REVIEW / SYNTHÈSE

Chemical ecology of predator–prey interactions in aquatic ecosystems: a review and prospectus[1]

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Abstract: The interaction between predator and prey is an evolutionary arms race, for which early detection by either party is often the key to success. In aquatic ecosystems, olfaction is an essential source of information for many prey and predators and a number of cues have been shown to play a key role in trait-mediated indirect interactions in aquatic communities. Here, we review the nature and role of predator kairomones, chemical alarm cues, disturbance cues, and diet cues on the behaviour, morphology, life history, and survival of aquatic prey, focusing primarily on the discoveries from the last decade. Many advances in the field have been accomplished: testing the survival value of those chemicals, providing field validation of laboratory results, understanding the extent to which chemically mediated learning may benefit the prey, understanding the role of these chemicals in mediating morphological and life-history adaptations, and most importantly, the selection pressures leading to the evolution of chemical alarm cues. Although considerable advances have been made, several key questions remain, the most urgent of which is to understand the chemistry behind these interactions.

Résumé : L'interaction entre les prédateurs et les proies constitue une course aux armements dans laquelle la détection précoce par l'un ou l'autre des protagonistes est souvent la clé du succès. Dans les systèmes aquatiques, l'olfaction est souvent une source essentielle de renseignements pour les proies et prédateurs et nous savons que de nombreux signaux jouent un rôle essentiel dans les interactions indirectes, par l'intermédiaire des traits biologiques dans les communautés aquatiques. Nous faisons ici une rétrospective de la nature et du rôle des kairomones, des signaux chimiques d'alerte, des signaux de perturbations et des signaux alimentaires sur le comportement, la morphologie, le cycle biologique et la survie des proies aquatiques, avec une attention particulière pour les découvertes de la dernière décennie. Il y a eu beaucoup de progrès dans le domaine : des tests de la valeur de survie de ces substances chimiques, la validation en nature des résultats de laboratoire, la détermination de l'importance du bénéfice pour la proie des connaissances associées aux signaux chimiques, l'évaluation du rôle de ces produits chimiques dans le contrôle des adaptations de la morphologie et du cycle biologique et surtout l'étude des pressions de sélection menant à l'évolution des signaux chimiques d'alerte. Malgré les progrès considérables accomplis, il reste plusieurs questions importantes à élucider, la plus urgente étant la compréhension des bases chimiques de ces interactions.

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Introduction

The interaction between predator and prey is an evolutionary arms race. There is selection on predators to become ever more efficient and effective at detecting and capturing prey. Concomitantly, there is selection on prey to become ever more efficient and effective at detecting and evading predators. At the ultimate or functional level of selection, stealth, teeth, and claws on the part of the predator are pitted against crypsis, spines, and rapid flight by prey. At the prox-imate or mechanistic level of selection, predator–prey interactions can be cast as a contest of sensory systems where predator and prey are each rewarded when they gain an information advantage over the other. Early detection is the key to gaining an advantage. Predators that catch prey unaware usually win (i.e., successfully capture prey). Prey with advanced knowledge of a predator's approach usually win because they evade detection through crypsis, area avoidance, seeking shelter, or initiating early flight in the event of an attack (Lima and Dill 1990; Smith 1992).

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Because the consequences of losing the contest differ for predator and prey (lunch versus life), one could argue that the selection gradient imposed on prey is greater than that on predators, resulting in prey being adept at predator detection and evasion. This review emphasizes aquatic ecosystems and therefore olfaction because semiochemicals, chemicals that transmit information between conspecifics and other species, are dominant in aquatic habitats.

Predation advances through successive escalating stages from initial detection (of prey by predator, and vice versa, independently), attack, capture, and ingestion (Lima and Dill 1990; Smith 1992). At different stages in the predation sequence, stage-specific forms of chemical information that reliably indicate the presence of predation risk are released and provide some additional information about the nature and imminence of the risk. At the stage of initial detection, prey detect predators through the predator's signature odour, i.e., a kairomone. A kairomone is a chemical released by one species (predator), received by a second species (prey), that is adaptively favorable to the second species but not the first. Kairomones allow prey to detect and evade predators from a distance or predators waiting in ambush. The kairomone literature is extensive, particularly with respect to behavioural and morphological responses of crustacean plankton to kairomones from midge larva *Chaoborus* Lichtenstein, 1800 or to the kairomones of various fish species (Tollrian and Harvell 1999; Lass et al. 2005). A second class of pre-attack chemical information comes from chemicals released by startled or disturbed prey. These are referred to as disturbance cues, and the consensus is that they involve a pulse release of urinary ammonia (Kiesecker et al. 1999). A third class of cues are damaged-released alarm cues. Predators may damage prey tissue, particularly epidermal tissue, during the attack and subsequent handling of prey prior to ingestion. Damaged epidermal tissues leak chemical compounds that are released in no other context and thus reliably advertise the presence of an actively foraging predator. All major groups of aquatic organisms, from protists to amphibians, show antipredator responses to chemical cues released from injured conspecifics (Wisenden 2003). These chemicals, known as alarm cues, invoke strong behavioural responses (and sometimes morphological and life-historical defences) that serve to reduce the probability of predation. Related to these are "dietary cues", presumably of similar chemistry as alarm cues or their metabolic derivatives, that are released postingestion from the predator's digestive system during digestion and defecation. They also invoke changes in behaviour, morphology, and life history (see below). The final type of chemical information that prey use to assess predation risk are those that have acquired ecological significance through learning. Minnows in particular have served as a productive study model in this regard (Brown 2003). Any novel chemical stimulus that is correlated with the presence of alarm cues can become associated with predation risk (Suboski 1990; Chivers and Smith 1994). This form of learning has the remarkable property of requiring only a single reinforcing event to form a virtually permanent association in many prey animals (Suboski 1990).

Chivers and Smith (1998) published a comprehensive review of the chemical ecology of aquatic predator–prey interactions. The paper provided an overview, primarily in tabular form, of the distribution of alarm-cue systems in different aquatic taxa and briefly considered the role of predator odours (kairomones) in mediating predator–prey systems. Chivers and Smith (1998) has had a considerable impact; it has been cited nearly 400 times, at least 30 times a year for each of the past 7 years (ISI Web of Science Search). Nevertheless, that review has become dated in light of a spate of new work since 1998. Hence, the goal of our current review is to consider many of the same themes discussed by Chivers and Smith (1998). We ask the following questions: What has been done over the past decade? Where are we making good progress? What have we missed? We refer readers to other more directed reviews that have attempted to synthesize smaller pieces of this complex literature (e.g., Wisenden 2000, 2003; Brown and Chivers 2006; Wisenden and Chivers 2006; Mathis 2009; Mirza 2009).

Over the past decade, chemical ecology has increasingly moved out of the laboratory and into the field. Also there has been an increasing emphasis on demonstrating the survival value of antipredator responses. The past decade has also seen many papers showing that alarm cues are important in mediating learning in the context of predator–prey interactions. We have made some progress on understanding the role of alarm cues in mediating morphology and life-history responses of prey. Another shift in studies of chemical alarm systems has been a greater focus on understanding the evolution of alarm cues. The field has moved away from discussion about alarm "pheromones" per se to discussion of alarm "cues" in the context of public information. In fact, the "alarm cells" of many fishes evolved primarily as part of the immune system (Halbgewachs et al. 2009) and only secondarily acquired a warning function as a by-product of being in tissue commonly damaged during predation. Perhaps the most conspicuous omission in the past decade has been our failure to advance significantly our understanding of the chemistry of alarm cues, predator odours, and the sensory receptors that detect them.

Response to predator kairomones

Many species of prey display antipredator behaviours upon detection of predator kairomones. The responses to predator odour can be innate, mediated through diet effects, or mediated through learning.

Innate predator recognition

Whereas most prey species require learning to be able to recognize predator odour as threatening, several aquatic species have been reported to display antipredator responses upon their first detection of the odour of some predators. Such responses have been shown in a variety of species, including freshwater snails (Turner 1996; Dalesman et al. 2007a) and salmonid fishes (Berejikian et al. 2003; Vilhunen and Hirvonen 2003; Hawkins et al. 2004, 2007; Scheurer et al. 2007), as well as larval toads (Laurila et al. 1997; Gallie et al. 2001) and salamanders (Mathis et al. 2003; Epp and Gabor 2008). In the majority of these studies, predator-naïve prey were obtained by bringing egg masses from the wild to the laboratory followed by testing of the young upon hatching. Although this constitutes a fair definition of predator-naïve individuals, recent findings show that

prey can acquire predator recognition as embryos still encased in their egg shells (Mathis et al. 2008; Ferrari and Chivers 2009a, 2009b). Hence, future studies will have to carefully consider the origin of "naïve" prey before drawing conclusions regarding their lack of experience with predators.

Effect of diet on predator labelling

Diet cues are postdigestion alarm cues released into the environment from the predator's digestive system. Chivers and Smith (1998) reported studies testing the effect of predator diet on the responses of prey: sea anemone (Howe and Harris 1978), fathead minnows (*Pimephales promelas*) (Mathis and Smith 1993a), and damselfly larvae (Chivers et al. 1996a; Wisenden et al. 1997). During the last decade, similar examples of predator labelling by dietary cues were reported in a dozen predator–prey systems (see Table 1). Only one study to date, on sculpins, reported no effect of diet on the responses of the prey (Bryer et al. 2001).

In some cases, individuals respond to conspecific odours as a kairomone if conspecifics represent a threat to them, as may be the case in cannibalistic species (Wildy et al. 1999). Quirt and Lasenby (2002) reported size-dependent responses of shrimp to conspecific odour. Particularly, immature and juvenile shrimp displayed a fearful response when exposed to odour from adult conspecifics, but not to similar-sized conspecifics. Similar responses to conspecific odour were reported by Mathis (2003) and Ferris and Rudolf (2007).

Effect of experience on the response of prey to predator kairomones

Experience affects how prey respond to predators. For many species, predator-experienced individuals respond to predator odour, whereas predator-naïve ones do not: clams (Smee and Weissburg 2006), fishes (Godard et al. 1998; Kristensen and Closs 2004; McLean et al. 2007), and amphibians (Eklöv 2000; Chivers et al. 2001a; Marquis et al. 2004; Smith et al. 2008). These species often acquire recognition of their predators through social learning (Mathis et al. 1996; Ferrari and Chivers 2008) or through conditioning with alarm cues (see below for more details about learned predator recognition mediated by alarm cues).

Through experience, prey adjust responses to predators to optimize trade-offs between predator avoidance and other activities. Fish and larval amphibians have been shown to increase their antipredator response upon exposure to more concentrated predator odour (Kusch et al. 2004; Fraker 2009) or adjust their response according to predator size (Kusch et al. 2004). Moreover, pike-experienced fathead minnows can distinguish the odour of individual northern pike (*Esox lucius* L., 1758) in an odour mixture of multiple pike, and can further adjust response intensity to the mixed cue according to pike density and proximity (Ferrari et al. 2006a; Fig. 1). Similar predator density-dependent responses occur in chironomid larvae (Hölker and Stief 2005).

Other factors also affect prey responses to predator odours (e.g., turbulence: Smee et al. 2008; body mass: Fraker 2008; body size: Mathis et al. 2003; age: Crumrine 2006; ecomorphs: Robinson et al. 2008).

Disturbance cues

Disturbance cues have been identified in a few species: sea urchin (Nishizaki and Ackerman 2005), virile crayfish (*Orconectes virilis*) (Hazlett 1985), Iowa darters (*Etheostoma exile* (Girard, 1859)) (Wisenden et al. 1995a), brook trout (*Salvelinus fontinalis*) (Mirza and Chivers 2002), convict cichlids (*Archocentrus nigrofasciatus* (Günther, 1867)) (Jordao 2004; Vavrek et al. 2008), slimy sculpins (*Cottus cognatus*) (Bryer et al. 2001), and larval Northern Red-legged Frogs (*Rana aurora* Baird and Girard, 1852) (Kiesecker et al. 1999). The active ingredient in disturbance cues is thought to be a pulse of urinary ammonia released by startled prey (Hazlett 1985; Kiesecker et al. 1999). Disturbance cues elicit weaker responses than alarm cues (Jordao 2004) and are thought to increase the receiver's vigilance. Although behavioural changes may be subtle, exposure to conspecific disturbance cues have been shown to increase survival of brook trout during staged encounters with predators (Mirza and Chivers 2002).

Alarm cues

Chivers and Smith (1998) reported more than 60 aquatic species possessing and responding to chemical alarm cues, including sea anemones, various gastropods, a number of aquatic arthropods, echinoderms, fishes, and larval amphibians. Since Chivers and Smith (1998), a large number of new species have been shown to possess and respond to conspecific alarm cues (Table 1). Overall, responses to chemical alarm cues have been shown to have survival benefits for the prey (Mathis and Smith 1993b; Wisenden et al. 1999; Mirza and Chivers 2003a; but for an exception see McCarthy and Dickey 2002).

Although the majority of studies report antipredator responses to conspecific alarm cues in a laboratory context, some studies have validated such results in the field, either through direct observations or through trap experiments (see Table 1).

Most antipredator behaviours include area avoidance, decreases in activity, and increases in shelter use (Lawrence and Smith 1989). In some cases, alarm cues have more subtle effects on prey. Examples of short-term effects include decreased efficacy of prey to locate other chemicals such as foraging cues (virile crayfish: Tomba et al. 2001), or change in foraging posture (convict cichlids: Foam et al. 2005a). Longer term changes also may occur. For example, crucian carp (*Carassius carassius*), which are usually nocturnal in the absence of predation risk, become aperiodic when chronically exposed to conspecific alarm cues (Pettersson et al. 2001).

A number of factors have been shown to affect the responses of prey to conspecific alarm cues. Extrinsic factors are those related to characteristics of the cues or the environment. Intrinsic factors are those related to the internal state of prey. In the following section, extrinsic and intrinsic factors affecting the way in which aquatic species respond to conspecific alarm cues are summarized.

Extrinsic factors affecting the responses to conspecific alarm cues

Concentration

Chemical cues may be somewhat unreliable in space and

Table 1. Summary of the studies on conspecific alarm cues, diet cues, and learned predator recognition via alarm cues since Chivers and Smith (1998).

	Respond to conspecific alarm cues	Respond to diet cues	Learn to recognize predators through pairing with alarm cues
Sponges			
Coral, *Discophyton rudyi* (Verseveldt and Ofwegen, 1992)	Goddard 2006	—	—
Flatworms			
Flatworm *Dugesia dorotocephala* (Woodworth, 1897)	Wisenden and Millard 2001	—	Wisenden and Millard 2001
Molluscs			
Marsh periwinkle, *Littoraria irorata* (Say, 1822)	Rahman et al. 2000	—	—
Eastern mudsnail, *Ilyanassa obsoleta* (Say, 1822) (= *Nassarius obsoletus* (Say, 1822))	Rahman et al. 2000	—	—
Pouch snail, *Physa gyrina* (Say, 1821)	McCarthy and Dickey 2002	—	—
Waved welk, *Buccinum undatum* L., 1758	—	—	Dalesman et al. 2006
Sitka periwinkle, *Littorina sitkana* Philippi, 1846	—	Rochette and Dill 2000	—
Checkered periwinkle, *Littorina scutulata* Gould, 1849	—	Rochette and Dill 2000	—
Swamp lymnaea, *Lymnaea stagnalis* (L., 1758)	—	—	Rochette et al. 1998
Northern quahog, *Mercenaria mercenaria* (L., 1758)	Smee and Weissburg 2006	Smee and Weissburg 2006	—
Baltic macoma, *Macoma balthica* (L., 1758); common cockle, *Cerastoderma edule* (L., 1758)	—	Griffiths and Richardson 2006	—
Insects			
Larval mosquito, *Culex restuans* Theobald, 1901	Ferrari et al. 2007*a*	—	Ferrari et al. 2008*a*
Larval mayfly *Siphlonurus* Eaton, 1868	Huryn and Chivers 1999	—	—
Larval mayfly *Siphlonisca* Needham, 1909	Huryn and Chivers 1999	Huryn and Chivers 1999	—
Larval damselfly *Enallagma antennatum* (Say, 1839)	—	McBean et al. 2005; Mortensen and Richardson 2008	—
Crustaceans			
Amphipod *Gammarus* Fabricius, 1775	Wisenden et al. 2001 (field)	—	—
Virile crayfish, *Orconectes virilis* (Hagen, 1870)	—	—	Hazlett et al. 2002
Rusty crayfish, *Orconectes rusticus* (Girard, 1852)	—	—	Hazlett and Schoolmaster 1998
Red swamp crayfish, *Procambarus clarkii* (Girard, 1852)	—	—	Hazlett and Schoolmaster 1998
European freshwater crayfish, *Austropatmobius pallipes* (Lereboullet, 1858)	—	—	Hazlett and Schoolmaster 1998
Annelids			
Annelid *Nereis virens* Sars, 1835	Watson et al. 2005	—	—
Echinoderms			
Variegated or green sea urchin, *Lytechinus variegatus* (Lamarck, 1816)	Vadas and Elner 2003	—	—
Sea egg, *Tripneustes ventricosus* (Lamarck, 1816)	Vadas and Elner 2003	—	—

Table 1 (*continued*).

	Respond to conspecific alarm cues	Respond to diet cues	Learn to recognize predators through pairing with alarm cues
Green sea urchin, *Strongylocentrotus droebachiensis* (Müller, 1776)	—	Hagen et al. 2002	—
Tunicate *Clavelina huntsmani* Van Name, 1931	Pelletier 2004	—	—
Fishes			
Common bully, *Gobiomorphus cotidianus* McDowall, 1975	Kristensen and Closs 2004	—	—
Fathead minnow, *Pimephales promelas* Rafinesque, 1820	Pollock et al. 2005a (field); Wisenden and Barbour 2005 (field); Friesen and Chivers 2006 (field)	—	—
Central mudminnow, *Umbra limi* (Kirtland, 1841)	Wisenden et al. 2008a (field)	—	—
Starry goby, *Asterropteryx semipunctata* Rüppell, 1830	McCormick and Larson 2007 (field)	—	Larson and McCormick 2005
Golden shiner, *Notemigonus crysoleucas* (Mitchill, 1814)	Godard et al. 1998	Godard et al. 1998	—
Blacknose shiner, *Notropis heterolepis* Eigenmann and Eigenmann, 1893	Wisenden et al. 2004a (field)	—	—
Goldfish, *Carassius auratus* (L., 1758)	—	—	Zhao et al. 2006
Crucian carp, *Carassius carassius* (L., 1758)	—	Pettersson et al. 2000	—
Northern redbelly dace, *Phoxinus eos* (Cope, 1861)	Pollock et al. 2005a (field); Wisenden and Barbour 2005 (field)	—	—
Glowlight tetras, *Hemmigrammus erythrozonus* (Durbin, 1909)	—	Brown and Dreier 2002; Brown and Zachar 2002	—
Brook stickleback, *Culaea inconstans* (Kirtland, 1840)	Friesen and Chivers 2006 (field)	—	—
Green swordtail, *Xiphophorus helleri* Heckel, 1848	Mirza et al. 2001a	—	—
Slimy sculpin, *Cottus cognatus* Richardson, 1836	Bryer et al. 2001	—	—
Reticulate sculpin, *Cottus perplexus* Gilbert and Evermann, 1894	Chivers et al. 2000	—	—
Roach, *Rutilus rutilus* (L., 1758)	Jachner and Rydz 2002	—	—
Arctic char, *Salvelinus alpinus* (L., 1758)	Lautala and Hirvonen 2008	Vilhunen and Hirvonen 2003	—
Brook trout, *Salvelinus fontinalis* (Mitchill, 1814)	—	—	Mirza and Chivers 2001a
Rainbow trout, *Oncorhynchus mykiss* (Walbaum, 1792)	—	—	Brown and Smith 1998
Chinook salmon, *Oncorhynchus tshawytscha* (Walbaum in Artedi, 1792)	—	—	Berejikian et al. 1999
Yellow perch, *Perca flavescens* (Mitchill, 1814)	Mirza et al. 2003	—	—
Pumpkinseed sunfish, *Lepomis gibbosus* (L., 1758)	Marcus and Brown 2003	—	—
Walleye, *Stizostedion vitreum* (Mitchill, 1818) (= *Sander vitreus* (Mitchill, 1818)	—	—	Wisenden et al. 2004b
Amphibians			
Larval Pacific Treefrog, *Hyla regilla* Baird and Girard, 1852 (= *Pseudacris regilla* (Baird and Girard, 1852))	Adams and Claeson 1998 (field); Chivers et al. 2001a	—	—
Larval Common Frog, *Rana temporaria* L., 1758	Marquis et al. 2004	—	—

Table 1 (*concluded*).

	Respond to conspecific alarm cues	Respond to diet cues	Learn to recognize predators through pairing with alarm cues
Larval Woodfrog, *Rana sylvatica* LeConte, 1825 (= *Lithobates sylvaticus* (LeConte, 1825))	Ferrari et al. 2007*b*; but see Petranka and Hayes 1998	—	Ferrari et al. 2008*b*
Iberian Green Frog, *Rana perezi* López-Seoane, 1885 (= *Pelophylax perezi* (López-Seoane, 1885))	—	—	Gonzalo et al. 2007
Larval Hallowell's Toad, *Bufo maculatus* Hallowell, 1854 (= *Amietophrynus maculatus* (Hallowell, 1854))	Spieler and Linsenmair 1999	—	—
African Common Toad, *Bufo regularis* Reuss, 1833 (= *Amietophrynus regularis* (Reuss, 1833))	Spieler and Linsenmair 1999	—	—
Larval American Toad, *Bufo americana*	—	—	Mirza et al. 2006*a*
Larval Long-toed Salamander, *Ambystoma macrodactylum* Baird, 1850	Wildy and Blaustein 2001	—	—

Note: Dashes indicate not applicable.

time (Ferrari et al. 2007*b*). Cue concentration represents a measure of time elapsed since a predation event occurred (temporal assessment) and (or) distance from the site of predation (spatial assessment). Either way, higher cue concentration likely indicates higher level of risk, independent of the absolute level of risk. Hence, prey should use cue concentration to adjust the intensity of their antipredator responses in a threat-sensitive manner (Helfman 1989) to optimize fitness in the trade-off between costly predator avoidance and fitness-related activities. Recent examples of species that match response intensity to cue concentration include larval mosquitoes (*Culex restuans*: Ferrari et al. 2008*a*; *Ochlerotatus triseriatus* (Say, 1823) (= *Aedes triseriatus* (Say, 1823)): Kesavaraju et al. 2007), roach (*Rutilus rutilus*) (Jachner and Rydz 2002), fathead minnows (Ferrari et al. 2005), goldfish (*Carassius auratus*) (Zhao et al. 2006), larval American Toads (*Bufo americanus*) (Mirza et al. 2006*a*), and larval Woodfrogs (*Rana sylvatica* (= *Lithobates sylvaticus*) (Ferrari et al. 2009*a*). Some studies, however, have reported all-or-nothing responses to gradients of conspecific alarm cues: northern clearwater crayfish (*Orconectes propinquus* (Girard, 1852)) (Bouwma and Hazlett 2001; but see Tomba et al. 2001), convict cichlids (Roh et al. 2004), rainbow trout (*Oncorhynchus mykiss*) (Mirza and Chivers 2003*a*) and pumpkinseed sunfish (*Lepomis gibbosus*) (Marcus and Brown 2003).

Degradation and water chemistry

Biodegradation is another mechanism by which cue age can be assessed. Cue decay is undoubtedly influenced by physical, chemical, and biological properties of a prey's environment (e.g., sunlight, dissolved organic carbon, bacterial composition) and background chemistry of the aquatic medium. For example, a pH of 6.4 or lower completely deactivates conspecific alarm cues of some fish species (pumpkinseed sunfish: Leduc et al. 2003; salmonids: Leduc et al. 2006; Smith et al. 2008). Hazlett (1999) reported that alarm cues of virile crayfish may stay active for at least 6 h under laboratory conditions. Ferrari et al. (2007*b*) found that

alarm cues of Woodfrog tadpoles under natural conditions persist for less than 2 h. Alarm cues of both *Gammarus* amphipods and fathead minnows remain fully active for more than 3 h but less than 6 h in the laboratory and field (Wisenden et al. 2009). Related to the effects of cue concentration and cue degradation is the idea of active space. One estimate conducted in the field on natural populations demonstrated that 2 cm^2 of skin of fathead minnows or northern redbelly dace (*Phoxinus eos*) generates an active space with a radius of at least 2 m for at least 2 h (Wisenden 2008).

Group size and social context

Grouping behaviour dilutes the statistical risk of predation to individuals in the group (dilution effect). Brown et al. (2006*a*) found that large groups of convict cichlids exposed to conspecific alarm cues showed lower intensity antipredator responses than small groups of cichlids. Similar results were reported by Lefcort (1998) using tadpoles of Southern Toads (*Bufo terrestris* (Bonnaterre, 1789) (= *Anaxyrus terrestris* (Bonnaterre, 1789))). Pollock et al. (2006*a*) and Wisenden et al. (2003, 2009) reported an interaction between the presence of shoals of conspecifics and the presence of alarm cues in field experiments. It seems that minnows that detect alarm cue are strongly motivated to shoal even if the nearest shoal is inside the trap whence the cue emanates.

Habitat and abiotic characteristics

Temperature and light both affect the way prey respond to conspecific alarm cues (Jacobsen and Stabell 1999; Gerald and Spezzano 2005). Arena size can have a great impact on the responses of snail to crushed conspecific cues (Dickey and McCarthy 2007). In small arenas, snails detected and responded to the cues by crawling out of the water. However, in large arenas, snails failed to respond to the cues, possibly because of cue dilution. Golub et al. (2005) reported that habitat complexity had no effect on the responses of sunfish to conspecific alarm cues. UV-B irradiation has also been

Fig. 1. (Top panel) Mean change in shoaling index for fathead minnows (*Pimephales promelas*) exposed to three treatments: (1) 60 mL of northern pike (*Esox lucius*) odour, 30 mL taken from each of 2 pike (2 PO); (2) 60 mL of pike odour, 5 mL taken from each of 12 pike (12 PO); or (3) 60 mL of dechlorinated tap water (water). $N = 16$ minnows per treatment. The overall volume of pike odour was constant in the 2 PO and 12 PO treatments, therefore the greater intensity of antipredator response by minnows in the 2 PO treatment indicates that minnows respond stronger to pike that are in close proximity. (Bottom panel) Mean change in shoaling index for minnows exposed to three treatments: (1) 50 mL of dechlorinated tap water plus 10 mL of pike odour (5 mL from each of 2 pike (2′ PO); (2) 60 mL of pike odour (5 mL from each of 12 pike (12 PO); or (3) 60 mL of dechlorinated tap water (water). $N = 16$ minnows per treatment. The greater intensity response to the 12 PO treatment indicates that minnows can determine pike odour concentration (i.e., predator density) irrespective of predator proximity. (Modified from Ferrari et al. 2006*a* and reproduced with permission of Anim. Behav., vol. 72, issue 4, pp. 930 and 931, © 2006 Elsevier Limited.)
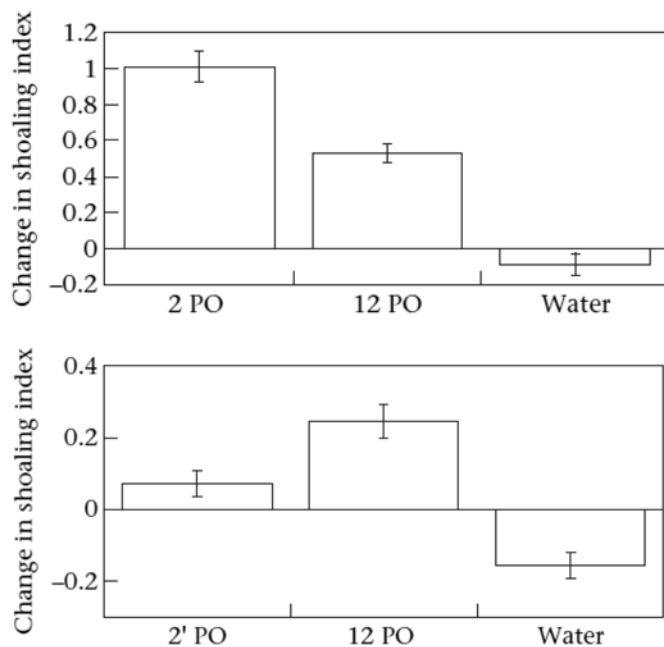
shown to decrease the responses of larval amphibians to conspecific alarm cues (Kats et al. 2000).

Intrinsic factors affecting the responses to conspecific alarm cues

Response intensity to indicators of risk varies among individuals because cost–benefit trade-offs between risk avoidance and foraging or reproduction (or all three) varies with internal state.

Trade-offs with foraging

Hungry individuals often reduce or give no overt behavioural responses to conspecific alarm cues, whereas satiated ones do (Chivers et al. 2000; Hazlett 2003*a*; McCormick and Larson 2008). The risk allocation hypothesis (Lima and Bednekoff 1999; Ferrari et al. 2009*b*) is a model predicting intensity of antipredator behaviour and foraging effort based upon short-term patterns of risk. For example, prey chroni-

cally exposed to risk initially display a high intensity of antipredator response, but gradually decrease responsiveness to risk (and conversely increase their foraging rate) because long bouts of vigilance cannot be sustained while meeting energy demands. This hypothesis was tested with cichlids and trout exposed once or three times per day to conspecific alarm cues for three consecutive days (Foam et al. 2005*b*; Brown et al. 2006*b*; Mirza et al. 2006*b*; Ferrari et al. 2008*d*) and then tested for their responses to alarm cues. In all cases, fish exposed to alarm cues three times a day responded to a given concentration of alarm cues with a lowered intensity of antipredator response than those exposed to alarm cues once per day.

Trade-offs with reproduction

A number of studies have shown trade-off responses between antipredator behaviour and reproduction (Magnhagen 1992; Chivers et al. 1995; Pollock et al. 2006*b*; Koch et al. 2007; Lastein et al. 2008). This general phenomenon extends to chemically mediated risk. For example, Evans et al. (2007) found that female guppies (*Poecilia reticulata* Peters, 1859) exposed to conspecific alarm cues shorten brood retention time compared with guppies not exposed to alarm cues. Female guppies are live-bearers and thus are more vulnerable to predators while gravid. Early release of young reduces the probability that young will be consumed while still in their mother.

Trade-offs with information-acquisition behaviours

Prey with advanced warning of predation risk have a lower probability of capture by predators (Mathis and Smith 1993*b*). Thus, information has great value and prey engage in a variety of behaviours to increase their access to, and quality of, information about predation risk. Accessing chemical information, while simultaneously remaining motionless to avoid detection, imposes a constraint on chemical sensing behaviour. Fish employ several modes of furtive sniffing. For example, darters raise their snouts above the substrate to access water currents passing over their head (Wisenden and Chivers 2006; Fig. 2). Fathead minnows hover motionless in mid-water and flick their pectoral fins to waft water past their nares. Other species increase the rates of opercular pumping that generate water currents to draw new chemical information over their nares (Commens and Mathis 1999). Glowlight tetras (*Hemigrammus erythrozonus*) approach and inspect predators to acquire chemical information about the nature and imminence of risk (Brown and Godin 1999; Brown et al. 2000). Zebra danios (*Danio rerio* (Hamilton, 1822)) seek shelters closer to the cue source when water flow is low, but prefer distant shelter when the flow is high (Wisenden et al. 2010). Similarly, wild populations of riverine minnows flee areas upstream of sources of chemical alarm cues when they are upstream of the source (where chemical information is not available) but remain in place when they detect upstream sources of alarm cues (Wisenden et al. 2010). This is akin to differential area avoidance by fathead minnows and brook stickleback. After 4 h, the number of fish using areas previously labelled with chemical alarm cues is not different from the number of fish that used labeled areas before cue release. However, fish using risky areas after 4 h are different individuals than the

Fig. 2. Chemical cues are distributed unequally throughout the water column for water in flow. In panel 1, a dye is released upstream of a stack of drinking straws lying on their side, producing stable laminar flow. In panels 2 and 3, resistance to flow from the surface and substrate retard advancement of the odour plume. For benthic fishes such as darters, elevated head posture during predator vigilance extends olfactory receptors into the leading edge of the plume. The cartoon fish on the downstream end of panel 3 indicate the advantage of head-up chemical sampling behaviour in providing earlier detection and continual updates of important chemical information. Panel 4 shows a johnny darter (*Etheostoma nigrum* Rafinesque, 1820) in normal head-down feeding posture. Panel 5 shows the same fish with its head partially raised. In full head-up posture, the snout points almost straight up and the pectoral fins are fully extended. Photographs taken by and reproduced with permission of Oscar Noriega. (From Wisenden and Chivers 2006 and reproduced with permission of © 2006 Science Publishers.)
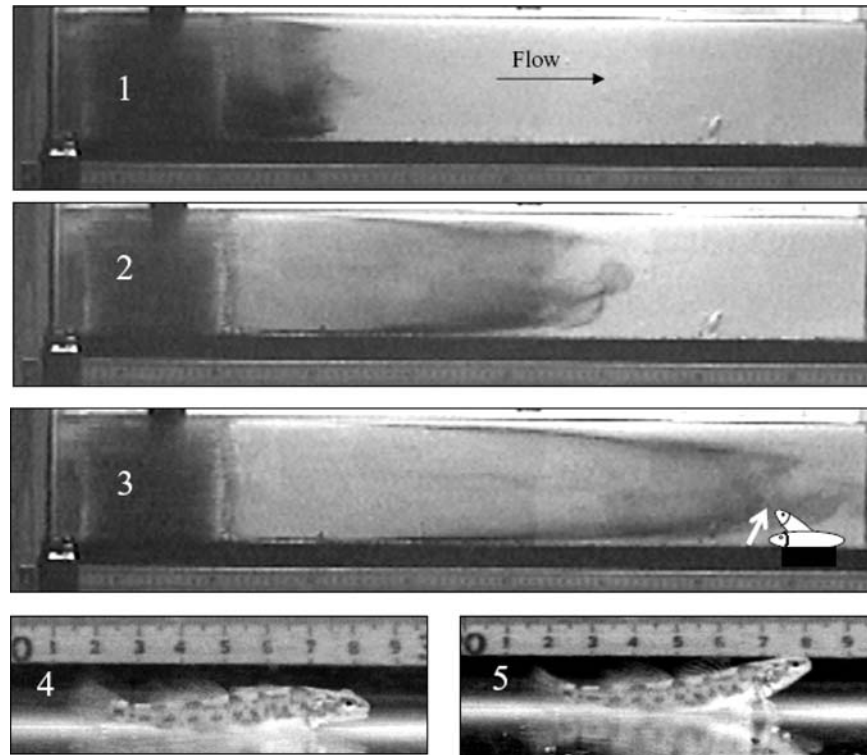
ones present at the time of cue release. Individual fish that experienced alarm cues directly avoid risky areas for 7 or 8 h (Wisenden et al. 1995*b*).

Hartman and Abrahams (2000) proposed a sensory compensation model for which minnows should respond to conspecific alarm cues when no visual information is available (e.g., in turbid environments), but should not respond to these cues when visual cues are available and no predators are detected. Although laboratory data supported these predictions, field observations with underwater video of natural populations showed that blacknose shiners (*Notropis heterolepis*) sum visual and chemical information additively by responding to either source of information when presented alone and with doubled intensity when visual and information were presented together (Wisenden et al. 2004*a*).

Ontogenetic switches

Factors such as body size and growth rate (Pollock et al. 2006*b*; Blanchet et al. 2007), body condition (Pollock et al. 2006*b*), sex (Mirza et al. 2001*a*), and age (Ichinose 2002) affect the way in which prey respond to conspecific alarm cues. For example, yellow perch (*Perca flavescens*) undergo an ontogenetic switch in which young-of-the-year respond to conspecific alarm cues with an antipredator response, whereas adult perch display a foraging response to the same cues (Harvey and Brown 2004). Similar ontogenetic switches occurred with pumpkinseed sunfish (Marcus and Brown 2003) and green sunfish (*Lepomis cyanellus* Rafinesque, 1819) (Golub and Brown 2003). However, factors such as experience (Scheurer et al. 2007) or the transition from larva to juvenile related to independence from parental care (i.e., pre- and post-independence of juveniles) did not affect how prey respond to alarm cues (Alemadi and Wisenden 2002).

Heterospecific alarm cues

A number of prey species respond to alarm cues from heterospecifics. These responses could result from phylogenetic conservation of chemical elements of skin extract among closely related species or a result of learning (discussed below). A number of studies of prey responses to heterospecific alarm cues support the hypothesis that these cues are conserved through phylogeny: freshwater snails (Dalesman et al. 2007*b*; Turner 2008), mayflies (Huryn and Chivers

1999), sea urchins (Vadas and Elner 2003), salmonids (Mirza and Chivers 2001b), and larval amphibians (Ferland-Raymond and Murray 2008).

Multiple cue assessment

In some cases, the presence of alarm cues alone is not sufficient to elicit an overt antipredator response. For example, Dalesman et al. (2007a) found that predator-naïve freshwater gastropods such as the swamp lymnaea (*Lymnaea stagnalis*) do not alter their behaviours upon detection of crushed conspecific cues alone or the odour of tench (*Tinca tinca* (L., 1758)) alone, but do so in the presence of both stimuli. Griffiths and Richardson (2006) reported that the bivalve Baltic macoma (*Macoma balthica*) burrow in response to the odour of crabs fed conspecifics but not to the odour of crushed conspecific cues alone. One must interpret these results with caution because in some cases prey have covert responses that only manifest themselves in altered future behaviour. For example, Brown et al. (2004) found that glowlight tetras did not overtly respond to subthreshold concentrations of the putative ostariophysan alarm cue (hypoxanthine-3-*N*-oxide, H3NO), but subsequently responded to secondary visual cues with increased intensity compared with glowlight tetras not exposed to the subthreshold concentration of H3NO. A few studies report effects of different cue potencies. Keppel and Scrosati (2004) reported that snails responded with increasing intensity of antipredator responses when exposed to the odour of a predatory crab alone, conspecific alarm cues alone, and both conspecific alarm cues paired with predatory crab odour. This pattern has been also reported for other species (Bryer et al. 2001; Jacobsen and Stabell 2004; Wisenden et al. 2004a; McCormick and Manassa 2008). McCarthy and Fisher (2000), however, reported that snails responded the strongest to conspecific alarm cues and displayed lower intensity of antipredator behaviour when exposed to predator odour alone or predator odour paired with conspecific alarm cues.

Predation cues mediate morphological adaptations

Developmental plasticity of phenotypes is a rapidly emerging subfield of evolutionary ecology (Fordyce 2006). There are energenic trade-offs not only in behavioural responses, but also in allocation of energy stores to somatic growth versus allocation to reproduction. Spines, tail shape and body forms that are best adapted to thwart predators impart an efficiency cost on foraging, therefore growth and ultimately reproductive success. Because of the stochastic nature of predation risk in time and space, many prey species have evolved mechanisms to employ costly morphological responses to predation risk only when they are needed (Clark and Harvell 1992; Chivers et al. 2008; Hammill et al. 2008). The defences are cued by an environmental trigger, commonly predator kairomones and (or) conspecific alarm cues that indicate a high risk of predation.

A wide diversity of aquatic prey animals exhibit changes in morphology in response to predation cues, including protozoans (Kusch 1993; Lass and Spaak 2003), cladocerans (Parejko and Dodson 1990; Barry 2000; Lass and Spaak 2003), rotifers (Stemberger and Gilbert 1984), bryozoans (Harvell 1986), gastropods (Hoverman et al. 2005; Bibby et al. 2007), insects (Johansson and Samuelsson 1994; Johansson and Wahlstrom 2002), fishes (Brönmark and Miner 1992; Chivers et al. 2008), and amphibians (Van Buskirk and Relyea 1998; McIntyre et al. 2004; Kishida and Nishimura 2006).

At the time of Chivers and Smith (1998), little was known about the role of alarm cues from injured prey in inducing morphological defences. Only three predator–prey systems had been considered and there was considerable variation in the responses observed. The first experiments, conducted on the colonial bryozoan *Membranipora membranacea* (L., 1767) failed to find evidence that alarm cues from injured conspecifics alone induce spine growth (Harvell 1986). This was in contrast to studies showing that contact with nudibranch predators such as *Doridella steinbergae* (Lance, 1962) induces spine growth in the bryozoan colonies (Harvell 1984). Interestingly, bryozoans adjacent to those being attacked also develop protective spines. This observation led to the hypothesis that a combination of predator odour and cues of injured conspecifics are required to induce the morphological change. In the marine gastropod *Thais lamellose* (Gmelin, 1791) – predatory crab *Cancer productus* Randall, 1840 system, Appleton and Palmer (1988) came to a similar conclusion.

Studies on crucian carp directly tested the importance of alarm cues in mediating induced defences, but the results were mixed. Brönmark et al. (1994) found that exposure to cues from predatory pike induced an increase in body depth to length ratio (a defence that works against gape-limited predators), but alarm cues from carp failed to produce the same effect. In contrast, Stabell and Lwin (1997) found that alarm cues alone were enough to induce the change in morphology. They speculated that differences in concentration of alarm cues may have led to the disparity between their results and those of Brönmark et al. (1994).

A survey of recent papers on predator-induced morphological changes show that alarm cues from injured conspecifics often, but not always, induce changes in morphology. For example, goldfish altered their depth to length ratio in response to conspecific alarm cues (Chivers et al. 2007a, 2008), but conspecific alarm cues did not alter tail morphology of tadpoles of the Gray Treefrog (*Hyla versicolor* LeConte, 1825) (Schoeppner and Relyea 2005).

By far, the majority of studies examining predator-induced changes in morphology have manipulated risk using predator odours (kairomones), and in most of these studies predators were fed conspecifics of the prey (Lass et al. 2005; Teplitsky et al. 2005). Hence, the relative role of alarm cues versus kairomones in mediating changes in morphology remains an open question. It may well be the case that only predictable metabolites of alarm cues trigger morphological responses (Stabell et al. 2003). Alarm cues are known to label predators as dangerous (reviewed by Chivers and Mirza 2001a). Would prey exhibit the change in morphology if the predator was fed a different diet that did not contain prey alarm cues? Schoeppner and Relyea (2005) exposed tadpoles of Gray Treefrogs to 10 different prey species that were either experimentally macerated or consumed by predators. Interestingly, alarm cues from crushed conspecifics induced behavioural defences (hiding

and reduced activity) but only consumed prey induced deeper tails and shorter bodies. Schoeppner and Relyea (2005) speculate that this may indicate that behavioural defences are more easily reversed than morphological defences.

Fässler and Kaiser (2008) provide additional support for the importance of the predator's diet in mediating morphological defences. Molluscs show altered shell growth when crabs were fed molluscs that were closely related to the test species. Moreover, Hoverman et al. (2005) demonstrated that snails show differential morphological responses to different predators. In response to cues of crayfish feeding on snails, the snails developed narrow, high shells, whereas in response to cues of water bugs feeding on snails, the snails developed wide shells with wide apertures. A change in shell growth can be induced throughout the snails life, but the thickness of the shell, and presumably its effectiveness at deterring predators, can be limited if the defence develops later in the snail's life (Hoverman and Relyea 2007; Fig. 3).

The importance of alarm cues and predator kairomones in mediating morphological defences was further examined by Stabell et al. (2003). They found that *Daphnia galeata* G.O. Sars, 1864 did not exhibit changes in morphology in response to fish that were fed earthworms, but they did in response to fish fed *D. galeata*. Extracts made from the intestine of earthworm-fed fish homogenized with earthworms gave no response, but extracts made from the intestine of earthworm-fed fish homogenized with *Daphnia* did induce a response. Given that *D. galeata* did not respond to crushed *D. galeata* alone, Stabell et al. (2003) argue that alarm cues are activated by intestinal or bacterial enzymes.

Alarm cues and adaptive plasticity in life-history characteristics

Studies examining the role of alarm cues in mediating adaptive changes in life-history characteristics often share the same experimental design issues as those that examine morphology; they do not differentiate the role of alarm cues from that of predator kairomones. Most studies use odour from predators that have been fed conspecifics of the prey. Studies of life history have been focussed largely on understanding the timing of switch points related to hatching and metamorphosis. We highlight these areas below and then discuss other studies that have shown that alarm cues induce changes in longevity and alter reproductive investment in prey.

Adaptive changes in life-history switch points

Theory dictates that the timing of the transition between life-history stages should vary with the costs and benefits associated with each stage (Werner 1986; Hammill et al. 2008). Specifically, prey should switch life stages when their mortality to growth ratio is lower in the following stage than the current stage. Amphibians have become a model system to study the effects of predation risk on the timing of hatching. Sih and Moore (1993) were the first to show that amphibians (Streamside Salamanders, *Ambystoma barbouri* Kraus and Petranka, 1989) could alter their timing of hatching in response to predation risk. Salamander eggs exposed to the odour of flatworms (a predator of salamander larvae) delay hatching until they had reached a developmen-

Fig. 3. Morphological responses of march rams-horn (*Helisoma trivolvis* = *Planorbella trivolvis*) to water bug colonization. The top snail was reared in the absence of water bugs, whereas the bottom two snails experienced water bug colonization early (bottom right) and late (bottom left) in the experiment. The open dots illustrate the approximate point in shell formation where the water bug was added. Note the difference in shell thickness (dark vs. light gray regions) between the snails exposed to water bug colonization early compared with late in the experiment. (From Hoverman and Relyea 2007 and reproduced with permission of Ecology, vol. 88, issue 3, p. 702, © 2007 Ecological Society of America.)
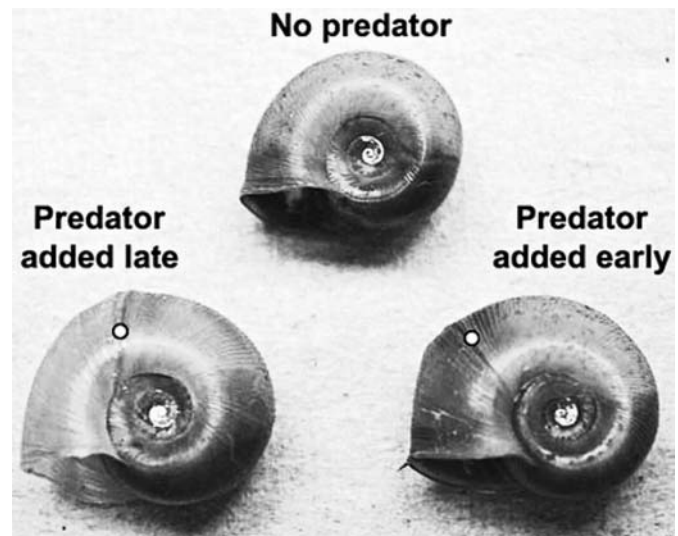

tal stage less susceptible to the predator. Chemical cues of predatory sunfish have a similar effect on salamander eggs (Moore et al. 1996).

Odours from egg predators have the opposite effect on hatching time as cues from larval predators. Chivers et al. (2001b) provided the first evidence that tadpoles hatch earlier than normal in response to odours from egg predators. They found that eggs of Pacific Treefrogs (*Hyla regilla* = *Pseudacris regilla*) and Cascades Frogs (*Rana cascadae* Slater, 1939) hatched earlier in response to chemical cues of leech predators feeding on amphibian eggs. Interestingly, the frogs also tended to hatch earlier when exposed to cues of injured eggs alone. Tadpoles that hatch early in response to predator and alarm cues should benefit by the early escape but are often smaller, less developed, and may suffer a survival cost (Fig. 4). The number of studies examining plasticity in hatching characteristics in other amphibian systems is quite striking (Laurila et al. 2001, 2002; Johnson et al. 2003; Saenz et al. 2003; Vonesh 2005; Capellán and Nicieza 2007; Lehman and Campbell 2007; Mandrillon and Saglio 2008). These papers generally support the hypothesis that early hatching is induced by the presence of predator kairomones. In one study, Mandrillon and Saglio (2008) did not find evidence of early hatching in response to whole crushed eggs, jelly envelopes, or embryos; however, these cues resulted in longer and deeper tails in the hatching tadpoles.

Studies on several species of *Daphnia* (Ślusarczyk 1999; Barry 2000; Ślusarczyk and Rygielska 2004; Lass et al.

Fig. 4. Time to hatching, as well as time, size, and Gosner developmental stage to leave jelly mass after hatching for Cascades Frogs (*Rana cascadae*) exposed to chemical cues of predatory leeches, non-predatory earthworms, injured eggs, or a distilled water control. Values are mean ± SE. Different letters over bars indicate significant differences at $P < 0.05$, based on Tukey's tests. Chemical cues from leeches and to a lesser extent alarm cues from injured eggs resulted in alterations in hatching characteristics. (Modified from Chivers et al. 2001*b* and reproduced with permission of Oikos, vol. 92, issue 1, p. 140, © 2001 John Wiley and Sons, Inc.)
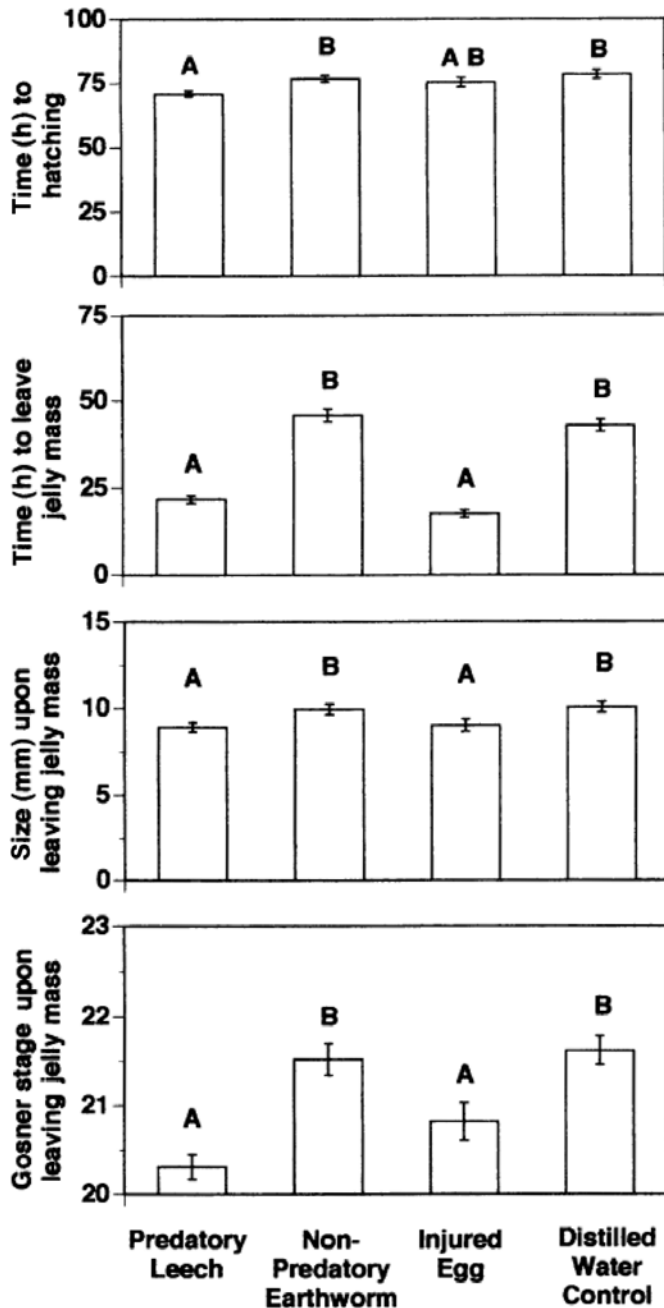
Moreover, studies with fishes have documented differences in the timing of nest emergence. In these cases, it is unknown whether the difference in emergence time reflects differences in the timing of hatching as opposed to a decision on when to emerge from the nest (Mirza et al. 2001*b*; Jones et al. 2003).

Metamorphosis is another major life-history switch point that is influenced by predation risk. Dahl and Peckarsky (2003) found that fish odours induced faster larval development and smaller size at maturity for larval mayflies. Such shorter developmental times could increase larval survival but may be costly in terms of reducing female fecundity. Likewise, Kiesecker et al. (2002) found that larval Red-legged Frogs metamorphosed earlier and at a smaller size when exposed to either predatory newts or to alarm cues from injured conspecifics than those raised in no-cue control treatments. Interestingly, the same change in life history was not seen when the tadpoles were exposed to newts fed caddisflies. Western Toads (*Bufo boreas* Baird and Girard, 1852 (= *Anaxyrus boreas* (Baird and Girard, 1852))) metamorphose earlier when exposed to predator odours and alarm cues from conspecifics; these changes do not seem to alter size at metamorphosis (Chivers et al. 1999). In contrast, Teplitsky et al. (2005) found that exposure to predators fed tadpoles results in delayed metamorphosis and smaller size, whereas Laurila et al. (2004, 2006) found that tadpoles raised in the presence of high risk had longer larval periods and were larger at metamorphosis. A clear pattern of metamorphic responses in anuran amphibians appears to be lacking. A study with larval Long-toed Salamanders (*Ambystoma macrodactylum*) demonstrated that exposure to odours from conspecifics that had been cannibalistic resulted in slower growth rate and an increase in time to metamorphosis (Wildy et al. 1999).

Changes in longevity and reproduction

Crowl and Covich (1990) provided strong evidence that alarm cues are important in mediating changes in longevity and reproduction in the snail *Physella virgata* (Gould, 1855). Snails were exposed to cues of undamaged snails, crayfish only, a combination of crayfish and undamaged snails, and to crayfish feeding on snails. Cues of crayfish feeding on snails resulted in significantly larger and older snails at the age of first reproduction and at death than the other three treatments. Snails appear to allocate resources to growth instead of reproduction to outgrow their vulnerability to crayfish. In another study, Hoverman et al. (2005) confirmed that march rams-horn (*Helisoma trivolvis* (Say, 1817) (= *Planorbella trivolvis* (Say, 1817))) delayed reproduction and grew larger before reproducing in response to cues from predators feeding on march rams-horns. March rams-horns exhibited a greater delay in reproduction in response to odours from crayfish than odours from water bugs. Pollock et al. (2005*b*) exposed pairs of convict cichlids to conspecific alarm cues and found that they were faster to start reproducing than those exposed to water controls. Another study showed that female guppies exposed to conspecific alarm cues shorten brood retention times (Evans et al. 2007). Guppies are live-bearers and thus are more vulnerable to predators while brooding.

2005) and fishes (Kusch and Chivers 2004; Kusch et al. 2005) have also examined alterations in the timing of hatching in response to alarm cues and predator kairomones.

Learned predator recognition

Prey responses to chemical cues are much more complex than a simple mechanistic stimulus–receptor interaction. In trade-offs discussed above, higher cognitive processes suppress or inhibit responses to alarm cues because phenotypes are selected to optimize overall fitness, not solely to minimize exposure to predation risk. Similarly, higher cognitive processes can attach adaptive significance to otherwise neutral stimuli if these stimuli are correlated with predation risk. Because of the prevalence and unforgiving nature of predation, prey are quick to form associations between risk and novel stimuli. Learning, therefore, greatly extends prey's ability to detect and evade risk. Rather than being limited by a finite set of genetic recognition templates of danger, prey that augment risk assessment with learning can track spatial and temporal variation in predator identity and dynamically adjust assessment of individual risk in response to ontogenetic changes in the prey's own ecology. Learned predator recognition has often been referred to as "adaptive", but tests demonstrating this point were lacking. In the last decade, a few studies have shown that learned predator recognition enhances survival during direct encounters with predators (Mirza and Chivers 2000; Gazdewich and Chivers 2002).

Single predation cue

Alarm cues can mediate learning when a naïve individual is simultaneously exposed to conspecific alarm cues and cues of a novel predator, such as its image, odour, or sound. Typically, experiments testing learned predator recognition consist of two phases: the conditioning phase, during which the prey is exposed to conspecific alarm cues paired with a novel cue, and the testing phase, during which the prey is exposed to the novel cue alone. A control treatment involves pairing water with the novel stimulus in the conditioning phase and the novel cue alone in the test phase. This methodology allows the researcher to ensure that learning indeed occurred, i.e., the prey now responds to the novel cue without any additional reinforcer (e.g., alarm cues). Chivers and Smith (1998) highlighted the ability of three fish species — European minnows (*Phoxinus phoxinus* (L., 1758)) (Magurran 1989), fathead minnows (e.g., Chivers and Smith 1994), zebra danios (Suboski et al. 1990) — to learn following a single conditioning event. This ability was also demonstrated in larvae of the damselfly *Enallagma* Charpentier, 1840 (Chivers et al. 1996*a*; Wisenden et al. 1997) and in Central Newts (*Notophthalmus viridescens louisianensis* (Wolterstorff, 1914)) (Woody and Mathis 1998). The last decade has seen many new additions to this literature (Table 1). Although most studies of aquatic species focused on the recognition of novel visual or chemical predatory cues, learning is not necessarily restricted to those two types of stimuli. Wisenden et al. (2008*b*) showed that fathead minnows and glowlight tetras could learn to associate conspecific alarm cues with a sound stimulus. Although most aquatic species rely heavily on visual or chemical cues, we must not forget that otophysan fishes (comprising the majority of the superorder Ostariophysi) possess Weberian ossicles, which are a series of specialized vertebrae that connect the air bladder to the inner ear, thus conferring great sensitivity to a wide range of underwater sound stimuli. It should be noted that there need not be an observable behavioural response during the conditioning phase for learning to occur. Brown et al. (2001*a*) found that fathead minnows acquire recognition of a novel predator when exposed to low concentrations of a putative alarm cue (H3NO) paired with the odour of a yellow perch, even in the absence of an overt behavioural response. This result was confirmed by Ferrari et al. (2005) using alarm cues derived from skin extract.

All of the learning studies identified in Table 1 report learned predator recognition in the laboratory. Only one species, juvenile Atlantic salmon (*Salmo salar* L., 1758), has been shown to acquire recognition of lemon oil as a negative stimulus when presented with conspecific alarm cues in the wild under fully natural conditions (Leduc et al. 2007*a*). In a related study, Mirza and Chivers (2000) trained brook trout to recognize predatory chain pickerel (*Esox niger* Lesueur, 1818) in containers beside a creek and then stocked them in an enclosure with predators. Trained individuals had higher survival than non-trained individuals.

A remarkable discovery was the ability of embryos to learn to recognize novel predators. Mathis et al. (2008) and Ferrari and Chivers (2009*b*) found that embryos of Woodfrogs and Ringed Salamanders (*Ambystoma annulatum* Cope, 1886), while still encased in their egg shells, learn to recognize a novel predator through pairing of injured conspecific cues and novel predator odour. The testing phase was performed posthatching, when the larvae were old enough to be tested. Saglio and Mandrillon (2006) tested a similar question using embryos of Common Frogs (*Rana temporaria*) exposed to predators fed tadpoles. They found an effect of embryonic exposure treatment on the morphology of the tadpoles but did not find any learning effects.

Multiple cues

Although the vast majority of studies on learned predator recognition focus on a single novel stimulus, there are three studies that investigated learning using multiple predation cues. Wisenden and Harter (2001) found that when confronted with alarm cue and two visual objects that differed in shape and one of which was in motion, fathead minnows ignore shape and associate danger only with the moving object. Darwish et al. (2005) conditioned predator-naïve glowlight tetras to conspecific alarm cues paired with a cocktail of odours of largemouth bass (*Micropterus salmoides* Lacepède, 1802), Honduran red point (*Amatitlania siquia* Schmitter-Soto, 2007), and comet goldfish, and then subsequently tested 48 h later for learned recognition of each odour individually. They found that glowlight tetras displayed an antipredator response to the odour of all three species. Bouwma and Hazlett (2001) conditioned northern clearwater crayfish to injured conspecific cues paired with visual and mechanical cues of a novel object. When subsequently tested, northern clearwater crayfish responded to the visual cue at a greater distance and with a stronger response. Similarly, the frequency of response and the magnitude of the responses shown to a tactile cue were higher when alarm odour was added, but only at night. This indicates a complex interaction between stimuli from different sensory inputs.

Threat-sensitive predator learning

Although learning to recognize novel predators is benefi-

cial for prey, new studies show that predator recognition is modified to the level of threat posed by novel predators. By varying the concentration of alarm cues during the conditioning period, Ferrari et al. (2005) found that fathead minnows exposed to increased concentrations of alarm cues paired with a novel predator odour subsequently displayed a greater intensity of antipredator response when subsequently exposed to the novel predator cues. Similar results were obtained by Zhao et al. (2006) using goldfish, by Ferrari et al. (2008a) using larval mosquitoes, and by Ferrari et al. (2009a) using larval amphibians. Moreover, Ferrari et al. (2006b) found that minnows were able to further adjust their responses when subsequently exposed to varying concentration of predator odour, displaying stronger responses to more concentrated predator odour and vice-versa.

Generalization of learning

Could associative learning with alarm cues allow prey to recognize not one, but several species of predators? Ferrari et al. (2007c) investigated this aspect of learning by conditioning predator-naïve fathead minnows to recognize the odour of lake trout (Salvelinus namaycush (Walbaum in Artedi, 1792)) and subsequently testing them for a response to odours of lake trout, brook trout, rainbow trout, northern pike, or white sucker (Catostomus commersoni (Lacepède, 1803)). They found that minnows displayed a fright response to lake trout odour, but also to brook trout odour and rainbow trout odour, but with a decreased intensity. However, minnows did not generalize their responses to non-salmonids. A follow-up study (Ferrari et al. 2008c) indicated that this generalization phenomenon was dependent on the concentrations of alarm cues used during the conditioning trials. If the reference predator is learned as a high threat through conditioning with high concentrations of alarm cues, then minnows generalize their antipredator response to similar novel predators, but if the reference predator is recognized as a mild threat, minnows limit their responses to that specific predator. A similar phenomenon has been shown in larval Woodfrogs (Ferrari et al. 2009a; Fig. 5).

Constraints on learning

A number of constraints on associative learning have been identified. First, a temporal mismatch between the presentation of alarm cues and presentation of predator cues throughout the day results in failure of prey to learn the predator (Hazlett 2003b). However, Korpi and Wisenden (2001) found that a 5 min delay between the presentations of the two cues still result in successful learning. Second, prior pre-exposures to the novel odour in the absence of alarm cues prevent learned associations from forming. For example, Acquistapace et al. (2003) exposed crayfish to goldfish odour 2 h/day for three consecutive days and then subsequently attempted the learning paradigm by exposing crayfish to crushed conspecific cues paired with goldfish odour. They found that goldfish odour pre-exposure prevented crayfish from associating injured cues with goldfish odour. This phenomenon, known as latent inhibition, has also been demonstrated in fathead minnows (Ferrari and Chivers 2006a), and more recently, has been shown to occur in embryonic Woodfrogs. Ferrari and Chivers (2009a) pre-exposed embryonic Woodfrogs to the odour of a predatory

Fig. 5. Proportion change (mean ± SE) in activity from the pre-stimulus baseline for Woodfrog (*Rana sylvatica*) tadpoles exposed to the odor of Red-bellied Newts (*Taricha rivularis* (Twitty, 1935)), Eastern Tiger Salamanders (*Ambystoma tigrinum*), or African Clawed Frogs (*Xenopus laevis* (Daudin, 1802)). One day earlier, the tadpoles were exposed to newt odor paired with either water (●), a low (■) concentration, or a high (▲) concentration of tadpole alarm cues. The tadpoles learned to recognize the Red-bellied Newt as a predator based on the association with alarm cues. The degree to which the tadpoles generalized their learned recognition to Eastern Tiger Salamanders and African Clawed Frogs depended on the danger level associated with the Red-bellied Newt (i.e. the concentration of alarm cues used during the conditioning). (Adapted from Ferrari et al. 2009a.)
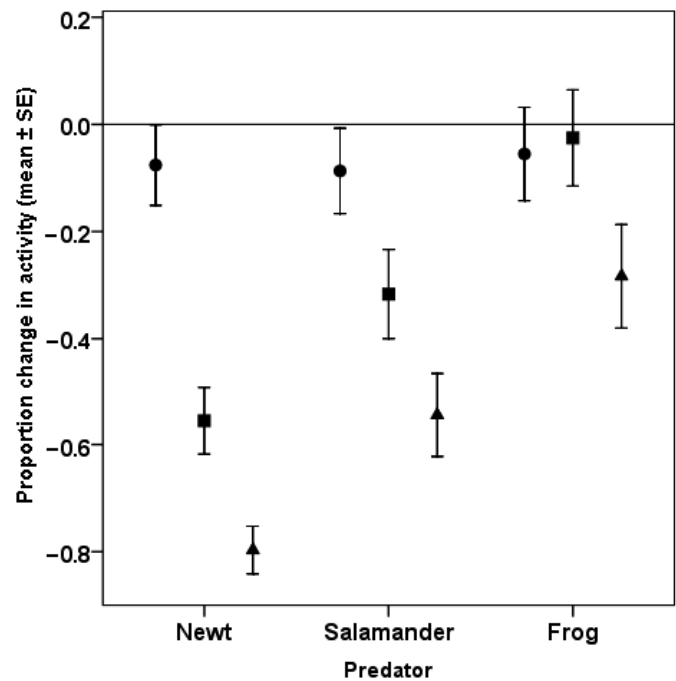
salamander, the Eastern Tiger Salamander (*Ambystoma tigrinum* (Green, 1825)), in the absence of negative reinforcement with alarm cues. Two weeks after hatching, they conditioned the tadpoles to recognize salamander odour as a threat through simultaneous exposure to crushed conspecific cues and salamander odour, but learning did not occur. Sometimes, the type of cues the prey are exposed to may facilitate differential learning of predators. For example, Wisenden and Harter (2001) found that when dealing with visual stimuli, motion, not shape, facilitates learned predator recognition. In addition, Hawkins et al. (2008) found that learning abilities may be sometimes limited by ontogeny, as 16- to 20-month-old juvenile Atlantic salmon have better learning performances than 3-week-old Atlantic salmon.

Abiotic factors may also constrain learning. Acidic environments (pH < 6.4) occurring from acid rains or industrial effluents deactivate the "alarm" function of alarm cues, hence, resulting in the absence of learned predator recognition under these conditions (Leduc et al. 2004). This phenomenon has also been demonstrated in the wild (Leduc et al. 2006, 2007b). Pollutants, such as heavy metals (Scott et

al. 2003) or herbicides (Mandrillon and Saglio 2007) also impair learned predator recognition. In addition, the pH of predator odour has been reported to affect learning. Smith et al. (2008) found that juvenile rainbow trout conditioned to recognize the odour of a predator at pH 6 or 7, subsequently responded to the odour at the same pH as the one used in the conditioning phase. This indicates that pH affects the ability of prey to recognize the chemistry of the predator odour.

Memory: a biological constraint to learned predator recognition

In addition to constraints on the detection of stimuli, there are other constraints on the evolution of learned predator recognition. Once prey have acquired recognition of a novel species as risky, how long do they retain this recognition? Chivers and Smith (1994) conditioned fathead minnows to visually recognize either a goldfish or a pike. When minnows were subsequently retested, they displayed antipredator responses only to the species to which they were conditioned. Although no differences in the responses of the pike-conditioned and goldfish-conditioned minnows were initially found, subsequent testing 2 months later revealed that pike-conditioned minnows responded to the sight of a pike with a greater intensity of response than goldfish-conditioned minnows tested for their responses to goldfish. This indicates that there may be some selection and constraints for prey to maintain the recognition of natural predators. Hazlett et al. (2002) conditioned four different species of crayfish — two native and two exotic species — and found that exotic species retained the responses for longer periods of time than the native species. Brook trout retained recognition of a novel predator after 10 days (Mirza and Chivers 2000) and juvenile rainbow trout lost recognition of their predator after 21 days (Brown and Smith 1998). This might be an adaptive way to avoid responding to non-threatening predators. Indeed, as trout grow, they outgrow their predators and hence should stop responding to them. Ferrari et al. (2010) recently developed a theoretical framework of intrinsic and extrinsic factors contributing to differential retention of learned predator recognition.

Complexity of learning

In most cases, associative learning occurs after a single conditioning trial. However, in nature, prey are repeatedly exposed to kairomones and conspecific alarm cues. Unfortunately, the role of continual information gathering and assessment over ecological time is not well understood. Ferrari and Chivers (2006b) found that when given several pieces of information regarding the level of threat associated with a predator, fathead minnows seem to have a "rule of thumb" to respond to risk: first, when given conflicting information, minnows respond conservatively by minimizing risk (i.e., by displaying the strongest intensity of response), and second, minnows rely more heavily on recent than old information. This pattern of response also occurs in larval Woodfrogs (Ferrari and Chivers 2009c). In addition, prey gather information regarding the time at which predators are the most dangerous and subsequently adjust their behavioural patterns and antipredator response in a threat-sensitive manner. Ferrari et al. (2008b) and Ferrari and Chivers (2009c) found that naïve larval tadpoles conditioned for 6 days with alarm cues can learn the activity pattern of a predatory salamander. When subsequently exposed to salamander odour, tadpoles displayed stronger antipredator responses at the time of day during which the predator was the most dangerous. It would seem that increased opportunities to learn would result in increased predator information, which in turn should allow prey to respond more adaptively to predators. Vilhunen (2006) tested this hypothesis by conditioning Arctic char (Salvelinus alpinus), and found increased survival in Arctic char that had experienced multiple conditioning compared with those that received only one conditioning event.

Learning through diet cues

Although alarm cues may be released during a predation event, we now know that alarm cues are also released by the predator after the predation event. Brown and Godin (1999) found that glowlight tetras learned to recognize a novel predator fed conspecifics through predator inspection behaviour. In addition, chemical cues can be released in the feces of predators, as they are not completely degraded by digestion (Chivers and Smith 1998). Mathis and Smith (1993a) and Chivers and Mirza (2001a, 2001b) have found that alarm cues detected from feces can mediate learned predator recognition, by chemically labelling the predator as threatening. What is interesting is that predators have, in turn, found a way to counter this phenomenon. Pike fed a diet of minnows defecated away from their hunting grounds, whereas pike fed a non-minnow diet did not show a preference of the location of their defecation (Brown et al. 1995, 1996).

Learning of heterospecific alarm cues

Learned response to heterospecific cues is expected within prey guilds, where ecologically similar species occur in sympatry. In this context, alarm cues from one species indicate predation risk for all guild members because they share the same predators. These learned cross-species reactions represent one of the arguments in support of the idea that alarm cues are a form of public information rather than specialized alarm pheromones (see below). Learning allows for the recognition of heterospecific alarm cues (Mirza and Chivers 2001a), which in turn can also mediate learned predator recognition (Mirza and Chivers 2003b).

Pollock et al. (2003) found that stickleback-naïve fathead minnows do not respond to brook stickleback (Culaea inconstans) alarm cues. However, when fathead minnows and brook stickleback are raised together in the presence of predators, minnows display antipredator responses when exposed to stickleback alarm cues. Fathead minnows and brook stickleback share the same habitat and the same predators; hence, responding to heterospecific alarm cues is likely beneficial for both species. However, factors such as habitat complexity and heterospecific density have been reported to act as a constraint on cross-species learning of heterospecific cues (Pollock and Chivers 2003, 2004). Other species have also been shown to display antipredator responses to heterospecific cues: sea urchins responding to alarm cues from blue mussels (Hagen et al. 2002) and larval

Pacific Treefrogs responding to alarm cues from larval Northern Red-legged Frogs (Adams and Claeson 1998).

Ontogenetic switches influence the way in which juvenile green sunfish respond to alarm cues from sympatric dace. Sunfish respond fearfully to dace alarm cues until they reach 90 mm standard length. Large individuals respond to the same cues with a foraging response (Golub and Brown 2003). Similar ontogenetic switches occur in juvenile large-mouth bass (Brown et al. 2002), pumpkinseed sunfish (Golub et al. 2005), and fathead minnows (Mirza and Chivers 2003c). Interestingly, Golub et al. (2005) found that although pumpkinseed sunfish exposed to bass alarm cues displayed this ontogenetic switch from antipredator to foraging behaviours in habitats of low or medium complexity, pumpkinseed sunfish of all sizes displayed a fearful response when exposed to bass alarm cues in highly complex habitat.

Learning through disturbance cues

There is only one study to date that investigated the possibility that disturbance cues can mediate learned predator recognition. Ferrari et al. (2008e) found that juvenile rainbow trout exposed to disturbance cues paired with a novel predator odour did not learn to recognize the predator as threatening. However, the presence of disturbance cues in conjunction with conspecific alarm cues result in a heightened intensity of antipredator response towards the learned predator.

The evolution of semiochemicals

There is some confusion over the distinction between alarm pheromone and alarm cue. Although this may at first appear to be a minor quibble over semantics, at the heart of the discussion is the evolutionary origin and maintenance of these cues, the receptors that detect them, and the behavioural, morphological, and life historical responses that have evolved in response to them. "Pheromone" was first defined 50 years ago by Karlson and Lüscher (1959) as a substance secreted to the outside of an individual and received by a second individual of the same species, in which they release a specific reaction in the form of a behaviour or a developmental process. Many of the examples given in the original description of pheromones were from insects. However, one of the examples of a pheromone given by Karlson and Lüscher (1959) was the "warning substance of the minnow", citing von Frisch (1941). We argue here that chemicals released from damaged minnow skin are categorically distinct from chemicals used by insects for attracting mates, colony recognition, aggregating, and significantly, signalling alarm.

The problem with the original definition by Karlson and Lüscher (1959) is that the ecological relationship between the pheromone sender and the pheromone receiver was vaguely defined. For example, do both the sender and receiver benefit from the release and reception of the chemical cue (a +/+ relationship) or does the sender benefit while the receiver is not influenced (a +/0 relationship)? Negative effects on the sender or receiver are also possible. A recent review by Dicke and Grostal (2001) categorized pheromones as any of +/–, –/+, or +/+. This is not helpful because one cannot develop ideas about the evolution of these chemicals without understanding the nature of the selection acting on the players involved.

The pheromones of the insects are maintained by +/+ relationships between the sender and the receiver. For example, a sex pheromone emitted by a female moth attracts males. The female (sender) benefits from attracting mates. Males (receivers) benefit from the pheromone by being able to locate the female. Because the sender accrues fitness benefits, there is selection on the sender to become ever more effective at producing and disseminating pheromone through the elaboration of specialized tissues or organs for that function. For their part, receivers are selected to evolve receptors to detect the pheromone and neural pathways to process and respond adaptively to this information. In another context, alarm pheromones emitted by an aphid, ant, or bee reduces the probability that kin will be eaten by a predator, thus the sender accrues benefits to its inclusive fitness through kin selection. These examples of pheromones are mutualisms (+/+).

In contrast, chemical compounds released from damaged prey tissue do not lead to the evolution of mutualisms because the sender does not benefit from the responses of receivers. Receivers exploit chemical information for their own benefit and evolve receptors and adaptive responses accordingly. However, prey in the clutches of a predator's jaws do not generally benefit from the responses of conspecifics to the public release of their internal fluids. In this case, the sender–receiver relationship is a commensalism (0/+). Damage-released chemical cues, we argue, are not specialized pheromones comparable with pheromones in arthropods, but simply detectable chemicals, or "public information" of value to receivers (Fig. 6). Evidence supports this view. There are no alarm pheromone glands to produce and release specialized alarm pheromones to be found among aquatic animals precisely because there has been no selection to favour the evolution of alarm pheromones. However, aquatic prey, as receivers, attend to these chemical cues to guide behavioural decision-making with respect to managing risk of predation.

The epidermal club cells of fishes in the superorder Ostariophysi presented evolutionary ecologists with a problem (Williams 1966, 1992; Hugie and Smith 1987). The superorder Ostariophysi (minnows, characins, catfish, suckers, etc.) comprises 27% of all known species of fish and 64% of freshwater ichthyofauna (Nelson 1994). Adding to the scale of the phenomenon, analogous large epidermal club cells also occur in non-ostariophysan fishes: Poeciliidae (Bryant 1987; García et al. 1992; Mirza et al. 2001a); Eleotridae (Kristensen and Closs 2004); Percidae (Smith 1979; Commens and Mathis 1999; Mirza et al. 2003); Centrarchidae (Brown and Brennan 2001); Cottidae (Chivers et al. 2000; Bryer et al. 2001); and Gobiidae (Smith and Lawrence 1992). These epidermal club cells (also known as "alarm substance cells") appear to satisfy the requirements of a specialized structure for the production and release of a chemical alarm pheromone (Pfeiffer 1977; Smith 1992). These cells are situated on the skin surface on the outside of the scales where even slight abrasion potentially ruptures them and releases their contents. However, release of this putative "alarm pheromone" is a passive by-product of tissue damage, not a voluntary act by the sender.

Fig. 6. The distinction between an alarm cue and an alarm pheromone is the absence or presence of a benefit to the sender, respectively. In both cases, there is selection for receivers to evolve specialized receptors to detect the chemical information because they accrue a benefit from doing so. Only in the case of an alarm pheromone does one see the elaboration of specialized tissues for the production of a specialized compound or compounds with which to manipulate the receiver. Damage-released chemicals from aquatic organisms constitute alarm cues. (Adapted from Bradbury and Vehrencamp 1998.)

ALARM CUE

SENDER → ENVIRONMENT → (+) RECEIVER

(0)

RESPONSE

ALARM PHEROMONE

SENDER → ENVIRONMENT → (+) RECEIVER

(+)

RESPONSE

Smith (1992) outlined 16 hypotheses for evolutionary mechanisms by which a sender could accrue fitness benefits for investment in epidermal club cells, of which 2 have now received empirical support. Interestingly, neither hypothesis posits that epidermal club "alarm substance" cells arose or are maintained by involvement in directly mediating predation risk.

Attraction of a secondary predator hypothesis

For senders to benefit from somatic investment in epidermal club cells, they must survive an encounter with a predator. This could occur if in addition to their role in alerting nearby conspecifics to the presence of predation risk, the chemical compounds in club cells also alert nearby predators of the presence of a potential meal to pirate away from another predator. By attracting a second predator, prey can escape if the predators fight over the prey or if the second predator to arrive is big enough to eat the primary predator. Laboratory and field experiments showed that predators are attracted to extract of minnow skin that contains club cells (Mathis et al. 1995; Wisenden and Thiel 2002). Chivers et al. (1996b) then found that the arrival of a second predator after the first predator has already grasped its prey, allows the prey to escape 50% of the time. In this scenario, the origin and maintenance of epidermal club cells is driven entirely by their role in a mutalism that co-evolved between minnows and their (secondary) predators, not as an "alarm substance".

Antipathogen or wound healing hypothesis

The antipathogen hypothesis maintains that epidermal club cells play a role in deterring bacterial infection, parasite penetration, and general wound healing. The epidermis provides physical protection to underlying layers and is also the first barrier against agents of disease. Pathogens and parasites are ubiquitous in aquatic habitats as anywhere and make for a compelling agent of selection for cellular responses in the epidermis. Although these ideas have been in the literature for some time (e.g., Al-Hassan et al. 1985; Blazer et al. 1997), connecting these functions to a mechanism for maintaining epidermal club cells was not the focus of the original authors. Recent data explicitly testing this hypothesis show that epidermal club cells in percids (yellow perch and johnny darters) are more abundant on the dorsal surface than on the lateral and ventral surfaces, suggesting a link between these cells and exposure to UV radiation (Chivers et al. 2007b). Experimental exposure to trematode cercariae and to zoospores of the pathogen fungus *Saprolegnia ferax* Kütz. and *Saprolegnia parasitica* Coker stimulate the production of club cells in fathead minnows (Chivers et al. 2007b; Fig. 7). Agar treated with skin extract of fathead minnows, but not skin extract of swordtails (*Xiphophorus helleri*) (a non-ostariophysan species) inhibits growth of *S. ferax*, affirming an antipathogenic component specific to minnow skin. Moreover, there is no correlation between epidermal club cell density and predation pressure in the source population (Chivers et al. 2007b). As with the "attraction of a secondary predator" hypothesis, the antipathogen hypothesis provides a mechanism for the maintenance of club cells over evolutionary time by avoiding the question of predation. These cells primarily serve an immune function (Halbgewachs et al. 2009) and have only secondarily acquired a role in mediating predator–prey interactions through selection acting on receivers to exploit public information.

Club cells, general damage-released chemical cues, and public information

Amid all the debate over how to explain the persistence of epidermal club cells over evolutionary time comes a recent result which suggests that club cells and their contents are not required for skin extract to elicit alarm behaviour (Carreau-Green et al. 2008). In this study, skin extract from larval fathead minnows that have not yet begun to produce epidermal club cells elicited full alarm reactions in adult minnows. This watershed result further supports the idea that club cells are not specialized for the production and release of an alarm (pheromone) cue. Rather, these data suggest that club cells serve other function(s) which provide direct benefits to the individual that makes them. This result, if corroborated by future study, will firmly place the "warning substances of minnows" squarely in the realm of chemical public information and not as the enigmatic anomaly it has posed to evolutionary theory for nearly half a century (Williams 1992; Wisenden and Chivers 2006).

True alarm pheromones can come about only when the individual emitting the chemical accrues a fitness benefit (Wisenden and Stacey 2005; Fig. 6). This occurs in kin groups where the sender gains inclusive fitness by increasing the probability that relatives survive. Alarm pheromones are well known in social insects where this condition is met (Hamilton 1964). Kin associations in aquatic taxa occur in some salmonids (Brown and Brown 1996) and amphibian

Fig. 7. Number (mean ± SE) of club cells per millimetre section of minnow skin for fathead minnows (*Pimephales promelas*) raised in the presence of water moulds. (*a*) Minnows raised for 16 days in the presence of water moulds (2 000 and 20 000 zoospores of *Saprolegnia parasitica* and 20 000 zoospores of *Saprolegnia ferax*) or a solution of dilute salts (control). (*b*) Minnows raised for 14 days in the presence of 20, 200, or 2 000 zoospores of *S. ferax* or a solution of dilute salts (control). Different letters over bars indicate significant differences based on Tukey post hoc comparisons ($p < 0.05$). (Modified from Chivers et al. 2007*b* and reproduced with permission of Proc. R. Soc. Lond. B Biol. Sci., vol. 274, issue 1625, p. 2615, © 2007 The Royal Society of London.)
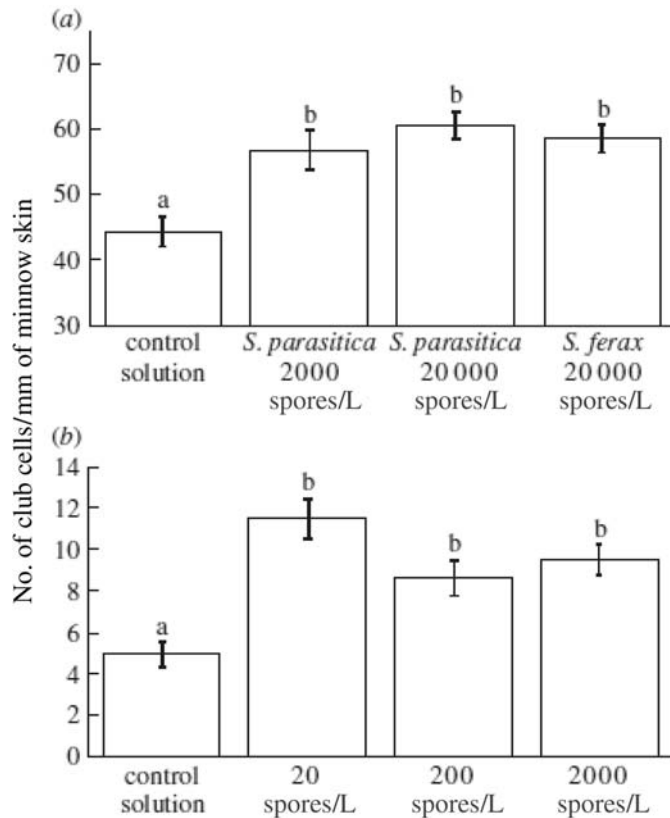
tadpoles (Halverson et al. 2006). Recent evidence is emerging that tadpoles of ranid amphibians possess epidermal secretory cells that release an alarm pheromone comprising at least two polypeptides smaller than 10 kDa (Fraker et al. 2009). No single high performance liquid chromatography (HPLC) fraction of skin extract produced an alarm reaction. However, when HPLC fractions were recombined, alarm reactions were re-established. Curiously, alarm reactions occurred in response to skin that had been poked with a needle but not from cues derived from homogenizations from freshly killed tadpoles, suggesting voluntary release of the pheromone. If supported by further study, this may be the first verified example of an alarm pheromone in aquatic 7vertebrates.

Hypoxanthine-3-*N*-oxide is a compound that has attracted attention as a candidate for the active ingredient in alarm cues of ostariophysan fishes (characins: Pfeiffer et al. 1985; minnows: Brown et al. 2001*b*). However, other work shows that one or more proteins in minnow skin is required for

alarm reactions to occur (Wisenden et al. 2009), intensity of alarm responses to heterospecific alarm cues declines with phylogenetic distance (Schütz 1956), and the active alarm chemicals in minnow skin is greater than 1500 Da (Lebedeva and Burlakov 1975; Kasumyan and Ponomarev 1987). Moreover, all chemical alarm cues identified to date from aquatic organisms have been proteinaceous (Atema and Stenzler 1977; Rittschof 1990). The paucity of work on the chemical characterization of alarm cues stands in sharp contrast to the amount of work done on the ecological role these cues play in the aquatic systems. We expect this will be addressed within the next decade.

Synthesis and future research directions

A decade ago, the field could be characterized as still exploring for the edges of the possible. We were still learning that alarm responses were not limited to fish of the superorder Ostariophysi. Ten years ago, we were grappling with the evolutionary paradox of ostariophysan epidermal club cells. We had just learned that fish could associate danger with novel stimuli, that diet affected a predator's odour, and that responses to alarm cues included changes in behaviour, morphology, and life history. Moreover, we had just started testing these new ideas in the field. The past decade has seen many developments that have clarified our understanding of the role of chemical cues in mediating predator–prey interactions in aquatic habitats and opened new ones. Several themes emerged that likely predict major trends for the next 10 years. The first is the application of learning to the ways in which aquatic animals assess risk. Although this area has made great strides, it still has much to learn from learning theory developed by psychologists and classic ethologists. The second area of growth is the extension of the antipredator phenotype to include embryonic development, which tunes behaviour and morphology to match prevailing environmental conditions. As behavioural ecology becomes increasingly reductionist, molecular tools will enable the next decade of researchers to delve into the epigenetic molecular switches that regulate development of antipredator competence. It is apparent that most researchers in this field are not physiologists or molecular biologists because proximate mechanisms of antipredator responses remain virtually unexplored. We expect this area to leap forward in the coming years.

The field reviewed here needs a better understanding of the chemistry of these cues. Of particular interest would be common properties of cues that would enable us to discern between phylogenetic conservation of chemicals and convergent evolution of chemical properties that work best as semiochemicals. There is a good possibility that epidermal cells that may form a component of alarm cues serve to protect these organisms from pathogens and (or) ultraviolet radiation. Thus, this research has potential pharmaceutical benefits. Understanding the chemistry of these cues will then open up the physiology of the olfactory system for detailedstudy with the application of such techniques as electroolfactograms. Knowing something about cue chemistry will allow the field to better assess and test for interference between these cues and common classes of industrial effluents.

In closing, we remind future researchers to bring these

ideas to the field and test them in manipulative field experiments. The stimulating effect of having one wake-up call this past decade (Magurran et al. 1996) propelled the field forward in new directions. With a little imagination and creativity, most ideas tested in the laboratory can be replicated under field conditions, bringing together the experimental power of hypothesis-driven research with the ecological realism of natural populations. It is in the field context that these responses evolved and continue to evolve.

Acknowledgements

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