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Dead Spadefoot Tadpoles Adaptively Modify Development in Future Generations: A Novel Form of Nongenetic Inheritance?

Katrina S. Pfennig¹ and David W. Pfennig²

Nongenetic inheritance—involving epigenetic, behavioral, or environmental factors—is increasingly viewed as being important in development and evolution. Here, we describe a possible novel form of nongenetic inheritance in the tadpoles of the Mexican Spadefoot (*Spea multiplicata*): the transmission of information about the environment from dead individuals to living individuals of a later cohort or generation. When we exposed live tadpoles to the remains of desiccated conspecifics from a naturally occurring dry pond, we found that they used phenotypic plasticity to adjust their development in ways that would increase their chances of escaping a drying pond. Specifically, compared to their siblings that were reared with soil lacking tadpole remains, those reared with soil containing desiccated conspecifics grew larger, developed faster, and were more likely to express an alternative, environmentally induced phenotype—a distinctive carnivore morph that is favored in rapidly drying ponds. We also found evidence of underlying genetic variation in the plasticity to produce carnivores, suggesting that this plasticity could mediate adaptive evolution when populations experience different environmental conditions. Such a tendency of living individuals to respond to cues associated with dead individuals from a previous generation may be vital in giving each generation a head start in their environment.

INHERITANCE—the ability to transmit biological information across generations (*sensu* Bonduriansky and Day, 2018)—is a fundamental property of life (Maynard Smith, 1986). Although genes have long been regarded as the sole mediators of inheritance (reviewed in Bonduriansky and Day, 2018), it is becoming increasingly clear that biological information can also be conveyed through various epigenetic, behavioral, or environmental factors; i.e., through ‘nongenetic inheritance’ (Jablonka and Lamb, 1995; Bonduriansky and Day, 2009). Not only can these factors influence phenotype production, they might even mediate evolutionary change (Bonduriansky and Day, 2009).

Research on nongenetic inheritance has focused primarily on epigenetic inheritance (Gilbert and Epel, 2015). This focus is understandable given that epigenetic inheritance is widespread and potentially important for human health (Feinberg, 2018). Yet, there are numerous other mechanisms of nongenetic inheritance, including parental effects as well as cultural, structural, microbiome, and ecological inheritance (reviewed in Bonduriansky and Day, 2018). For instance, ecological inheritance occurs when organisms modify their local environment and then pass to future generations the resulting modified conditions as well as the altered selective pressures that are associated with these new conditions (as when bacteria first evolved photosynthesis and then bequeathed to future generations the resulting increased oxygen levels and modified selective pressures; Odling-Smee et al., 2003). The existence of such diversity of nongenetic inheritance mechanisms points to the need to identify additional examples. Moreover, greater research effort is needed to gauge the extent to which phenotypic change wrought by nongenetic inheritance is adaptive. Most nongenetic changes are likely maladaptive for the same reason that genetic changes are: they both result from errors (Bonduriansky and Day, 2018). However, just as beneficial mutations occur occasionally, natural selection should be

capable of co-opting some nongenetic inheritance mechanisms for adaptive functions. Yet, relatively few studies have investigated the adaptiveness of nongenetic inheritance (for examples, see Bonduriansky and Day, 2018).

Here, we present a novel example of what might constitute nongenetic inheritance: the transmission of fitness-enhancing information about the environment from dead individuals to living individuals belonging to a later cohort or generation. To do so, we studied Mexican Spadefoots, *Spea multiplicata*. This species occurs in deserts of northern Mexico and the southwestern USA where the adults breed, and their tadpoles develop, in highly ephemeral, rain-filled ponds (Pfennig, 1990, 1992a; Fig. 1A, B). These ponds often dry before the tadpoles reach metamorphosis, resulting in the death of an entire cohort and the desiccation of their remains (Fig. 1C). To increase their chances of metamorphosing before their pond dries, tadpoles of *Spea* have evolved two forms of phenotypic plasticity. First, in response to lowering levels of water, they can facultatively speed development (Denver et al., 1998; Morey and Reznick, 2000; Gomez-Mestre and Buchholz, 2006). This response appears to be due to the reduced swimming volume of a drying pond (and perhaps the proximity to the surface) and not to increased temperature, concentration of compounds in the water, or chemical or physical interactions among conspecifics (Denver et al., 1998). At the same time, these fast-developing tadpoles often metamorphose at a smaller size (e.g., Newman, 1989; in *S. multiplicata*, however, the first tadpoles to metamorphose tend to also be the largest; Pfennig et al., 1991). Second, tadpoles of *Spea* can facultatively shift from a slowly developing ‘omnivore’ morph to a rapidly developing (and morphologically distinctive) ‘carnivore’ morph (Pfennig, 1992b; Fig. 1D). This carnivore morph has an additional advantage in a drying pond: it can reduce competition and

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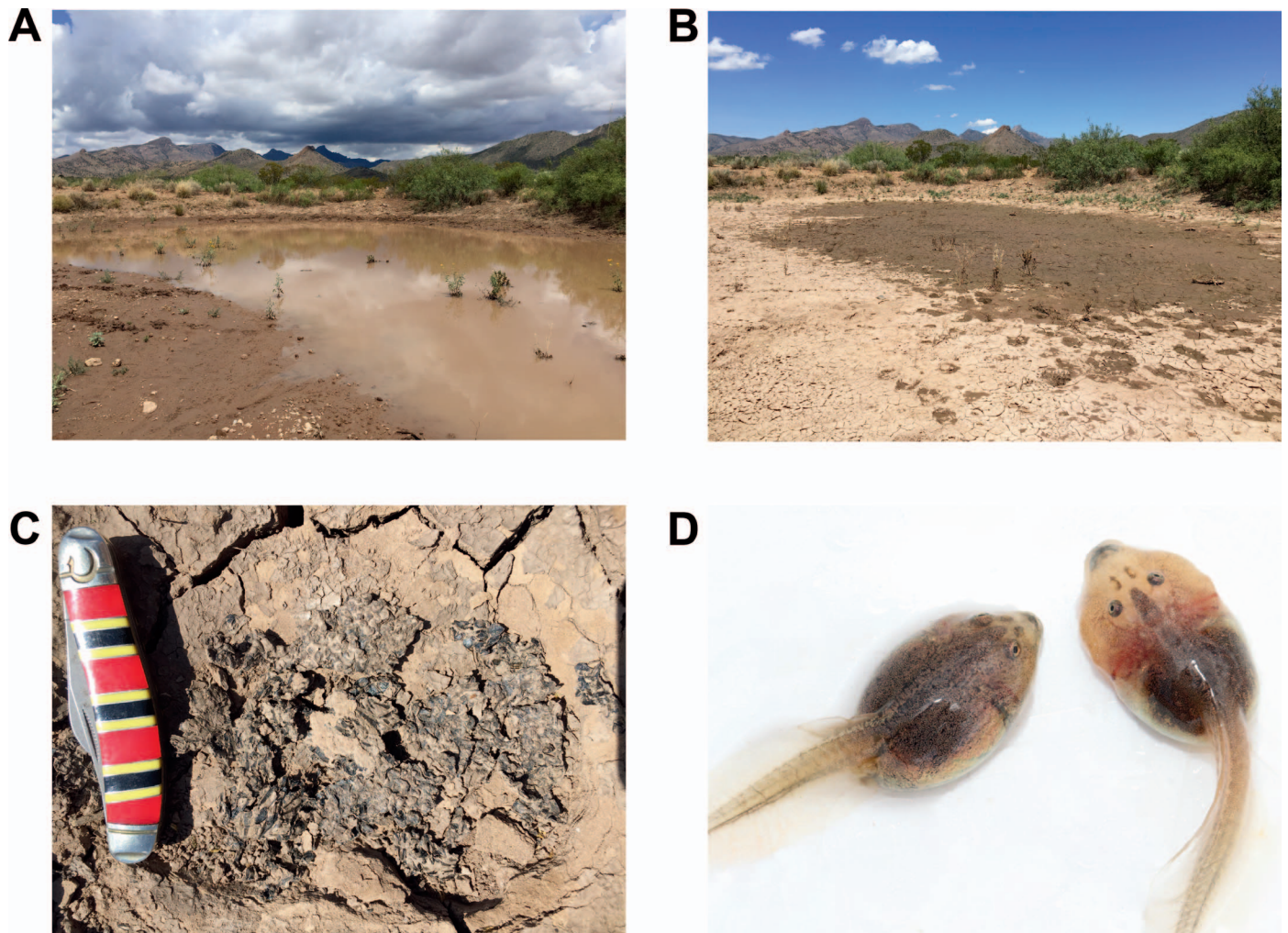


Fig. 1. Study system. Mexican Spadefoots, *Spea multiplicata*, breed in (A) ephemeral pools that (B) dry rapidly (this is the same pond as in panel 'A,' but nine days later). (C) Consequently, the tadpoles often desiccate before reaching metamorphosis. (D) To speed development, *Spea* tadpoles have evolved phenotypic plasticity to shift from an 'omnivore' morph (left) to a more rapidly developing 'carnivore' morph (right).

enhance growth and development by eating other tadpoles (Pfennig, 2000).

There is a possible third strategy that spadefoots might use to escape a drying pond: the presence of desiccated tadpoles from previous pond fillings could stimulate the developmental rate of a subsequent cohort or generation (Bragg, 1950). Indeed, Bragg (1950) showed experimentally that exposure to dead tadpoles increased development rate in Hurter's Spadefoot tadpoles, *Scaphiopus hurterii*. Yet, it is unclear if any such facilitation extends to carnivore-morph production. We therefore sought to perform a similar experiment using a species of spadefoot (*S. multiplicata*) that can produce carnivores.

As we describe below, our data suggest that information associated with dead individuals can indeed influence development in a later generation in ways that would likely enhance fitness. This tendency of dead individuals to facilitate development in future generations might constitute a novel form of nongenetic (possibly, ecological) inheritance in which information acquired from a previous generation gives a later generation a head start in the environment that it is likely to encounter.

MATERIALS AND METHODS

On 30 July 2018, we identified the remains of desiccated tadpoles in a dry pond near Portal, Arizona in which *S. multiplicata* have bred annually for at least the past 30 years ('Figure 8 Pond'; 31.932931°N, 109.086052°W). Specifically, in several locations in what was formerly the pond bottom, we found patches (about 80 mm diameter x 2 mm thick) of dried tadpoles from a previous breeding (Fig. 1C). Based on their size and shape, as well as the location of the pond, we identified these as remains of *S. multiplicata* (about 10 mm in snout-vent length [SVL] and Gosner [1960] stage 30, suggesting that they were about one week old when they died). Moreover, given that the tadpole remains had not been blown away, we concluded that these remains were likely from a breeding earlier in the same year. Because it had not rained at this location since mid-May, the remains were therefore at least 2 months old (in Arizona, *S. multiplicata* breed anytime following warm rains; pers. obs.).

We sampled three such patches of dead tadpoles ('tadpole-remains soil'), each containing about 100 desiccated tadpoles. We also sampled—from the same pond—the top 2 mm

Table 1. Summary statistics for the effects of soil type (control soil vs. tadpole-remains soil) on SVL, GS, and MI.

Response variable	Estimate (mean±s.e.m.) on:				
	Control soil	Tadpole-remains soil	F	df	P
Body size (SVL)	8.313±0.369	10.015±0.402	8.32	1, 31.1	0.0070
Developmental stage (GS)	28.157±0.44	30.187±0.486	15.93	1, 30.2	0.0004
Trophic morphology (MI)	-0.646±0.437	0.767±0.365	35.52	1, 30	<0.0001

of nearby (<10 cm) soil that lacked any visible tadpole remains ('control soil'). Back in the lab, we ground each type of soil separately into a fine powder. We did not quantify the nutritional content of each soil type, but, other than differing in the presence of tadpole remains, both likely contained the cysts (eggs) of anostracan fairy shrimp (*Thamnocephalus* sp. and *Streptocephalus* sp.) and tadpole shrimp (*Triops* sp.; as evidenced by the fact that live shrimp were later observed in most of the experimental microcosms), as well as dried shrimp, algae, bacteria, and organic material washed in from the area surrounding the pond. Indeed, previous studies had established that sufficient nutrition is usually present in the soil of such dry ponds for *S. multiplicata* tadpoles to survive, grow, and develop at similar rates to those observed in natural ponds (Pfennig et al., 2006; Martin and Pfennig, 2010).

To start the experiment, we bred four pairs of *S. multiplicata* that had been collected in earlier years from a nearby pond ('PO2 Pond'; 31.914131°N, 109.083437°W). PO2 Pond is <1 km from Figure 8 Pond (the source of the soil), and it has a hydroperiod similar to Figure 8 Pond. For these breedings, we artificially paired the parents with each other, but all sires had been collected in amplexus with a female in an earlier, natural breeding in PO2 Pond. The eggs from each parent were kept in separate mesocosms (390 L x 255 W x 140 mm D plastic boxes) filled with 11 L of dechlorinated water and maintained adjacent to each other in a room kept at 23.5°C and on a 14 hr light:10 hr dark photoperiod. Once the tadpoles hatched (about two days after oviposition), we placed 10 ml of each type of soil into separate microcosms (180 L x 125 W x 80 mm D plastic boxes) filled with 800 mL of dechlorinated water. Although we were unable to quantify the exact number of desiccated tadpoles in the soil provided to each microcosm, we estimate that each likely contained the remains of about 15 dead tadpoles.

The next day, we introduced into each microcosm a single, two-day old tadpoles of *S. multiplicata* from this breeding. Each sibship was replicated five times per soil type (20 tadpoles per soil type). We did not provide the tadpoles with any food other than naturally occurring material in their soil (see above). All microcosms were maintained on the same rack in a room kept at 23.5°C and on a 14 hr light:10 hr dark photoperiod (the positions of different sibships were interspersed on this rack). We let the water from the mesocosms dry naturally, simulating a drying pond. We ended the experiment after 15 days for two reasons. First, in naturally occurring, drying ponds, *S. multiplicata* can metamorphose as soon as 14 days post-hatching (Pfennig et al., 1991). Second, 15 days was the point in time when about half of the water was gone from each microcosm (this evaporation rate was within the range of rates observed in natural ponds; Pfennig, 1990).

We recorded the number of tadpoles that survived to the end of the experiment. We also recorded each tadpole's body size (i.e., SVL) and Gosner developmental stage (GS; Gosner, 1960). To assess each tadpole's resource-use morphology, we calculated its 'morphological index' ('MI'; see Martin and Pfennig, 2011 and references therein). To calculate each tadpole's MI, we measured the width of its orbitohyoideus muscle (OH; carnivores have a larger OH) and scored its mouthparts (MP) on an ordinal scale that ranged from 1 (most omnivorous) to 5 (most carnivorous). After correcting OH for body size [by regressing ln(OH) on ln(SVL)], we combined OH and MP into a principal component analysis (PCA) using JMP Pro, version 14.0 (SAS Institute, Inc., Cary, NC; https://www.jmp.com/en_us/software/data-analysis-software.html). OH and MP each contributed 50% to the PCA. Each tadpole's MI consisted of the first principal component, which explained 78% of the variance in resource-use morphology among our tadpoles. Larger values of the MI correspond to more carnivore-like tadpoles.

To determine if there was an effect of treatment (soil type) on our response variables (SVL, GS, or MI), we used two approaches. First, we used the mixed model function in JMP Pro 14.0 and included treatment (soil type) as a fixed effect and sibship as a random effect. We then used a model that included both treatment and sibship as fixed effects to determine if there was a significant interaction between the two (i.e., to test if different sibships responded differently to the treatment effect). Finally, because we found a significant interaction for MI only (see below), we performed a Tukey HSD test in JMP Pro 14.0 to determine which sibships differed in MI from the others on the different treatments.

RESULTS

Desiccated tadpoles did not increase survival of living conspecifics: 16 of 20 tadpoles in the tadpole-remains soil survived, whereas 19 of 20 tadpoles in the control soil survived ($\chi^2 = 2.057$, $P = 0.1515$). Desiccated tadpoles did, however, increase growth and development rate of living conspecifics. Compared to their siblings reared with control soil, tadpoles reared with tadpole-remains soil grew larger (Table 1, Fig. 2A) and developed faster (Table 1, Fig. 2B). Additionally, compared to their siblings reared with control soil, tadpoles reared with tadpole-remains soil were more carnivore-like in their trophic morphology (Table 1, Fig. 2C).

We also found that the four sibships differed in their responses to the different soil types. Although there was no effect of sibship on SVL (Table 2A) or GS (Table 2B), there was a significant effect of sibship on MI (Table 2C). Moreover, there was a highly significant interaction of sibship and soil type on MI (Table 2C), indicating that sibships varied in likelihood of producing a carnivore morph (as revealed by their MI). Indeed, two sibships (Sibships 2 and 4) responded to the presence of tadpole remains strongly by producing

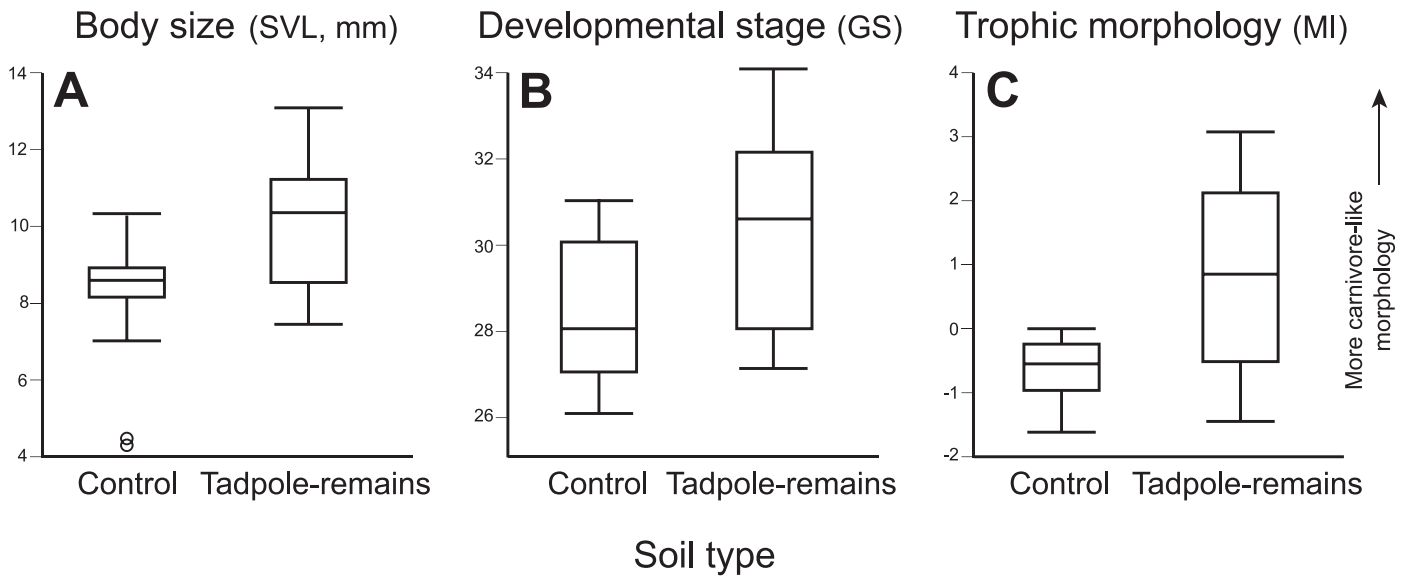


Fig. 2. Effects of soil type on growth, development, and trophic morphology. Compared to their siblings reared in the absence of tadpole remains (control soil), by the end of the experiment, those reared in the presence of desiccated conspecifics (tadpole-remains soil) were: (A) larger, (B) more developmentally advanced, and (C) more carnivore-like in trophic morphology. Box plots show quintiles and median (middle horizontal line).

more carnivore-like tadpoles, whereas the other two sibships (Sibships 1 and 3) did not respond at all (Fig. 3).

DISCUSSION

In the presence of the remains of desiccated conspecifics from a previous generation or cohort that had likely been dead for more than two months, living tadpoles of *S. multiplicata* used phenotypic plasticity to modify their development. Compared to their siblings that were reared with soil lacking tadpole remains, those reared with soil containing desiccated conspecifics grew larger, developed faster, and were more carnivore-like (Fig. 2). Given that larger, faster-developing, and more carnivore-like tadpoles are more likely to escape a drying pond (Pfennig, 1992a), such facilitation of development by dead conspecifics is likely adaptive. Presumably, in a large (and, hence) long-duration pond, cues from dead conspecifics would be diluted and perhaps not be detected by living tadpoles. In such situations, no facilitation of development is needed and none would likely be manifest. By contrast, in a small (and,

hence) short-duration pond, cues from dead conspecifics would be concentrated and thereby likely to be detected by living tadpoles. In such situations, facilitation of development is needed and would likely be manifest. It is even possible that cues associated with dead conspecifics are used in concert with other cues that tadpoles use to assess pond duration, such as swimming volume and perhaps the proximity to the surface (Denver et al., 1998). Thus, dead individuals can influence development in future cohorts or generations in ways that would likely enhance fitness.

Not only did tadpoles respond to the presence of tadpole remains by becoming more carnivore-like, different sibships (i.e., different genotypes) varied in this plastic response

Table 2. Summary statistics for the effects of sibship, soil type, and their interaction on (A) SVL, (B) GS, and (C) MI.

Source	F	df	P
(A) Body size (SVL)			
Sibship	1.333	3, 3	0.2843
Soil type	8.589	1, 1	0.0068
Sibship x Soil type	0.430	3, 3	0.7332
(B) Developmental stage (GS)			
Sibship	0.183	3, 3	0.9068
Soil type	8.554	1, 1	0.0069
Sibship x Soil type	0.938	3, 3	0.4358
(C) Trophic morphology (MI)			
Sibship	27.252	3, 3	<0.0001
Soil type	59.427	1, 1	<0.0001
Sibship x Soil type	9.934	3, 3	0.0001

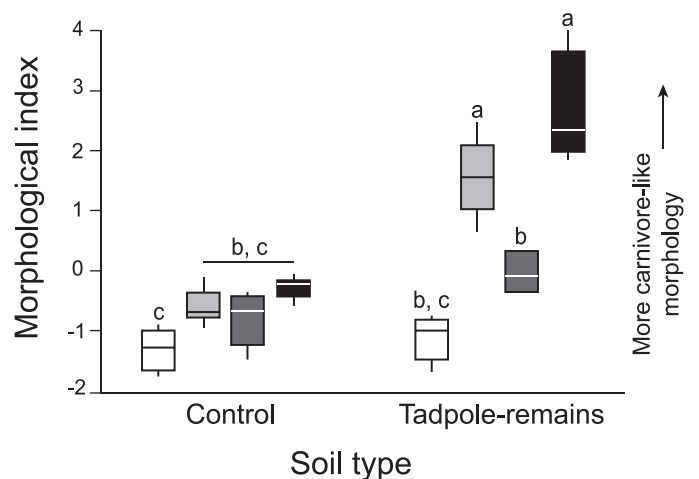


Fig. 3. Evidence of genetic variation in plasticity. Different sibships varied in propensity to produce carnivores in response to the absence vs. presence of desiccated conspecifics. Similar-shaded boxes are siblings (i.e., similar genotypes; within each soil type, the four boxes refer to sibships 1–4 reading from left to right). Box plots show quintiles and median (middle horizontal line). Groups not connected by the same letter above the box plots are significantly different from each other ($P < 0.05$; Tukey HSD test).

(Table 2C, Fig. 3). This sibship-specific variation suggests underlying genetic variation in plasticity to produce a carnivore when desiccated tadpoles are present. Such genetic variation in this plasticity could mediate adaptive evolution in response to different environmental conditions. For example, a genotype that is not plastic in response to tadpole remains might be selectively favored in wet years (when ponds do not dry rapidly), whereas genotypes that are highly plastic might be selectively favored in dry years (when ponds do dry rapidly). Substantial pond-to-pond and year-to-year variation in pond drying exists in our study area (Pfennig, 1990, 2007) and could explain why such genetic variation is maintained.

The mechanism by which the observed facilitation occurs is unknown. Because we ground the tadpole remains into a fine powder, visual cues could not have played a role. Instead, some substance(s) must have triggered the plastic response. One possibility is that increased growth and development might have simply reflected a greater nutritional value of soil containing dead tadpoles. Many studies have established that tadpoles fed high protein diets grow and develop quickly (Kupferberg, 1997), and earlier work has shown that *S. multiplicata* grow larger on a diet of tadpoles (Pfennig, 2000). However, prior studies with *S. multiplicata* have also shown that increased protein alone does not influence carnivore production (Pfennig, 1990). Yet, we found that tadpoles reared with tadpole remains were more carnivore-like (Fig. 2C). A second (non-mutually exclusive) possibility is that specific chemicals from dead tadpoles may have been concentrated in the soil. Although many unique chemicals occur in dead tadpoles, a plausible candidate is thyroxine (or its precursors: tyrosine and iodine). Thyroxine is a potent accelerator of development in larval amphibians (Dodd and Dodd, 1976; Denver, 1997), and it may even trigger carnivore production in *S. multiplicata* (Pfennig, 1992b). Although it is unclear if thyroxine can last long enough in the environment to act as a cue for future generations, iodine can persist in soil for years (Shetaya et al., 2012), and earlier work has shown that iodine, by itself, can speed tadpole development (Spaul, 1924). Future studies are needed to clarify the mechanism underlying the observed facilitatory effects.

It is also unclear how these effects could have evolved in the first place. Obviously, dead individuals receive no direct benefit. Therefore, it seems highly unlikely that individuals would evolve an ability to signal to the next generation that their pond is at risk of drying. Instead, the ability to detect and respond to cues associated with dead conspecifics likely evolved solely because of the benefits accruing to the recipients. This seems plausible in *S. multiplicata*. In this species, failing to achieve metamorphosis is lethal, ponds frequently dry prematurely, *Spea* have evolved multiple forms of plasticity to hasten development (see Introduction), and cues associated with desiccating conspecifics can serve as reliable indicators of future conditions (this study). Essentially, these cues are redolent of ‘alarm cues’ found in certain plants (Agrawal et al., 1999) and many aquatic animals (Ferrari et al., 2010), in which individuals that are injured by predators passively release pheromones that, if detected, can cause nearby conspecifics to modify their phenotype in ways that decrease their risk of predation (Smith, 1992).

Our data also suggest how eating conspecifics could be adaptive. Generally, predators experience enhanced growth and development by eating conspecifics, presumably because

conspecifics contain the right proportions of nutrients (Meffe and Crump, 1987; Crump, 1990; Wildy et al., 1998). At the same time, feeding on conspecifics might enhance the risk of acquiring disease-causing parasites (Pfennig et al., 1998; Rudolf and Antonovics, 2007). However, if desiccation kills some parasites (such as fungi; see Wilson and Sherman, 2010), then individuals that feed on desiccated conspecifics might reduce the risk of disease while obtaining the nutritional benefits (assuming these nutritional benefits do not break down over time).

Finally, if we define ‘inheritance’ as the transmission of biological information across generations (*sensu* Bonduriansky and Day, 2018), then the observed transmission of information (albeit passive) about the environment from dead individuals to living conspecifics might constitute a novel form of nongenetic inheritance. This ability to acquire information from dead members of a previous cohort or generation might be akin to ecological inheritance, where organisms modify their local environment and then pass to future generations the resulting modified conditions as well as the altered selective pressures that are associated with these new conditions (*sensu* Odling-Smee et al., 2003). Although the effects described here might not persist for more than one or two generations, they could be vital in giving individuals a head start in the environment that they are likely to encounter (Agrawal et al., 1999; Bonduriansky and Day, 2009).

DATA ACCESSIBILITY

Supplemental information is available at <https://www.copeiajournal.org/ce-19-286>.

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