



Amphibians breeding in refuge habitats have larvae with stronger antipredator responses



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Antipredator responses are a key determinant of the successful persistence of prey, and behavioural modifications are a frequent antipredator strategy. However, conspecific populations often inhabit heterogeneous environments. This can determine local adaptations, and might also induce variation in antipredator responses. Nevertheless, there is limited information on whether heterogeneity of predation risk among populations determines variation in antipredator response. Here we studied the fire salamander, *Salamandra salamandra*, a species that can breed in both surface streams and caves, habitats that are predator-rich and predator-free, respectively, and measured differences in antipredator responses across populations with different predation risk. We combined field surveys and laboratory experiments to understand the role of predation risk on the activity patterns of larvae, while measuring behavioural differences between populations. We reared larvae from different habitats in safe and risky conditions and tested their response to predator cues before and after rearing. In the field, predation risk was much higher in surface streams than in caves; larvae moved more in the absence of predators and when the light intensity was low. During laboratory experiments, larvae were less active if reared in risky conditions, but cave larvae showed a stronger response to risk than stream larvae. Therefore, larvae from sites without predators showed higher antipredator responses than those from risky habitats. This response fits the predictions of the risk allocation model, in which prey from habitats with a high background level of risk need to be active even when predators are present, to satisfy their energetic demands. Our findings show that antipredator behaviour may differ strongly between populations and stress the importance of integrating this variability in studies on predatory responses.

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Predators can affect prey through consumption, but also through nonconsumptive effects that alter the morphology, life history and behaviour of prey (Davenport & Chalcraft, 2013; Preisser & Bolnick, 2008; Winandy & Denoël, 2015), with major impacts on prey population dynamics (Davenport & Chalcraft, 2013). For instance, semiaquatic organisms with complex life cycles are able to assess the predation risk in a water body and modulate breeding activity by selecting habitats with fewer predators (Stav, Blaustein, & Margalit, 2000; Winandy, Darnet, & Denoël, 2015). Several studies have assessed the nonconsumptive effects of predation risk by evaluating how antipredator responses

enhance fitness and by measuring the costs and the trade-offs of such responses, which are keystones to understanding several ecological and conservation aspects (Amo, Lopez, & Martin, 2003; Blanchet, Bernatchez, & Dodson, 2007; Yorzinski et al., 2015). Such studies often use individuals of the same origin, without taking into account potential variation between populations (Blaustein, 1997; Hernandez & Peckarsky, 2014; Kishida, Trussell, Nishimura, & Ohgushi, 2009). However, local adaptations are common among populations that inhabit heterogeneous environments; thus spatial heterogeneity in predation pressure might induce variation in antipredator responses.

The reduction in activity levels under high predation risk is common antipredator behaviour (Kishida et al., 2009, 2011). Movements increase the risk of being detected by predators, but are often necessary to find resources such as food or partners, leading to a trade-off between reducing mortality and acquiring resources

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(Carlson & Langkilde, 2014). Some studies have underlined how individuals from populations living in risky habitats can display specific behavioural adaptations, which limit predation risk. In some cases, larvae of amphibians from habitats with high levels of predation risk (e.g. predatory fish) show a lower level of activity (e.g. moving less) and an even stronger reduction in activity rates in the presence of predators (Chivers, Wildy, Kiesecker, & Blaustein, 2001; Storfer & Sih, 1998). However, cases exist in which individuals from populations exposed to predators have higher activity levels, as this can improve their foraging and allow them to rapidly grow to a large size, thus reducing the period during which individuals suffer predation risk (Urban, 2007). In practice, anti-predator adaptations can be highly variable, suggesting that knowledge of how the heterogeneity of predation risk among populations and habitats determines the variation in antipredator response between populations is incomplete.

Predation risk is variable over space and time, and this variability is crucial in determining how prey respond to risk (Ferrari, 2014). As a consequence, the background level of risk is an additional factor potentially affecting the outcome of prey responses, as it can influence the readiness of a species to respond to predators (Ferrari, 2014; Ferrari, Crane, Brown, & Chivers, 2015). For instance, prey inhabiting habitats with high level of risk can decrease their vigilance and be particularly active during brief periods of safety (paradox of risk allocation hypothesis: Ferrari, Sih, & Chivers, 2009; Lima & Bednekoff, 1999). Furthermore, the background level of risk can strongly modify the overall activity level of prey, and this influences the outcome of their interactions with predators, with increase or decrease of survival depending on the predator type (Ferrari et al., 2015).

The fire salamander, *Salamandra salamandra*, is a usually epigeous taxon that breeds in streams, but some populations have also colonized subterranean environments in which larvae successfully complete their development (Manenti, Denoël, & Ficetola, 2013). On the one hand, subterranean environments can provide advantages, such as more stable environmental conditions and limited predation risk. On the other, salamanders in these habitats face major challenges, such as food scarcity (Manenti, Pennati, & Ficetola, 2015). Evidence suggests that local adaptations to underground environments are present, with cave populations also showing a higher behavioural plasticity than surface stream populations. This plasticity allows them to modulate activity levels in relation to environmental conditions and availability of prey, thus helping the colonization of such challenging habitat (Manenti, Denoël, et al., 2013; Manenti & Ficetola, 2013).

In this study, we combined field surveys and laboratory experiments to assess whether antipredator responses of salamander larvae differ between populations facing different levels of predation risk. First, we evaluated in the field whether movement is reduced in habitats with a higher predation risk. Second, we reared larvae from populations with a different level of predation risk (caves: absence of aquatic predators for salamander larvae; streams: presence of predators), and tested (1) whether larvae reared under risky conditions or in the presence of predatory cues are less active and (2) whether the response to risky conditions is similar or differs between populations that experience different predation risks.

METHODS

Field Surveys

We studied fire salamander populations from Lombardy (northwest Italy; approximately 45°48'N, 9°02'E). In this area, the fire salamander is ovoviviparous and usually produces larvae in

streams, but also often in caves (Supplementary Fig. S1). All these salamander larvae are fully aquatic and have external pairs of gills. Adult females actively enter caves and select them as breeding sites; no larvae in the chosen sites could have drifted into this environment from superficial waters, because all sites are springs that receive water exclusively from the subterranean aquifer (Manenti & Ficetola, 2013; Manenti, Ficetola, Bianchi, & De Bernardi, 2009). In these underground habitats, salamander larvae successfully grow and metamorphose (Manenti, Ficetola, Marieni, & De Bernardi, 2011).

We surveyed 52 sites (15 cave pools and 37 outdoor springs and stream pools; Fig. S1) between February 2014 and June 2015 during the day and at night. We visited each site twice and the same observer performed all the surveys. On all the sampling occasions, we recorded the number of active salamander larvae, i.e. the number of larvae visible from the pool border in 5 min visual surveys. To do this, we approached the pools in the dark and once at the border of the pool, we shone a torch on it (Petzl Ultra Vario) and directly counted the larvae. Subsequently, we estimated the total number of larvae using two successive removal samplings with a fine mesh net and applying the removal method (Chao & Chang, 1999). Larvae were released at their place of capture immediately after the census. We then calculated the frequency of active larvae as a proportion of the total number of larvae. As environmental variables, we recorded the maximum light intensity (illuminance) on the pool surface using a CEM DT8820 lux meter (CEM-instruments, Shenzhen, China), and estimated the biomass of predators (dragonfly larvae; g/m²) through pipe sampling (diameter: 25 cm; Dodd, 2010; see Limongi, Ficetola, Romeo, and Manenti (2015) for additional details on invertebrate samplings). All the studied pools were devoid of fish and we excluded from the analyses a few surface sites ($N = 5$) in which we found native crayfish, *Austropotamobius italicus*.

Laboratory Experiments

We performed behavioural experiments to assess the variation in movement between salamander larvae born under different risk conditions in underground and surface streams. We collected larvae at developmental stage 1 (newborns: well-developed tail fin and the tip of the fin bluntly rounded; Juszczak & Zakrzewski, 1981) from underground pools (67 individuals from six sites) and neighbouring surface pools or slow-running water streams (96 individuals from eight sites). Larvae were individually maintained at a mean temperature of 18 °C, exposed at the natural photoperiod, in 10 × 11 cm perforated (diameter of perforations: 2 mm) transparent plastic containers placed in six independent water-filled blocks (i.e. plastic containers of 40 × 50 cm; water depth: 5 cm). Larvae were randomly assigned to three rearing treatments, with two blocks per treatment (each containing 12 larvae). The rearing treatments were a control (absence of dragonfly larvae), predator without contact ('no contact') and predator with contact ('contact'). Under the predator without contact treatment, two dragonfly larvae, *Cordulegaster bidentata*, were free to move within the block. Salamanders could receive dragonfly cues through the perforated walls of their container, but were protected from predation or direct contact. In the predator with contact condition, a dragonfly larva was placed in the container of the larva (see Ethical Note below), twice weekly, for 30 s. All *C. bidentata* larvae used were at the premetamorphosis stages (mean length ± SE = 31.8 ± 0.4 mm) and are major predators of salamander larvae within the study area (Manenti, Siesa & Ficetola, 2013). *Salamandra salamandra* larvae were fed ad libitum every 2 days with *Chironomus* sp. larvae. Chironomids were also provided ad libitum to *C. bidentata* larvae for a total of 8–10 prey per week. Salamander larvae were kept without food for 3 days before

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