



KNOCK-ON EFFECTS OF ENVIRONMENTAL
INFLUENCES DURING EMBRYONIC DEVELOPMENT
OF ECTOTHERMIC VERTEBRATES

BROR JONSSON

*Norwegian Institute for Nature Research
0855 Oslo, Norway*

E-MAIL: BROR.JONSSON@NINA.NO

NINA JONSSON

*Norwegian Institute for Nature Research
0855 Oslo, Norway*

E-MAIL: NINAFOTOGRAFI@GMAIL.COM

MICHAEL M. HANSEN

*Department of Biology, Aarhus University
8000 Aarhus C, Denmark*

E-MAIL: MMH@BIO.AU.DK

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ABSTRACT

Environmental factors influencing parents or offspring during embryogenesis can have knock-on effects at later life stages of the offspring. These effects may prepare the progeny for conditions that they may encounter as larvae, juveniles, and/or adults. Here, we give examples on how knock-on effects of temperature and predator cues can affect phenotypes of fish, amphibians, and reptiles. Such effects are best described in reptiles, but are generally widespread among ectotherms. Most of the species are oviparous with egg incubation outside the mother's body. The eggs can be exposed to highly different and variable environmental conditions, and developmental plasticity may help offspring cope with influences they may encounter at a later stage, e.g., whether the habitat will be warmer or colder and/or safer or riskier

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than what they a priori are adapted for. Knock-on effects can be considered a subset of phenotypically plastic responses. They can be instantaneous or delayed, have a physiological foundation, and can be manifested as temperature-dependent sex determination and changes in morphological, physiological, life-history, and behavioral characters. They are often, but not exclusively, assumed evolutionarily favorable, particularly beneficial for invasive species and during periods of rapidly changing environments. However, although several studies suggest that plasticity in some cases increases survival and reproductive success, the fitness gain is still virtually untested. It is assumed that epigenetic mechanisms, such as DNA methylation and histone modifications, could ultimately be important components of molecular mechanisms that allow early perceived cues to be expressed at a later stage in life. Although some empirical cases support this, evidence is still mostly circumstantial. Future research should investigate mechanisms and fitness effects of early environmental stimuli. These effects are important for the ecology of species and should be taken into account in experiments on ecological effects of environmental variables. This is of particular interest today because of climate change and increasing anthropogenic habitat alterations.

INTRODUCTION

ENVIRONMENTS are changing more rapidly than ever before. This global change is largely caused by anthropogenic influence of climate and habitats resulting from human population growth with increased urbanization and industrialization, overharvesting of natural populations, pollution, damming and regulations of rivers, new modes of operation in agriculture and forestry, and invasions of exotic species (Bronzizio et al. 2019).

Are organisms able to cope with these challenges, and how? Many populations and species are not coping and have gone or will likely go extinct in the near future (Jonsson et al. 1999; Román-Palacios and Wiens 2020). Others may be able to persist in altered environments through mechanisms such as phenotypic plasticity and local adaptation (Fusco and Minelli 2010; Valladares et al. 2014; Donelan et al. 2020).

Phenotypic traits of individuals play crucial roles for the likelihood to survive and reproduce. Although phenotypic variation is often attributed to genetic and environmental factors and interactions between the two (Falconer and McKay 1996), it is becoming increasingly evident that environments can affect phenotypes in complex ways and with considerable time lag. Such environmentally induced plasticity is widespread especially among ectothermic animals, may have lifelong effects on individual phenotype and fitness (Lafuente and Beldade 2019), and is responsible for a significant amount of interindividual phenotypic variation (Parsons et al. 2020).

A major challenge in ecology is to understand how environmental factors influence organisms (Bosch et al. 2014). A large array of factors affects phenotypes, but two of the most central variables affecting ectothermic animals are environmental temperature and predation (Noble et al. 2018). Temperature governs their biochemical and physiological reactions with subsequent effects on morphology, ecology, and behavior (Hochachka and Somero 1984; Schulte 2015). Thermal conditions affect functional structures in cells and patterns of gene expression influencing phenotypes (Burggren 2020), and play a critical role in brain development and flexibility influencing cognition, behavior, social skills, stress responsiveness, and personality development (Malekpour 2007; Dantzer et al. 2013). Predation is a central concept because it concerns the energy flow in ecosystems and affects the structure, size, distribution, density, and functions of prey populations (Ormerod 2002). At the individual level, risks of predation lead to morphological, physiological, and behavioral changes, and reduce prey fitness (Sheriff et al. 2020). In a modern world with increasing temperature, the warmer climate will increase metabolic and developmental rates and influence body size of ectotherms (Atkinson 1994; Berrigan and Charnov 1994; Jonsson et al. 2013), augment thermal stress with oxidative damage of biomolecules, and accelerate the rate of aging (Burraco et al. 2020). Increased temperature will influence predation rate because faster developing animals accelerate food consumption rate and change resource availability, habitat characteristics, and size

and condition of animals (Morin et al. 2021). Furthermore, mothers stressed by predators may transfer stress to their offspring by altered hormone and/or other contents of their ova. This may lead to changed offspring morphology, physiology, and/or behavior (Mommer and Bell 2013; O'Brien et al. 2017; Ensminger et al. 2018; McGhee et al. 2020), induce developmental plasticity, and be suggestive of the trophic conditions that the offspring may encounter later (Meylan et al. 2012; Warner and Lovern 2014).

In this review, we provide examples of how temperature and predator cues during early development or at a parental phase may have knock-on effects that indirectly cause phenotypic change later in life. There are other environmental factors, such as habitat stability and hypoxia, that might have similar effects, but it is beyond the scope of this review to include the effects of these other variables.

Knock-on effects can be considered a subset of the general concept of phenotypic plasticity, which is the ability of a genotype to express different phenotypes in response to environmental differences (Schlichting 1986; Kelly et al. 2012). Hence, knock-on effects consist of cues or imprints experienced in individuals' early life, transferred as a parental effect, or induced at embryo or larval stages, which later in life affect the ability to change developmental trajectories, activities, and resource allocations within an organism's life span. Early environmental effects may not only influence embryo development and hatching success, but also influence sex ratio and offspring morphology, life history, physiology, and behavior (Deeming 2004; Booth 2006, 2018). These phenotypically plastic effects may be particularly important for ectothermic and oviparous species with embryos developing outside the mothers' body, where environmental conditions are highly variable. The effects can be long term and prepare offspring for conditions that they may encounter at a later stage in life, and buffer otherwise detrimental effects of environmental change (Elphick and Shine 1998; Richards et al. 2010; Rey et al. 2016). Such parental or early environmental effects are expected to be advantageous when parents or early environment provide a reliable fore-

cast about the conditions that the offspring may encounter later in life (Hu and Barrett 2017; Donelson et al. 2018; Tariel et al. 2020). However, it may be maladaptive in unpredictably changing environments (Bateson et al. 2014), and there are very few quantitative studies demonstrating how beneficial such early programming is (Warner and Shine 2005, 2008; Bell et al. 2016).

Phenotypically plastic reactions (i.e., the ability of an organism to change its phenotype in response to stimuli from the environment) are rapid and typically occur within a generation (Fox et al. 2019). Responses to prenatal or early postnatal environments may influence organisms all of the way to reproduction and, in some cases, influence the course of life in future generations (Salinas and Munch 2012; Warner et al. 2013; Dias and Ressler 2014; Shama and Wegner 2014). Across generations, parents influence offspring, e.g., by breeding at an appropriate time or place or by a physiological effect such as the provisioning of a larger amount or higher quality yolk to the embryo, improving larval growth and survival (Stratman and Taborsky 2014). Parents may also have longer-term effects such as changed age at maturity or length of life span of the offspring (Heath and Blouw 1998). Studies have demonstrated that parental effects may have important ecological and evolutionary consequences (Räsänen and Kruuk 2007; Stratman and Taborsky 2014). Maternal effects can be mediated by variation in provisioning of the eggs (Braun et al. 2013; Arnold et al. 2018) or by selection of oviposition sites that determine risks and feeding opportunities for offspring (Burton et al. 2013). Maternal nutrition can affect the number or size of offspring produced (Lovern and Adams 2008) and nutrients available to their developing embryos (Moczek 1998). This may affect immune function, morphology, life history, and behavior of offspring (Kelly and Coutts 2000; Rutkowska and Cichon 2002; Warner et al. 2007; Fuiman and Perez 2015). Also, fathers may influence their young through fertilization success and parental care, growth, and associated life-history traits affecting their competitive abilities. For instance, male guppy *Poecilia reticulata* ejaculates influence offspring size at birth (Evans et al.

2017), and male parental care in threespined sticklebacks *Gasterosteus aculeatus* reduces predator stress linked to the expression of a DNA methyltransferase in the brain of the progeny (McGhee and Bell 2014).

Phenotypically plastic responses may or may not be adaptive and apply to all characteristics of an organism other than its genes. That being said, reaction norms of phenotypic characters can also be under genetic control and subject to genetic change through selection (Pigliucci and Schlichting 1998). In some cases, phenotypically plastic responses may be governed by transcriptional regulators to DNA, where methylation of CpG sites in DNA sequences (that is “C” followed by “G”) is the most thoroughly studied epigenetic mechanism in ecological and evolutionary sciences (Feil and Fraga 2012; Verhoeven et al. 2016). In vertebrates, methylation of CpG sites in regulatory regions acts to down-regulate genetic expression and, conversely, demethylation leads to upregulation (Greenberg and Bourc’his 2019). Other epigenetic mechanisms involve histone modifications and microRNA (miRNA) that alter the transcriptional capabilities of the genome (Handel et al. 2010; Verhoeven et al. 2016). However, to date, there is little information about to what degree phenotypic plasticity is genetically or epigenetically regulated.

Epigenetic effects across generations as a result of epigenetic variation are controversial in vertebrates (Anastasiadi et al. 2021b), although well demonstrated in plants (Heard and Martienssen 2014; Nadeau 2015; Horsthemke 2018; Anastasiadi et al. 2021b). Still, phenotypic responses transferred over generations may be manifested in the germ cells, where long-lived RNA molecules appear to be the most likely transgenerational carrier (Galan et al. 2020). However, the molecular mechanisms involved in transgenerational transfer of phenotypically plastic characters are largely unresolved and need further research efforts (Miska and Ferguson-Smith 2016).

Here, we will primarily provide insight into how temperature and predator cues have knock-on effects on ectothermic vertebrates. We do this because few if any studies have shown how early environmental factors affect phenotypes across fish, amphibians, and

reptiles. There are similarities, but also some differences among these vertebrate groups. We begin the review by presenting environmental sex determination (ESD) and provide examples from fish and reptiles. We chiefly use examples of and discuss temperature-dependent sex determination (TSD), although we briefly mention other environmental factors that may influence sex determination. We also discuss the evolution of TSD. Next, we present how temperature before and shortly after conception has knock-on effects on later-appearing morphological, physiological, life-history, and behavioral traits. We provide examples from fish through amphibians to reptiles. Thereafter, we present similar effects of predator cues on the same taxa. Then, we discuss epigenetic mechanisms that may underlie some phenotypic knock-on effects. There are many commonalities in response patterns of environmental stressors across these large groups of species. We summarize similarities and differences across the taxonomic groups and discuss adaptive values of environmental knock-on effects of early environmental influences. We end by examining the wider ecological significance of early induced phenotypic knock-on effects and present needs for future research in this field.

KNOCK-ON EFFECTS OF ENVIRONMENTAL SEX DETERMINATION

Sex determination initiates the process of sexual differentiation, i.e., forming the differences between males and females. Most ectothermic vertebrates have genetic sex determination (GSD) where different inherited genes or even chromosomes determine their sex. However, some have environmentally induced sex determination where external factors signal the gonadal sex well after the fertilization (Singh et al. 2020). Among ESD species, temperature during a sensitive period of the embryonic/larval development is the most common variable that determines the sex of the offspring (Janzen and Phillips 2006). TSD is widespread among reptiles, but is also known from some species of fish (Roush and Rhen 2018). In addition, sex determination may be influenced if eggs or larvae are exposed to extreme temperatures, but not under regularly occurring thermal conditions.

This phenomenon is not viewed as TSD *sensu stricto*.

TEMPERATURE-DEPENDENT SEX DETERMINATION

Temperature influences the fitness of organisms by influencing vital variables such as developmental rate (Arrighi et al. 2013), metabolic rate (Neubauer and Andersen 2019), growth rate (Boltaña et al. 2017), body size (Atkinson 1994), and length of life span (Keil et al. 2015). However, these variables may influence the fitness of males and females differently, and for some species and populations, it may be more favorable to develop into males at some temperatures, and females at others. Furthermore, temperature during early life should be a reliable cue for the temperature level that the organism experiences later in life.

Research indicates that TSD is a threshold trait—i.e., a quantitative trait based on a continuously distributed factor (temperature) that contributes to the underlying liability trait (sex; Singh et al. 2020). In TSD, there is a pivotal temperature where the sex ratio is 1:1 (Mrosovsky and Pieau 1991). A male surplus may be produced when the temperature is colder, and more females when it is warmer than the pivotal temperature. In other species, it is the other way around with more females at low and more males at higher temperatures. There are also cases where only females or males are produced at both warm and cold temperatures, and the other sex or both at intermediate temperatures. The favored sex is fitness dependent as proposed by Charnov and Bull (1977; further described in the section titled Evolution of ESD Systems below). Thus, TSD has a genetic basis where different individuals are more or less responsive to temperature (Scheiner 1993; Singh et al. 2020), with genetic variation in temperature sensitivity of the embryos (Rhen et al. 2011). The magnitude and duration of exposure to temperature during the thermosensitive period may also influence how many in an embryo clutch develop testes or ovaries (Rhen et al. 2015). Probably, this is because temperature influences the production of sex hormones that stimulate sex determination. Below, we give examples of how tem-

perature at an early stage in life influences sex determination in fish, amphibians, and reptiles.

Fish

TSD is reported from approximately 60 species of fish (Shen and Wang 2014). This includes some Cichlidae, Atherina, Ictaluridae, Sebastidae, Moronidae, Rivulidae, Embiotocidae, and Paralichthyidae). Often, more males are produced at relatively high temperatures (Hasyashi et al. 2010), but in channel catfish *Ictalurus punctatus* (Patiño et al. 1996), Korean rockfish *Sebastes schlegeli* (Omoto et al. 2010), European sea bass *Dicentrarchus labrax* (Baroiller and D’Cotta 2000), and dwarf perch *Micrometrus minimus* (Schultz 2008), more females are produced at high temperatures. In olive flounder *Paralichthys olivaceus*, both high and low temperatures induce males, and intermediate temperatures yield an even sex ratio (Baroiller and D’Cotta 2000). Mangrove killifish *Kryptolebias marmoratus* have a mixed strategy, where individuals can either be self-fertilizing hermaphrodites or crossbreeding where the ambient temperature modulates their sexual identity (Taylor 2012).

When is the thermosensitive period in fishes? Few species have been investigated, but in tilapia *Oreochromis mossambicus*, elevated proportions of females were induced when the embryos were exposed to low temperatures from fertilization to five days posthatching. More males, on the other hand, were produced when fish were exposed to elevated temperatures 10 days after hatching. But, at that time, exposure to low temperatures had no effect on sex determination (Baroiller and D’Cotta 2000). In European sea bass *D. labrax*, treatment with 15°C from 57 to 137 days posthatching induced higher proportions of males, whereas more females were produced when exposed to cold water (13–15°C) 30 hours after fertilization (at the stage of half-epiboly; Baroiller and D’Cotta 2000). At that developmental stage, more males were produced when the temperature was 20°C. Thus, two different thermosensitive windows may exist at least in some cases, and there appears to be variation as to whether the sensitive period is in the early embryonal or larval stage.

The sex determination of sockeye salmon *Oncorhynchus nerka*, rainbow trout *Oncorhynchus mykiss*, medaka *Oryzias latipes*, Nile tilapia *Oreochromis niloticus*, and zebrafish *Danio rerio* is influenced if the eggs are affected by much higher temperatures than the eggs typically experience in nature, but these species are not recognized as TSD species (Azuma et al. 2004; Tessema et al. 2006; Ospina-Álvarez and Piferrer 2008).

In fish, other environmental factors can also influence sex determination. For instance, larval food consumption and early growth may influence sex determination of lampreys (Kuwamura et al. 2002), zebrafish (Lawrence et al. 2008), and roach *Rutilus rutilus* (Paull et al. 2009). Also, these are factors that may influence the fitness of species (Dmitriew 2011) and, in many fish species, there is a stronger relationship between size and reproductive success in females than in males (Fleming 1996), which may also be the case in these species. In sea lamprey *Petromyzon marinus*, slow growth increases the probability of becoming male (Johnson et al. 2017). But once the lampreys have entered the juvenile period, the sex is defined and does not change (Beamish and Barker 2002). For southern brook lamprey *Ichthyomyzon gagei*, the sex ratio is influenced by growth rate, larval density, pH, and temperature (Beamish 1993). In lampreys, however, the mechanism of ESD is not well understood.

Water acidity can also influence sex determination in the cichlids *Pelvicachromis pulcher*, *P. subocellatus*, *P. taeniatus*, *Apistogramma borellii*, *A. cacatuoides*, and the poeciliid *Xiphophorus hellerii* (Rubin 1985). When broods were developed at low pH (5–6), the sex ratio of the cohort was skewed toward males. At higher pH (7), the ratio was skewed toward females. Poor water quality may have long-lasting negative effects on growth and this may be the reason for its influence on the sex determination of some freshwater fishes where males are typically smaller than females.

Amphibians

Amphibians have GSD and not TSD under normal environmental conditions (Flament 2016). Extreme temperatures, however, may

influence sex differentiation. This sex change may be hormonally induced, is not considered adaptive and, consequently, not recognized as TSD. In several anurans, such as the wood frog *Lithobates sylvaticus*, Japanese brown frog *Rana japonica*, American bullfrog *Lithobates catesbeianus*, and common toad *Bufo bufo*, low temperatures have a masculinizing effect and high temperatures a feminizing effect (Witschi 1929; Chardard et al. 2004; Nakamura 2009). In the Indian skipper frog *Euphlyctis cyanophlyctis*, on the other hand, exposure of tadpoles to very high temperatures (greater than 28°C) produced male-biased sex ratios (Phuge 2017). High temperatures also resulted in early metamorphosis at a reduced body size, stimulated testis, and disturbed ovary development. Possibly, stress hormones that surge at extreme temperatures are responsible for the skewed sex ratio and favor the smaller-sized sex (Phuge 2017).

Temperature-dependent sex reversal (i.e., redirection of sexual phenotype during larval development) is common in several amphibians, which may have replaced TSD in this group (Ruiz-Garcia et al. 2021). For species with temperature-dependent sex reversal, embryo temperatures may be a poor predictor of the temperatures they experience later in life, so that the phenotypic sex changes from the genetic sex during the tadpole stage. The responsible mechanism is, however, still not well understood.

Reptiles

Although GSD is most common among reptiles, TSD is known in crocodiles, tuatara, turtles, and various lizards, including geckos, Scincidae, anguimorphs, and acrodonts (Roush and Rhen 2018; Cornejo-Páramo et al. 2020). No other known factor induces ESD in reptiles (Singh et al. 2020), although Lolavar and Wynneken (2020) claim that moisture in nests, in addition to temperature, may impact sex determination of loggerhead sea turtles *Caretta caretta*. TSD species typically mate and nest at sites where the ambient temperature is about 25°C, suggesting that circa 25°C is an optimal temperature for nesting and embryo development of TSD species. Lower temperatures result in one sex and

warmer temperatures typically induce another (Warner and Shine 2008). In many turtles, eggs predominantly hatch males at lower temperatures and predominantly females if incubated above it (Lance 2009). However, in tuatara, females are produced at low temperatures and males if it is warm (Bull 1980). In crocodylians, some turtles, and lizards, males are more prevalent at intermediate temperatures and females at both warmer and colder temperatures (Graves 2008).

Temperatures that produce female lizards will in some cases exert feminizing effects on behavior, and temperatures that produce predominantly males tend to have masculinizing effects on behavior. This is the case in the leopard gecko *Eublepharis macularius* (Flores and Crews 1995), whereas no similar effect was observed in jacky dragon lizards *Amphibolurus muricatus* (Warner et al. 2010). There can also be interaction between egg incubation temperature and egg size as in the veiled chameleon *Chamaeleo calyptrotus* (Andrews 2018). At 28°C, females are more likely to be produced from large eggs and males more likely to be produced from small eggs, while at 25 and 30°C, the pattern of sex allocation is reversed.

EVOLUTION OF ESD SYSTEMS

Several factors have been proposed to drive the evolution of ESD systems. Among these are sexual dimorphism, unequal survival rates of the sexes, different ages at maturity, inbreeding avoidance, and mating competition (Bókony et al. 2019). However, the prime hypothesis explaining environmental sex determination was first formulated by Charnov and Bull (1977), which predicts that selection favors ESD over genetic or chromosome-based sex determination when the fitness of each sex varies differently among environments. A specific environment makes it beneficial to become one sex and not the other. By that, they formulated a conceivable, common mechanism for why it might be favorable to develop into a male at some temperatures, but a female at other temperatures.

The Charnov and Bull (1977) model appears to hold for Atlantic silverside *Menidia menidia* (Conover 1984). Atlantic silversides

occurring at different latitudes compensate for differences in thermal environment and seasonality by adjusting the sex ratio according to the prevailing temperature (Conover and Heins 1987). Environmental temperature may serve as predictor of seasonality, and each sex is produced at the time of year when its fitness is maximized. Similarly, Warner and Shine (2005), using short-lived, early maturing jacky dragon lizards, investigated how seasonality influenced sex determination. TSD allowed overproduction of daughters early in the nesting season and sons later. Early hatching enhanced body size during the first year and allowed females to reproduce in the second year, one year younger than females produced late in the season. These authors incubated eggs at different temperatures, deconfounded sex and incubation temperature, and quantified their lifetime reproductive success in field enclosures. Warner and Shine (2005) interpreted this pattern as adaptive because any early maturing males were still too small in the second year to compete efficiently for territories with older, larger males. Thus, unlike young females, juvenile males presumably benefit from an additional year of growth prior to maturity. Furthermore, Warner and Shine (2008) showed that incubation temperature affected reproductive success differently in males and females, and that fitness of each sex was maximized by the incubation temperature that produced that sex. Similar results were shown for the scincid lizard *Niveoscincus microlepidotus* (Shine 2005) and agamid lizard *Agama picticauda* (Steele and Warner 2020). They found that females produced from female-biased incubation temperatures had greater survival than those from male-biased temperatures, and male survival was lowest for individuals produced from a female-biased temperature. As an alternative to these studies indicating that the sexes produce most offspring at different temperatures, Lawson and Rollinson (2021) revisited the sex allocation theory and found support for that in long-lived chelonians and crocodylians, where males are produced at optimal incubation temperatures optimizing health and vigor whereas females are produced at less beneficial temperatures. This is because

reproductive success of males depends largely on the number of matings they perform whereas the fitness of females is constrained by the number of mature eggs they produce, which is less dependent on health and vigor. Lawson and Rollinson (2021) based their study on data from 28 investigations that supported their hypothesis.

Not all studies lend support to these adaptive hypotheses. For instance, sexes may change at extreme temperatures that the organisms do not experience under conditions they encounter in nature such as in sockeye salmon *O. nerka*, rainbow trout *O. mykiss*, and Nile tilapia *O. niloticus* (Tessema et al. 2006). In such cases, a hormonal stress mechanism is probably responsible for the sex determination.

In reptiles, TSD may influence nest-site selection by mothers adjusting offspring sex ratios by choosing nest sites that will have special thermal properties (Mitchell et al. 2013). TSD systems in reptiles are chiefly found in places where the sexes mate and nest at approximately 25°C, which is at low but not high latitudes (Cornejo-Páramo et al. 2020). TSD may be disadvantageous in patchy environments and under variable climatic conditions. There, GSD may be selectively favored (Cornejo-Páramo et al. 2020). However, there is still little empirical evidence that underpins the Charnov-Bull (1977) hypothesis. Booth (2018) calls for more studies that may show how TSD is adaptively favorable as this is important knowledge, for instance, under the present conditions of rapid climate warming. Increased temperature regimes may influence the distribution and sustainability of TSD species by influencing sex ratios and long-term productivities.

KNOCK-ON EFFECTS ON MORPHOLOGICAL AND PHYSIOLOGICAL TRAITS

There is a distinct relationship between body shape and function of animals (Arnold 1983). For instance, body shape and size of appendages influence their ability to move, compete for resources, and escape from threats and survive. Research shows that thermal influences at the embryo stage have knock-on effects on later expressed morph-

ological traits with evidence from studies of fish, amphibians, and reptiles. These morphological changes are associated with their behavior and physiology, influence their defense capacity and fitness, and are therefore probably adaptive.

TEMPERATURE

It is well known that temperature has a direct effect on the body size of ectotherms (Atkinson 1994). However, it is less well known that temperature during embryonic development has knock-on effects on the morphology and size of larvae, juveniles, and adults. In the following, we provide several examples.

Fish

Egg incubation temperature may influence body shapes of juvenile teleosts (Corral and Aquirre 2019). For instance, body shape differentiation from hatching to larval metamorphosis of European sea bass *D. labrax* is influenced by the temperature experienced by the embryos in the eggs. Georgakopoulou et al. (2007) incubated eggs at two temperatures, 15°C and 20°C, and observed that sea bass incubated at 15°C had a slenderer body shape than those incubated at 20°C. Furthermore, Sfakianakis et al. (2011a) demonstrated a similar body shape effect of embryo temperature on larval zebrafish *D. rerio*. Low water temperature at the embryo stage may prepare the offspring for relatively low temperature later, as a more streamlined body improves swimming performance and the probability to escape endothermic predators, which in contrast to ectotherms perform well even at low temperatures (Blake 2004; Sfakianakis et al. 2011b). However, a slenderer body shape makes sea bass an easier target for gape-limited predators, which may be a disadvantage (Nilsson and Brönmark 2000).

On the other hand, a study on juvenile Atlantic salmon *Salmo salar*, which is a cold water species, demonstrated that higher egg temperature, 6 versus 3°C, resulted in juveniles with more streamlined bodies and smaller pectoral fins (Greenberg et al. 2021; Table 1).

TABLE 1
Phenotypic effects of increased egg incubation temperature of fish

Species	Effect	References
Sea bass <i>Dicentrarchus labrax</i>	Stouter body shape	Georgakopoulou et al. (2007)
Zebrafish <i>Danio rerio</i>	Stouter body shape, poorer swimming performance	Sfakianakis et al. (2011a,b)
	Changed expression of genes involved in energy metabolism, angiogenesis, cell stress, muscle contraction, and apoptosis and thermal acclimation capacity	Scott and Johnston (2012)
Atlantic salmon <i>Salmo salar</i>	Slenderer and more streamlined body shape and smaller pectoral fins of juveniles	Greenberg et al. (2021)
	Higher maximum growth rate and larger at adulthood, larger gonads, and eggs scaled for body size	Finstad and Jonsson (2012); Jonsson et al. (2014)
	Younger at smolting	Burgerhout et al. (2017)
	Later return from the ocean for spawning	Jonsson and Jonsson (2018)
Senegalese sole <i>Solea senegalensis</i>	Enhanced energy production and growth rate	Carballo et al. (2018)
Haddock <i>Melanogrammus aeglefinus</i>	Enhanced growth of fry	Martell et al. (2005)
Common carp <i>Cyprinus carpio</i>	Enhanced growth of fry	Korwin-Kossakowski (2008)
European whitefish <i>Coregonus lavaretus</i>	Polyphenism	Steinbacher et al. (2017)

Warmer water has lower solubility of oxygen, and for Atlantic salmon, which is an oxygen-demanding species, a more streamlined body means that they require less oxygen for swimming, and more easily perform normal functions without exceeding the aerobic scope. This reduces the likelihood of mortality. Even in fully oxygenated water, their performance is constrained by the oxygen content in the water at temperatures above 18–20°C (Jonsson and Jonsson 2011). The slimmer body shape and smaller pectoral fins may be beneficial for cruising fish in lakes and oceans, but may be disadvantageous for salmon fry before they smolt and migrate out of the nursery river. Young Atlantic salmon typically live in turbulent, fast-flowing rivers where they rest their pectoral fins on the bottom, and make short excursions to take drifting food items. In rivers and streams, a deeper, laterally more compressed body shape with more flexible maneuverability may be advantageous during swimming (Webb 1984). Thus, there may also be a fitness cost involved in this morphological flexibility. Atlantic salmon fry tend to smolt younger when the eggs are incubated in warmer water (Burgerhout et al. 2017),

but we do not know if they also smolt smaller, although this is a reasonable suggestion, because younger smolts are often smaller (Økland et al. 1993; Vanhooydonck and Van Damme 1999). Experiments with brown trout *Salmo trutta* indicate that this fish will leave the nursery river earlier and smaller when the eggs are incubated in warmer water (Jonsson and Greenberg 2022).

How can temperature during embryogenesis influence morphological traits? Proximate causes are changes in skeleton and muscle development. Tåning (1952) reviewed experiments showing that the average number of vertebrae of brown trout varied with temperature during embryonic development. At 6°C constant temperature, this fish developed the fewest vertebrae, and more vertebrae developed at lower and higher temperatures. Vertebral numbers were determined during gastrulation when the embryo was about 165 degree-days old. Tåning (1952) also reported that the number of rays in the dorsal, anal, and pectoral fins of brown trout varied with embryo temperature. The highest number of fin rays in the dorsal and pectoral fins were developed at 8–10°C, and at 5–6°C in the anal fin. Later, relationships between

water temperature at early ontogeny and meristic characters have been demonstrated for some other fishes, for instance, galaxids (McDowall 2003, 2008), ladyfish (Elopidea; McBride and Horodysky 2004), Atlantic silverside (Billerbeck et al. 1997), and three-spined sticklebacks *G. aculeatus* (Ahn and Gibson 1999). The effect of increased temperature may also be transferred from parents to offspring. In mangrove rivulus *K. marmoratus*, Swain and Lindsey (1986) showed that a parental temperature of 30°C produced offspring with fewer vertebrae, pectoral, and caudal fin rays than it does when incubated at 25°C. With the change in vertebral numbers, body shape and fin sizes are altered (Aquirre et al. 2019), which may influence the swimming performance of the species (Swain 1992). Furthermore, Corral and Aquirre (2019) studying *Astyanax mexicanus* showed that number of precaudal vertebrae increased at low embryo temperatures, and caudal vertebrae increased at high embryo temperatures. Thus, high and low temperatures may affect their swimming performance differently, although the numbers of vertebrae are similar.

Early temperature also influences the rate of myogenesis, including composition of the functional structures within the cells, number, size, and distribution of muscle fibers, fiber diameters, myofibril areas, and the development of heart muscle (Johnston 2006; Scott and Johnston 2012). Atlantic salmon fry, incubated at higher temperatures, develop larger but fewer muscle fibers than those incubated at lower temperatures (Stickland et al. 1988; Johnston 2006). Similarly, incubation temperature influences growth and muscle cellularity in Senegalese sole *Solea senegalensis* (Carballo et al. 2018), suggesting a generality of this finding. By affecting muscle development, embryo temperature may also affect the swimming performance of the fish.

Prehatching temperature appears to be the environmental cue informing organisms whether they will later experience relatively warm or cold climates. The countergradient variation (CGV) hypothesis suggests that cold environments favor high metabolic rates to compensate for the negative effect of low tem-

peratures, and warm environments favor low metabolic rates enabling organisms to conserve energy in otherwise costly environments (Conover and Schultz 1995). This reduces the phenotypic effect of differences in thermal climate. Thus, at least partly, phenotypic effects of temperature experienced by embryos may explain differences in metabolic rates of species with changing altitude or latitude. This plasticity may alter the efficiency of the cardiovascular system or lead to changes in mitochondrial function, resulting in lower metabolic rates and physiological capacities in warmer temperatures. This may stem from altered metabolic activity because of reduced activity of oxidative enzymes such as cytochrome *c* oxidase, citrate synthase, and pyruvate kinase in the swimming muscles (Schnurr et al. 2014). Additionally, elevated developmental temperatures have been shown to alter cardiac anatomy (increased ventricular roundness), lower aerobic exercise performance, and affect gene upregulation in zebrafish. These are conditions that persist into adulthood (Dimitriadi et al. 2018). Thus, CGV may have a purely plastic background not involving genetic variation, illustrating the need for carefully designed studies before interpreting phenotypic differences among populations as genetically based local adaptation (Kawecki and Ebert 2004).

Embryo temperature may influence metabolic rates in accordance with the CGV hypothesis by affecting energy metabolism pathways and acclimation capacity as reported from a study on zebrafish, a much-used model organism (Schnurr et al. 2014). Also, in wild populations, higher egg incubation temperature reduces metabolic rates and aerobic scope as shown for juvenile brown trout (Durtsche et al. 2021), and standard metabolic rate of brook trout *Salvelinus fontinalis* (Cook et al. 2018). In a common garden experiment, Durtsche et al. (2021) used genetically similar study groups and found that temperature during egg incubation alone produced metabolic patterns among juvenile fish consistent with the CGV hypothesis. This shows that this is a phenotypically plastic trait, which should be taken into account when studying differences among populations in metabolic rates.

TABLE 2
Phenotypic effects on larvae of increased egg incubation temperature of amphibians

Species	Effect	References
Rough-skinned newt <i>Taricha granulosa</i>	Longer and more developed at hatching	Smith et al. (2015)
Oriental fire-bellied toad <i>Bombina orientalis</i>	Larvae have smaller tails, slower locomotor activity	Kaplan (1992); Kaplan and Phillips (2006)
Striped marsh frog <i>Limnodynastes peronii</i>	Higher energy expenditure and thermal tolerance; growth, burst locomotor, and lactate dehydrogenase activity maximized at egg incubation temperature	Seebacher and Grigaltchik (2014)
Chorus frog <i>Pseudacris hypochondriaca</i>	Higher oxygen consumption and critical thermal maximum, slower locomotor activity	Mueller et al. (2019a)

Amphibians

There are studies showing that egg temperature influences the size or morphology of amphibian larvae (Table 2). For instance, larval size of rough-skinned newts *Taricha granulosa* increased with higher temperatures during egg incubation independent of the temperature during larval development (Smith et al. 2015). On the other hand, the tail length and height of oriental fire-bellied toad *Bombina orientalis* larvae decreased with increasing egg incubation temperature (Kaplan 1992; Kaplan and Phillips 2006). Furthermore, temperature variation during egg incubation had positive effects on body length, but negative effects on tail length and height relative to rearing under stable conditions. However, in the wood frog, egg temperature had no effect on the size of the larvae (Watkins and Vraspir 2006), showing that the effect of temperature during embryogenesis differs among species. Whether egg temperature will influence larvae size may depend on the fitness effect in the proper ecological context (Kaplan and Phillips 2006).

In parallel with these morphological conditions, physiological and behavioral modifications occur. Warmer egg incubation temperatures result in higher metabolic rate and thermal tolerance for larvae of the striped marsh frog *Limnodynastes peronii* (Niehaus et al. 2011). Furthermore, the temperature during embryonic development can affect the behavioral performance of the tadpoles, with maximum larvae performances at the incubation temperature. The breadth of the performance curve of burst locomotor per-

formance of the striped marsh frog was greatest when egg developmental and acclimation temperatures coincided. The activity of the glycolytic enzyme, lactate dehydrogenase, paralleled the pattern of burst locomotor performance. The locomotion performance of the tadpoles appears associated with tail size and myofibril activity (Van Buskirk and McColm 2000). Furthermore, the egg incubation temperature can affect oxygen consumption rate and critical thermal maximum as shown for chorus frog *Pseudacris hypochondriaca* larvae (Mueller et al. 2019a). Warmer ambient egg temperatures between 10 and 25°C typically resulted in similar or higher maximum oxygen consumption rate and critical thermal maximum. Increased embryonic temperature raised thermal tolerance, and the effect was retained even following larval acclimation to a colder temperature. Thus, embryonic developmental conditions modulated the performance curves of the tadpoles to better respond to environmental conditions later in life. However, the relationship between incubation temperature and larval physiology and behavior may be species or even population specific and related to whether organisms are breeding in relatively cold or warm habitats.

Reptiles

Morphology and Locomotor Performance

Higher egg incubation temperatures increase metabolic and developmental rates of hatchlings in reptiles, and have knock-on effects on their morphology, body size, and locomotor performance (Table 3). These

TABLE 3
Phenotypic effects of increased egg incubation temperature of reptile hatchlings

Species	Effect	References
Green sea turtle <i>Chelonia mydas</i>	Better swimming performance Developed faster and were smaller at hatching	Burgess et al. (2006) Stubbs and Mitchell (2018)
Loggerhead sea turtle <i>Caretta caretta</i>	Lower growth rate, faster crawling and initial swimming speed, better righting response and crawling speed, but poorer sustained swimming, higher blood glucose concentration	Fisher et al. (2014); Kobayashi et al. (2018); Usategui-Martín et al. (2019)
Leatherback sea turtle <i>Dermochelys coriacea</i>	Broader carapaces, shorter flipper reach, slower locomotion	Mickelson and Downie (2010)
Smooth softshell turtle <i>Apalone mutica</i>	Faster growing, faster locomotion	Janzen (1993)
Snapping turtle <i>Chelydra serpentina</i>	Smaller hatchlings with lower resting metabolic rate and thyroxine level	Packard et al. (1987); O'Steen and Janzen (1999); Steyermark and Spotila (2000)
Cagle's map turtle <i>Graptemys ouachitensis</i>	Lower innate immune response	Freedberg et al. (2008)
Softshelled turtle <i>Pelodiscus sinensis</i>	Lower immune competence and higher mortality; immunorelated enzyme activity, and best growth at intermediate temperatures	Du and Ji (2003); Li et al. (2013); Dang et al. (2015)
Painted turtle <i>Chrysemys picta</i>	Shorter and thinner with slower growth and locomotor activity, and preferred lower temperature	Tamplin and Cyr (2011); Warner et al. (2011)
Bearded dragon lizard <i>Pogona vitticeps</i>	Grew more slowly, were slower at learning and completing social tasks, but ran and fed faster	Siviter et al. (2017, 2019)
Jacky dragon <i>Amphibolurus muricatus</i>	Slower growth, smaller hatchlings, poorer survival	Esquerré et al. (2014)
Wall lizard <i>Podarcis muralis</i> ; Grass lizard <i>Takydromus wolteri</i> ; Oriental garden lizard <i>Calotes versicolor</i>	Slower growth, smaller hatchlings with shorter appendages, and poorer locomotor performance	Van Damme et al. (1992); Braña and Ji (2000); Pan and Ji (2001); Ji et al. (2002)
Maccay's skink <i>Nannoscincus maccoyi</i>	Shorter body and tail, ran slower, reacted less strongly to snake scent, and were more vulnerable to snake predation	Downes and Shine (1999)
Garden skink <i>Lampropholis delicata</i> ; Southern skink <i>Saproscincus mustelinus</i> ; Suter's skink <i>Oligosoma suteri</i>	Longer body and tail, grew and ran faster, reacted more strongly to snake scent, and were less vulnerable to snake predation	Downes and Shine (1999); Hare et al. (2004, 2008)
Three-lined skink <i>Bassiana dupereyi</i>	Larger body size, faster movement speed, and improved learning ability	Amiel and Shine (2012); Amiel et al. (2014)
Cuban rock iguana <i>Cyclura nubila</i>	Faster growth	Alberts et al. (1997)
Madagascar ground gecko <i>Paroedura pictus</i>	Decreased preferred temperature	Blumberg et al. (2002)
Keelback <i>Tropidonophis mairii</i>	Faster locomotion	Bell et al. (2013)

changes appear adaptive and influence their ability to protect themselves in a warmer climate. For instance, hatchlings of green sea turtles incubated at 30°C developed faster and hatched earlier, but smaller than hatchlings incubated as eggs at 26°C. However, they had more residual yolk left that could support dispersal to offshore habitats than those produced at lower temperatures (Burgess et al. 2006; Stubbs and Mitchell 2018). Furthermore, warm-incubated hatchlings had higher stroke rate frequency and larger force output than those incubated at lower temperatures. This may be because muscles of hatchlings from cooler temperatures fatigue at a faster rate than those from warmer eggs (Burgess et al. 2006). These differences may compensate for their smaller size, which make warm-incubated hatchlings more susceptible to predation, and thus result from adaptive priming (Godfrey and Mrosovsky 2006).

Other species may develop different traits that increase predator protection. Warm-incubated loggerhead sea turtles have broader carapaces and swim and crawl at a higher speed because they have a longer flipper reach (Fisher et al. 2014; Kobayashi et al. 2018). However, they have lower sustained swimming performance compared to conspecifics incubated at lower temperatures decreasing the advantage they have from the faster speed. But still, the morphological and behavioral changes may increase survival of the hatchlings in warmer water by this change in predator-avoidance capability (Read et al. 2012; Wood et al. 2014; Sim et al. 2015; Mueller et al. 2019b). Also in garden skinks *Lampropholis delicata*, southern skinks *Saproscincus mustelinus*, and Suter's skinks *Oligosoma suteri*, warm-incubated embryos produce more agile hatchlings that avoided predation better when they develop at higher egg temperatures (Hare et al. 2004, 2008).

Larger body size also protect prey against predation, and the hatchlings of smooth softshell turtles are larger and move faster if they, as embryos, were incubated at relatively high temperatures (Janzen 1993). The same was observed for the three-lined skink *Bassiana duperrayi*, warmer egg incubation temperature increased hatchling body size

and movement speed (Amiel and Shine 2012; Amiel et al. 2014). Also in these cases, the knock-on effects appeared adaptive and increased subsequent survival.

In many cases, however, it is unclear if the knock-on effects increase fitness. For instance, warm-incubated hatchlings are smaller and move more slowly in jacky dragons *A. muricatus* (Esquerré et al. 2014), wall lizards *Podarcis muralis* (Van Damme et al. 1992; Braña and Ji 2000), grass lizards *Takydromus wolteri* (Pan and Ji 2001), oriental garden lizards *Calotes versicolor* (Ji et al. 2002), and Maccoy's skinks *Nannoscincus maccoyi* (Downes and Shine 1999). The latter also has shorter heads, tails, and appendages relative to their body length, and move more slowly than those incubated at lower temperatures. This variation in size and locomotor performance may not be adaptive priming but associated with the sex-determining temperature where only females are developed at extreme temperatures. It is also possible that the offspring are stressed by the extreme temperature, which instead decreases their fitness.

Immune Effect

Immunocompetence is influenced by temperature during embryogenesis. Thus, responses to pathogens vary with embryo temperature in changing environments. Dang et al. (2015) reported that hatchlings of Chinese softshelled turtles *Pelodiscus sinensis* had lower mortalities when eggs were incubated at 24 rather than 28°C (Table 3). Both temperatures are experienced by the eggs in natural nests. Moreover, in Cagle's map turtles *Graptemys ouachitensis*, higher (female-producing) temperatures yielded hatchlings with poorer innate immune response as compared to lower (male-producing) temperatures. Hatchlings from the low incubation temperature had higher immunoglobulin levels (IgM, IgD) and T-cell surface glycoprotein (CD3 γ) expressions than those from warmer incubation temperatures. Furthermore, Les et al. (2009) reported that developmental rates and immune responses of painted turtles *Chrysemys picta* and red-eared sliders *Trachemys scripta* were increased by temperature fluctuation during egg incubation.

The eggs were incubated at temperatures near the critical minimum 23°C or critical maximum 31°C. Near the critical minimum, developmental rate and survival were increased by fluctuations, whereas the opposite was observed near the critical maximum. In addition, individuals incubated with a low frequency of temperature fluctuations had reduced total antioxidant capacity, while incubation at a lower average temperature was associated with enhanced total antioxidant capacity. Total antioxidant capacity differences may be temperature-mediated through changes in metabolic rate (Treidel et al. 2016). Thus, egg incubation temperatures clearly influence developmental rate, immunity and antioxidant capacity, and survival of the hatchlings, and thereby may affect their fitness.

Most studies reporting significant associations between egg incubation temperature and later developing performance traits have not tested potential effects on offspring fitness. But studies on immunity function may correlate with survival of offspring and provide an indirect measure of offspring fitness. This may be a link to understand the role of developmental plasticity in adaptive traits in future studies (Dang et al. 2015).

Cognitive Function and Thermal Preference

The ability to learn quickly and thereby meet environmental challenges provides an adaptive advantage (Amiel et al. 2014), and embryo temperature seems to influence this in reptiles (Siviter et al. 2017). This appears associated with a change in brain anatomy that is influenced by the egg incubation temperature as was demonstrated for bearded dragons (Amiel et al. 2014). Low temperatures during embryogenesis resulted in hatchlings with larger telencephalons and neurons in the median cortices. Offspring incubated at warmer temperatures had fewer neurons in the medial cortex but higher neuronal density. Associated with these differences, hatchlings of scincid lizards incubated in warmer conditions demonstrated enhanced learning ability (Amiel and Shine 2012) as shown by use of Y-mazes, were bolder in the short

term (Siviter et al. 2017), and better able at discriminating colors (Clark et al. 2014).

In bearded dragons and velvet geckos *Amalosa lesueurii*, on the other hand, eggs incubated at colder temperatures yielded hatchlings with better learning ability. Furthermore, Siviter et al. (2017) showed that cold-incubated bearded dragons more quickly learned how to open a slide door in front of food. Dayananda and Webb (2017) and Abayarathna and Webb (2020) demonstrated that the spatial learning ability and survival of this species in the field was better if they came from cold eggs. Higher egg incubation temperature has little if any effect on the critical maximum temperature of velvet geckos (Dayananda et al. 2017; Dayananda and Webb 2020), but may shift the critical minimum temperature upward (Abayarathna et al. 2019).

Egg incubation temperature influences experimentally induced temperature preferences. For instance, snapping turtles incubated at 21.5°C chose 28°C water, while turtles from 30.5°C selected 24.5°C (O'Steen 1998). These temperature preferences were repeatable even after a six-month hibernation period at 7°C. Esquerré et al. (2014) incubated jacky dragon lizards at 25, 28, and 32°C. Hatchlings incubated at 28°C had lower and more stable preferred temperatures than those incubated at higher and lower temperatures. Thus, incubation temperature may influence the preferred temperature of the offspring.

In total, these plastic reactions caused by higher egg incubation temperature are no cure against effects of global warming, but may influence thermal preferences and maternal nest-site selection and affect the ability of offspring to learn novel tasks. These results show that egg incubation temperature influences the social cognitive abilities of oviparous reptiles. In several cases, the effects last beyond the hatchling stage and should affect the fitness of the animals.

GROWTH AND LIFE-HISTORY EFFECTS

Growth and reproductive traits such as fecundity, egg, and gonad size have strong fitness effects (Braun et al. 2013), and embryonic temperature is the main abiotic

factor with knock-on effects that influence growth and life-history traits later in life (Jonsson et al. 2014). Below, we give examples of this indirect thermal effect.

FISH

In fish, temperature influences food consumption rate and growth, given sufficiently high oxygen density in the water. The assimilated energy is used for maintenance, activity, stored within the body (e.g., as growth), and disseminated as gametes. Temperature has a direct effect on the rate of metabolism, and an indirect knock-on effect associated with the temperature experienced during embryogenesis. For instance, temperature during embryogenesis influences growth of juvenile Atlantic salmon (Finstad and Jonsson 2012). Atlantic salmon eggs incubated in warmer water yielded faster growing juvenile offspring than those produced from eggs incubated in colder water (Table 1). The size advantage that warm-incubated offspring acquired lasted to adulthood as shown in experiments by Jonsson et al. (2014). Similarly, Burgerhout et al. (2017) reported that higher egg incubation temperature accelerated growth and developmental rate of juvenile Atlantic salmon, causing them to be younger when they transformed to smolts that tolerate sea water (approximately 35 ‰ salt). However, it is not verified whether younger age at seaward migration results only from being larger, or if they can also be smaller when they smolt and adapt to sea water. The relationship between egg incubation temperature and later growth may be more general as a similar relationship between embryo temperature and later growth has been reported for fish as different as haddock *Melanogrammus aeglefinus* (Martell et al. 2005), common carp *Cyprinus carpio* (Korwin-Kossakowski 2008), and Senegalese sole (Carballo et al. 2018). Exceptions occur, however, as in brown trout, where egg incubation temperature had no significant effect on the growth rate of juvenile fish (Jonsson and Jonsson 2021).

Growth rate depends on the rate of energy consumption of the fish (Jonsson et al. 2001),

and apparently juvenile Atlantic salmon feed more when developed from eggs incubated in warmer water and food presented *ad libitum*. Faster growth rate may compensate for higher mortality and shorter life span in warmer water (Jonsson and Jonsson 2011). A similar relationship between early growth rate and life expectancy was reported for threespined stickleback (Lee et al. 2013).

Temperature during embryogenesis influences energy allocation to eggs and sperm in Atlantic salmon (Table 1). When incubated in warmer water, they later produce larger eggs with higher yolk content, and have higher gonad mass at maturity. Fecundity and age at maturity appear, on the other hand, to be unaffected by egg incubation temperature (Jonsson et al. 2014). Also, females kept at higher temperatures during egg maturation give offspring that in turn produce larger eggs as compared to egg size in females kept at ambient water temperature during maturation (Jonsson and Jonsson 2016). Larger eggs have more yolk, and the offspring may survive better at reduced oxygen concentrations than those from smaller eggs (Einum et al. 2002; Braun et al. 2013). Furthermore, high water temperature reduces the efficiency of yolk conversion to body tissue (Fleming and Gross 1990). This increases the advantage of larger eggs in warmer environments. How this maternal effect is transferred over to subsequent generations is unknown, but possibly it is associated with the transfer of nutrients (Goncalves et al. 2010), energy rich matter (Brooks et al. 1997), or hormones (Gagliano and McCormick 2007; Beddington and Groot-huis 2021) within the eggs.

Temperatures during embryogenesis may influence later behavioral decisions (Table 1). Jonsson and Jonsson (2018) released groups of juvenile Atlantic salmon (smolts) produced from eggs incubated at either ambient (approximately 4°C) or 3°C warmer water temperature. After hatching, both experimental groups were reared under similar thermal conditions. The fish migrated to sea as juveniles, and after feeding in the ocean for one or two years they returned to the experimental river for spawning. Atlantic salmon that were developed from eggs incubated in warmer water returned from the

sea approximately two weeks later in the summer/autumn than adults of the same age developed from colder eggs. The later return was independent of the body size of the juveniles at outmigration and similar for offspring of three different populations tested. Hence, thermal conditions during early development appeared to prepare the offspring, when adult, to spawn later in the year. Later return to a warmer (or earlier return to a colder) river may be advantageous because egg incubation time decreases with increasing temperature, so the fish may spawn later under warmer conditions. The mechanism driving this phenotypic plastic response has not been investigated, but may be linked to the maturation process.

Effects of temperature prior to spawning can influence egg size and reproductive success in threespined sticklebacks. Fuxjäger et al. (2019) reared parental fish at either 17°C or 21°C. Females developed at 17°C produced smaller eggs in 21°C water than those developed in 21°C water, and males that were developed at 21°C exhibited lower overall mating success compared with 17°C males in 17°C water, but higher mating success in 21°C water. Thus, reproductive success was highest when offspring experienced the same temperature during gonad maturation as their parents. In this way, the fitness of offspring was adjusted by the temperature experienced by their mothers during egg maturation, similar to the findings from Atlantic salmon reported above (Jonsson and Jonsson 2016). Whether these effects are adaptive depends on the match between the temperatures experienced by parents and offspring. Fuxjäger et al. (2019) suggest that the mechanistic background of these transgenerational effects may involve maternal provisioning of resources, somatic factors, and parental variation in epigenetic state.

Temperature prior to egg fertilization can affect offspring growth as a maternal effect through changes in egg mass (Mousseau and Fox 1998). For instance, mass of eggs produced by next generation Atlantic salmon females were larger when their mothers experienced warmer water during egg maturation (Jonsson and Jonsson 2016). In spiny chromis *Acanthochromis polyacanthus*, in-

creasing parental temperature by 1.5 or 3°C as compared to the standard temperature of 28.5°C, reduced the length of the breeding season of their offspring. In addition, an increase of 1.5°C yielded earlier breeding offspring, whereas a 3°C higher acclimation temperature of the parental fish gave later breeding offspring. Furthermore, parents acclimated to 3°C warmer water yielded offspring with smaller and fewer eggs (Donelson et al. 2016). The reason for these differences are unknown. Sheepshead minnow *Cyprinodon variegatus*, reared in either 24, 29, or 34°C water for 30 days during egg maturation, produced offspring that had the highest growth rate at temperatures matching those that their mothers experienced during egg maturation. The growth of offspring increased by 30% over one generation, i.e., an order of magnitude more than could be expected in terms of a single-generation rate of adaptive evolution (Salinas and Munch 2012). However, effects of parental temperature on offspring growth vary among species. Shama and Wegner (2014) tested threespined sticklebacks and found that developmental acclimation of mothers at elevated temperatures had negative effects on offspring body size at adulthood. The offspring were smaller when mothers were reared at 21°C than at 17°C. A smaller body in warmer water may be beneficial in terms of lower oxygen demands (Forster et al. 2012), but smaller fish produce fewer offspring, showing that there are also fitness costs involved.

Experimental evidence from studies on guppies *P. reticulata* showed that developmental plasticity can be transferred across more than two generations (Le Roy et al. 2017). These authors reared the F0 generation at either 23°C or 29°C, and their offspring at 26°C in F1, F2, and F3 generations. The positive effect of higher grandmother temperature on locomotor performance lasted these three generations.

Early thermal variability may also affect growth and survival of fish (Hokanson et al. 1977). For instance, Pisano et al. (2019) showed that recently hatched brook trout *S. fontinalis* reared at either constant or fluctuating temperatures with the same mean (10°C) differed in survival and growth.

Variability influenced survival positively and growth negatively relative to stable thermal conditions. They interpreted this in the context of Jensen's Inequality saying that performance at average conditions is unequal to average performance across a range of conditions and will depend on whether the functional relationship between performance and temperature is convex or concave (e.g., Ruel and Ayres 1999). However, virtually nothing appears to be known about effects of variable versus constant prehatching temperatures in fish.

Polymorphism and polyphenism (two or more distinct phenotypes produced by the same genotype) occurs in several fish species. For instance, among salmonid fishes there are differently sized sympatric forms in Arctic charr *Salvelinus alpinus* (Jonsson and Jonsson 2001), whitefishes *Coregonus* spp. (Bernatchez et al. 2010), and brown trout *S. trutta* (Ferguson and Taggart 1991; Ferguson and Prodöhl 2022). Sympatric phenotypes often occur in pairs exhibiting a large and a dwarf form, and sometimes there are more than two sympatric forms of the same species (Snorrason et al. 1994). The morph differentiation is partly inherited (Hindar and Jonsson 1993) and, in several cases, clear genetic underpinnings of morph differentiation have been demonstrated (Bernatchez et al. 2010) along with signals of the divergence history (e.g., Rougeux et al. 2017). However, differences in egg incubation temperature may also lead to phenotypic differentiation.

In a German lake, two forms of European whitefish *Coregonus lavaretus* segregate vertically and show metabolic adaptations to, as well as behavioral preferences for, different temperatures. Steinbacher et al. (2017) revealed that the two forms diverged by incubating embryos at either 2 or 6°C (i.e., the typical temperature during embryogenesis of the two). Both groups of offspring were reared and subjected to similar thermal treatments after hatching. The offspring differentiated in body size and muscle growth depending on the egg incubation temperature; fish incubated at 2°C grew larger than those at 6°C, regardless of whether their parents were large or small whitefish. Results also demonstrated that muscle hypertrophy

(increased fiber size) and hyperplasia (increased fiber number) were similarly affected by thermal histories. Immunolabeling provided evidence that the cellular mechanisms leading to increased growth after cold incubation in both ecotypes were increased proliferation and reduced differentiation rates of muscle precursor cells, most probably associated with epigenetic differences. Similar differences in egg incubation temperatures may initiate polyphenic variation also in other salmonids. According to Scott and Johnston (2012), thermal plasticity arises through changes in physiological and endocrinological pathways, in which epigenetic gene regulation is likely to play an essential role.

Some fish populations are facultatively migratory (Jonsson and Jonsson 1993), and early growth influences whether a fish becomes migratory or not. Migratory white perch *Morone americana* tend to originate from slow-growing, early spawned egg cohorts and residents from later spawned, faster developing individuals (Kerr and Secor 2010). Possibly, the migratory propensity is controlled by an early threshold switch point that determines whether a migratory or a resident phenotype is expressed, and growth during early life may influence the choice made. Decisions about migration, however, may be also taken at later occasions depending on the energetic state of the individuals as reported for brown trout by Forseth et al. (1999).

AMPHIBIANS

Temperature has a direct effect on the rate of development, growth, and life history of amphibians such that tadpoles grow more slowly when incubated from the egg stage in colder water (Darrow et al. 2004; Seebacher and Grigaltchik 2014; Goldstein et al. 2017). This parallels the fact that populations at higher altitudes and latitudes have a longer larval period, are larger at metamorphosis and at adulthood, older at maturity, and produce fewer but larger clutches per year (Morrison and Hero 2003). However, the embryo temperature does not seem to have any effect on growth rate in later developmental stages.

REPTILES

Egg incubation temperature during embryonic development can affect lizard growth. Bearded dragon lizards *Pogona vitticeps* grew faster during 18 weeks posthatching when eggs were incubated at 27°C than 30°C (Siviter et al. 2017, 2019; Table 3).

In some cases, a factor in addition to temperature can influence offspring success. For instance, in some viviparous reptiles, such as McCann's skink *Oligosoma maccanni*, growth rates and phenotypes of hatchlings vary both with thermal conditions and basking opportunities during the ovarian cycle of the mothers (Hare and Cree 2010). Maternal pregnancy success at the same temperature was lower and offspring slower growing and smaller when basking opportunities were constrained, suggesting long-term influences on population dynamics of the basking, possibly related to effects of the ultraviolet light of the sun. Importantly, the latter could partly explain why body size and growth in this species differ with latitude and time of nesting season in some reptiles (Stubbs and Mitchell 2018; Bodensteiner et al. 2019).

Cuban rock iguanas *Cyclura nubila* were studied as long as 14 months posthatching. Also in this species higher embryo temperature increased later growth (Alberts et al. 1997). In Madagascar ground geckos *Paroedura pictus*, high embryo temperatures decreased the preferred temperature of the hatchlings (Blumberg et al. 2002). However, many of the changes measured for hatchlings may not proceed to the adult stage. For instance, egg incubation temperature did not influence thermal tolerance of adult brown anoles *Anolis sagrei* (Gunderson et al. 2020). Overall, few studies have evaluated the effects on subsequent adult phenotypes needed to estimate the fitness gain of the plasticity, which is important when evaluating possible effects of, for example, climate change (Mitchell et al. 2018; Noble et al. 2018).

PHENOTYPIC EFFECTS OF PREDATORS

Predator-prey interactions are a central theme in ecology because removal of prey

has major effects on the function of ecological systems. However, there are also important nonconsumptive effects on prey that reduce the likelihood of being detected, captured, and eaten (Lima 1998) and influence prey density and fitness (Peacor et al. 2020; Wirsing et al. 2021). Phenotypic effects are changes in shape and mobility that make the prey more difficult to consume and/or increase the mobility helping them to escape. Also, increased rate of growth helps prey to exceed the gape size limitations of a predator. Predation is often strongest shortly after hatching (Elliott 1994), and cues experienced at the embryo stage can initiate the full suite of prey responses mentioned above. In some cases, maternal prey recognition can trigger similar reactions with effects across generations. Already during embryogenesis, many species have an innate ability to recognize predator cues (Bestion et al. 2014). A large literature quantifies prey plastic responses on body shape, life history, physiology, and behavior in relation to predator cues, which we review in more detail below.

FISH

Early exposure to predators can influence body shape of potential prey improving predator avoidance behavior (Table 4). For instance, fry shorter than 12 mm of both eastern mosquitofish *Gambusia holbrooki* and western mosquitofish *Gambusia affinis* responded phenotypically to early predator cue exposure of largemouth bass *Micropterus salmoides* by developing more streamlined and hydrodynamic body shape and wider caudal area (Arnett and Kinnison 2017). This led to stronger propulsion effect and less drag when swimming, positively affecting movement efficiency and improving opportunities to avoid predator threats. The behavior of the prey species differed, however, as western mosquitofish became bolder and were more plastic in this trait when exposed to early cues of predators as compared to eastern mosquitofish that became shyer. Possibly, bolder behavioral types may be more plastic in their behavioral tendencies in the presence of predators (Thomson et al. 2012).

Male fathead minnows *Pimephales promelas* change their morphology in response to predation risk. With early alarm cue exposures males develop deeper heads and bodies, shorter caudal peduncles and tails, and longer dorsal fin basis (Meuthen et al 2019). Furthermore, Kusch and Chivers (2004) showed that fathead minnow embryos that were exposed to cues of predatory crayfish, hatched earlier so they could seek shelter and, by that, reduce predation risk. However, early hatching involves a cost by reducing developmental time within the egg. Embryos responded differently to different kinds of predators. If embryos were exposed to adult alarm cues, they did not exhibit early hatching as they did when exposed to embryo predator cues. This demonstrates ontogenetic specificity in the hatching response of embryonic minnows (Horn and Chivers 2021a). Furthermore, embryonic exposure to one of three different concentrations of an alarm cue (skin from adult fathead minnows) were paired with the odor of predatory northern pike. Then the offspring were tested after between 102 and 319 days, and juvenile fish from all three groups responded to the predator odor by reducing their movements (Horn and Chivers 2021b). However, only those exposed to the highest concentration of the alarm cue increased their shelter use. These responses were maintained over at least 10 months and show that the conditioned juveniles were threat sensitive and could distinguish between degrees of predation risk.

Embryonic predator cues can also induce increased growth at the juvenile stage, but this may decrease adult body size as reported from a study on threespined stickleback (Bell et al. 2011). Juveniles exposed to predator cues early grew faster initially, but matured younger and therefore smaller when exposed to cues of predatory rainbow trout *O. mykiss* (Table 4). The increased early growth of juvenile sticklebacks appeared adaptive because larger juveniles were more likely to escape predation and, hence, were expected to surpass the the gape limitation of the predator sooner. Early growth stagnation and smaller adult size may be a cost of rapid growth and development (Bell et al. 2011).

Other species may grow larger in the presence of gape-limited predators. For example, crucian carp *Carassius carassius* reared in water with olfactory cues of predatory northern pike *Esox lucius* developed larger and deeper bodies that sooner exceeded the gape-size limitations of the pike (Brönmark and Pettersson 1994). Deeper bodies are also beneficial by producing more thrust that increases bursting abilities of the crucian carp (Domenici et al. 2008). On the other hand, deep-bodied fish experience higher drag, and therefore experience an energetic disadvantage during cruising compared with more shallow-bodied fish (Webb 1984). Thus, plastic responses in morphology may enhance the survival of prey species occurring in sympatry with predators at the cost of higher energy use when swimming. It is not known, however, at which stage crucian carp are sensitive to cues of northern pikes.

Predator stress can influence egg size transgenerationally. When maturing female threespined sticklebacks were exposed to the threat of predation, they produced larger eggs with higher cortisol content, which consumed more oxygen shortly after fertilization compared with untreated control fish (Giesing et al. 2011). As juveniles, the offspring of predator-exposed mothers exhibited tighter shoaling behavior, which is an anti-predator tactic. The higher cortisol content may give the offspring a metabolic advantage, and larger eggs have a positive effect on fry feeding and swimming abilities. This may give fry a survival advantage in a high predation environment. However, there is a tradeoff between size and number of eggs (Jonsson and Jonsson 1999). With larger investments in each egg, there will be fewer eggs produced. In parallel, predator cues perceived by the mouth brooding, striped goby *Eretmodus cyanostictus* produced larger and heavier eggs with more yolk, but smaller clutches than conspecific females without prior predator experience (Segers and Taborsky 2012). Apparently, the mothers prepared their offspring for challenges that they might meet after birth by adjusting the amounts of yolk serving as food for the larvae. Thereby, they increase the size of the offspring at the commencement of external

TABLE 4
*Examples of how predator cues affect the development of morphological
 and life-history traits of fish and amphibians*

Taxonomic group	Affected species	Predators	Traits changed	References
Fish	Eastern mosquitofish <i>Gambusia holbrooki</i> ;	Largemouth bass <i>Micropterus salmoides</i> ;	Slenderer body, wider caudal peduncle, males	Arnett and Kinnison (2017)
	Western mosquitofish <i>G. affinis</i>	bluegill sunfish <i>Lepomis macrochirus</i>	smaller gonopodium, personality changed	
	Fathead minnow <i>Pimephales promelas</i>	Crayfish, skin of adults; northern pike <i>Esox lucius</i>	Deeper body, shorter caudal peduncle and tail fin, longer dorsal fin base in males, and behavioral changes	Kusch and Chivers (2004); Meuthen et al. (2019); Horn and Chivers (2021a,b)
	Crucian carp <i>Carassius carassius</i>	Northern pike <i>Esox lucius</i>	Deeper bodies	Brönmark and Pettersson (1994)
	Guppy <i>Poecilia reticulata</i>	Millet <i>Crenicichla alta</i>	Offspring smaller at birth	Monteforte et al. (2020)
	Threespined stickleback <i>Gasterosteus aculeatus</i>	Rainbow trout <i>Oncorhynchus mykiss</i>	Offspring with faster growth of juveniles, younger and smaller adults, larger eggs, changed social behavior	Bell et al. (2011); Giesing et al. (2011)
	Striped goby cichlid <i>Eretmodus cyanostictus</i>	Hore's haplo <i>Ctenochromis horei</i>	Offspring with larger eggs, smaller egg clutches	Segers and Taborsky (2012)
	Daffodil cichlid <i>Neolamprologus pulcher</i>	Reduced predation risk by introducing guarding helpers	Offspring with smaller eggs, they are less neophobic toward novel objects	Taborsky et al. (2007); Bannier et al. (2017)
	Damselfish <i>Acanthochromis polyacanthus</i>	Coral trout <i>Plectropomus leopardus</i>	Offspring with increased heart rates	Atherton and McCormick (2020)
	Amphibians	Red-eyed treefrog <i>Agalychnis callidryas</i>	Nicaraguan mosquitofish <i>Gambusia nicaraguensis</i> ; globe skimmer <i>Pantala flavescens</i> ; hemipteran <i>Belostoma</i> sp.	Larvae developed deeper tail muscles and fins, and darker pigmentation
Streamside salamander <i>Ambystoma barbouri</i>		Flatworms <i>Phagocotus gracilis</i> ; green sunfish <i>Lepomis cyanellus</i>	Delayed hatching	Sih and Moore (1993); Moore et al. (1996)
Ringed salamander <i>Ambystoma annulatum</i>		Cannibalistic ringed salamander larvae	Reduced activity and greater shelter-seeking behavior	Mathis et al. (2008)
Green frog <i>Rana clamitans</i>		Freshwater leech <i>Macrobdella decora</i> ; freshwater leech <i>Nepheleopsis obscura</i> ; nymphs of <i>Aeschna canadensis</i>	Accelerated or delayed development and hatching depending on the predator type	Schalk et al. (2002); Ireland et al. (2007)
Gray treefrog <i>Hyla versicolor</i>		Nymphs of <i>Aeschna</i> ; crawfish Cambarinae; freshwater leech Euhirudinae	Slower development and smaller larvae	Smith et al. (2005)

TABLE 4
Continued

Taxonomic group	Affected species	Predators	Traits changed	References
	Agile frog <i>Rana dalmatina</i>	Emperor dragonfly <i>Anax imperator</i>	Hatched smaller and later with stronger antipredator response	Gazzola et al. (2015)
	American toad <i>Anaxyrus americanus</i> ;	Green darner <i>Anax junius</i> ;	Hatched earlier, were less developed, and more so in presence of	Skelly and Werner (1990); Wilbur and Fauth (1990); Touchon et al. (2006); Watkins and Vraspir (2006); Smith et al. (2009)
	Wood frog <i>Rana sylvatica</i>	eastern newt <i>Notophthalmus viridescens</i> ;	pathogenic water molds (Saprolegniaceae)	(2006); Watkins and Vraspir (2006); Smith et al. (2009)
	Common frog <i>Rana temporaria</i>	pathogenic water molds Saprolegniaceae Freshwater leech <i>Haemopsis sanguisuga</i> ;	Population-specific effects on body proportions, developmental rate, and size at hatching	Laurila et al. (2002); Orizaola et al. (2013)
Reptiles	Common lizard <i>Zootoca vivipara</i>	Nymphs of <i>Aeshna</i> spp.; Threespined stickleback <i>Gasterosteus aculeatus</i>	Offspring had longer tail relative to body length, selected lower temperatures, and dispersed more	Bestion et al. (2014)
	Scincid lizard <i>Pseudemoia pagenstecheri</i>	Green whip snake <i>Hierophis viridiflavus</i>	Offspring were heavier, had longer tails relative to body length, and were more sensitive to snake odor	Shine and Downes (1999)

feeding. This should improve their likelihood of survival, as predation risk is highest when they start external feeding. Similarly, in the daffodil cichlid *Neolamprologus pulcher*, mothers adjusted egg size according to selective forces offspring might experience (Tabor-sky et al. 2007). When offspring were cared for by parents or alloparents (individuals that are not biological parents but undertake parental tasks), protection reduced the predation risk of the offspring, and the mothers reduced their investment in yolk per egg (Table 4).

Recently, Atherton and McCormick (2020) provided evidence of transgenerational predator recognition. Breeding damselfish *A. polyacanthus* were subjected to treatment with cues of predatory coral trout *Plectropomus leopardus*. In response to the exposure of the

predator cues of the parents, the offspring exhibited a mean increase in heart rate two times higher than that of offspring from untreated parents in the control groups. Possibly, the heart rate increase prepared the offspring against predator attacks. On the other hand, there are also examples showing that predator-exposed mothers can give offspring a disadvantage. Guppies (*P. reticulata*) are live bearers and, in the presence of predators, females reduce the time from egg fertilization to parturition (Evans et al. 2007), resulting in smaller offspring (Monteforte et al. 2020). By that, the females increase their own likelihood of survival, but they produce smaller offspring with impaired locomotor skills. This may be a stress reaction caused by the predation threat during gestation. Thus, there are differences across species as to

whether predator cues produce a positive or negative phenotypic effect on the offspring.

AMPHIBIANS

Predator cues adaptively change morphology and behavior of amphibians (Table 4). Chemical cues indicative of predator presence exposed to eggs may change behaviors of tadpoles. For instance, after hatching, ringed salamanders *Ambystoma annulatum* showed reduced activity and more pronounced shelter-seeking behavior (Mathis et al. 2008), whereas larvae that had not been exposed to similar predator cues at the egg stage did not show similar avoidance behavior. Thus, “negative” experiences at the egg stage appear to prime the offspring for a more adequate behavior after hatching in a more risky environment.

Darker coloration camouflaging the tadpoles appears to be a general response to predator cues in *Hyla* spp. (Kruger and Morin 2020). Furthermore, morphological changes are observed in tadpoles when the eggs are incubated in water with predator cues. Tadpoles of the common European frog *Rana temporaria* developed shorter bodies and deeper tail fins when they, as eggs, were exposed to diving beetle *Dytiscus marginalis* larvae (Laurila et al. 2001). Similarly, red-eyed treefrog *Agalychnis callidryas* tadpoles developed deeper tail muscles and larger fins and became darker in coloration when exposed to cues of fish predators at the egg stage (Touchon and Wojdak 2014). However, the tadpoles altered morphology to a lesser degree when exposed to dragonfly naiads or waterbugs than to fish, indicating that amphibians can distinguish between the severity of threats and respond accordingly.

The phenology of amphibian prey may also change when predator cues are present. For instance, egg hatching time can change according to perceived predation risk. Egg hatching in streamside salamanders *Ambystoma barbouri* was delayed in response to chemical cues of flatworms that prey on larvae but not on eggs (Sih and Moore 1993; Moore et al. 1996). With later hatching, the embryos were more developmentally advanced, making the larvae better able to escape predation.

The embryos also delayed hatching in response to cues of sunfish (Centrarchidae) that prey on salamander larvae. In some other cases, however, eggs hatched earlier in the presence of predator cues. Offspring of the red-eyed tree frog *A. callidryas*, which has their eggs attached to tree branches hanging out over water, hatched early when they are attacked by snakes, and the tadpoles escaped by rapidly falling into the water below (Warkentin 1995, 2005). Incidental acoustic and vibrational cues generated by predator attacks induced hatching, and the embryos distinguished between vibrations caused by predators and other environmental occurrences (Caldwell et al. 2009). The aquatic predators were less effective in preying on tree-frog larvae than the arboreal snakes. The earlier hatched larvae experienced higher mortality posthatching (Willink et al. 2014), but faster growth to metamorphosis, and they left the water with longer tails. This at least partly compensated for being younger and smaller at hatching (Touchon et al. 2013; Touchon and Wojdak 2014). Similarly, embryos of American toads *Anaxyrus americanus* hatched early in response to chemicals from crushed conspecific eggs, a putative cue of predation (Skelly and Werner 1990; Wilbur and Fauth 1990). Furthermore, presence of green darner *Anax junius* (Aeshnidae) larvae and predatory eastern newt *Notophthalmus viridescens* had a similar effect on the American toad. In parallel, wood frog embryos hatched early in response to predatory mosquitofish (Watkins and Vraspir 2006), whereas green frog embryos accelerated hatching in response to cues from an egg-eating leech and delayed hatching in response to cues from a dragonfly that preys on tadpoles but not on eggs (Ireland et al. 2007). In other cases, hatching is delayed in response to predator cues as, for instance, in green frogs *Rana clamitans* (Smith et al. 2015) and agile frogs *Rana dalmatina* (Gazzola et al. 2015).

Predator risks can also induce size effects on the prey. In the gray treefrog *Hyla versicolor*, tadpoles were smaller when exposed to cues of various invertebrate predators during embryogenesis, and when cues of predatory leeches were used, the tadpoles were both smaller and older at hatching

(Smith et al. 2005). Furthermore, agile frog tadpoles exposed as embryos to dragonfly chemical cues (kairomones), were smaller than the control tadpoles. They showed increased neuronal activity when exposed to the predator cue 30 days posthatching, as assessed by the frequency of spontaneous excitatory postsynaptic events. The firing rate of mitral cells was higher among tadpoles from treated versus untreated control groups. At the same time, tadpole activity of agile frogs was reduced because of embryonic predator cue treatment. But unlike the neural activity, the defensive behavior appeared adjusted to the current level of predation risk. If the predator chemical cues were removed from the environment, the antipredator behavioral response disappeared. This is probably because there are costs to pay by the predator defense behavior (Gazzola et al. 2015).

At the embryo stage, amphibians can acquire additional information about their future predators, such as level of threat and the time of day that is most dangerous. Ferrari and Chivers (2010) and Ferrari et al. (2010) exposed wood frog embryos to different concentrations of injured tadpole cues paired with the odor of predatory tiger salamanders *Ambystoma tigrinum* between 1500 and 1700 hours for five consecutive days and raised them for nine days after hatching. Tadpoles that had hatched from exposed embryos exhibited stronger antipredator responses to the salamander. Furthermore, responses of tadpoles were stronger when the tadpoles were exposed to salamander odor between 1500 and 1700 hours than before and after. Thus, the tadpoles appeared to foresee when the risk was highest and adjusted the intensity of their antipredator response accordingly because of exposure during embryogenesis.

REPTILES

Reptile eggs are incubated, often buried, on land and responses to predator cues experienced at the embryo stage appear few if any. However, fetus-carrying mothers exposed to predator cues may cause phenotypic effects in offspring as shown for common lizards (*Zootoca vivipara*) exposed to the odor of a lizard-feeding snake (Bestion et al. 2014). Offspring

from predator-exposed lizard mothers grew longer tails, selected lower temperatures, and dispersed three times more than offspring from unexposed mothers. Tail anatomy influences the ability of lizards to escape the grip of predators by breaking, and with the tail functioning as a decoy, the lizard can reach a safe hide (Bateman and Fleming 2009). This is a widespread antipredator defense among most lizard families (Downes and Shine 2001). In addition, the increased dispersal propensity from the risky habitat and moving to a colder and safer habitat is an antipredatory tactic suggesting that mothers adjusted offspring phenotype to enhance their survival in risky natal environments.

Transgenerationally, odors of predators may influence offspring development and size. Shine and Downes (1999) exposed female viviparous scincid lizards *Pseudemoia pagenstecheri* to the scent of sympatric lizard-eating snakes. This treatment increased the size of their offspring at birth. The offspring also had unusually long tails relative to body length, and became highly sensitive to the odor of the snakes. The modifications in body mass, tail length, and response to snake scent probably reduced the offsprings' vulnerability to predatory snakes and constituted a maternal effect on the offspring.

The stress response of the offspring may be mediated by hormonal transfer. Corticosterone is a steroid hormone that surges when the mothers are stressed by predators, and can be administered to animals when simulating predator attacks (Welberg and Seckl 2001). Injection of corticosterone to pregnant common lizards did not alter the size or developmental rate of offspring, but changed their behavioral stress response (Uller and Olsson 2006). Offspring of corticosterone-treated mothers spent a longer time in shelter after predator attacks than offspring of untreated mothers. Thus, differential steroid exposure during development, possibly mediated as a maternal stress response, may explain some of the variation in behavior among individuals in natural populations.

EPIGENETIC MECHANISMS

In the preceding sections we have reviewed different categories of knock-on effects in a

range of vertebrate organisms. For the most part, however, knowledge of the mechanistic underpinnings remain scarce. Epigenetic factors are strong candidates underlying several observed knock-on effects. This would essentially follow the route that environmental factors lead to epigenetic imprints that subsequently affect expression of genes, which ultimately modulates phenotypes. Epigenetics encompasses a number of mechanisms including, but not restricted to, methylation, histone modifications, and microRNAs (miRNAs) that may have later appearing phenotypic effects (Dupont et al. 2009; Anastasiadi et al. 2021b). These mechanisms themselves can interact. For instance, miRNA, short sequences of RNA, interfere with messenger RNA (mRNA) thereby affecting gene expression, but miRNAs can themselves be regulated by methylation of CpG islands (Wang et al. 2013). Hence, whereas significant progress has been made, the mechanistic background of epigenetics is complex and much remains to be learned.

There is evidence that phenotypically plastic adaptations can be mediated by epigenetic mechanisms (Schlichting and Wund 2014; Vogt 2017), and there are numerous examples demonstrating that epigenetic imprints are affected by environmental conditions (Heijmans et al. 2008; Lea et al. 2016; Verhoeven et al. 2016). Yet, whereas methylation scans surveying the full or reduced representations of the genome can be readily applied for studying general epigenetic patterns in different ecological settings (e.g., Le Luyer et al. 2017; Ryu et al. 2018), it is highly challenging to associate specific traits with specific methylated genomic regions. Le Luyer et al. (2017) were able to identify candidate genes with putative functions that were associated with general epigenetic responses of salmonids to hatchery or wild environments, but not specific traits. Similarly, Ryu et al. (2018) analyzed genome-wide methylation in the coral reef fish *A. polyacanthus* and identified candidate genes associated with different temperature regimes but not traits. A third example involves the American eel *Anguilla rostrata*, which is panmictic (Côté et al. 2013) and at the same time shows considerable morphological and life-history var-

iation. Côté et al. (2014) analyzed global gene expression (6144 expressed sequenced tags) in eels from different localities and observed significant differences in expression under different experimental, environmental conditions, even translating into different reaction norms of individuals from different sites. Given the panmictic status of the species, this suggests phenotypic plasticity and an underlying epigenetic background (and/or selection at specific genes in early life stages), although the specific phenotypic traits affected by this are unknown. Finally, a noteworthy example potentially reflecting knock-on effects was reported by Anastasiadi et al. (2021a). They exposed juveniles of European sea bass (*D. labrax*) to a simulated marine heat wave and demonstrated that this resulted in differential methylation at a number of genes relative to a control group. Moreover, for some genes differential methylation also led to differential expression, hence suggesting that this could have important phenotypic effects. When seen in conjunction with a previous paper by the same authors (Anastasiadi et al. 2017), showing altered muscle and organ formation along with DNA methylation and gene expression changes resulting from exposing larvae to a 2°C increase in temperature, then this comes close to bridging the gap between changes at epigenomic and phenotypic levels.

The current general lack of associating epigenomic scans with specific traits is akin to the complexities of identifying the genetic architecture of complex phenotypic traits. Whereas in the latter case efficient methods for genome-wide association studies (GWAS) has led to significant progress (Tam et al. 2019), this requires large sample sizes and remains costly. Using related approaches for associating traits with epigenetic markers is therefore presently mostly realistic for a few model organisms. Therefore, most progress in identifying the epigenetic background of phenotypic traits has been made in cases where candidate genes affecting the specific traits were already known. Below we highlight some examples where the molecular mechanisms underlying knock-on effects have been studied and where epigenetic factors may ultimately be involved. It should be noted that the examples represent within-generational

exposure to environmental cues that then modulate phenotypes later in life. Transgenerational epigenetic imprints, in contrast, are generally poorly documented in vertebrates. It is the current view that at least in mammals and presumably other vertebrates methylation undergoes extensive reprogramming in the germline precluding transgenerational transfer of methylation imprints; however, this view may be up for revision (Anastasiadi et al. 2021b).

SEX DIFFERENTIATION

Environmental sex determination is hormone dependent. The sex can be changed by modulating the activity of steroidogenic enzymes affecting the hormonal environment of the embryo (Janzen 1994). In TSD, the gene expression is thermally sensitive in a short period during embryogenesis (Yntema 1976, 1979; Valenzuela et al. 2003, 2006). The steroid hormones, estrogens in females and 11-oxygenated androgens in males, regulate key physiological steps of gonadal sex differentiation (Baroiller and D'Cotta 2000). The temperature-sensitive cytochrome P450-aromatase enzyme catalyzes the estrogen biosynthesis and feminization by conversion of androgens to estrogens. Thus, changes in sex ratios of populations are mediated by changes in gonadal aromatase gene expression. Can epigenetic factors ultimately explain these mechanisms? A recent study by Ge et al. (2018) on the red-eared slider turtle *T. scripta* has revealed the molecular mechanisms, which implies a strong role of epigenetics. Here, a temperature-sensitive epigenetic regulator histone demethylase *KDM6B* affects methylation/demethylation in the promoter of the sex-determining gene *Dmrt1*.

In fishes, aromatase gene expression is responsible for the balance between androgens and estrogens in the gonads (Guiguen et al. 2010). The aromatase gene is down-regulated by masculinizing temperature treatments, but may not be fully inhibited (Piferrer et al. 2019). Masculinization at high temperatures has been ascribed to stress and elevated cortisol concentration during gonadal sex differentiation (Yamaguchi et al.

2010). Cortisol may promote the level of the androgen 11-ketotestosterone and thereby induce the masculinization as demonstrated for Argentinian silverside *Odontesthes bonariensis* (Fernandino et al. 2012). For Atlantic silverside, Blázquez and Somoza (2010) suggested that an aromatase enzyme encoded by the *cyp19a1b* gene can convert testosterone to 17 β -estradiol, and by that control testis differentiation. There is evidence that DNA methylation in sexually dimorphic gene promoters of aromatase (*cyp19a1a*) is involved in TSD. Hence, in European sea bass Navarro-Martín et al. (2011) identified two of seven CpG loci in the *cyp19a1* promoter that were temperature sensitive, and thermal sex determination appeared partly mediated by changes in the methylation level of the aromatase promoter. In experiments it was found that at high temperatures, juvenile males had double the DNA methylation levels of females in the promoter region of the gonadal aromatase (Navarro-Martín et al. 2011). Exposure to high temperatures increased the promoter methylation levels inhibiting the development of the ovaries. Later, more species have been tested, and mean DNA methylation levels of this gene were less than 50% in ovaries and greater than 75% in testes (Piferrer et al. 2019). Thus, there was higher expression of *cyp19a1a* in ovaries than in testes. Furthermore, DNA methylation levels of the *Dmrt1* encoding the doublesex and mab-3 related transcription factor 1 were approximately 30% in ovaries and less than 10% in testes, also in accordance with higher expression of *Dmrt1* in testes than in ovaries (Herpin and Scharl 2011). Thus, there are inverse relationships between the DNA methylation and expression levels in these two genes (Piferrer et al. 2019). Therefore, they have been used as sex markers in turbot *Scophthalmus maximus* (Ribas et al. 2016) and medaka (Herpin and Scharl 2011).

It should be noted that methylation of other genes may also play a role in environmental sex determination (Piferrer et al. 2019), and histone modifications could be also involved. For instance, histone deacetylation appears involved in the sex differentiation of rice eels *Monopterus albus* (Zhang et al. 2013). For painted turtles, several genes

involved in DNA methylation (*Dnmt3b*) and histone methylation (*Nsd1*, *Setd1a*, *Carm1*, *Prmt1*, *Ash1l*, and *Prdm2*) appears differentially regulated between male and female producing temperatures (Radhakrishnan et al. 2018).

PHENOTYPIC PLASTICITY IN OTHER TRAITS

As an effect of embryo temperature, Scott and Johnston (2012) observed differences in later expression of individual genes involved in energy metabolism, cell stress, and muscle contraction that influenced the reaction norm for growth of zebrafish. The thermal plasticity arose through changes in a multitude of physiological and endocrinological pathways, in which epigenetic gene regulation is likely to play an essential role, as also demonstrated for Senegalese sole where higher egg incubation temperatures enhance the mRNA abundance of thyroid-related genes and of a retinoic acid-degrading enzyme, influence growth performance, and initiate metamorphosis (Carballo et al. 2018). There was also a change in the expression of DNA methyltransferases as well as histone modifications at hatching. In this species, incubation temperature modulates embryogenesis and later development and growth through endocrinological changes. There is an inverse relationship between DNA methylation and embryo temperature that may silence gene transcription (Simonet et al. 2013). Note, however, that this represents an example of associating traits with general epigenetic factors without strictly identifying specific genes and mechanisms, as is also the case for several of the following examples.

Burgerhout et al. (2017) studied body growth of Atlantic salmon developed from embryos incubated at 4° and 8°C until the embryonic “eyed-stage” followed by rearing at the production temperature of 8°C. The warm-incubated fish were about twice as heavy as the cold-incubated fish at smolting and transfer to seawater. Burgerhout et al. (2017) showed that larval myogenin expression was approximately four- to sixfold higher in the fastest growing group treated with heated water than in the other groups. The fast growth was associated with relative low

DNA methylation levels. Thus, DNA methylation appears to play a major role in phenotypic plasticity in structural muscle growth.

Temperature influences the intensity of DNA methylation, and it occurs more abundantly in polar than in tropical and temperate marine species (Kakutani 2002; Varriale and Bernardi 2006). The latter authors also reported that Antarctic icefishes (Channichthyidae) had the highest methylation level that they found. These results confirm the existence of an inverse relationship between DNA methylation and body temperature. However, little is known about its functioning for ecological traits (Simonet et al. 2013). Morán and Pérez-Figueroa (2011) hypothesized that an environmentally induced methylation pattern of the genome, which alters its transcriptional properties, can induce maturation of young male Atlantic salmon (parr), hence being the basis for male size dimorphism of this species. Furthermore, in Atlantic cod *Gadus morhua*, an increase of 4°C during egg incubation resulted in changes in DNA methylation pathways and the expression of genes involved in 1-carbon metabolism (Skjærven et al. 2014). Baerwald et al. (2016) reported that DNA methylation was associated with smolt-transformation in rainbow trout *O. mykiss*. Similar to some other salmonids like, for example, brown trout, this species exhibits populations consisting of both anadromous and nonanadromous phenotypes.

Metzger and Schulte (2018) investigated phenotypic plasticity of threespined sticklebacks and its underlying molecular processes. They found that gene expression changed in response to temperature during early development, and that this could be observed in the muscle transcriptome of adults. Han et al. (2016) reported that the DNA methylation level of the genome increased after short-term exposure (five days) and decreased after long-term exposure (30 days) in cold water (18°C) relative to similar exposures in warm water (28°C). In all, 21% of DNA methylation peaks were differentially affected by cold relative to warm treatments of zebrafish. Methylation of genes involved in multiple cold responsive biological processes were significantly affected, such as the antioxidant

TABLE 5
Effects of embryo temperature and predator cues early in life affecting morphological, ecological, behavioral, and physiological characters later in life

Environmental influence	Character affected	Fish	Amphibians	Reptiles
Embryo temperature	Sex determination	+		+
	Body shape, color, and size	+	+	+
	Length of appendages	+		+
	Growth rate	+		+
	Polyphenism	+		
	Eggs and gonad size	+		
	Metabolic rates	+	+	+
	Thermal tolerance		+	
	Muscle development	+		
	Immune response			+
	Thermal preference and tolerance			+
	Antioxidant capacity			+
	Behavioral decisions	+		
	Locomotor performance	+	+	+
	Learning performance			+
Predator cues	Body shape and size	+	+	+
	Developmental rate	+	+	
	Egg size	+		
	Hatching time and developmental rate		+	
	Neural response		+	
	Transgenerational influence	+		+

For references, see the text.

system, programmed cell death (apoptosis), chromatin modification, and immune system development. These processes are responsive to cold stress through regulation of DNA methylation, possibly in concert with histone modifications (Han et al. 2016).

MicroRNAs are substantial contributors to regulatory networks of development and adaptive plasticity (Jaenisch and Bird 2003; Campos et al. 2014). Experimentally, this was exemplified by Campos et al. (2013), who incubated Senegalese sole embryos at 15° or 21°C until hatching, and then reared the fish at a common temperature of 21°C. The higher incubation temperature was associated with expression of some miRNAs positively related to growth during segmentation and at hatching. The expression of the miRNAs was involved in lipid metabolism and energy production that differed between the temperatures. Furthermore, Bizuayehu et al. (2015) reported that temperature shifts during early ontogeny (embryonic and larval development) affected the miRNA repertoire of Atlantic cod with long-term consequences in the miRNA profile. Long-term effects of

embryonic incubation temperature were observed regarding expression of some miRNAs in juvenile pituitary glands, gonads, and liver. Bizuayehu et al. (2015) concluded that increased sea temperature seemed to affect the life history of Atlantic cod. Thus, miRNAs may play a role in temperature-induced phenotypic plasticity of growth and life-history traits of at least some fishes. However, there is still little knowledge about the mechanisms regulating environmental effects during early life on later emerging traits.

DISCUSSION

SIMILARITIES AND DIFFERENCES BETWEEN FISH, AMPHIBIANS, AND REPTILES

Fish, amphibians, and reptiles are ectothermic, and most have eggs that develop outside the body of the mother. Therefore, environmental influences on embryos are many and strong. Among the most conspicuous similarities are findings that embryo temperature and predator threats influence the morphology of all three groups reviewed (Table 5). However, whether warmer temperature or

increased predator risk lead to more streamlined body shapes and longer appendages or vice versa vary. Color changes are typically associated with daylight camouflage against predators, and the morphological alterations appear associated with locomotor performance and predator defense. We hypothesize that these changes depend on the environmental cue; for instance, whether the organism expects to encounter fewer or more, larger or smaller, endothermic or ectothermic predators, and what habitat they may use later on.

Also, metabolic rates of juveniles typically decrease when the egg incubation temperature increases. As a knock-on effect, organisms incubated as embryos in relatively warm environments prepare for higher temperatures and reduce metabolic rates and aerobic scopes relative to those incubated at a lower temperature. This metabolic effect reduces phenotypic differences between individuals living at different altitudes or latitudes in agreement with the CGV hypothesis (Levins 1968; Conover 1984). CGV may be a reflection of local adaptation (Marcil et al. 2006), but in brown trout, evidence suggests that this is a phenotypically plastic knock-on effect (Durtsche et al. 2021), and possibly this is also the case for other species.

The most noticeable difference among groups concerns the lack of TSD in amphibians (Table 5). However, amphibians exhibit temperature-induced sex reversal, and can change sex even by small changes in temperature, which may play a similar role as TSD does for fish and reptiles (Ruiz-Garcia et al. 2021). Another possible reason could be that embryo temperature may not influence fitness of the sexes differently, as it may do for some fish and reptiles in accordance with the Charnov-Bull (1977) hypothesis. Furthermore, in amphibians embryonic temperature does not seem to influence growth rate or length of appendages as it does for fish and reptiles. Most metamorphosed amphibians live in a different environment than the eggs and larvae and, perhaps, egg temperature is a poor indicator of later climatic conditions for these species.

Predator cues do not seem to influence reptiles at the egg stage in contrast to the other

two groups. Eggs of reptiles have harder shells, are laid on land, and often buried in the soil. Fish and most amphibians have softer egg shells, which typically develop in water. Therefore, reptile embryos may have difficulties in sensing predator cues. This view is supported by the fact that hatchlings of viviparous reptiles—where the mothers nourish their embryos directly as, for instance, in scincid lizards (Shine and Downes 1999) and the common lizard (Bestion et al. 2014)—show predator defense behavior as a maternal effect. In fish, transgenerationally induced predator defense behavior is reported from a few species with well-developed parental care (Taborsky et al. 2007; Giesing et al. 2011; Segers and Taborsky 2012; Atherton and McCormick 2020). We found no examples of transgenerational predator defense among amphibians. To perform studies of transgenerational effects, animals have to be reared for two generations or more. There may be few such long-term experiments with amphibians (Tariel et al. 2020).

There are a number of traits that are only discovered in one of the groups. For instance, in Atlantic salmon there are knock-on effects in egg size, gonad mass, and the timing of adult return to the river from the ocean (Jonsson et al. 2014; Jonsson and Jonsson 2018). In zebrafish, European whitefish, and Senegalese sole, muscle growth is influenced by embryo temperature (Scott and Johnston 2012; Carballo et al. 2018). Furthermore, amphibian larvae may exhibit altered hatching time, developmental rate, and shelter-seeking behavior because of predator cue exposure during embryogenesis (Mathis et al. 2008; Orizaola et al. 2013; Gazzola et al. 2015). These changes may all influence fitness and be favorable if the environmental change is as predicted by the environmental cue.

ADAPTIVE AND NONADAPTIVE CHANGE

The knock-on effects may be adaptive, non-adaptive, or even maladaptive relative to the fitness of individuals. Adaptive effects increase the fitness of organisms and may ameliorate establishment and persistence in new environments. Adaptive plasticity is favored

when the environment varies frequently, and reliable cues inform organisms about what is happening and how to respond adequately (Xue and Leibler 2018).

Developmental knock-on effects initiated at the embryo stage or as a maternal effect should occur when the environment varies predictably, and early environmental conditions are stable indicators of the juvenile or adult environment they will experience later. Similar to local adaptation (Kawecki and Ebert 2004), developmental knock-on effects should evolve through natural selection in response to the environments the offspring are repeatedly and consistently exposed to over evolutionary time, and responses to novel or atypical environments may generally be disadvantageous (Lea et al. 2016). Our ability to predict how species respond to environmental change will at least partly depend on our understanding of knock-on effects (Donelan et al. 2020).

Nonadaptive plasticity means any plastic, phenotypic reaction that is not improving the fitness of organisms, whereas maladaptive plasticity is when the plastic reaction reduces the fitness of organisms. The latter is likely to occur in response to extreme temperatures and novel environmental stress such as influences caused by human-induced habitat changes, exotic predators, and new pollutants not present in the evolutionary history of the species (Levis and Pfennig 2016). In such cases, organisms can be trapped by their evolutionary response and make a poor response to the environmental cue they experience with reduced fitness as the outcome (Schlaepfer et al. 2002; Donelan et al. 2020).

Adaptive plasticity should promote establishment and persistence in a new environment, but depending on how close the plastic response is to the new favored phenotypic optimum (Ghalambor et al. 2007). Gunderson et al. (2017) investigated whether plasticity in heat tolerance was beneficial or not. They calculated the number of days predicted to exceed the heat tolerance limits of 103 ectotherm populations, and found heat tolerance plasticity reduced the predicted number of overheating events. The effects provided greater benefits to amphibians than to reptiles, but overall plasticity in heat toler-

ance benefited both of these ectotherm groups. In most cases studied, the effect on fitness of developmental knock-on effects is unknown.

Not all individuals in a population will benefit from early initiated knock-on effects. In fluctuating environments, there is always the possibility that individuals express a sub-optimal phenotype, e.g., when environments differ from what the early cue indicated (Auld et al. 2010). There are also costs associated with the ability of being phenotypically plastic (DeWitt et al. 1998). Such costs have been suggested in several cases in this review but, in many instances, the cost is unknown (Murren et al. 2015).

ECOLOGICAL SIGNIFICANCE OF KNOCK-ON EFFECTS

Through phenotypic knock-on effects, organisms may better cope with directionally changing conditions (Jonsson et al. 2005, 2014; Finstad and Jonsson 2012; Jonsson and Jonsson 2016, 2018). The phenotypic effects of early environments in Atlantic salmon is an example where knock-on effects are assumed to be adaptive rather than caused by some form of developmental stress. Such changes may be particularly important for invasive species as they facilitate colonization of novel habitats (Vogt 2017; Ardura et al. 2018). It is assumed that invasive species typically exhibit higher phenotypic plasticity than noninvasive species although the plasticity is not always associated with a fitness benefit, especially when resources are limited (Davidson et al. 2011; Wang and Althoff 2019). Also, in cases of indigenous species where individuals may stray from their home environment into different environments, knock-on effects could be important. For instance, in Atlantic salmon, not all adults return to their home river, as some stray and end up in a foreign river (Jonsson et al. 2003). Because of knock-on effects, the offspring may respond to the thermal conditions in the new river, instead of retaining all traits that were favorable in the river of past generations.

Knock-on effects prepare offspring for environmental conditions that they may

encounter later. This can contribute to adequate responses as it facilitates adaptive evolutionary reactions to directional change (Kingsolver and Buckley 2017). This is essential in periods of rapid climate change (Kelly 2019). Similarly, adaptive plasticity may prepare organisms to cope with other changes as those caused by industrialization and urbanization (Alberti et al. 2017).

EPIGENETIC UNDERPINNINGS OF KNOCK-ON EFFECTS

In the preceding sections we have explored the possibility that epigenetic factors play key roles in determining knock-on effects. Despite a current scarcity of results, particularly when relating genome-wide methylation patterns to phenotypic traits, we nevertheless find several convincing cases where methylation of specific genes is involved in determining phenotypic traits later in life, particularly noteworthy in the case of environmental sex determination (e.g., Navarro-Martín et al. 2011; Ge et al. 2018). As DNA methylation is sensitive to environmental changes (Anastasiadi et al. 2017), thermal climate (Varriale and Bernardi 2006), water quality, nutrition, and environmental structure (Morán et al. 2013; Le Luyer et al. 2017), it does seem plausible that epigenetic imprints represent the fundamental “bridge” linking environmental conditions to subsequent change of gene expression affecting phenotypes later in life. However, we also caution against ascribing all knock-on effects to epigenetic mechanisms, particularly due to the unclarified role of transgenerational epigenetic inheritance in vertebrates (Anastasiadi et al. 2021b).

In a broader perspective, what could be the longer term evolutionary significance of knock-on effects? It has been hypothesized that epigenetic mechanisms may have the potential to develop into genetic variation and ultimately trigger speciation, although evidence is still meager (Venney et al. 2020). One such proposed mechanism is “Plasticity First” (e.g., Levis and Pfennig 2016), where phenotypic plasticity leads to a range of phenotypes, some of which are favored by selection. Over time,

mutations fixing the favored phenotypes accumulate and, ultimately, the phenotypes initially resulting from plasticity will have a genetic basis. For example, Smith et al. (2016) hypothesized that heritable epigenetic marks that increase fitness should increase in frequency in populations of North American darters (Percidae), and that these changes may result in novel morphology, behavior, physiology and, ultimately, reproductive isolation.

Whereas “Plasticity First” represents a plausible scenario by which phenotypic plasticity could ultimately turn into genetically based adaptations, it would be premature to conclude that this would be a likely evolutionary outcome of many knock-on effects. The essence of knock-on effects consists in somehow sensing the environment, using this as a cue of the future environment, and modulating the phenotype in order to maximize fitness. Hence, it is exactly the plasticity that is adaptively important, with the relative importance of developmental and/or transgenerational plasticity along with genetic evolution being determined by environmental predictability and accuracy of environmental cues (McNamara et al. 2016).

FUTURE RESEARCH

To better understand the nature of adaptive developmental plasticity, more studies should focus on estimating its costs and benefits for organisms. Early influences can affect the outcome of ecological experiments and, if not taken into account, can lead to wrong interpretations of trait differences among conspecific populations by, for example, reporting that differences are genetically adapted while they in fact are results of early knock-on effects. Such misinterpretation may lead to wrong decisions when managing populations in changing environments.

Many studies on the effects of thermal influences have used constant temperatures in the experiments. This has been criticized as it does not mimic the situation in natural settings where temperatures are variable. According to Usategui-Martín et al. (2019), incubation temperature regimes influence

hatchling performances, and temperature patterns of natural conditions should be used in laboratory tests of thermal effects. Thus, it is important that future studies also include effects of variable or fluctuating temperatures. Varying temperatures may influence the size of the thermal effects, but will not change the fact that incubation temperature influences later trait development.

Much evidence shows that cues experienced in early life can affect the development of phenotypes with consequences for life in environments encountered at a later stage. As of yet, however, there are few examples that actually test if observed changes are adaptive and improve the fitness of organisms (and the assumption that they are is still controversial; Bateson et al. 2014). Thus, tests of whether observed changes are adaptive are needed, as responses of populations in changing environments are critical to their persistence. Their capacity to display adaptive plasticity to changing environments may determine their future success. One may start by releasing organisms in novel but controlled environments, and measure phenotypic and fitness changes of individuals with embryonic experience from the new environment relative to those with embryo experience from the old environment before being transferred at the time of hatching.

It is hypothesized that environmentally induced plasticity may facilitate and speed up the processes of adaptive evolution (e.g., Ghalambor et al. 2007; Levis and Pfennig 2016). However, there is still little evidence exploring the role of plasticity in facilitating the evolution of natural populations (Warner et al. 2010, 2014) and, consequently, an obvious need for further research.

The understanding of how knock-on effects influence the development of phenotypes will in many cases involve epigenetic processes. Whereas some studies have convincingly demonstrated the role of epigenetics in knock-on effects, the whole field of epigenetics is still in its infancy. Hence, most studies to date have focused on methylation of specific candidate genes, whereas whole genome approaches (e.g., whole genome bisulfite sequencing) could reveal more com-

plex relationships between phenotypes and epigenetic determinants. This will likely be required in order to understand the basis of phenotypic variation for which molecular pathways are poorly understood as compared to, for example, sex determination. We also reiterate the general need for understanding the significance and mechanisms of transgenerational epigenetic inheritance in vertebrates.

CONCLUSIONS

1. Sex of several fish and reptile species is determined by temperature or some other environmental cues during early development.
2. Morphology, life-history, physiological, and behavioral traits of several fish, amphibian, and reptile species are influenced through knock-on effects, by temperature or other environmental factors affecting offspring during egg, embryonic, or larval development.
3. These phenotypically plastic responses may adapt offspring to function better in anticipated, future environments, and appear important for species colonizing novel areas and habitats. Such responses must also be considered important during times of rapid climate or other environmental changes.
4. Epigenetic mechanisms such as DNA methylation, histone modifications, or miRNA may be important for the proposed adaptive programming that occurs without changes in DNA sequences. However, a deeper epigenomic understanding is required that goes beyond the currently few select examples of candidate genes known *a priori*.
5. Adaptive knock-on effects may facilitate evolutionary change and speciation.
6. Future research should investigate mechanisms and fitness effects of early environmental stimuli, and how these induce specific phenotypes.

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