



# Safe as a cave? Intraspecific aggressiveness rises in predator-devoid and resource-depleted environments

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Received: 10 December 2018 / Revised: 11 April 2019 / Accepted: 12 April 2019

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## Abstract

Intraspecific aggressiveness can be affected by multiple environmental pressures. In several cases, aggressiveness can grade into full-scale cannibalism, particularly when resources are scarce. However, limited information exists on how intraspecific aggressiveness varies among populations experiencing different environmental pressures, and on the role intraspecific predation plays for the exploitation of harsh habitats. The fire salamander, *Salamandra salamandra*, is an excellent model species to study factors affecting intraspecific aggressiveness, because of its ability to breed in habitats with contrasting food resources and predation pressure. Here, we evaluated the influence of predation risk and habitat of origin on aggressive interactions. To this extent, we reared larvae from cave (scarce resources; nearly-absent predators) and surface (abundant resources and predators) populations under different risk conditions and measured aggressive behavior towards conspecifics. During behavioral trials, larvae were exposed to different combinations of predator and wounded conspecific chemical cues. Intraspecific aggressiveness increased in large and late-development larvae. Larvae from all the populations significantly reduced aggressiveness under both typologies of risk experienced during rearing (constant presence of predator; pulses of high predation risk), and also when stimulated by predator cues. However, larvae from cave populations exhibited a more pronounced aggressiveness, especially when exposed to wounded conspecific cues. Intraspecific aggressiveness can be modulated by the complex interaction between multiple variables, and both behavioral plasticity and local adaptations can determine its variation across populations. Our findings reveal that aggressive interactions are favored in cave environment, suggesting intraspecific predation can play a key role in the exploitation of resource-depleted habitats.

## Significance statement

In this study, we investigated how intraspecific aggressiveness of salamander larvae is shaped under predation risk in populations originating from contrasting environments, such as cave and surface habitats. Larvae experiencing predator presence during their development or exposed to predator cues significantly reduced their aggressive interactions, both in cave and surface populations. Interestingly, cave-originating individuals reacted to wounded conspecific cues by increasing the frequency of their aggressive displays, suggesting cannibalistic behavior is locally enhanced in populations from resource-depleted habitats. The present study offers new insights on the importance of intraspecific aggressiveness for the adaptation to harsh environments.

**Keywords** Intraspecific aggressiveness · Cannibalism · Chemical signaling · Cave environment · Predation risk · *Salamandra*

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Communicated by C. R. Gabor

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**Electronic supplementary material** The online version of this article (<https://doi.org/10.1007/s00265-019-2682-z>) contains supplementary material, which is available to authorized users.

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## Introduction

Intraspecific aggressiveness is a plastic behavioral trait that can deeply modulate interactions with conspecifics. Intraspecific aggressiveness can have profound impact on populations, by modulating competition and determining access to resources, and often has cascading effects on fitness and population dynamics (Reques and Tejedo 1996; Whitehouse 1997; Arnott and Elwood 2008). This is particularly relevant in contexts where conspecifics become a potential trophic resource, and aggressive interactions often result into full-scale cannibalism (Wise 2006; Manenti et al. 2015). Cannibalistic behavior can, at the same time, provide additional foraging resources to the cannibals and release them from intraspecific competition pressure, with potential benefits such as a faster development rate and better survival (Polis 1981; Crump 1983). These benefits are particularly relevant in environmental contexts where resources are limited, conditions are harsh, or risk is elevated (Fox 1975; Crump 1983). Therefore, aggressive interactions can be more frequent in ephemeral habitats, when food availability is scarce or conspecific densities are elevated (Reques and Tejedo 1996; Wildy et al. 2001; Amat et al. 2008; Cooper et al. 2015; Manenti et al. 2015). Moreover, intraspecific aggressiveness can be higher in age- or size-structured populations (e.g., where cohorts from different breeding seasons coexist) and, in these conditions, predation on conspecifics by large, late-stage individuals is facilitated by size asymmetry (Ziemba and Collins 1999; Eitam et al. 2005; Wissinger et al. 2010).

The benefits of intraspecific aggressiveness are often context-dependent. Aggressiveness is frequently a plastic or conditional strategy which is subjected to multiple ecological trade-offs (Fox 1975; Polis 1981; Pizzatto and Shine 2008). The occurrence of predators is often a major determinant of intraspecific aggressiveness, nonetheless its effects on cannibalism occurrence may be complex and difficult to predict. First, predators directly affect the availability of conspecifics through consumption, thereby reducing intraspecific encounter rate (Polis 1981). Second, predation pressure often determines non-consumptive effects in prey populations, such as behavioral responses that allow minimizing predation risk (Peckarsky et al. 2008; Davenport and Chalcraft 2013). Non-consumptive effects can affect the incidence of aggressiveness in diverse ways. On the one hand, predation risk is known to determine the decrease of activity level across multiple taxa (Lima and Dill 1990; Anholt et al. 2000; Barbosa and Castellanos 2005), which in many cases can limit or even suppress the occurrence of cannibalistic behavior (Wissinger et al. 2010; Kishida et al. 2011). For instance, dragonfly larvae are predators that can cause a dramatic reduction of activity and aggressive interactions in the Ezo salamander (*Hynobius retardatus*) larvae, thus inhibiting the occurrence of cannibalistic individuals (Kishida et al. 2011).

On the other hand, when the risk of being predated is constantly elevated, a prolonged reduction of activity can be too costly, as it would hamper foraging (Lima and Bednekoff 1999; Ferrari et al. 2009). Under persistent risky conditions, an increase in foraging may even result more advantageous, favoring faster growth and rapid development, which can limit exposure to predators of most vulnerable stages or size-classes (Ferrari et al. 2009; Kishida et al. 2015; Manenti et al. 2016). An increase in cannibalistic behavior under heavy predation risk was observed in spadefoot toads, which showed a higher frequency of cannibalistic tadpoles in sites where their main predators (salamanders) were present (Ghioca-Robrecht et al. 2009).

Non-consumptive effects and the degree of anti-predatory responses strongly depend on the ability of prey to perceive predator presence and to assess predation risk (Lima and Dill 1990; Palmer et al. 2017). In aquatic environments, risk is typically perceived through chemical cues released by the predator (kairomones) (Chivers and Smith 1998; Kats and Dill 1998). Chemical signals can be also released by conspecifics, for instance when they are stressed, wounded, or eaten by a predator (stress, alarm, and diet cues) (Mirza and Chivers 2001; Wisenden 2003; Ferrari et al. 2010b). The simultaneous perception of predator kairomones and conspecific cues often produces synergic effects on prey behavior and can induce or enhance antipredator responses (Bryer et al. 2001; Keppel and Scrosati 2004; Dalesman et al. 2007). Moreover, anti-predator response can be modulated on the basis of experienced conditions (Wisenden and Millard 2001; Gonzalo et al. 2007; Epp and Gabor 2008) thus previous encounters with predators or risk cues can determine refined responses (McCollum and VanBuskirk 1996; Martin and Lopez 2003; Ferrari et al. 2007; Ferrari et al. 2008). However, when exposure to predators is continuous, predator-associated stimuli can lose their effectiveness and the intensity of anti-predator behavior can decrease (Turner 1997; Ferrari and Chivers 2011; Gonzalo et al. 2013). Overall, mechanisms regulating cannibalism under predation risk are difficult to disentangle, and complex trade-offs likely determine its occurrence and intensity (Nilsson et al. 2011; Kishida et al. 2015). Despite environmental conditions being expected to affect the benefits of cannibalism, only a few studies have analyzed the variation of aggressive interactions between populations subjected to considerably diverging predatory and environmental pressures (Griffiths 1994; Nilsson et al. 2011).

In our study, we evaluated how predation risk affects intraspecific aggressiveness of salamander larvae in populations originating from extremely diverging habitats, such as surface and cave environments. The fire salamander (*Salamandra salamandra*) typically breeds in surface streams, where predators are abundant (Lanza et al. 2009; Manenti et al. 2009b, 2016). Nevertheless, several populations breed in underground streams or pools (Manenti et al. 2009a, 2011). These environments are virtually devoid of interspecific predators,

are characterized by limited trophic resources, and can host high salamander densities (Manenti et al. 2015). Theory predicts that cannibalistic behavior is favored under these conditions (Polis 1981; Crump 1983).

Cannibalism is frequent in fire salamander larvae (Joly 1968) and is known to occur both in surface and cave populations (Manenti et al. 2015). In this species, the frequency of aggressive interactions is associated with cannibalism intensity, thus intraspecific aggressiveness represents a good proxy for the occurrence of this behavior (Markman et al. 2009; Limongi et al. 2015; Manenti et al. 2015). To evaluate the complex interplay among factors determining cannibalism, we investigated the plasticity and variability of aggressive displays linked to cannibalistic behavior in salamander larvae from cave and surface populations, after the exposure to risk conditions and risk-associated cues. We predict that (i) long-term exposure to predators during development decreases the occurrence of aggressive interactions among larvae; (ii) the degree of anti-predator behavior is affected by the temporal pattern of experienced conditions (e.g., less pronounced response under constant risk regime compared to periodical exposure); moreover, (iii) acute exposure to chemical cues associated to predation risk should affect the perceived level of risk, decreasing intraspecific aggressiveness; finally, (iv) we expect higher aggressiveness in larvae facing environmental conditions that favor intraspecific predation (e.g., cave populations). Understanding mechanisms regulating cannibalism occurrence and intensity in natural environments can offer important insights on the relative role played by cannibalism in favoring ecological plasticity and the exploitation of harsh, resource-deprived habitats.

## Methods

### Collection of larvae

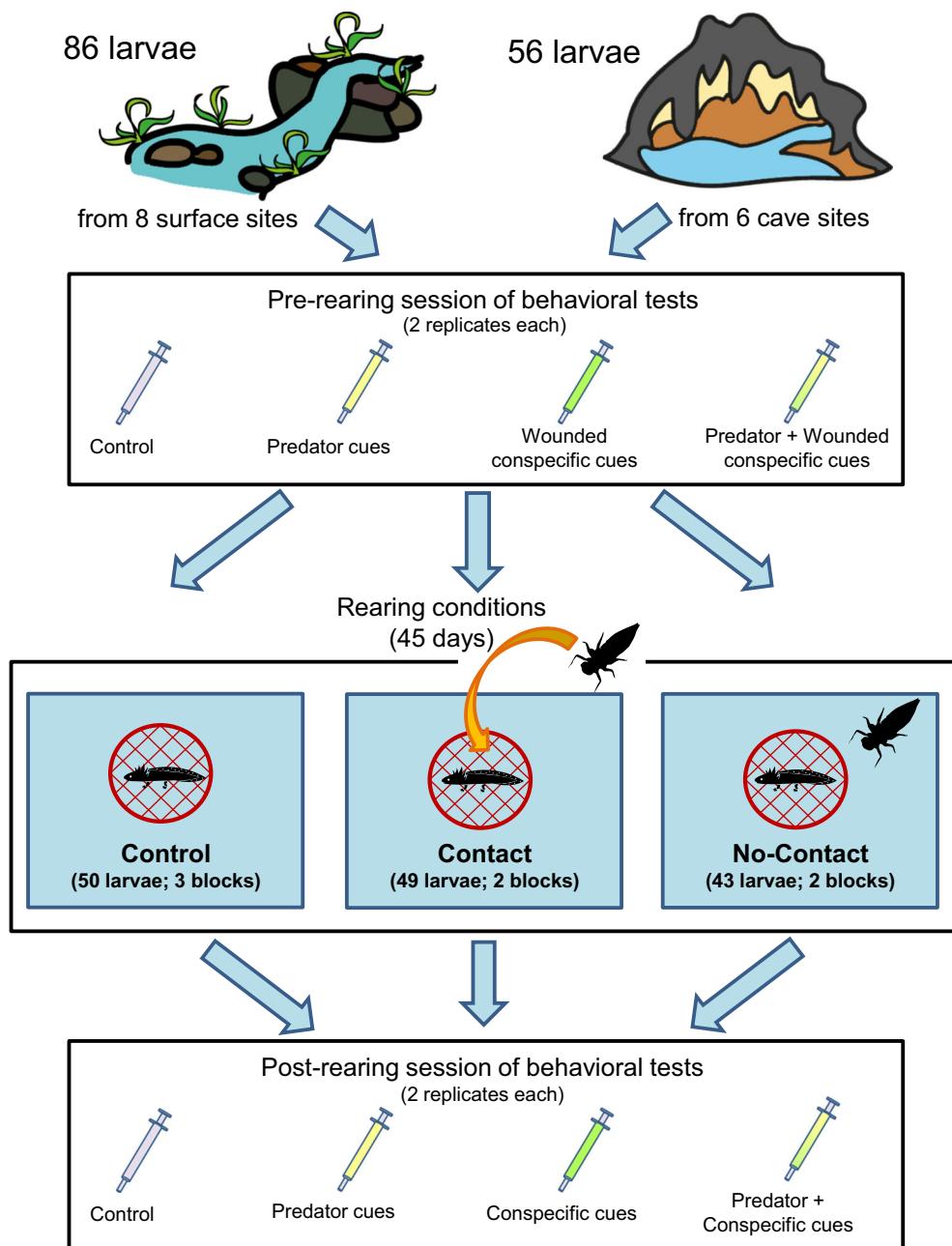
The study individuals were collected in the districts of Como and Lecco (Lombardy, NW Italy. Approximately 45.8° N, 9.2° E). This area is characterized by hilly and mountainous reliefs with scattered woodlands, predominantly composed of deciduous trees and a dense hydrographic network. In this region, karstic areas are frequent, with numerous cavities constituting a suitable habitat for multiple terrestrial and aquatic invertebrates. In this area, the fire salamander is common and gives birth to fully-aquatic larvae both in surface sites (e.g., pools and small streams (Manenti et al. 2009b)) and in underground springs (Manenti et al. 2009a). In underground sites, larvae prey upon cave-dwelling invertebrates, but food availability is scarce (Romero 2009). Therefore, development rate is generally slower than in surface sites (Manenti et al. 2011; Limongi et al. 2015), still salamanders are able to successfully complete metamorphosis.

In spring 2014, 142 newborn fire salamander larvae (developmental stage 1, Zakrzewski 1987) were collected from six underground pools ( $N=56$  individuals, average 9.3 individuals per site; range 5–12) and from eight surface sites ( $N=86$ , average 10.7 individuals per site; range 7–12; Fig. 1), located between 250 and 970 m a.s.l. The distance between sites ranged between 350 m and 29 km. Nearby sites were separated by natural barriers like deep valleys with steep slopes, thus larvae from different sites belong to separate populations. All underground sites were emitting springs inside caves; therefore, no accidental drift of larvae from outdoor sites was possible (Manenti et al. 2009a; Manenti and Ficetola 2013). For the surface sites, only habitats with permanent water were selected, because temporary wetlands have very different selective pressures (Reinhardt et al. 2013). Fire salamanders are ovoviparous; thus, larvae could only be collected after deposition. To limit age differences and minimize the effect of possible prior experiences, we daily monitored breeding sites and collected newborn larvae immediately after deposition.

### Rearing conditions

Immediately after collection, each larva was photographed to allow individual identification through the unique pattern of their tail (Eitam and Blaustein 2002). Larvae were then individually hosted in transparent plastic containers (10 cm diameter, 15 cm height), and arranged in large plastic tanks (40 × 50 cm), filled with 5 cm of aged tap water (blocks). All the individual containers were perforated (2 mm perforations); therefore, water freely flowed between the tank and the individual containers. Water temperature (15 °C) and oxygenation were kept constant and larvae were exposed to natural photoperiod. Five days after collection, cave and surface larvae were equally divided into three rearing conditions differing in risk exposure: constant predator exposure with no direct predation risk (No-contact), short periodical predator encounters (Contact), and a control condition with no exposure to predators (Fig. 1). The predator used for the experiment was a large (35 mm) dragonfly (*Cordulegaster bidentata*) larva. Dragonfly larvae were collected from surface sites, where they represent a common predator of salamander larvae. Dragonfly larvae can also occur in cave environments, but their frequency is extremely low (Manenti et al. 2013b). In the No-contact conditions ( $N=43$  larvae, subdivided in two blocks), two dragonfly larvae were added to the tanks hosting the containers with salamanders and allowed to freely move inside the tank for the whole rearing period. In this condition, predation was impossible but larvae were constantly exposed both to predator's visual and chemical cues. In the Contact conditions ( $N=49$  larvae, two blocks), individuals were subjected to brief pulses of risk with an abrupt exposure to predator presence (with the simultaneous perception of visual, chemical, and tactile stimuli),

**Fig. 1** Experimental design and sample sizes. We collected 142 fire salamander larvae (*Salamandra salamandra*) from six caves ( $N=56$ ) and eight surface ( $N=86$ ) populations. Larvae were exposed for 45 days to three rearing conditions: Control, absence of predator ( $N=18$  cave larvae + 32 surface larvae); Contact, periodical exposure to 30-s encounter with predator ( $N=20$  cave larvae + 31 surface larvae); No-contact, constant to non-lethal exposure to predator ( $N=18$  cave larvae + 23 surface larvae). We conducted two sessions of behavioral tests: before rearing period and after rearing period. During each behavioral test, the focal larva was exposed to each chemical treatment in two replicates ( $N=8$  tests per larva per session)



larvae were exposed every 4 days to direct encounters with predators, by inserting one dragonfly larva in the plastic container for 30 s (total: 11 encounters throughout the rearing period). This brief exposure prevented predation attempts but was sufficient to be perceived as a threat by salamander larvae, which showed startled escape responses when the dragonfly larva was inserted into their container. The escape response was observed even at the last exposure, suggesting no habituation to this treatment. Predator exposure in Contact and No-contact conditions differed both in time and modality: while Contact-reared animals experienced risk during limited

but acute stress events, individuals reared in No-contact conditions were exposed to persistent and but less pronounced risk conditions. Contact and No-contact conditions aimed at comparing differential risky conditions, which could differentially affect behavior (Turner 1997; Lima and Bednekoff 1999; Sih and McCarthy 2002). Finally, larvae under Control conditions never experienced predator presence ( $N=50$  larvae, three blocks). Rearing lasted 45 days, and during this period, both fire salamander and dragonfly larvae were fed ad libitum every second day with fresh *Chironomus* spp. larvae.

## Chemical cues

To test the influence of predation-related cue exposure, two chemical treatments were prepared: predator cues and wounded conspecific cues. Cue extraction was performed before rearing and behavioral tests as in Manenti et al. (2016). Previous studies have demonstrated that salamander larvae perceive dragonfly larvae as a threat, as they heavily reduce activity (Manenti et al. 2016). Therefore, predator chemical cues were obtained leaving 6 *C. bidentata* specimens in 1.5 l of decanted tap water for 24 h. Conversely, in order to obtain cues from a wounded conspecific, the tail tip (< 30%) of a fire salamander larva was cut off with a sterilized scalpel, and the individual was left in 1.5 l of decanted tap water for 24 h. Tail loss is very frequent in natural populations (up to 40% of salamander larvae in populations with abundant predators) (Manenti et al. 2013b). Moreover, salamander larvae are able to quickly regenerate tail, and this operation does not impact larval survival or subsequent performance (Segev et al. 2015). The wounded individual was separately reared; its conditions were monitored for 40 days, and it was released in its site of origin. The two cue solutions were collected, divided into 10 ml aliquots, and stored at -20 °C until the behavioral tests. Tap water was collected using the same procedure and used as control treatment. Salamander and dragonfly larvae used during this procedure were not used for any rearing treatment or behavioral trial, and were maintained separated from the individuals used for the experiment.

## Behavioral tests

The experimental design consisted of two behavioral sessions: before and after the 45-day rearing period. During these sessions, the aggressive behavior of individuals was measured by different cue exposures. At each behavioral session, each individual was tested in two replicates for all the combinations of cue exposures (predator; wounded conspecific; predator + wounded; control; see Fig. 1). In total, individuals were subjected to 16 behavioral trials ( $N=8$  trials per individual per session); in each session, the order of cues was randomized. This procedure made it possible to perform all the test combinations in a reasonable and comparable time; the randomization of test order allows the minimization of potential biases related to the sequence of cue exposure (Altmann 1974; Ferrari et al. 2010a). Aggressiveness trials were performed after a 3-day starvation period to promote the occurrence of aggressive interactions and standardize individual motivation to attack. Before each experimental session, all larvae were photographed on graph paper to measure total length. Behavioral tests were conducted under daylight conditions in a 13.5 × 18.3-cm plastic arena filled with 250 ml of decanted tap water. To test for intraspecific aggressiveness, the focal individual was exposed to a so-called “prey larva”

in the experimental arena. The prey larva was a newborn fire salamander larva originating from a different site of collection, and not subjected to any rearing treatment. Both the focal and the prey larvae were gently introduced at the opposite side of the same arena and let acclimatize for a 5-min period. During acclimation, larvae were kept separated by means of a removable plastic barrier, which divided the arena into two equal-size sectors. After the acclimation phase, 1 ml of the selected cue treatment was injected by the same experimenter in the prey larva sector, then the plastic barrier separating the two larvae was cautiously removed and the test started.

Aggressiveness tests lasted 7 min. During tests, three behavioral displays were recorded for focal larvae: total number of bites or biting attempts towards the prey larva (Attack), the latency of the first movement towards the prey (Latency), and the time spent by the focal larvae approaching the prey larva (Following). An Attack was any effective bite, a snap trying to catch the conspecific, or a sudden rush towards the prey larva. Latency was the time occurring until the first approach, such as when the larva performed an attack or at least two consecutive movements towards the prey larva. Following was the total duration of approaching events towards the prey larva (approaching events were three or more consecutive movements towards the prey larva). Data were not blindly recorded to avoid the risk of mismatching errors.

Between trials, both focal and prey larvae were placed in their plastic boxes for a 15-min recovery time, while arenas were carefully washed twice to remove cues; previous studies showed that this procedure is sufficient to detect the effect of exposure to different cues (Manenti et al. 2016). In total, we used 47 prey larvae and randomly assigned them to the focal larva during each trial to minimize repeated encounters. For each trial, we also calculated size difference between larvae (i.e., the total length difference between focal and prey larva). During the trials, two clear cannibalism attempts occurred. In both cases, the consumption was promptly interrupted, and the trial stopped. The prey larvae were replaced, separately allowed to recover and never used in any subsequent trial.

## Statistical analysis

Data were analyzed using linear mixed effects models (LMMs) and generalized linear mixed effects models (GLMMs), which take into account random factors determining non-independence of observations (Pinheiro and Bates 2000). Gaussian LMMs were used to analyze the factors determining Following and Latency displays, while Poisson GLMMs were used for the number of attacks. As fixed effects, we considered size difference between focal and prey larva, period (before or after rearing), origin (cave or surface population), rearing condition (No-contact, Contact, Control), and chemical treatment. The two sessions of behavioral trials (before and after rearing) were analyzed simultaneously; we

**Table 1** Influence of independent variables on Attack, Latency, and Following displays performed by fire salamander larvae. For Attack, we used Poisson GLMMs (test statistics:  $\chi^2$ ); for Latency and Following, we used Gaussian LMMs (test statistics:  $F$  value). Significant effects are in italic

Display	Fixed effects	df	Test statistic	P
Attack	Size difference	1	4.160	<i>0.041</i>
	Period	1	4.212	<i>0.040</i>
	Origin	1	3.099	0.078
	Rearing	2	14.962	< 0.001
	Predator cues	1	0.003	0.960
	Conspecific cues	1	2.016	0.156
	Period $\times$ Predator cues	1	4.351	<i>0.037</i>
	Rearing $\times$ Origin	2	16.372	< 0.001
	Rearing $\times$ Predator cues	2	8.735	<i>0.013</i>
	Rearing $\times$ Conspecific cues	2	8.875	<i>0.012</i>
Latency	Size difference	1, 126.9	5.68	<i>0.019</i>
	Period	1, 91.64	1.33	0.253
	Origin	1, 81.6	0.53	0.467
	Rearing	2, 100.4	1.64	0.199
	Predator cues	1, 168.0	0.001	0.972
	Conspecific cues	1, 176.3	0.02	0.893
	Origin $\times$ Conspecific cues	1, 172.1	7.32	<i>0.008</i>
Following	Size difference	1, 73.8	6.47	<i>0.013</i>
	Period	1, 48.8	3.52	0.067
	Origin	1, 151.99	5.43	<i>0.021</i>
	Rearing	2, 120.31	8.79	< 0.001
	Predator cues	1, 148	4.81	<i>0.029</i>
	Conspecific cues	1, 151.99	0.19	0.666
	Origin $\times$ Conspecific cues	1, 150.7	4.93	<i>0.028</i>

included period in the mixed models to take into account differences occurring through time. We also included length difference between larvae as a covariate. Random factors were larva identity, rearing block, and population of origin. Preliminary analyses including the identity of prey larva as a further random factor showed higher AIC values and were qualitatively identical.

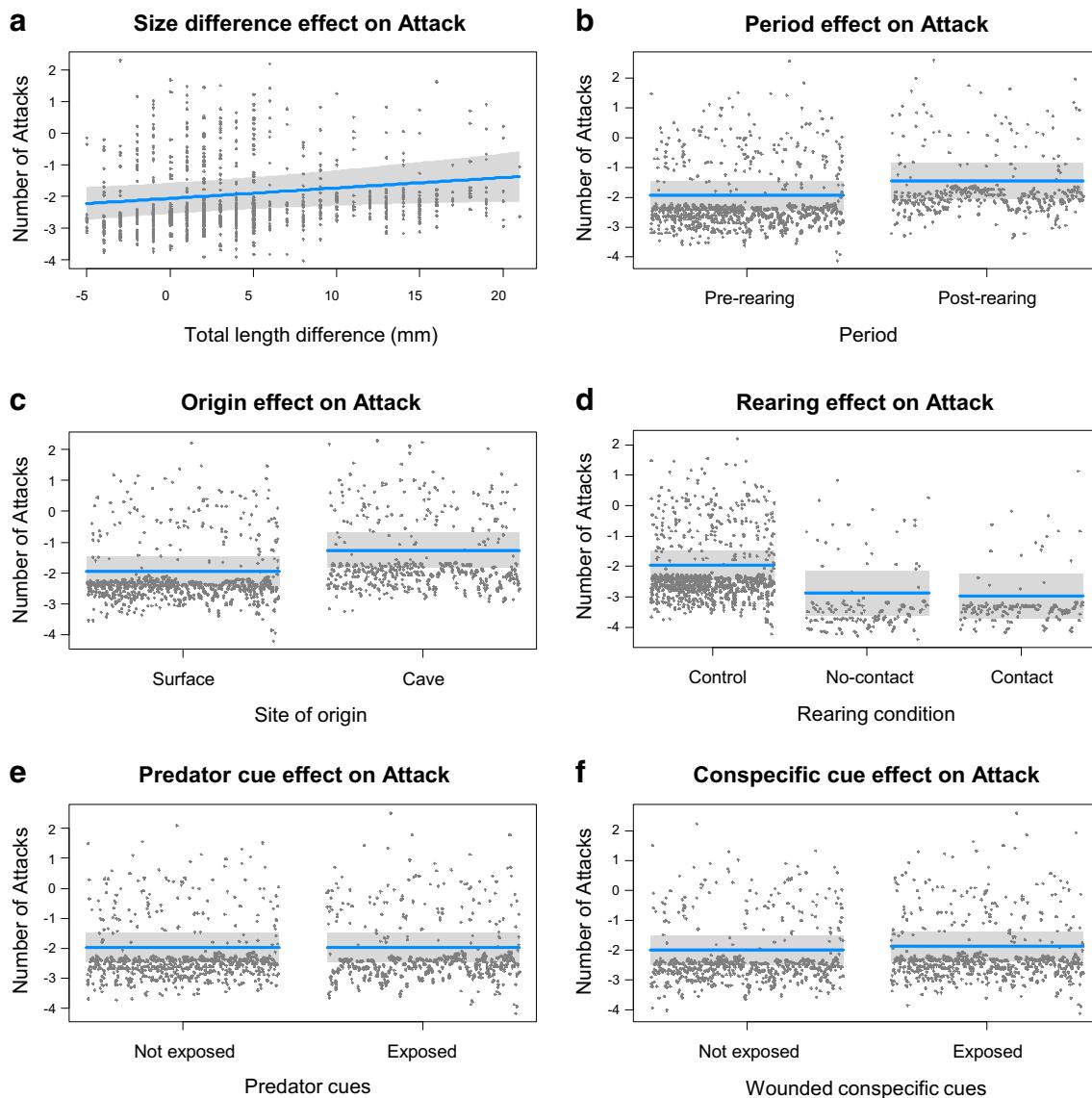
We used orthogonal contrasts (or “planned comparisons”) to perform the comparison between rearing conditions. Orthogonal contrasts allow pairwise comparisons without increasing type I and type II errors, as it would occur when using post-hoc tests (Field et al. 2012). We first used contrasts to compare predator-rearing conditions (Contact- and No-contact) against Control-larvae. Subsequently, we tested the significance of differences between Contact and No-contact conditions. For each behavioral display, two-way interactions between period, origin, rearing condition, and chemical treatment were tested; non-significant interactions were not included in the final models. Testing statistical interactions between chemical stimuli (predator and wounded conspecific cues) was used to assess the possibility of joint effects between them. The analysis of latency and following behaviors was performed on the subset of trials in which larvae approached or followed conspecifics (i.e., 196 and 160 trials, respectively;

see Appendix S1). To visualize the effects of GLMMs, we built conditional partial regression plots using visreg 2.4 (Breheny and Burchett 2017). All analyses were performed under the R 3.4.1 environment using the packages lmerTest and lme4 (Pinheiro and Bates 2000), while the visreg package was used to generate plots presented hereafter.

The datasets generated during and/or analyzed during the current study available from the corresponding author on reasonable request.

## Results

Overall, we performed 1520 behavioral trials. During trials, differences between focal larva and prey larvae for the total length ranged between – 5 and 21 mm (mean = 3.44, SD = 5.37 mm). None of the correlations between behavioral displays was strong. We detected a significant correlation between the duration of Following and the number of Attacks and ( $r = 0.472$ ,  $P < 0.001$ ), while correlations between Attacks and Latency ( $r = 0.002$ ,  $P = 0.979$ ) and between Following and Latency ( $r = -0.111$ ,  $P = 0.120$ ) were weak and non-significant. Survival rate after rearing was 70.4%. The mortality of salamander larvae in nature is often > 90% even in



**Fig. 2** Conditional partial residual plots, showing the relative influence of size difference (a), period (b), origin (c), rearing (d), predator cues (e) and conspecific cues (f) on fire salamander Attack display. Shaded areas are 95% confidence bands

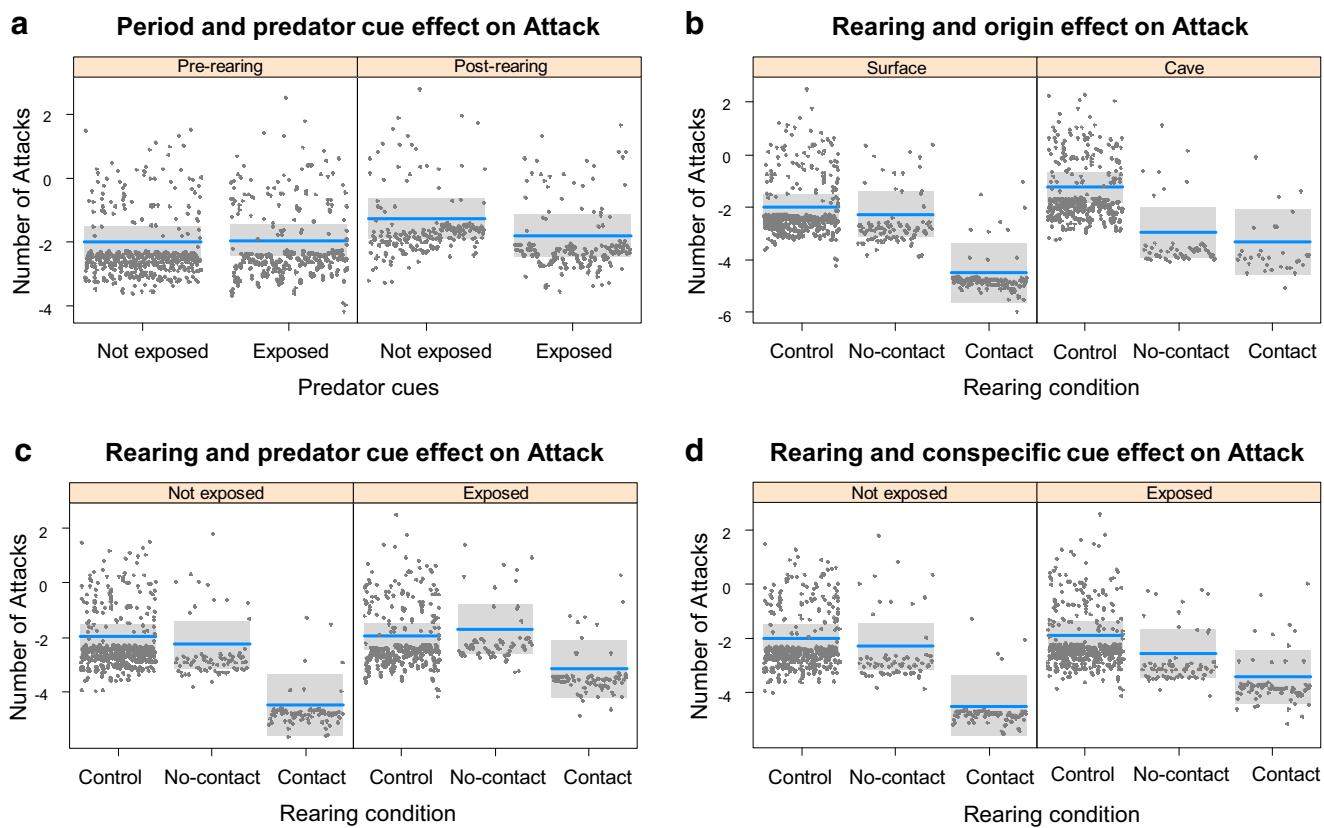
environments with limited predators (Limongi et al. 2015); therefore, the observed values are not unexpected. Mortality was not significantly different between rearing conditions or origin (binomial generalized linear mixed model; all  $P > 0.05$ ).

## Attack

During behavioral tests, mean ( $\pm$  SD) Attack rate was  $0.34 \pm 0.88$ , and the total number of attacks ranged from 0 to 6 per trial. The number of attacks significantly increased when size differences among larvae were largest ( $P = 0.041$ ), and after 45 days ( $P = 0.040$ ; Table 1; Fig. 2a, b). Furthermore, rearing under risky conditions significantly decreased the Attack rate ( $P < 0.001$ ; Fig. 2d). Orthogonal contrasts showed that both

rearing conditions significantly reduced Attack rate compared to Controls ( $\chi^2_1 = 11.37$ ;  $P < 0.001$ ), while we did not detect differences between the Contact and the No-contact conditions ( $\chi^2_1 = 0.08$ ;  $P = 0.781$ ). We found no significant effect of origin, predator cues, or wounded conspecific cues on this display (all  $P > 0.05$ ; Table 1, Fig. 2c-f).

We also detected multiple significant interactions between independent factors (Fig. 3, Table 1). First, larvae reduced their Attack rate in the presence of predator cues, but only after 45 days of rearing ( $P = 0.037$ ; Fig. 3a). Second, cave larvae reared under No-contact conditions reduced Attack rate more than surface larvae ( $P < 0.001$ ; Fig. 3b). Finally, larvae reared under Contact conditions reduced their aggressiveness less when exposed to predator ( $P = 0.013$ ; Fig. 3c) and to conspecific cues ( $P = 0.012$ ; Fig. 3d), compared to the other



**Fig. 3** Conditional partial residual plots, showing the significant interaction effects on fire salamander Attack display: period and predator cues exposure (**a**), rearing conditions and origin (**b**), rearing

conditions and predator cues exposure (**c**), rearing conditions, and conspecific cues exposure (**d**). Shaded areas are 95% confidence bands

conditions. We found no significant interaction of the paired exposure to the two chemical cues nor between any other fixed factor.

## Latency

Approaches towards prey larvae were detected in 12.9% of trials, with Latency time ranging between 0 and 417 s (mean =  $189.22 \pm 127.85$  s). The time before approaching prey was significantly shorter when size differences between the two larvae were largest ( $P = 0.019$ ; Table 1, Fig. 4a). By contrast, we did not detect a significant effect of period, origin, rearing, predator cues, or conspecific cues (all  $P > 0.05$ ; Table 1, Fig. 4b–f). Besides, when exposed to wounded conspecific cues, cave larvae showed a shorter time to first approach the prey larvae, compared to surface larvae ( $P = 0.008$ ; Fig. 5a). No other interactions between factors showed significant effects on latency.

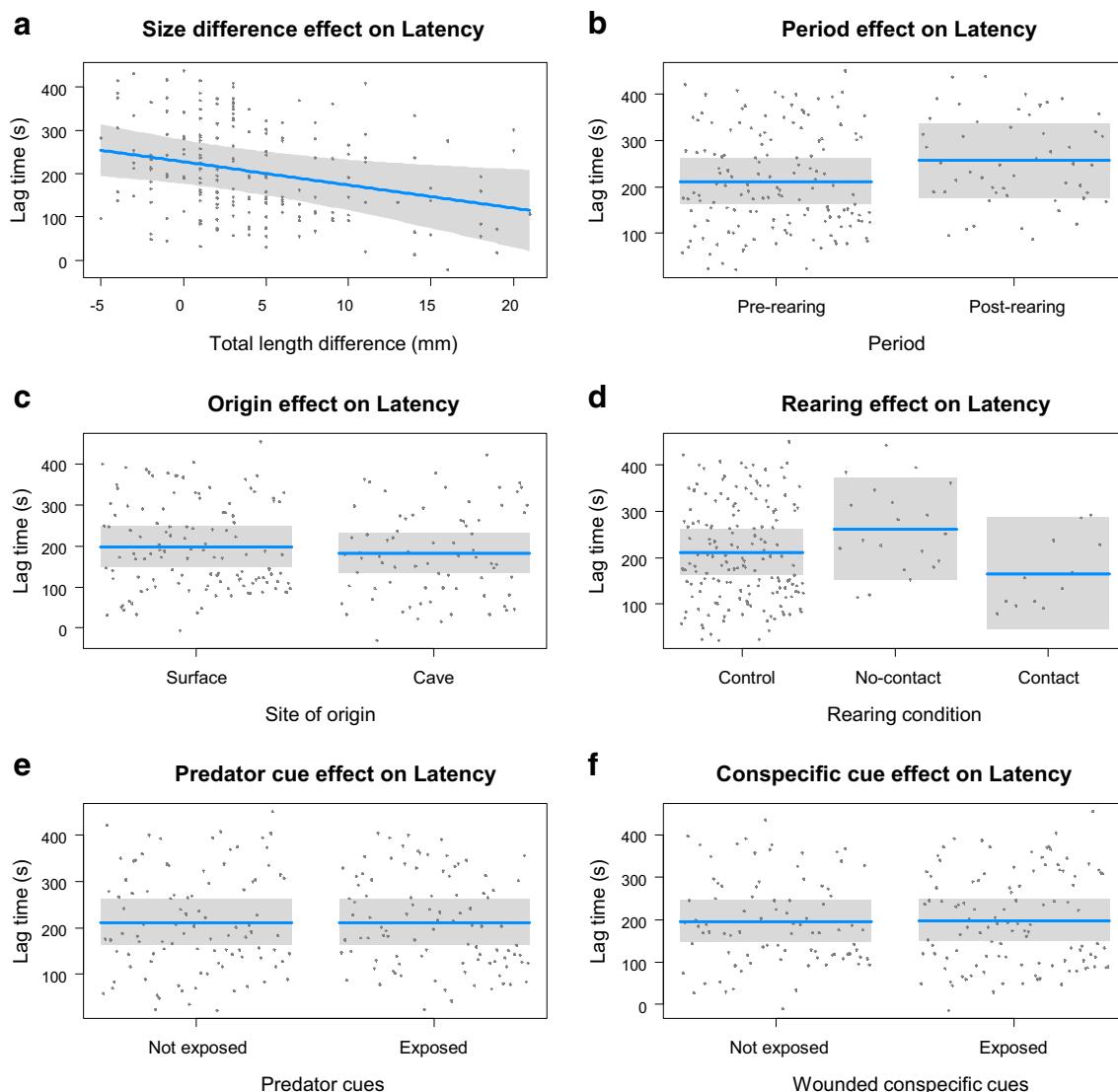
## Following

The Following behavior occurred in 10.5% of trials. The total time pursuing prey larvae ranged from 10 to 267 s (mean =  $43.53 \pm 46.48$  s). The Following time was

significantly longer when length differences between larvae were largest ( $P = 0.013$ ; Table 1; Fig. 6a). Furthermore, less prolonged Following was observed in larvae from surface populations ( $P = 0.021$ ; Fig. 6c), in the presence of predator cues ( $P = 0.029$ ; Fig. 6e), and in larvae reared with predators ( $P < 0.001$ ; Fig. 6c). Larvae reared under both risk conditions showed significantly shorter Following behavior, compared to Controls (orthogonal contrasts:  $F_{1, 118.4} = 13.9$ ;  $P < 0.001$ ; Fig. 6d), while differences between the Contact and No-contact conditions were not significant ( $F_{1, 150.7} = 0.74$ ;  $P = 0.390$ ). We did not detect significant effects of period or wounded conspecific cues on Following (all  $P > 0.05$ ; Fig. 6b, f). Finally, a significant interaction between origin and wounded cues indicated that only cave larvae increased their Following activity when exposed to wounded cues ( $P = 0.028$ ; Fig. 5b). No other interaction between fixed factors significantly affected Following duration.

## Discussion

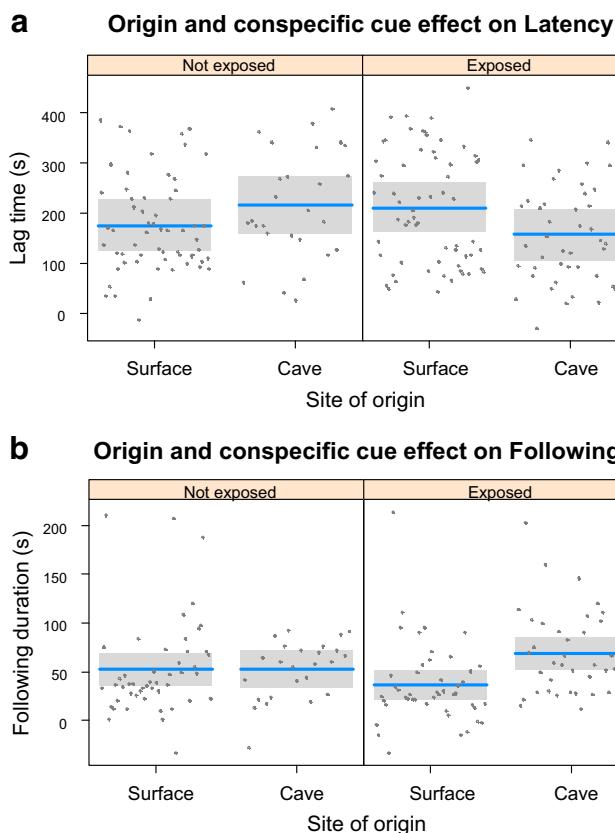
Environmental pressure can determine strong variation of aggressive behavior, and we observed increased agonistic



**Fig. 4** Conditional partial residual plots, showing the relative influence of size difference (a), period (b), origin (c), rearing (d), predator cues (e), and conspecific cues (f) on fire salamander Latency display. Shaded areas are 95% confidence bands

interactions in larvae from cave populations, where the fitness advantages of aggressive individuals can be particularly effective. Our study confirms that the expression of aggressive behavior can be affected by habitat pressures, and that populations can show differences in their responses to environmental conditions. Different typologies of risk exposure (constant presence of predator; pulses of high predation risk; presence of chemical cues) yielded a consistent reduction of aggressiveness through all the populations, still larvae from cave populations exhibited a more pronounced aggressiveness, especially when exposed to wounded conspecific cues. Individuals from cave populations also tended to follow more actively the perspective prey larvae, suggesting a stronger propensity to start agonistic interactions. This supports the prediction that aggressive interactions are favored in cave environment and suggests a key role of intraspecific predation on the exploitation of resource-depleted habitats.

The higher aggressiveness of cave larvae is probably related to their peculiar environment. Theory predicts that food scarcity, high conspecific density, and absence of predators shall enhance cannibalistic tendency (Fox 1975; Polis 1981), and these conditions are generally experienced by salamander larvae from cave populations (Limongi et al. 2015; Manenti et al. 2015). Moreover, when exposed to wounded conspecific cues, cave larvae considerably decreased their Latency to approach prey larvae, and increased their Following duration. Examples of conspecific cues eliciting an active foraging strategy are described for some cannibal species (Harvey and Brown 2004; Tran 2014; Carlson et al. 2015), and resource-poor environments, such as caves, may further favor this response. Cannibalism is often favored in size- or age-structured populations (Fox 1975; Reques and Tejedo 1996). As expected, size differences promoted aggressive displays by increasing the number of attacks and the following intensity, and by



**Fig. 5** Conditional partial residual plots, showing the significant interaction effects of origin and conspecific cues exposure on fire salamander Latency (a) and Following (b) displays. Shaded areas are 95% confidence bands

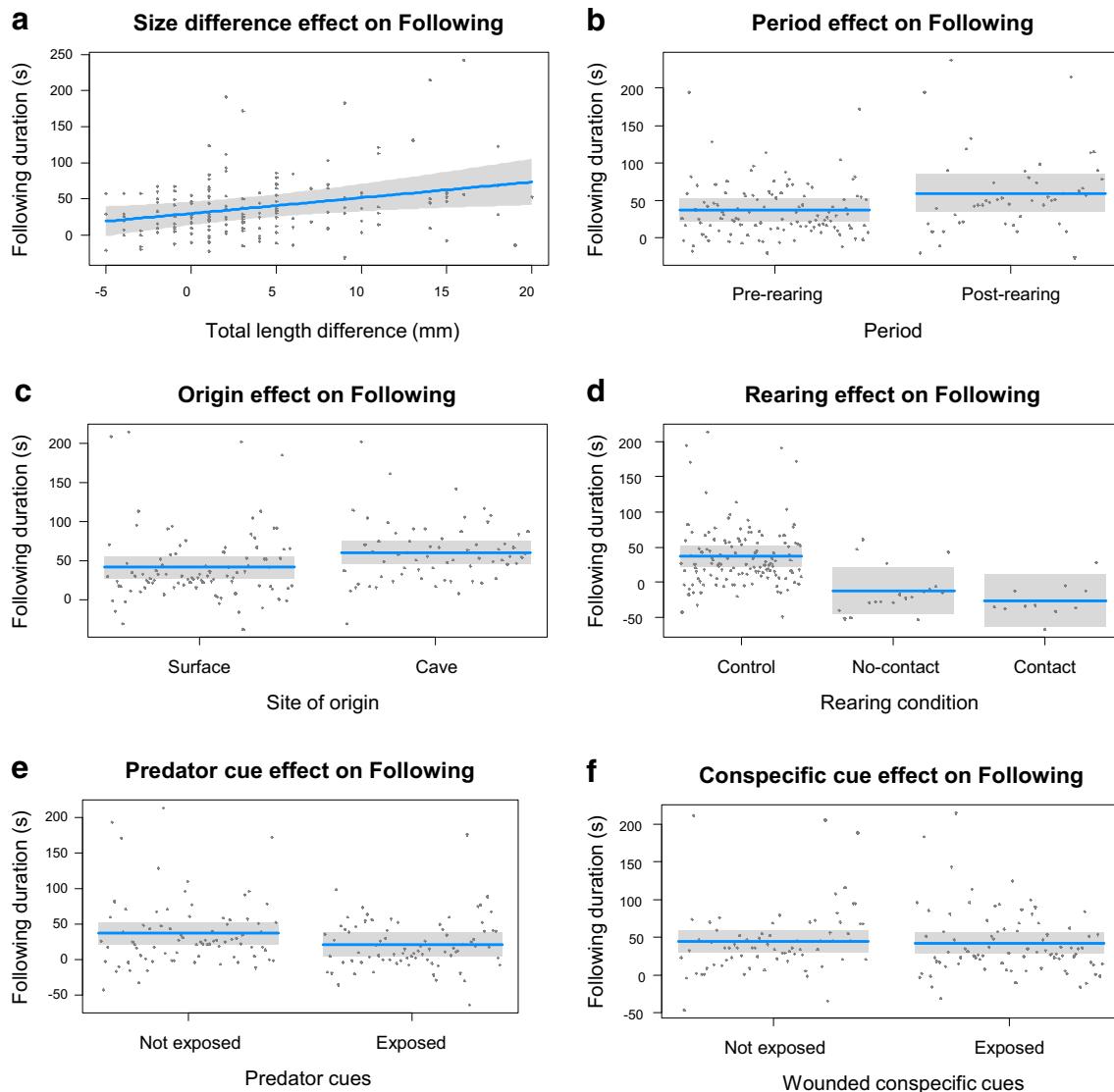
decreasing the latency of aggressive behaviors. Moreover, an increased aggressiveness was detected after 45 days of rearing, in agreement with studies suggesting that aggressive behaviors and cannibalism are more frequent in older larvae (Sadeh et al. 2009; Wissinger et al. 2010). In cave environments, prey are scarce and new-born conspecifics likely constitute an important resource for older, larger, and more aggressive larvae to survive and successfully achieve metamorphosis. Our results suggest that larvae from cave populations can be particularly prone to adopt risky behaviors and actively search for prey (Blecha et al. 2018), and perceive the cues of wounded conspecifics as a signal of trophic opportunity rather than an alarm signal.

The different behavioral strategies between cave and surface larvae (Figs. 5, and 6c) support the hypothesis of local adaptation in populations facing different environmental pressures (Baur 1994; Caspers et al. 2015). High foraging plasticity and cannibalism are traits that can facilitate the exploitation of resource-depleted environments (Polis 1981) and favor the colonization of novel habitats such as caves (Romero 2009; Manenti et al. 2013a). Moreover, in these environments, strategies offering access to alternative trophic resources, such as intraspecific predation and active search for the prey, should

be positively selected and can become established as local adaptations (Hüppop 1987; Manenti and Ficetola 2013). Cave and surface populations often live nearby; therefore, some gene flow between populations is possible. Nevertheless, local adaptations might be maintained by multiple processes, such as the strong difference in selective pressure between the two environments and assortative mating (Caspers et al. 2009).

Predation pressure can determine complex anti-predatory responses. A reduction of activity and higher refuge exploitation are frequent non-consumptive effects allowing to limit encounter rate with predators (Lima and Dill 1990; Davenport and Chalcraft 2013; Manenti et al. 2016); thus, we expected a reduction of intra-specific aggression in salamander larvae exposed to predators. Our findings were in agreement with this prediction, as a strong decrease of aggressiveness was evident in salamanders from both cave and surface populations experiencing predator presence during rearing (i.e., Contact and No-Contact conditions), or exposed to predator cues during behavioral tests.

Attack rate and Following duration were significantly reduced in larvae reared under both Contact and No-contact conditions, confirming the hypothesis that risk exposure can lead to important non-consumptive effects in fire salamander (Manenti et al. 2016). On the one hand, the strong risk pulses of Contact were expected to determine a pronounced increase of anti-predator responses and thus limit the occurrence of aggressive interactions. On the other hand, a continuous exposure to predator, without direct experience of negative consequences as in the No-contact condition, was supposed to cause a lower anti-predator response (Turner 1997; Lima and Bednekoff 1999; Sih and McCarthy 2002). Nevertheless, we did not detect significant differences between the Contact and No-contact conditions, as both caused a similar reduction in aggressiveness. While such lack of difference might also be favored by the good nutritional regime of larvae, which can limit the need for an active search of resources, the reduction of aggressiveness in No-contact larvae strongly suggests that any occurrence of habituation to predator presence was unlikely. In contrast, these results support the idea that perceived predation risk, even if extremely differing both in time and modality, can elicit a strong anti-predator response causing deep consequences on behavioral interactions between conspecifics. Moreover, we detected complex interactions between chemical cues and rearing conditions, as larvae reared under Contact condition showed a lower reduction in their aggressiveness when exposed to cues of predators and wounded conspecifics (Fig. 3). During the Contact condition, animals experienced pulses of risk with the direct presence of the predator (with co-occurring visual, tactile, and chemical stimuli). In contrast, during behavioral trials, animals were exposed to just the chemical cues released by predators. The lower response to predator cues in Contact-reared animals seems to suggest that animals experiencing the contemporary exposure to multiple stimuli



**Fig. 6** Conditional partial residual plots, showing the relative influence of size difference (a), period (b), origin (c), rearing (d), predator cues (e), and conspecific cues (f) on fire salamander Following display. Shaded areas are 95% confidence bands

could have improved their capability to discriminate between stimuli associated to predators, compared to individuals that never experienced direct contact with predators. However, the assessment of this hypothesis would require focused tests.

Chemical signals are assumed to be the most common cues used for risk perception by amphibian larvae (Chivers and Smith 1998). Our study showed that chemical signals are important also for fire salamanders, as a small amount of cues from predators and/or conspecifics was enough to entail significant behavioral responses. While predator cue exposure determined a general anti-predator response, with a significant reduction of some aggressive displays, cues of wounded conspecifics did not determine anti-predator behaviors, suggesting that in fire salamander, they are not perceived as alarm cues potentially inhibiting intra-specific aggressiveness. Several studies showed that other amphibian larvae reduce activity rate when exposed to the cues of wounded conspecifics (Gonzalo et al. 2007; Ferrari et al. 2010b).

However, most of these studies have been performed on anuran tadpoles, which rarely are predators (Wells 2007), and more studies are necessary to unravel the complex effects of wounded conspecifics in aquatic predators.

Both exposure to predators during rearing and the presence of predator cues during behavioral trials led to pronounced decreases of intraspecific aggressive interactions. Aggressiveness decreased in both cave and stream larvae, and in both newborn and older larvae. Such a reduction of aggressiveness led by predator occurrence may result in a waning or even a complete suppression of cannibalism in risky habitats (Kishida et al. 2011; Líznarová et al. 2018). As cannibalism plays a key role in many aquatic ecosystems (Rudolf 2008; Wissinger et al. 2010; Takatsu and Kishida 2015; Takatsu et al. 2017), its suppression may impact the survival and life-history of individuals (Kishida et al. 2011), with potential broad consequences on population dynamics (Claessen et al. 2004; Rudolf 2008).

Behavioral decisions under predation risk are driven by a complex interplay between multiple conditions (e.g., background level of risk, experience, prey energetic state). Their expression can be fine-tuned by the multifaceted nature of the environmental pressures experienced, but is also affected by adaptations to local conditions. Integrated analyses, considering multiple behavioral displays, are essential to better understand how prey responses are modulated under the complex environmental variation that can occur in nature.

#### Acknowledgments

We are grateful to Benedetta Barzaghi for her help with field sampling and to Prof. Roberta Pennati for helping edit during the drafting of this manuscript. The comments of two anonymous reviewers and C. Gabor greatly improved previous versions of the manuscript.

**Funding** GFF is funded by the European Research Council under the European Community's Horizon 2020 Programme, Grant Agreement no. 772284 (IceCommunities).

#### Compliance with ethical standards

The study design was approved by the ethical committee of the Lombardy Region Authority and was authorized as complying with the regional law 10/2008, p.n.: F1.2013.0002091. Larvae were subjected to the same rearing conditions as in Manenti et al. (2016). The aim of the present study was to evaluate the non-consumptive effects of dragonfly larvae on salamander larvae aggressive behavior. Consequently, care was taken to plan the experiment accordingly and, thus, to avoid any larvae being exposed to any actual predation. To this end, during rearing, direct contact with predator was restricted to 30-s encounters, which were short enough to prevent predation events. Whatever the case, we were always ready with tweezers to block snaps or stop them from extending their mouthparts. Similarly, full cannibalistic interactions were not allowed. During behavioral trials, when an aggressive interaction lasted more than a single bite event, conspecifics were promptly separated, thus, preventing injuries and intraspecific predation events. It should be also noted that in natural conditions, fire salamander larvae show very often aggressive interactions (Joly 1968), facing much more severe outcomes (e.g., being cannibalized) than those experienced in the study design that we adopted during behavioral trials and that was approved by the ethical committee. Conspecific cues were extracted from a single larva by removing the tail tip (far less than 30% of the tail) with sterilized scissors, a procedure that has been assessed to have no impact on individual survival or subsequent performance (Segev et al. 2015). After tail removal, the conditions of this individual were monitored and it perfectly recovered during a 40-day rearing period before releasing it in the site of origin. Overall, the survival rate of larvae was 70.4%, being much higher than that observed in natural populations (Limongi et al. 2015). All individuals were checked daily and fed every 2 days (see also Winandy and Denoel 2013, 2015). All the larvae were released at their site of origin at the end of the study, following the recommendations of the permit.

**Conflict of interest** The authors declare that they have no conflict of interest.

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