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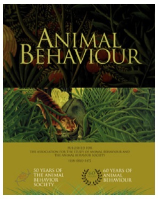

Foraging plasticity favours adaptation to new habitats in fire salamanders

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Predators often show strong plasticity of optimal foraging strategies. A major difference in foraging strategies occurs between sit-and-wait and active predators. Models predict that the efficiency of these strategies is affected by environmental conditions, active predators being favoured when prey are scarce and their detection difficult. The shift between the two strategies may occur through both phenotypic plasticity and local adaptations. Larvae of the fire salamander, *Salamandra salamandra*, are typically stream-dwelling sit-and-wait predators, but some populations breed in caves. We evaluated whether local adaptations or phenotypic plasticity determine shifts in foraging strategy between stream and cave populations. The foraging behaviour of salamander larvae was evaluated under all combinations of three test conditions during trials: light versus darkness, prey presence versus absence and food deprived versus fed; larvae originated from caves and streams and were reared in epigeous photoperiod or in darkness. Observations and video tracking showed that salamander larvae modified their behaviour in response to environmental conditions. In the darkness, larvae showed higher average velocity and moved longer distances. Movements were higher in food-deprived larvae and in the presence of prey compared to fed larvae and prey absent conditions. Furthermore, larvae from cave populations showed higher behavioural plasticity than stream larvae, and better exploited the available space in test environments. Variation in foraging behaviour was strong, and involved complex interactions between plasticity and local adaptations. Larvae from cave populations showed higher behavioural plasticity, supporting the hypothesis that this trait may be important for the exploitation of novel environments, such as caves.

When populations colonize new environments, selection pressures may determine phenotypic divergence for multiple traits, including morphology, physiological tolerance and behaviour (Kawecki & Ebert 2004). Phenotypic divergence can occur through both local adaptations and phenotypic plasticity. First, divergent selection may favour genotypes determining locally adapted ecotypes. Second, one single genotype can determine multiple phenotypes (phenotypic plasticity), enhancing fitness under specific environmental conditions (Lande 2009; Torres-Dowdall et al. 2012). However, local adaptation and plasticity are not mutually exclusive and, under certain conditions, natural selection may favour individuals that are able to express strong reaction norms, showing the highest values of phenotypic plasticity. This can be particularly valuable when the colonized habitats are heterogeneous, in the presence of gene flow between habitats, and during the early phases of the adaptation process (Crispo 2008). The interplay between local adaptation and plasticity is rarely assessed in natural populations, but may be detectable by ecotype-by-environment interactions, that is, when the slope of reaction norms differs between ecotypes (Crispo 2008; Torres-Dowdall et al. 2012).

Predators often show strong plasticity for the foraging strategies employed because optimal foraging can be influenced by multiple factors, such as physiological constraints, features of both the environment and prey, and risks associated with the predatory behaviours (Delclos & Rudolf 2011). A major difference in foraging strategies occurs between the sit-and-wait (also named 'ambush') predators, and the active (also named 'widely foraging') predators (Huey & Pianka 1981). Sit-and-wait predators usually remain hidden for more or less long periods waiting for prey to come close. In contrast, active predators widely explore their habitat (Scharf et al. 2006), performing wandering displacements that may increase the probability of encountering prey (Hodar et al. 2006). These two

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strategies are most effective under opposite environmental conditions. The sit-and-wait strategy requires the occurrence of moving prey and the possibility to detect it at long distances, while active predators are favoured when prey are encountered infrequently, when predators can move faster than their prey, and when predators' energy requirements are low in relation to the prey capture rate (Huey & Pianka 1981; Scharf et al. 2006). Sit-and-wait and active search are two extremes of the foraging mode spectrum, and predators can modify their strategies in response to the environmental context and prey identity (Perry 1999; Scharf et al. 2006).

Hypogeous (i.e. underground) environments have multiple features that differentiate them from epigeous habitats and that can have a strong impact on the optimal foraging strategy for predators that colonize them. First, lack of light makes it difficult to detect prey visually over long distances (Dumas & Chris 1998). Furthermore, in underground environments both predators and prey occur in limited abundance (Uiblein et al. 1992, 1995; Hervant et al. 2000). Therefore in underground environments a mesopredator (i.e. a predator at an intermediate level of the food web) has a low encounter rate with its prey, but also a limited risk of being predated. Theoretical models predict that under these conditions a more active foraging strategy would be more advantageous than the sit-and-wait strategy (Scharf et al. 2006; Hawlena et al. 2011). Both phenotypic plasticity and local adaptations may determine variation for behavioural traits, optimizing foraging strategies in cave fauna (Gordon & Matson 1991; Hervant & Renault 2002; Romero 2009). Understanding the importance of phenotypic plasticity in cave colonization is challenging (Poulson 2011; Romero 2011). Facultative cave dwellers, in which only some populations exploit caves, can be extremely helpful for assessing the relative role of plasticity and local adaptations in the variation of foraging behaviour.

In this study, we compared foraging strategies between cave and epigeous breeding populations of the fire salamander, *Salamandra salamandra*. The fire salamander is usually an epigeous species breeding in streams (Manenti et al. 2009b; Ficetola et al. 2011) but is well able to adapt to new environments (Weitere et al. 2004; Steinfartz et al. 2007; Caspers et al. 2009). Previous studies showed that, in the presence of contrasting breeding habitats, salamander females can show a preference for a specific breeding habitat, and assortative mating can cause genetic differentiation between ecotypes (Weitere et al. 2004; Steinfartz et al. 2007; Caspers et al. 2009). In several areas, the fire salamander often also gives birth to larvae in caves (Manenti et al. 2009a, 2011; Ianc et al. 2012). The peculiar cave features probably expose salamanders to strong selection pressures, and analyses of predatory performance suggest that cave-breeding populations show local adaptations to the underground environments (ecotypes), as they have a better predation performance in complete darkness (Manenti & Ficetola 2013). We used common environment experiments to assess whether phenotypic plasticity or local adaptations enable salamanders to optimize their foraging strategy depending on the environmental conditions. We reared salamander larvae from different origins (cave versus epigeous streams) under contrasting environmental conditions (complete darkness versus normal photoperiod), and tested their behaviour under two light conditions (light versus darkness). We considered two parameters representing foraging behaviour: active search of prey and use of space. First, active search of prey is favoured when prey organisms are scarce, and when they are more difficult to detect (Scharf et al. 2006). If behavioural plasticity determines optimal foraging strategies, then we predicted a more active search for prey in darkness than under the light condition. By contrast, if there are local adaptations, we predicted a different prey search strategy between larvae originating from caves and streams.

Second, in epigeous streams, salamander larvae often remain on the sides of pools, near rocks where they can hide and reduce the risk of being detected by predators (Krause et al. 2011). This risk is lower in caves, where predators are essentially lacking, and in darkness, when predators cannot use visual detection. If variation in space use is determined by behavioural plasticity, we predicted that peripheral sectors will be more frequently used under light conditions. If it is determined by local adaptations, we predicted a higher use of peripheral sectors by stream populations in comparison to cave populations. As foraging strategy may be affected by multiple additional factors (e.g. nutritional status, prey presence, previous experience), we also considered their potential impact. Finally, we evaluated potential ecotype-by-environment interactions, to assess the interplay between plasticity and local adaptation.

METHODS

Study System

We studied fire salamander populations from a karstic area in Lombardy, northwest Italy (approximately 45.8°N, 9.3°E). The area is located between the districts of Lecco and Como and ranges between 340 and 980 m above sea level. The area is characterized by mountainous and hilly reliefs covered by broadleaved woodlands and a dense hydrographic network. In this area, the fire salamander is ovoviviparous and usually gives birth to larvae in streams and creeks (Manenti et al. 2009b; Ficetola et al. 2011). However, there are several natural and artificial caves regularly used for parturition by fire salamanders (see Manenti et al. 2011). These caves are characterized by underground springs which receive water exclusively from the subterranean aquifer; therefore larvae found in caves could not have drifted from superficial water. Females actively enter caves, and select them as breeding sites if they have suitable environmental features (accessibility, presence of prey; Manenti et al. 2009a, 2011). In these environments, salamander larvae are able to develop and metamorphose successfully (Manenti et al. 2011). Salamander larvae are generalist predators feeding on a wide range of benthic invertebrates (e.g. chironomids, culicids, oligochaetes, plecopterans, small larvae of other insects, and small crustaceans: Weitere et al. 2004).

Experimental Setting

We performed a behavioural experiment to assess the foraging strategy of larvae born in hypogeous and epigeous streams under different conditions. We collected newborn larvae (less than 1 week old; larval development stage one: Zakrzewski 1987) from underground springs (11 different caves) and neighbouring epigeous streams (nine different streams). To avoid using related larvae, we used one larva per location. Larvae were transported to the laboratory in separate boxes. In the laboratory, larvae were individually maintained at an average temperature of 18 °C in 10 × 11 cm plastic containers (water depth: 5 cm). Containers with larvae were randomly assigned to one of two different rearing conditions (i.e. giving different experience to larvae): total darkness (light intensity constantly <0.01 lx) and normal day:night photoperiod (12 h light and 12 h darkness). Containers were randomly arranged in two blocks (tanks) per treatment; thus they were not independent. Larvae were fed every second day: 20 live prey items per week during the first 3 weeks and 30 live prey items per week from the fourth week. Prey items were *Tubifex* sp. specimens and chironomid larvae (*Chironomus* sp.) depending on the week.

Behavioural tests started after 45 days of rearing. Each larva was tested under all the combinations of three test conditions: light