

# Conspecific alarm cues, but not predator cues alone, determine antipredator behavior of larval southern marbled newts, *Triturus pygmaeus*

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Received: 28 November 2011 / Revised: 26 January 2012 / Accepted: 3 February 2012  
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**Abstract** Predation imposes selection on the ability of prey to recognize and respond to potential threats. Many prey species detect predators via chemoreception, particularly in aquatic environments. Also, chemical cues from injured prey are often perceived as an indication of predation risk. However, because antipredatory behavior can be costly, prey responses should depend on the current level of risk that each predator poses, which may depend on the type of chemical cues detected. We exposed larval newts, *Triturus pygmaeus*, to chemical cues from predator larval beetles or to alarm cues from conspecific larval newts and examined the behavioral changes of larval newts. Results showed that larval newts reduced activity levels when conspecific alarm cues were present but not when the predator cues alone were present. These results might suggest that larval newts are unable to recognize predator chemicals. To avoid costs of unnecessary antipredatory behaviors, larval newts may benefit by avoiding only predators that represent a current high level of threat, showing only antipredatory responses when they detect conspecific alarm cues indicating that an actual predatory attack has occurred.

**Keywords** Alarm cues · Chemoreception · Newts · Predator recognition · Risk assessment

## Introduction

The ability to recognize and respond to a potential predator is an important component of antipredator behavior because a failure increases the probability that the predator captures or injures the prey (Lima and Dill 1990). As a result, there should be strong selective pressure for prey to identify potential predators (Sih 1987; Lima and Dill 1990). Many animals discriminate among predators using a variety of sensory modes, one of the most common being chemoreception (Dodson et al. 1994; Chivers and Smith 1998; Kats and Dill 1998; Ferrari et al. 2010). Although information provided through other sensory modes (e.g., visual or tactile cues; Boothby and Roberts 1995; Amo et al. 2004a) may help prey in locating predators, chemical cues may be particularly useful for prey species that are nocturnal (Chivers et al. 1996a), that live in highly complex or turbid environments (Petranka et al. 1987; Cabido et al. 2004), or that deal with cryptic or sit-and-wait predators (Mathis and Smith 1993a; Chivers et al. 1996a; Amo et al. 2004a). Diverse types of prey, such as many invertebrates, fish, amphibians, reptiles, or mammals, can detect and discriminate chemically between a predator and a non-predator (reviewed in Kats and Dill 1998; Ferrari et al. 2010), and, in many cases, only predators of significant threat elicit avoidance behaviors (e.g., Thoen et al. 1986; López and Martín 2001; Amo et al. 2004b).

Chemical cues from predators can be important indicators of risk that elicit antipredator responses in many aquatic animals (Kats and Dill 1998; Tollrian and Harvell 1999; Ferrari et al. 2010). Also, in some cases, combined chemical information from both the predator and prey appears to induce a selective response in prey. For example, predatory attacks cause injury to prey and the passive release of chemical compounds from internal body tissues of prey. These prey chemicals may therefore serve as alarm cues

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that induce antipredator behavior in nearby conspecific prey. Given the selective pressure imposed by predation, many aquatic organisms, from ciliates to fish and amphibians show antipredatory responses to injury or damage cues from conspecifics (reviewed in Smith 1992; Chivers and Smith 1998; Wisenden 2003; Ferrari et al. 2010). Conspecific alarm cues are not necessarily evolved signals per se but passively released chemical cues that inform and benefit nearby conspecific prey of the predator without any benefit accruing to the individual releasing the cue. A wide variety of larval amphibians exhibit avoidance responses to conspecific alarm cues (Adams and Claeson 1998; see reviews by Chivers and Smith 1998; Ferrari et al. 2010). Although some controversy exists concerning the function of alarm signals based on particular negative results (Magurran et al. 1996; but see Smith 1997), there exists considerable evidence for the antipredatory function of alarm signals (Smith 1992, 1997; Chivers and Smith 1998). Antipredatory behavioral responses to alarm signals can include freezing, area avoidance, tighter shoaling, increased shelter use, or decreased foraging activity and movement rates (Mathis and Smith 1993b; Chivers et al. 1995). Receivers of alarm signals may even alter their life history patterns or morphology (Stabell and Lwin 1997; Chivers et al. 1999).

Many animals can significantly reduce predation risk by responding to predator chemical cues or conspecific alarm cues (Kats and Dill 1998; Ferrari et al. 2010). However, although there are clear benefits to behavioral responses to predator cues, there can also be costs (Lima 1998). For example, avoiding particular habitats or reducing foraging activity can compromise an animal's foraging success (e.g., Skelly 1992; reviewed by Lima and Dill 1990; Lima 1998). In these cases, according to the threat-sensitive predator avoidance hypothesis (Helfman 1989), natural selection should favor individuals that take action appropriate to the magnitude of threat, which would require an accurate discrimination of the current level of risk that each predator poses. Thus, responses of prey to predators may be context-dependent (Maerz et al. 2001). For example, in the laboratory, many prey species only respond to predator chemical cues when the predator is experimentally fed a diet that contains conspecifics (e.g., Mathis and Smith 1993a; Wilson and Lefcort 1993; Chivers et al. 1996b). Similarly, green frog tadpoles exposed to alarm cues and predatory snake scent together reduce their movement rates to a greater extent than when the snake scent is found alone (Gonzalo et al. 2007), and responses to alarm cues are greater than to disturbance cues alone (Gonzalo et al. 2010).

In this study, we tested whether larvae of the southern marbled newt were able to detect and respond to chemical cues from a predator larval beetle and/or to conspecific alarm cues. The southern marbled newt, *Triturus pygmaeus*

(Wolterstorff 1905) is a small newt widespread in southwestern Spain. Adults typically breed at temporal ponds with well-developed aquatic vegetation (Montori and Herrero 2004; Reques 2007). The larvae of the great diving beetle, *Dytiscus marginalis*, is a generalist ambush predator that inhabits the same ponds as newts and usually feed on larval newts and tadpoles (e.g., Eklöv and Halvarsson 2000; Reques 2007). In this study, we exposed *T. pygmaeus* larvae to *D. marginalis* larvae or to alarm cues from conspecific larval newts and examined the ability of larval newts to modify their antipredatory behavior accordingly. For fish and larval amphibians, activity level is often correlated with predation risk (Godin and Smith 1988; Skelly 1994). Therefore, changes in activity level can be used as an indication of antipredator behavior of larval newts. We predicted that *T. pygmaeus* larvae will change their activity level when exposed to the predator and to alarm cues. However, the magnitude of the antipredatory response could be higher to alarm cues than to predator cues alone, as alarm cues should represent a stronger indication of current risk.

## Materials and methods

### Study species

During summer, we captured by netting *T. pygmaeus* larvae (snout-to-vent length,  $\bar{X} \pm SE = 21.8 \pm 0.3$  mm;  $N=20$ ) at several small temporary ponds in Collado Mediano (Madrid province, Central Spain). These ponds were complex habitats, with abundant aquatic vegetation. The ponds dry entirely through the summer. This forces larval newts to reach metamorphosis size in a short time, which may render very costly the unnecessary antipredator responses that decrease time available for foraging (see Lima and dill 1990). Newt larvae were individually housed at a laboratory of "El Ventorrillo" Field Station (Navacerrada, Madrid Province), 10 km from the capture area, in plastic aquaria (20×20 and 10 cm high) with water at ambient temperature and under a natural photoperiod. They were fed live little earthworms (*Lumbricus* sp.) everyday.

We also captured in the same ponds two *D. marginalis* larvae to be used as predator scent donors. These larval beetles are voracious generalist predators who mainly feed on other insects, fishes, and amphibian larvae (e.g., Eklöv and Halvarsson 2000). These *D. marginalis* larvae occur in the same microhabitat as that of southern marbled newts and represent a high predation threat for larval newts (Reques 2007). We housed *D. marginalis* larvae in the same conditions as larval newts but in a different room to avoid contact before starting the experiment. To avoid potential confounding effects of the diet on the results (Mathis and

Smith 1993a; Chivers et al. 1996b), all *D. marginalis* larvae were only fed live mealworms (*Tenebrio molitor*) for 2 weeks before starting the experiments.

All the animals were healthy during the trials. All larval newts metamorphosed into subadult newts and all larval beetles into adult beetles. The newts and the beetles were returned to their exact capture sites. The experiments were carried out under license from the “Consejería de Medioambiente de la Comunidad de Madrid”. Procedures were conformed to recommended guidelines for use of live amphibians in laboratory research (ASIH 2004).

### Experimental procedure

We exposed larval newts to a predator (*D. marginalis* larvae) and to conspecific alarm cues and noted whether there were changes in behavior of larval newts. Conspecific alarm cues were prepared from three larval newts. They were cold anesthetized by placing them at 4°C for 20 min, inducing them into deep hypothermia, and then euthanized with a quick blow to the head to avoid suffering (ASIH 2004). We did not use a chemical anesthetic, because these chemicals may interfere with natural chemical cues of larval newts in subsequent trials. The extract was then prepared by putting 0.8 g of larvae skin tissue (the three individuals mixed) in a clean disposable plastic dish and macerating it in 100 ml of distilled water. The stimulus water was then filtered through absorbent paper to remove solid particles, diluted in distilled water to make a final volume of 533 ml, and immediately frozen in 10-ml portions until used (Woody and Mathis 1998; Gonzalo et al. 2007, 2009).

We tested the responses of larval newts in an aquarium (40×50 and 20 cm high) containing dechlorinated clean water. Water was collected from a nearby high mountain spring that did not house newts or *D. marginalis* larvae. At the beginning of the experiment, we gently placed a single larval newt in the center of the aquaria and waited 5 min for habituation. Then, we started the experiment and observed the behavior of the larvae in clean water during the following 5 min. This initial period of the trial allowed us to measure basal levels of activity in clean water in absence of chemical cues. The aquaria had two small cages (10×5 cm) fixed at both ends and sunk at the water surface. After the initial observation period, we gently placed inside one of the cages randomly chosen a live larval beetle or 10 ml of the alarm cues (i.e., after the ice aliquots had entirely thawed). The cages were made of opaque plastic but had the laterals open and covered with a green net of fine mesh (2 mm) that allowed chemical cues to be released into the test aquaria while maintaining the larval beetle out of sight from the larval newts. We observed the behavior of the larval newt during the following 5 min. We considered that this time should be enough to test the existence of an

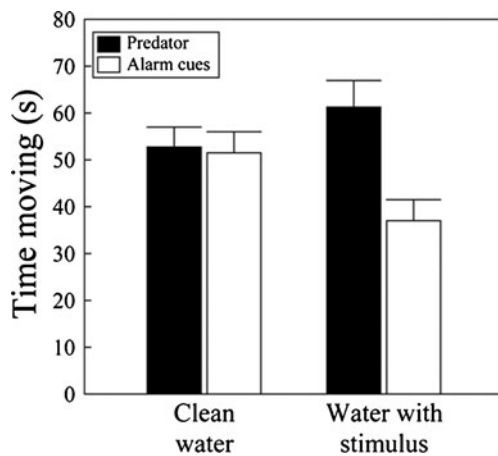
effective antipredator response of larval newts, as this response should be elicited immediately after appearing the threatening stimulus, which would require a quick detection of the predator or alarm chemicals. Each larval newt participated in two trials, in different days, with the different stimuli (predator or alarm cues) presented in a random order.

We recorded trials on videotape (Hi-8 format, 25 frames s<sup>-1</sup>) using a JVC GR-AX5 compact VHS video-camera aligned above the aquaria to avoid interferences of the observer on the activity of larval newts. As a measurement of activity levels, we noted the total time spent moving by larval newts in each of two periods of 5 min (before and after adding the chemical stimuli to water). The same experimenter (AG) performed these measurements. Preliminary tests with a few individuals had showed no change in activity levels of larval newts comparing 5 min before and 5 min after adding clean water without chemical stimuli (Wilcoxon matched pairs test,  $Z=0.14$ ,  $N=8$ ,  $P=0.88$ ). Thus, any change in activity in the tests could be assigned to the chemical cues added in the second period.

To tests for differences in time spent moving between treatments, we used a repeated-measures two-way analysis of variance (ANOVA) with treatment (“predator” vs. “alarm cues”) and period of the trial (“clean water” and “water with stimulus”) as within factors. We included the interaction between variables in the model to test for changes in movements through the trial (before vs. after adding the chemical stimuli) depending on the type of chemical cues added. Data were log-transformed to ensure normality (Shapiro-Wilk’s test). Tests of homogeneity of variances (Levene’s test) showed that variances were not significantly heterogeneous after transformation. Pairwise comparisons used Tukey’s honestly significant difference tests (Sokal and Rohlf 1995).

### Results

The type of chemical stimuli affected the activity level of larval southern marbled newts (Fig. 1). The significant interaction among effects showed that there were significant differences between the two treatments in the change in time spent moving, after adding the stimulus in relation to previous basal activity in clean water (two-way repeated-measures ANOVA; stimulus effect,  $F_{1,15}=3.41$ ,  $P=0.08$ ; treatment effect,  $F_{1,15}=3.70$ ,  $P=0.07$ ; interaction,  $F_{1,15}=12.61$ ,  $P<0.005$ ). Thus, larval newts spent the same amount of time moving at the beginning of the trials when water was clean in both treatments (Tukey’s test,  $P=0.98$ ) but spent significantly less time after adding conspecific alarm cues than after adding predator chemicals ( $P=0.0005$ ). Time spent moving when the alarm cue was present was significantly less than the time spent moving in clean water ( $P=0.011$ ). Thus, in the presence of alarm cues, larval *T. pygmaeus*



**Fig. 1** Time (seconds; mean $\pm$ SE) spent moving by larval newts during 5 min in clean water and during 5 min after being exposed to predator chemicals or to conspecific alarm cues

spent 28.1% less time moving than in the absence of such cues. However, there was not a significant difference between the amount of time that larval newts spent moving when the predator chemicals were present than when they were in clean water ( $P=0.53$ ) (Fig. 1).

## Discussion

In our study, *T. pygmaeus* larvae showed a reduction of activity when conspecific alarm cues were present. Reduced activity is a common behavioral response of amphibian tadpoles to predators (e.g., Hokit and Blaustein 1995; Kiesecker et al. 1996; Gonzalo et al. 2007, 2009). Also, some species of salamanders use immobility as their primary response to predators (Arnold 1982; Dodd 1989; Ducey and Brodie 1983). This suggests that *T. pygmaeus* larvae use conspecific alarm cues to assess predation risk and modify their activity levels as an antipredatory response. The use of chemosensory predation risk assessment should be especially advantageous in complex habitats such as the temporal ponds with abundant vegetation inhabited by *T. pygmaeus* (Montori and Herrero 2004).

In contrast, in our study, *T. pygmaeus* larvae did not show reduced activity in response to predator *D. marginalis* larvae. Because we used a live larval beetle in the experiments, we cannot rule out that other types of cues in addition to chemical cues, such as visual or vibrational cues, were also present in the tests. However, because larval newts did not respond to the predator presence, we can ensure that no type of predator cues, including chemical cues, elicited any antipredatory response in the larval newts. Recognition of predator odor is innate in some species (Sih and Moore 1993; Storfer and Sih 1998; Polo-Cavia et al. 2010) but not in many others (Chivers and Smith 1998; Polo-Cavia et al.

2010). This may depend mainly on whether predator and prey have a previous long-time co-existence in the evolutionary time, which may select for innate predator recognition (Kats and Dill 1998; Ferrari et al. 2010; Polo-Cavia et al. 2010). In the case of absence of predator recognition, naïve prey show no response when first presented with a novel predator odor. However, in many cases, the same naïve prey that are presented with a novel stimulus simultaneously with conspecific alarm cues may later learn to associate risk with the novel stimulus presented alone (Chivers and Smith 1994; Gonzalo et al. 2007, 2009).

A possibility to explain the lack of predator recognition is that larval newts might only recognize predators if they were “marked” with the prey included in its diet. This diet-related chemical labeling of predators has been demonstrated in several studies. For example, pike-naïve fathead minnows, *Pimephales promelas*, show anti-predator responses to chemical stimuli from pike-fed fathead minnows but not to pike-fed swordtails (Mathis and Smith 1993a). Larval damselfly can learn to recognize predators from chemical cues in the predator’s diet (Chivers et al. 1996b). However, in our experiment, *D. marginalis* larvae were fed only mealworms during the 2 weeks prior to the experiment, so larval beetles were not “marked” with *T. pygmaeus* alarm cues. This raises the possibility that larval southern marbled newt might only recognize a predator when it is marked with alarm cues of a conspecific; otherwise, *D. marginalis* larvae would not be considered as a predator.

An alternative explanation to the lack of responses to the predator cues alone could be a change in predation risk assessment linked to the late ontogenetic stage of the larval newts. Vulnerability to predation has typically been considered to increase during metamorphosis in many amphibians (e.g., Arnold and Wassersug 1978). However, some late-stage larval newts have been reported to be unpalatable to predatory larval diving beetles (*Dytiscus verticalis*) (Formanowicz and Brodie 1982), thus decreasing vulnerability to predation. The change from palatable to unpalatable was associated with the development of granular epidermal (poison) glands. Similar developmental changes in palatability have been reported in some anuran tadpoles (Brodie et al. 1978; Formanowicz and Brodie 1982; Brodie and Formanowicz 1987) and might also occur in southern marbled newts. Late-stage larval newts may not discriminate between chemical stimuli from predators and nonpredators in this phase, as it occurs in *Notophthalmus viridescens* (Mathis and Vincent 2000), which suggests that fright responses of larval newts are plastic and dependent on risk level. However, even if larval newts were unpalatable to most predators, they should respond to alarm cues because these indicate that an actual predation event has occurred. So, this would indicate that, at least for that predator, unpalatability alone was not effective and that an additional antipredatory response (i.e., immobility) is required.



On the other hand, antipredator behavior has associated costs such as decreased food intake efficiency (Lawler 1989; Skelly 1992; Lima 1998), because a decrease in activity may be the usual response to the presence of any “unknown” threat stimulus. Although this defensive approach has obvious benefits for predation avoidance, decreasing activity in response to neutral stimuli may unnecessarily limit foraging opportunities. The consequences of reduced foraging success may be severe because populations of larval newts often experience intense intraspecific competition (Morin 1983; Harris et al. 1988) and larvae that inhabit temporary ponds have a limiting time to grow and reach the metamorphosis. So, in this context, the antipredator efficiency should depend largely on the correct identification of actual threat situations (Mathis and Vincent 2000). However, reduced activity affects food intake, so it could be too costly to respond to all potential predators (Lima and Dill 1990; Lima 1998) because the survival of adult amphibians is positively related with size reached at the metamorphosis (Laurila et al. 2002).

In small temporary ponds, with reduced visibility and highly populated, larval newts attempting to avoid all potential predators would spend a great amount of time in avoidance behaviors and subsequently miss an excessive number of foraging opportunities. Larval newts should benefit by avoiding only predators that represent a current high level of threat, showing only an antipredator response when they detect conspecific alarm cues or predators previously marked with alarm cues. Therefore, in southern marbled newts, alarm cues may have two functions: first, to mark a non-familiar predator as an actual predator which could eventually be or not be a high threat in the future or, second, when responding to all potential predators is too costly, alarm cues could be used to mark actual current high threats, avoiding costs of responding to other minor threats (Gonzalo et al. 2010).

More studies are needed to examine ontogenetic changes in antipredatory mechanisms and the ability to detect predators of larval newts and to investigate whether different costs of the antipredator responses in highly competitive situations or unfavorable situations may favor variations in predator detection and antipredatory responses. This information would allow us to determine the scope of variation of potential antipredatory responses under natural conditions.

**Acknowledgments** We thank two anonymous reviewers for helpful comments and El Ventorrillo MNCN Field Station for use of their facilities. Financial support was provided by MEC-FPU grants to A. G. and C.C. and by the projects MCI-CGL2008-02119/BOS and MICIIN-CGL2011-24150/BOS.

**Integrity of research and reporting** The manuscript submitted for publication complied with the current laws of Spain, and the experiments were carried out under license from the *Consejería de Medio ambiente de la Comunidad de Madrid* (the Environmental Agency of the local Government of Madrid). The authors declare that they have no conflict of interests.

## References

- Adams MJ, Claeson S (1998) Field response of tadpoles to conspecific and heterospecific alarm. *Ethology* 104:955–962
- Amo L, López P, Martín J (2004a) Wall lizards combine chemical and visual cues of ambush snake predators to avoid overestimating risk inside refuges. *Anim Behav* 67:647–653
- Amo L, López P, Martín J (2004b) Chemosensory recognition and behavioral responses of wall lizards, *Podarcis muralis*, to scents of snakes that pose different risks of predation. *Copeia* 2004:691–696
- Arnold SJ (1982) A quantitative approach to antipredator performance: salamander defense against snake attack. *Copeia* 1982:247–253
- Arnold SJ, Wassersug RJ (1978) Differential predation on metamorphic anurans by garter snakes (*Thamnophis*): social behaviour as a possible defense. *Ecology* 59:1014–1022
- ASIH (2004) Guidelines for use of live amphibians and reptiles in field and laboratory research. Lawrence, Kansas: Herpetological Animal Care and Use Committee (HACC) of the American Society of Ichthyologists and Herpetologists
- Boothby KM, Roberts A (1995) Effects of site of tactile stimulation on the escape swimming responses of hatchling *Xenopus laevis* embryos. *J Zool* 235:113–125
- Brodie ED Jr, Formanowicz DR Jr (1987) Antipredator mechanisms of larval anurans: protection of palatable individuals. *Herpetologica* 43:369–373
- Brodie ED Jr, Formanowicz DR Jr, Brodie ED III (1978) The development of noxiousness of *Bufo americanus* tadpoles to aquatic insect predators. *Herpetologica* 34:302–306
- Cabido C, Gonzalo A, Galán P, Martín J, López P (2004) Chemosensory predator recognition induces defensive behavior in the slow-worm (*Anguis fragilis*). *Can J Zool* 82:510–515
- Chivers DP, Smith RJF (1994) Intra- and interspecific avoidance of areas marked with skin extract from brook stickleback (*Culaea inconstans*) in a natural habitat. *J Chem Ecol* 20:1517–1524
- Chivers DP, Smith RJF (1998) Chemical alarm signalling in aquatic predator–prey systems: a review and prospectus. *Ecoscience* 5:338–352
- Chivers DP, Wisenden BD, Smith RJF (1995) The role of experience in the response of fathead minnows (*Pimephales promelas*) to skin extract of Iowa darters (*Etheostoma exile*). *Behaviour* 132:665–674
- Chivers DP, Kiesecker JM, Anderson MT, Wildy EL, Blaustein AR (1996a) Avoidance response of a terrestrial salamander (*Ambystoma macrodactylum*) to chemical alarm cues. *J Chem Ecol* 22:1709–1716
- Chivers DP, Wisenden BD, Smith RJF (1996b) Damselfly larvae learn to recognize predators from chemical cues in the predator’s diet. *Anim Behav* 52:315–320
- Chivers DP, Kiesecker JM, Marco A, Wildy EL, Blaustein AR (1999) Shifts in life history as a response to predation in western toads (*Bufo boreas*). *J Chem Ecol* 25:2455–2463
- Dodd CK Jr (1989) Duration of immobility in salamanders, genus *Plethodon* (Caudata: Plethodontidae). *Herpetologica* 45:467–472
- Dodson SI, Crowl TA, Peckarsky BL, Kats LB, Covich AP, Culp JM (1994) Nonvisual communication in fresh-water benthos: an overview. *J North Am Benthol Soc* 13:268–282
- Ducey PK, Brodie ED (1983) Salamanders respond selectively to contacts with snakes: survival advantage of alternative antipredator strategies. *Copeia* 1983:1036–1041
- Eklöv C, Halvarsson H (2000) The trade-off between foraging activity and predation risk for *Rana temporaria* in different food environments. *Can J Zool* 78:734–739
- Ferrari MCO, Wisenden BD, Chivers DP (2010) Chemical ecology of predator–prey interactions in aquatic ecosystems: a review and prospectus. *Can J Zool* 88:698–724

- Formanowicz DR Jr, Brodie ED Jr (1982) Relative palatabilities of members of a larval amphibian community. *Copeia* 1982:91–97
- Godin JGJ, Smith SA (1988) A fitness cost of foraging in the guppy. *Nature* 333:69–71
- Gonzalo A, López P, Martín J (2007) Iberian green frog tadpoles may learn to recognize novel predators from chemical alarm cues of conspecifics. *Anim Behav* 74:447–453
- Gonzalo A, López P, Martín J (2009) Learning, memorizing and apparent forgetting of chemical cues from new predators by Iberian green frog tadpoles. *Anim Cogn* 12:745–750
- Gonzalo A, López P, Martín J (2010) Risk level of chemical cues determines retention of recognition of new predators in Iberian green frog tadpoles. *Behav Ecol Sociobiol* 64:1117–1123
- Harris RN, Alford RA, Wilbur HM (1988) Density and phenology of *Notophthalmus viridescens dorsalis* in a natural pond. *Herpetologica* 44:234–242
- Helfman GS (1989) Threat-sensitive predator avoidance in damselfish-trumpetfish interactions. *Behav Ecol Sociobiol* 24:47–58
- Hokit DG, Blaustein AR (1995) Predator avoidance and alarm-response behaviour in kin-discriminating tadpoles (*Rana cascadae*). *Ethology* 101:280–290
- Kats LB, Dill LM (1998) The scent of death: chemosensory assessment of predation risk by prey animals. *Ecoscience* 5:361–394
- Kiesecker JM, Chivers DP, Blaustein AR (1996) The use of chemical cues in predator recognition by western toad tadpoles. *Anim Behav* 52:1237–1245
- Laurila A, Karttunen S, Merilä J (2002) Adaptive phenotypic plasticity and genetics of larval life histories in two *Rana temporaria* populations. *Evolution* 56:617–627
- Lawler SP (1989) Behavioural responses to predators and predation risk in four species of larval anurans. *Anim Behav* 38:1038–1047
- Lima SL (1998) Stress and decision making under the risk of predation: recent developments from behavioral, reproductive, and ecological perspectives. *Adv Stud Behav* 27:215–290
- Lima SL, Dill LM (1990) Behavioral decisions made under the risk of predation: a review and prospectus. *Can J Zool* 68:619–640
- López P, Martín J (2001) Chemosensory predator recognition induces specific defensive behaviours in a fossorial amphibia. *Anim Behav* 62:259–264
- Maerz JC, Panebianco NL, Madison DM (2001) Effects of predator chemical cues and behavioral biorhythms on foraging activity of terrestrial salamanders. *J Chem Ecol* 27:1333–1344
- Magurran AE, Irving PW, Henderson PA (1996) Is there a fish alarm pheromone? A wild study and critique. *Proc R Soc Lond B* 263:1551–1556
- Mathis A, Smith RJF (1993a) Fathead minnows, *Pimephales promelas*, learn to recognize northern pike, *Esox lucius*, as predators on the basis of chemical stimuli from minnows in the pike's diet. *Anim Behav* 46:645–656
- Mathis A, Smith RJF (1993b) Intraspecific and cross-superorder responses to chemical alarm signals by brook stickleback. *Ecology* 74:2395–2404
- Mathis A, Vincent F (2000) Differential use of visual and chemical cues in predator recognition and threat-sensitive predator-avoidance responses by larval newts (*Notophthalmus viridescens*). *Can J Zool* 78:1646–1652
- Montori A, Herrero P (2004) *Triturus pygmaeus* (Wolterstorff, 1905). In: Ramos MA (ed) *Amphibia, Lissamphibia. Fauna Iberica vol 24*. Museo Nacional de Ciencias Naturales (CSIC), Madrid, pp 221–232
- Morin PJ (1983) Competitive and predatory interactions in natural and experimental populations of *Notophthalmus viridescens dorsalis* and *Ambystoma tigrinum*. *Copeia* 1983:628–639
- Petranka JW, Kats LB, Sih A (1987) Predator-prey interactions among fish and larval amphibians: use of chemical cues to detect predatory fish. *Anim Behav* 35:420–425
- Polo-Cavia N, Gonzalo A, López P, Martín J (2010) Predator-recognition of native but not invasive turtle predators by naïve anuran tadpoles. *Anim Behav* 80:461–466
- Reques R (2007) Tritón pigmeo—*Triturus pygmaeus*. In: Carrascal LM, Salvador A (eds) *Enciclopedia Virtual de los Vertebrados Españoles*. Museo Nacional de Ciencias Naturales, Madrid. Available online at <http://www.vertebradosibericos.org/>
- Sih A (1987) Predator and prey lifestyles: an evolutionary and ecological overview. In: Kerfoot WC, Sih A (eds) *Predation: direct and indirect impacts on aquatic communities*. University Press of New England, Hanover, pp 203–224
- Sih A, Moore RD (1993) Delayed hatching of salamander eggs in response to enhanced larval predation risk. *Am Nat* 142:947–960
- Skelly DK (1992) Field evidence for a cost of behavioural antipredator response in a larval amphibian. *Ecology* 73:704–708
- Skelly DK (1994) Activity level and the susceptibility of anuran larvae to predation. *Anim Behav* 47:465–468
- Smith RJF (1992) Alarm signals in fishes. *Rev Fish Biol Fish* 2:3–63
- Smith RJF (1997) Does one result trump all others? A response to Magurran, Irving and Henderson. *Proc R Soc Lond B* 264:445–450
- Sokal RR, Rohlf FJ (1995) *Biometry*. WH Freeman, New York
- Stabell OB, Lwin MS (1997) Predator-induced phenotypic changes in crucian carp are caused by chemical signals from conspecifics. *Env Biol Fishes* 49:145–149
- Storfer A, Sih A (1998) Gene flow and ineffective antipredator behavior in a streambreeding salamander. *Evolution* 52:558–565
- Thoen C, Bauwens D, Verheyen RF (1986) Chemoreceptive and behavioural responses of the common lizard *Lacerta vivipara* to snake chemical deposits. *Anim Behav* 34:1805–1813
- Tollrian R, Harvell CD (1999) *The ecology and evolution of inducible defenses*. Princeton University Press, Princeton, New Jersey
- Wilson DJ, Lefcort H (1993) The effect of predator diet on the alarm response of red-legged frog, *Rana aurora* tadpoles. *Anim Behav* 46:1017–1019
- Wisenden BD (2003) Chemically mediated strategies to counter predation. In: Collin SP, Marshall NJ (eds) *Sensory assessment of the aquatic environment*. Springer, New York, pp 236–251
- Woody DR, Mathis A (1998) Acquired recognition of chemical stimuli from an unfamiliar predator: associative learning by adult newts, *Notophthalmus viridescens*. *Copeia* 1998:1027–1031