Does one result trump all others? A response to Magurran, Irving and Henderson

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SUMMARY

Magurran, Irving and Henderson have reported that a population of European minnows, *Phoxinus phoxinus*, did not show an obvious behavioural fright reaction when they were presented with conspecific skin extract in a wild situation. Fish from the same population show a strong response when tested in aquaria. From these data the authors conclude that the fright reaction may be contingent on such factors as assessed risk and hunger. From this reasonable hypothesis they progress to the assertion that the Schreckstoff of ostariophysan fishes should not be considered an alarm pheromone. Much of their paper is devoted to arguments supporting their hypothesis that Schreckstoff cannot operate as an alarm pheromone. I argue that it is appropriate and adaptive to respond to alarm signals in a contingent manner, and attempt to answer the various arguments regarding the validity of terming Schreckstoff an alarm pheromone.

1. INTRODUCTION

Magurran *et al.* (1996) report the very interesting observation that European minnows (*Phoxinus phoxinus*) in the River Frome did not show an overt behavioural response when conspecific skin extract was presented to them in the wild, although fish of this same population respond strongly when tested in aquaria. They see this finding as casting doubt upon the hypothesis that minnow skin extract contains an alarm pheromone (see Smith (1992) for a review). Much of the paper seems to be devoted to trying to find doubt rather than to analysing the meaning of the specific results presented. The question is, do their conclusions logically follow from their results? I will briefly present, then respond to, the arguments they present to support the conclusion that 'further doubt' is cast on 'the hypothesis that Schreckstoff is an alarm pheromone' (p. 1551).

For convenience, in this paper I will refer to the active component in ostariophysan skin extracts that releases antipredator behaviour in conspecifics as 'Schreckstoff' (von Frisch 1938, 1941) to distinguish it from analogous, injury-released alarm pheromones in other taxonomic groups of fishes, e.g. darters (Smith 1979), gobies (Smith 1989), brook stickleback (Mathis & Smith 1993), poeciliids (Garcia *et al.* 1992), a sculpin (Hugie *et al.* 1991), a cichlid (Wisenden & Sargent 1997) and rainbow trout (Brown & Smith, submitted), and from analogous pheromones in amphibians (e.g. Lutterschmidt *et al.* 1994).

2. ARGUMENTS

The authors argue (p. 1551) that Schreckstoff cannot function by kin selection because there is no good evidence that fish schools are composed of kin and

heterospecific fish respond to the alarm pheromone. First, there is no absolute evidence that fish schools do not contain subgroups of kin, the minimum requirement for kin selection. Naish *et al.* (1993) did not exclude kin selection because their results did not exclude the possibility of kin subgroups within larger shoals. There is evidence that some fishes preferentially associate with kin (e.g. salmonids, Brown & Brown (1996); stickleback, FitzGerald & Morrisette (1992)). Both rainbow trout (Brown & Smith, submitted) and stickleback (Mathis & Smith 1993; Brown & Godin, submitted) have alarm pheromone systems that appear analogous to the Schreckstoff system of the ostariophysans.

There may be benefits favouring alarm signalling if fish shoal with familiar individuals that provide reliable and effective coordination of antipredator behaviour, even if the familiar companions are not kin (Smith 1986). Brown & Smith (1994) have shown that fathead minnows (*Pimephales promelas*) can recognize former companions from wild shoals after months of separation and are attracted to them. Chivers *et al.* (1995) found that groups of familiar fathead minnows were more efficient in performing antipredator behaviour than unfamiliar minnows and Mathis *et al.* (1996) found that fathead minnows are able to transfer predator recognition by cultural transmission. Therefore, the apparent absence of kin is not proven, and kin are not necessary for senders to benefit by warning others.

The fact that other species (p. 1551) in the same prey guilds respond to skin extract in no way excludes kin benefits. Alarm signals are not mating signals and species specificity is not necessary. Alarm signals are widely used by heterospecific animals within a prey guild, e.g. lemurs respond to the alarm calls of sifakas

(Oda & Masataka 1996). Trivers (1971) has argued that prey could benefit from reduced predator attention if hunting success in the prey's region is reduced by alarm signals. So, there could even be selection for alarm signals that elicit a broad taxonomic response because senders, and possibly their kin, could benefit if predators are generally unsuccessful in an area. There are data (Smith & Lemly 1986) showing that minnows can survive to benefit after predation injuries. The 'heterospecific response' argument does not hold water.

Christensen & Sorensen (1996) have recently commented on the application of the term 'pheromone' to vertebrate chemical signals. They argue (p. 242) that 'the original intent of the term was ... to ... describe those socially active odorants that evoke specific reactions and greatly improve an organism's chances for reproductive success and survival', and that this criterion 'and not ... the requirement for strict species specificity' is 'the key to defining a substance ... as a pheromone'.

Magurran *et al.* (1996) state: 'It is not clear how fish gain from ... club cells' (p. 1551). They discuss the study of Mathis *et al.* (1995) reporting that pike, *Esox lucius*, are attracted to Schreckstoff. There is a second paper (Chivers *et al.* 1996), which was not available to Magurran *et al.*, showing that the presence of a second pike significantly increases the chance of escape by a minnow that has been captured by a pike. The Schreckstoff attracts more predators to the predation event and their presence increases the probability that the sender will escape. Thus there is one clearly demonstrated direct benefit to the sender from the club cell contents. This is communication between prey and predators that benefits the prey, and thus, by definition, is an allomone (Brown *et al.* 1970).

Magurran *et al.* contend that loss of club cells in breeding males of some species '... can be explained by the known tendency of testosterone to suppress the immune system' (p. 1551). There are species in which club cells are not reduced by androgen treatment (e.g. pearl dace *Margariscus margarita*, Smith & Smith (1986)) and there is no evidence that the club cells are part of the immune system, so the idea that their loss in some breeding males (and breeding females in some species) 'can be explained by the ... tendency of testosterone to suppress the immune system' is mere speculation.

Magurran *et al.* suggest (p. 1551) that use of the term 'pheromone' implies the presence of 'special signalling machinery' (Williams 1992, p. 111). The club cells, large fragile epidermal cells, seem to fit the definition of 'specialized sending machinery'. The teleost olfactory system is demonstrably very sensitive to components of club cell contents (e.g. Lawrence & Smith 1989) and there is very clear evidence of responses by conspecifics to minute amounts of club cell contents (see Smith (1992) for a review). The phrase 'would not be there except for its usefulness in communication' is difficult to apply to many chemical signals. Would boars still have a submaxillary gland if it did not secrete a mating signal? Probably they would. Does that mean the active component of the submaxillary secretion is not a

mating pheromone? The objections raised by Magurran *et al.* do not apply to the ostariophysan Schreckstoff system.

Their argument (p. 1552): 'most ... work ... has examined ... fish in aquaria or in relation to their willingness to enter traps' seems to imply that we don't know if fish respond to Schreckstoff in the wild. Later (p. 1554), trap data are dismissed as being based on a special circumstance because of the confining nature of the traps. The naive reader might be misled about just how convincingly the trap studies support the hypothesis that some ostariophysans, in the wild, respond to Schreckstoff. To sum up several studies very briefly, fathead minnows readily enter traps scented with control odours, but are much less likely to enter traps scented with Schreckstoff or placed in areas where Schreckstoff had previously been released. Mathis & Smith (1992) caught 849 fathead minnows in a 4.5 h set of 16 pairs of traps. Each Schreckstoff-scented trap was paired with a control trap across the stream; the traps were identical except for the presence of Schreckstoff and the traps were set in a 'wild' stream. The control traps caught 822 minnows, the Schreckstoff traps caught 27. Something was happening. These basic results have been confirmed in several later studies (Mathis & Smith 1993; Wisenden *et al.* 1994, 1995; Chivers *et al.* 1995). The suggestion by Magurran *et al.* that the well established response to Schreckstoff in laboratory aquaria and field trap studies is an artefact of enclosure is groundless, misleading and contrary to field evidence. Wisenden *et al.* (1995) followed the movements of marked fathead minnows after exposure to either Schreckstoff or distilled water at their place of capture. Fish from areas scented with Schreckstoff were less likely to be recaptured in their original location than fish from control areas. However, contrary to the assertions of Magurran *et al.*, fish from Schreckstoff areas were more likely than control fish to enter traps in adjacent areas. These results indicate that minnows avoid areas where Schreckstoff has been released and that exposure to Schreckstoff does not alter their propensity to enter traps. Traps are free of the immediate presence of humans and, I feel, offer clear evidence from controlled experiments that Schreckstoff can alter the behaviour of wild minnows in ways appropriate for predator avoidance.

As well as trap studies, there have been convincing field observations on fish responding to Schreckstoff. The original observations of von Frisch (1938, 1941) were models of simple elegance. He found that the same species as used by Magurran *et al.* did respond to skin extracts in the wild. Similarly Newsome (1975) and Smith (1976) found that wild populations of creek chub (*Semotilus atromaculatus*) and fathead minnows, respectively, responded in the wild. We will probably never know how many positive and negative field tests have been carried out and not reported, or not accepted for publication, because the question was assumed to have been settled.

Magurran *et al.* point out that '... the response of fish to alarm substance is contingent on the availability of food' (p. 1552), and imply that this reduces its

validity as a chemical signal. This is one variation of the argument they present repeatedly, that if the response to Schreckstoff is 'contingent' on other factors, such as foraging opportunity or risk assessment, then the Schreckstoff is not a 'real' pheromone. Behavioural ecologists are regularly finding that animals adjust their behaviour according to the contingencies of the moment, as Magurran *et al.* state (p. 1554). For example, Robertson *et al.* (1995) have recently pointed out that insects are 'notoriously variable' in their responses to semiochemicals. We do not consider courtship 'not real' if it is contingent upon low predation risk (Magurran & Seghers 1990; Magurran & Nowak 1991; Magnhagen 1993), nor should we consider antipredator behaviour 'not real' if it is modified by foraging requirements. I am reminded of a recent news photograph of a woman braving sniper fire in Sarajevo in order to get bread and water. Her 'antipredator behaviour' was suppressed by hunger and thirst but that doesn't mean that humans don't fear bullets. The normal expectation would be that fish would titrate their predation risk, as assessed by Schreckstoff and other stimuli, against their other needs. This does not invalidate the quantifiable responses shown to Schreckstoff.

Magurran *et al.* cite our work (Brown & Smith 1996) for suppression of an overt fright reaction in fasting minnows. However, the fasting minnows did learn predator recognition when predator odours were paired with Schreckstoff. 'Covert' responses such as learned predator recognition (Göz 1941; Magurran 1989) and induced morphological change (Stabell & Lwin 1997) are valid and appropriate responses to an alarm pheromone but would not have been detected by the methods of Magurran *et al.*

The 'contingent response argument' is raised in another guise with regard to trap entry (pp. 1552 and 1554). If Schreckstoff increases the fish's wariness about entering confined spaces like traps, that would make it a 'priming pheromone' that primes the animal to respond in an appropriate manner to certain stimuli (Wilson & Bossert 1963).

Regarding methods (p. 1552), were all the observations conducted at the same season and were wild fish ever caught and lab tested at the same season in the same year with the same batch of skin extract? Is there possibly a 'seasonal hunger' factor suppressing the response? Also, were stimuli that had been run through the field introduction tube ever tested on lab fish? This could be different from using extracts prepared 'in the same way' or fish collected from the same sites in other years or seasons. Could one bad batch of Schreckstoff or some problem with the tube introduction method account for the negative results?

These may seem minor points, but if one is going to base conclusions on one set of negative data it behoves one to control the study carefully. As the information is currently presented it is not evident if the particular batch of skin extract used in the river was effective in the laboratory, if these particular fish would respond in the lab, or if running the stimulus through a tube (length? material?) might inactivate it.

On p. 1559 Magurran *et al.* state that pike swallow

minnows in a few seconds, but this depends on the relative size of the pike and the prey. Chivers *et al.* (1996) found long handling times (e.g. 120–300 s) for very small pike taking fathead minnows. Small pike are the most abundant size class during some seasons and may drive the evolution of prey defences more effectively than large pike, which are less abundant, less likely to allow any escape and tend to feed on larger prey than minnows. It is asserted on p. 1552 that 'pike tend to swallow their prey whole and do relatively little damage to the skin...'. Actually, small pike with big minnows often cause considerable skin damage while struggling to manipulate the prey into a headfirst position for swallowing (personal observation). These observations cast doubt on the assertion that wild minnows were exposed to Schreckstoff for considerably longer in the experiment than during a natural predation event.

On p. 1553 Magurran *et al.* also state that: 'No pike were attracted to the Schreckstoff release point even though these predators were often observed in the vicinity of the sites.' Presumably this is a reference to the report by Mathis *et al.* (1995) that pike are attracted to Schreckstoff. This raises the question, were pike ever observed from the remote operated vehicles (ROVs), even though they were '... often observed in the vicinity...'? If pike did not approach the ROV then it would constitute a refuge for the minnows and could account for reduced response to Schreckstoff when the fish are near the ROV. The literature on fish attraction devices (FADs) and artificial reefs often suggests that prey fish congregate around artificial objects because the object is a refuge from predation (e.g. Klima & Wickham 1971).

Magurran *et al.* state that: 'We know that wild fish can exhibit a fright response (Smith 1976) but...this is clearly not a universal reaction...' (p. 1554). But failure to respond is not universal either. The current score on published non-trap field observations is: response 4 (von Frisch 1938, 1941; Newsome 1975; Smith 1976), non-response 1 (Magurran *et al.*). Inclusion of trap studies would shift the balance further. So, rather than assert that one data set trumps all others, a more reasonable course of action would be to conduct observations and experiments that reveal the conditions that lead to response or non-response.

Magurran *et al.* argue that 'There is a strong case for further work... in natural communities of fish' (p. 1555). We strongly concur, but the work should take into account studies using traps (Mathis & Smith 1992) and direct observations of behaviour (von Frisch 1941; Newsome 1975; Smith 1976) and give a balanced account of the results. In addition, studies of 'natural communities' should take into account responses to Schreckstoff that may have profound biological significance but are not visible as an immediate and overt behavioural response. For example, Brown & Smith (1996) found that fasting fathead minnows showed no overt behavioural response to Schreckstoff, but did learn to recognize stimuli presented with the Schreckstoff. Similarly, Stabell & Lwin (1997) have shown that Schreckstoff induces defensive morphological changes in Crucian carp, *Carassius carassius*.

This is another 'covert effect' that would not be detected by video observation from an ROV. There is evidence for rapid, population-wide changes in predator recognition (Chivers & Smith 1995; Brown *et al.* 1997) occurring in wild populations. Based on Brown and Smith (1996) this could be largely accomplished without overt fight reactions being observed.

On p. 1555, Magurran *et al.* argue that if '... Schreckstoff is a substance with another function...' then '... there is no evolutionary anomaly'. The problem here is sorting out multiple possible functions and assigning priority to one. This may be particularly difficult for semiochemicals where the evolutionary origin is often still obvious. Does a male dog urinate to communicate or to excrete water and nitrogenous wastes? If you proved that dogs need to urinate for excretory purposes does that mean that there is no 'pheromone' in their urine? Obviously secretions may contain more than one active component: some components of dog urine communicate, others excrete, some may do both. In the case of minnow skin extracts Magurran *et al.* mention an unpublished report of antipathogenic activity that we may contrast with a large number of published reports of defensive responses by conspecifics. It behoves us to see whether the antipathogen effects and the communication effects are due to the same components in skin extract. The work of Mathis *et al.* (1995) and Chivers *et al.* (1996) also removes the 'evolutionary anomaly' by presenting a proven benefit to the sender for producing club cells: the attraction of secondary predators.

One could hypothesize that there may be at least three pathways to the evolution of injury-released alarm pheromones: from repellants, predator attractants or antipathogen/antiparasite secretions. In each case receivers might learn or evolve appropriate antipredator responses to the secretion if it was a reliable indicator of predation on members of their prey guild and did not interfere with their own feeding responses to the damaged tissues of their prey. As a third stage, senders could modify the signal in response to benefits such as inclusive fitness or predator discouragement. Any of the three proposed 'ancestral functions' might be retained to varying degrees during the subsequent evolution of the pheromone. A careful look at the variety of injury-released alarm pheromones (e.g. cichlids, cottids, darters, gobies, poeciliids, sticklebacks, salmonids, amphibians, etc.) could provide examples of each type of system. Such work could be efficiently carried out by controlled laboratory experiments combined with field studies.

3. FINAL COMMENTS

What can laboratory studies tell us? Laboratory experiments, conducted under conditions where factors such as food abundance and quality and the presence or absence of predators or refuges are controlled, can tell us whether or not an animal possesses the capability to perform a behaviour pattern or respond to a particular stimulus. If, as Magurran *et al.* contend, we

have a situation where responses are clear in the laboratory but are not obvious in 'wild' situations, then this presents an 'evolutionary anomaly' at least as interesting as the occurrence of an alarm pheromone. What was it about the particular wild situation that inhibited or blocked the responses seen in the laboratory? There are conditions that are known to inhibit Schreckstoff responses in the lab, for example habituation (Krause 1993) and hunger (Brown & Smith 1996). Do any of these apply to the wild situation? This could be tested experimentally. For example, if the wild fish are too hungry to show an overt response then they would probably not respond in the lab either immediately after capture, but would respond after a few days on a good diet. They might also respond in the field after supplementary feeding. If they are habituated then they would probably not respond in captivity even after a few days of feeding. Pollutants such as detergents (Kasumyan & Paschenko 1982), pesticides, e.g. Diazinon (Moore & Waring 1996), and acid (Smith & Lawrence 1988) can interfere with fish olfactory responses, including the response to Schreckstoff. If the olfactory system is damaged then the fish should not respond in the lab situation until they have had time for recovery of the olfactory epithelium. If another factor, such as confinement or lack of known refuges, is at work then the Frome fish should respond soon after being placed in tanks.

It is interesting that the study of amphibian alarm pheromones has had a stronger tradition of reporting field observations (e.g. Petranks 1989) than has the study of fish responses. One possibility is that fish researchers have assumed that field verification was already taken care of through von Frisch's observations and early experiments. One of the benefits of the current exchange of views may be an increased awareness of the need to field test laboratory ideas and a willingness of reviewers and editors to accept documentation of field responses as an important element in the study of semiochemicals.

The preparation of this manuscript was supported by the Natural Sciences and Engineering Research Council of Canada and by the University of Saskatchewan. R. S. Mirza and Dr G. E. Brown, Dr D. P. Chivers and Dr B. D. Wisenden contributed valuable comments.

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Received 14 October 1996; accepted 6 November 1996