited in the yolk. The production of small offspring, which exhibit accelerated growth, may represent a manipulative strategy of mothers. Why should mothers pursue such a manipulative strategy? If favorable conditions are a good predictor for mothers that their offspring will manage to catch-up in growth, mothers may benefit from reducing their energy investment per egg. They may use this energy to invest in current fecundity or in their future reproductive potential, leaving it to their offspring to make up for a small size at the onset of life.

5.2.3 Offspring Reverse Negative Parental Effects

In cooperative societies, parental effects may predetermine offspring to take up a particular role or behavioral specialization, which may or may not coincide with the individual fitness interests of the offspring (parental

manipulation). In eusocial species, offspring are often programmed by dominant breeders to follow a particular social trajectory, which is not malleable by the young and may involve irreversible morphologic specializations. In contrast, if behavioral development is plastic, as it is the case in many cooperative breeders (English, Browning, & Raihani, 2015), offspring may be able to disagree with the parental program.

In *N. pulcher*, a similar conflict about egg size appears to exist as it does in mouthbrooders. Female *N. pulcher* produce smaller eggs giving rise to smaller offspring if they have many helpers (Taborsky et al., 2007). Although smaller offspring would face higher predation risk, this egg size reduction is possible, because in large groups survival of offspring is significantly enhanced (Brouwer et al., 2005). Thus, in this species the large number of helpers compensates for an increased potential mortality risk of small offspring.

In cooperative societies, parent—offspring conflicts can have an additional dimension. Offspring are not only dependent on care but also become carers themselves later during their ontogeny. The optimal contribution to alloparental care dominant breeders need and subordinate helpers are willing to give may diverge quite substantially and depend on the outside options for dispersal and independent breeding by subordinates (Russell & Lummaa, 2009). A conflict between parents and offspring about which social trajectory to pursue appears to exist in *N. pulcher*, which is apparently “won” by offspring. This was revealed by a rearing experiment, in which *N. pulcher* offspring grew up in large or small family groups. They did so either only during larval development (10 days) or also during the first 2 months after the larval period. This means that some fish were mostly under the influence of parental effects when they were separated from their original family groups, whereas others had sufficient time to sample their social environment themselves. After the experience phase, 70 days after the larval phase, juveniles were exposed to an encounter with a larger, dominant conspecific. Juveniles that had stayed in their family groups only during larval development were more aggressive but less submissive when originating from large groups. However, when they had the chance to make own experiences in the family groups, they developed exactly the opposite behavioral tendencies: now fish from large groups behaved less aggressive and more submissive toward dominant fish (Fig. 4). It seems that these fish reversed the initial influence of parental effects on their social behavior type. Why should they do so? Fischer (2014) showed that those subordinates that exhibit stronger submissive tendencies tend to stay in groups for extended periods after

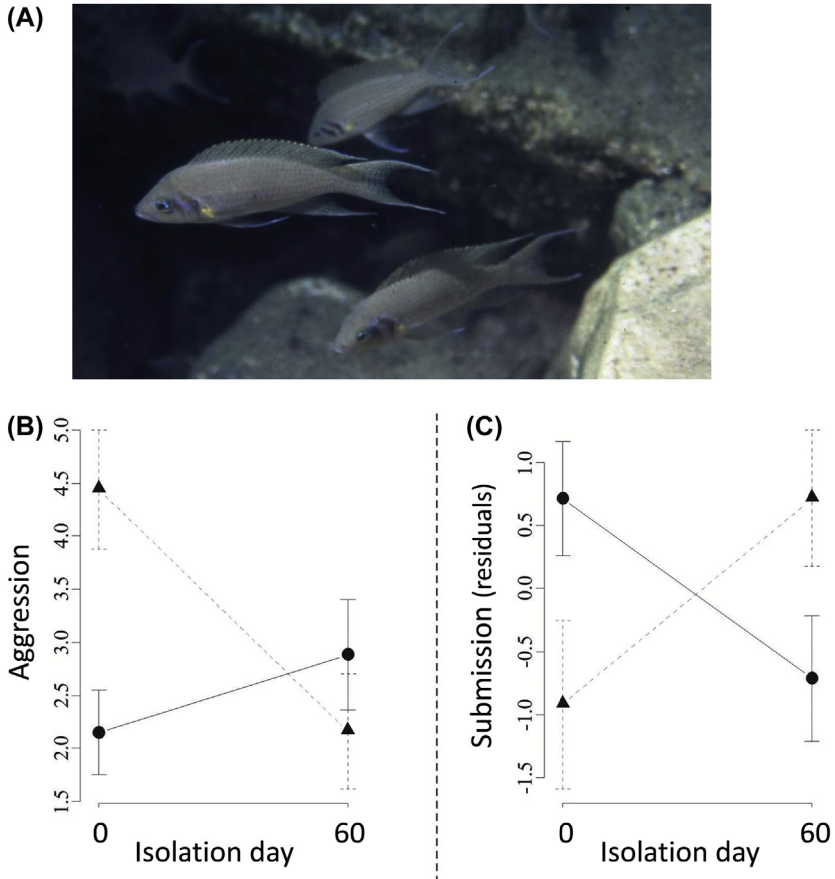


Figure 4 (A) A group of *Neolamprologus pulcher* in its natural habitat in Lake Tanganyika: a breeder pair is seen in the front, and a helper in the back. (B) Aggressive and (C) submissive behavior by juvenile focal fish toward a larger conspecific in a hierarchy formation test after being isolated from their family groups either at “day 0” (end of larval phase) or 60 days later. Triangles and dashed lines represent fish originating from large groups; circles and solid lines represent fish from small groups. Residuals are shown in (C), as submission frequency was corrected for the number of aggression received by the dominant individual. Modified after Fischer, S., Bessert-Nettelbeck, M., Kotrschal, A., & Taborsky, B. (2015). Rearing group size determines social competence and brain structure in a cooperatively breeding cichlid. *American Naturalist*, 186, 123–140.

maturation, whereas nonsubmissive (helper type) fish tend to disperse early. Thus, a speculative explanation of the reversal of parental effects in *N. pulcher* is that parents living in small groups produce the submissive phenotype because in the long run it would contribute to enhance group size. In the

field, large groups are able to persist over time much longer than small groups (Heg et al., 2005). However, the interest of subordinate group members differs from the parents. They prefer to join groups that are already large (Reddon, Balk, & Balshine, 2011). Thus, fish from small groups may be more likely to develop the disperser type and leave the small groups as soon as they reach a size when this is possible (Stiver et al., 2004).



6. FITNESS

6.1 Theory

Life history traits have a direct bearing on fitness. Therefore, investigating how parental effects and early experience influence the ontogeny of life history traits should give immediate insight in fitness consequences of developmental plasticity. The trade-off between growth, maintenance, and reproduction, also addressed as “general life-history problem” (Schaffer, 1983), is arguably the most prominent life history trade-off. A suite of life history traits is connected to this trade-off, such as growth rates, age and size at metamorphosis and maturation, age- and size-dependent survival, reproductive rates, and fecundity. As often survival and reproductive rates are a function of body size, the growth strategy of an individual chosen during development in dependence of features of its environment is a promising candidate to explore fitness effects of developmental plasticity.

English et al. (2016) analyzed a model, in which organisms simultaneously invest in growth by taking up food and obtain information about the food availability in their environment, followed by a step at which the previous belief about the environment is updated by the new information. The model explored how early life food availability and predation risk influence growth trajectories and size and age at maturation, when predation risk correlates either positively or negatively with food availability. As one might expect, organisms grew faster and matured later in high-food environments. As in previous models (e.g., Stamps & Krishnan, 2014), the value of the obtained information and the plasticity of behavior was highest during early life and steadily decreased with age. Interestingly, the large differences between life history traits in rich and poor environments, in particular with respect to age and size at maturation, did not significantly affect fitness. The authors proposed that this may have happened because individuals continually adjusted decisions about foraging effort and timing of maturation to the prevailing conditions to maximize their expected reproductive success.

6.2 Experimental Studies

In laboratory experiments, we can get close to measuring fitness effects of developmental plasticity, if we can follow the entire reproductive life history of organisms reared in different conditions to obtain an estimate of life time reproductive success. Nevertheless, fitness estimates from the laboratory should be interpreted with caution, as in the laboratory conditions are typically more benign than in nature, for instance, because the relevant predators or parasites are absent or cannot be kept in direct contact with the experimental animals for ethical reasons.

Results of a long-term experiment in *S. pleurospilus* investigating the influences of food ration on life history schedules (Taborsky, 2006a) are partly in agreement with the theoretical predictions about fitness effects by English et al. (2016). Females that grew up on a low-food (L) diet grew more slowly, matured at smaller size, had fewer offspring, but they reared their first successful clutch earlier and had a faster reproductive rate than females raised on a high-food (H) diet. Around maturation, half of the females were switched to the opposite food regimen, from high to low food (HL) or vice versa (LH), whereas the other half of the females remained in the original diet (LL and HH, respectively). Switched females adjusted their growth trajectories to the new ration. Consequently, HL females remained smaller than HH females and LH females grew larger than LL females. At around 1 year of age, the growth curves of the two switched treatments crossed: LH females became similar in size to HH females, and HL females approached the growth trajectory of LL females.

Remarkably, the treatments with similar final size, i.e., the treatments kept under the same *adult* food rations, had a similar life time reproductive success, irrespective of their juvenile ration (Taborsky, 2006a). When calculating the total biomass of young produced during the reproductive life span, it did not differ significantly between HH and LH and between LL and HL females. Similarly, zebra finches, reared as nestlings on a poor diet resulting in reduced growth and immune function of juveniles, became phenotypically almost indistinguishable as adults from birds reared on a normal diet (Birkhead et al., 1999). This suggests that after the nesting stage they compensated through a differential allocation of resources. Thus, in line with the predictions by English et al. (2016), it seems that organisms are able to compensate for their early life conditions by adjusting their growth and maturation schedules to the changing conditions. Nevertheless, in the

case of zebra finches, animals from the poor-nutrition treatment faced long-term costs toward the end of life, as they had a reduced longevity compared with normal reared birds (Birkhead et al., 1999).

There are cases, however, in which harsh early conditions are too severe to allow for full compensation. For instance, zebra finches facing strong resource competition induced by brood enlargement reached a smaller adult size than birds reared with fewer siblings (Naguib et al., 2004), an effect that carried over to adult sizes and the reproductive success of females in the next generation (Naguib et al., 2006; see also above). Along the same lines, male zebra finches growing up in experimentally reduced broods were more successful in obtaining copulations (Mariette, Cathaud, Chambon, & Vignal, 2013).



7. ADDED VALUE FROM ADDING COMPLEXITY?

Theoretical insights about the temporal patterns of environmental sampling and information use and about cue integration are plausible. When the environmental state fluctuates during an organisms life time, maintaining plasticity can be beneficial (B. Fischer et al., 2014). Only toward the end of life no plastic changes should be made as the benefits of these changes cannot be reaped anymore. In contrast, when environments are stable and further sampling of the environment does not yield new information, plasticity should decline as soon as a good match with the prevailing conditions is reached (Fawcett & Frankenhuis, 2015; Panchanathan & Frankenhuis, 2016; Stamps & Frankenhuis, 2016). Theory further predicts that it can be optimal to integrate cues from parents and own experience over a wide range of environmental conditions and that strong environmental autocorrelation combined with high transgenerational transmission accuracy of cues favors the use of parental cues over own experience or cues from own genes (Leimar et al., 2015; McNamara et al., 2016). These general theoretical predictions are valuable and could possibly be tested in a general comparative framework once sufficient information about temporal or spatial stability of environments, accuracy of cues, and their transgenerational transmission is available.

However, the reviewed empirical evidence indicates that the complexity of “real life” asks for more differentiated models. Models typically assume stationary, autocorrelated environments, such that the more recent a perceived environmental cue is, the better it can predict the future. The

results from long-lived vertebrates illustrate that this view is too simple. When adults and juveniles occupy different niches, parental cues experienced long time ago, for instance, in the juvenile stage of parents, may predict offspring conditions better than do more recent conditions parents experience in their adult environment (Taborsky, 2006b; Burton & Metcalfe, 2014). The reviewed case studies also provide a quite complex picture of when costs of plasticity are due. Although we often stop to survey the fitness consequences of a given plastic change once we “proved” its beneficial effects, the beneficial periods of these changes may be short and its costs may be paid only during an organism’s later life time (e.g., Metcalfe & Monaghan, 2001; Ruuskanen et al., 2013). These results emphasize that we have to survey fitness across full life cycles, which becomes particularly essential if we aim to test predictions from evolutionary models.

In contrast to the assumptions made in some theoretical models, the integration of cues from multiple sources is often not additive. At least for behavioral traits such as foraging or social behaviours, cues obtained from different environmental variables interactively affected the behavioral phenotypes of several vertebrate species (Fischer, 2014; Herczeg et al., 2016; Honarmand et al., 2015; Segers & Taborsky, 2011). Furthermore, parental and own cues do not always combine in positive synergy. Changeable environments (Champagne & Meaney, 2007) or conflicting interests between parents and offspring (Fischer et al., 2015) can result in complete compensation or even reversal of parental effects.

To conclude, both theory and experimental research made first steps toward incorporating the complexity of natural environments in the study of developmental plasticity. Nevertheless, we are only at the beginning to understand the multitude of interactions between developing phenotypes and their environment. Future research of both fields faces the challenge to better take account for developmental processes occurring during multiple ontogenetic stages in a multivariate environment without losing the tractability of models or experimental designs. We need to face this challenge if we want to avoid flawed conclusions about the evolution of developmental plasticity. As Chevin and Lande (2015) pointed out, “when phenotypic plasticity has evolved in response to multiple correlated environmental variables, misleading conclusions may be reached by analyzing plastic responses to any of these variables in isolation.” The field of developmental plasticity could certainly profit, if further steps toward a better understanding of the complexities of developmental processes were pursued hand in hand by theoreticians and experimental researchers.

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