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Review

Non-visual crypsis: a review of the empirical evidence for camouflage to senses other than vision

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I review the evidence that organisms have adaptations that confer difficulty of detection by predators and parasites that seek their targets primarily using sensory systems other than vision. In other words, I will answer the question of whether crypsis is a concept that can usefully be applied to non-visual sensory perception. Probably because vision is such an important sensory system in humans, research in this field is sparse. Thus, at present we have very few examples of chemical camouflage, and even these contain some ambiguity in deciding whether they are best seen as examples of background matching or mimicry. There are many examples of organisms that are adaptively silent at times or in locations when or where predation risk is higher or in response to detection of a predator. By contrast, evidence that the form (rather than use) of vocalizations and other sound-based signals has been influenced by issues of reducing detectability to unintended receivers is suggestive rather than conclusive. There is again suggestive but not completely conclusive evidence for crypsis against electro-sensing predators. Lastly, mechanoreception is highly understudied in this regard, but there are scattered reports that strongly suggest that some species can be thought of as being adapted to be cryptic in this modality. Hence, I conclude that crypsis is a concept that can usefully be applied to senses other than vision, and that this is a field very much worthy of more investigation.

Keywords: acoustic crypsis; chemical crypsis; olfactory crypsis; predation; mimicry

1. INTRODUCTION

The aim of this paper is to review the evidence that organisms have adaptations that have been selected because they confer difficulty of detection by enemies (principally predators and parasites) using sensory systems other than vision. That is, I will review the empirical evidence for non-visual crypsis and explore how our understanding of visual crypsis can be expanded to non-visual sensory systems. The review is arranged in terms of different sensory modalities.

As an important preliminary, we must consider how the concept of visual crypsis extends to other systems. Definitions of visual crypsis are discussed specifically in the companion paper by Stevens & Merilaita (2009). Here, I have attempted to stay close to their definition of crypsis. Specifically, I consider an organism to be cryptic if it possesses traits that hinder a receiver's ability to detect the organism as a discrete entity and locate its position. This focus on detection separates crypsis from traits that act to hinder the correct identification of the organism, the latter type of traits are typically called *mimetic* or *masquerading*. However, I believe the same trait can have both a cryptic function and a masquerading function. For example, the visual appearance of a stick insect may make it difficult for a viewer to detect the insect as an entity when presented against a background of plant parts, and even if detection occurs the insect may subsequently be misidentified as a stick. Further, I consider that a cryptic organism still has some impact on the relevant sensory system of the viewer, such that if the cryptic organism were removed, then the flow of information to the viewer would be changed. That is, I consider that a cryptic organism must make some impact on the sensory system of the viewer, although this impact is such as to make detection of the organism difficult. Another way to put this is that detection of a cryptic organism should be difficult but not impossible. For example, if a rabbit has colours and textures similar to the substrate on which it is feeding, then I would consider it likely to be visually cryptic. If the rabbit has a tendency to remain in its burrow at times when predation risk is the highest, then this is clearly an anti-predatory trait that reduces the likelihood of visual detection. However, I would not consider this crypsis, because when this trait is deployed detection becomes impossible; if the rabbit were removed from the burrow, then there would be no change in the flow of visual stimuli reaching the viewer on the surface. I would term such traits (which make detection impossible at certain times or under certain circumstances)

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hiding, rather than cryptic. This definition of crypsis expands naturally to cover any sensory system, and will be referred to throughout this review.

2. SOUND

There are many examples of organisms that are adaptively silent (curtail vocalizations) at times or in locations when or where predation risk is higher or in response to detection of a predator (Schevill 1964; Curio 1976; Spangler 1984; Jefferson *et al.* 1991; Luczukovich *et al.* 2000; Magrath *et al.* 2007). Such 'acoustical avoidance' (as coined by Curio 1976) requires some predictability in predation risk, either because times and places of heightened predation risk can be reliably detected, or because predators can be detected before they have detected the prey. Such avoidance probably incurs costs, since the sexual, social or other function of the calls is not fulfilled when the animal is silent. This cost can be reduced if calls are modified to make detection by the predator more difficult; and this may be the preferable approach where predation risk is permanently high or in situations where no reliable warnings of predation risk or individual attacks are available. Acoustical avoidance is an example of hiding as defined in the introduction, and thus is not what I would consider crypsis. However, modification of structure of calls in ways that make detection by predators more difficult (but not impossible) does fit with my definition of crypsis.

An example of real-time modulation of call type due to perceived increase in predation risk is described by Ryan *et al.* (1982), involving the response of calling male frogs to the presence of predatory bats. This study demonstrated that although more complex calls were favoured by female frogs, they were also preferentially targeted by bats in choice trials in an aviary. The complex call is only used by males when other males are calling at the same time, and so competition for females is more intense. Thus call selection is seen by the authors as a trade-off between complexity offering enhanced attractiveness to females but also enhanced predation risk. The higher predation risks are only acceptable when competition for females is higher. An alternative explanation could be that the presence of many males compensates (due to dilution of the predation risk of an individual male) for the increased predation risk caused by the complex call. In any case, it seems that the less complex calls offer protection from predation, and it seems plausible that this is due to the less-complex call making detection of the frog more difficult for bats. If so, this would be an example of auditory crypsis, however it may be that the nature of the call influences post-detection processes of recognition and target selection by the bats. Thus, although this system may provide an example of auditory crypsis, more research is needed to confirm this.

Mougeot & Bretagnolle (2000) demonstrated that terns stopped their own calling in response to playbacks of territorial calls of their skua predators. Again, I would consider this hiding, rather than crypsis. Bayly & Evans (2003) report changes in a sequence of alarm calls by male fowl, with later calls having properties that have been considered to reduce the ability of detectors to localize the sender; specifically the first call only in a sequence began with a high-amplitude, broadband pulse that the authors argue gives strong locational cues.

Marler (1955) suggested that the high-frequency 'seet' calls of many smaller passerines have the property of making the emitter difficult to locate by predatory receivers. High frequencies are certainly known to attenuate across distances more than low frequencies (hence thunder sounds 'deeper' when a storm if further away), reducing the ability of high frequency calls even to be heard at a distance. However, several authors have argued that at a given distance, larger-headed birds have reduced ability to localize sounds. This might be highly relevant, since as a generality predators tend to be larger-headed than their prey. Such papers (e.g. Brown 1982) generally cite works by Coles *et al.* (1980) and Hill *et al.* (1980) in support of this mechanism, but my reading of these papers suggested that if anything larger headed taxa should have an advantage in direction finding (see also Denny 1993). Nevertheless, the most comprehensive test of the hypothesis that seet calls are difficult to localize involved observation of the behaviour of several predatory species in an aviary in which seet calls and control calls were played on a loudspeaker (Jones & Hill 2001). Predators generally responded to both types of calls, but their head movements suggested more accurate location of the loudspeaker playing the control calls. Krams (2001) showed that dummy passerines associated with 'long-range contact calls' were attacked by predatory sparrowhawks (*Accipiter nisus*) more often than those paired with these high-frequency seet calls, which Krams put down to the attenuation effect. Brown (1982) and Wood *et al.* (2000) found that captive birds of prey responded to high-frequency alarm calls but generally failed to localize them, in contrast to a high ability to localize mobbing or distress calls played through the same speakers. Thus it does seem that some avian calls do have a form of anti-predator crypsis, however here crypsis may work more by hindering the predator's ability to localize the prey rather than to detect its existence.

Rednondo & De Reyna (1988) argue that the structure of begging calls of nestling altricial birds (involving dispersal of energy across a wide frequency spectrum) would reduce the ability of predators to estimate the distance to the callers. They suggest that these properties are less pronounced in cavity nesters because fewer predators can access cavity nests even if they locate them, thus producing less selection pressure to hide nest position. However, the very different acoustic properties within a cavity compared with open nests might select for different properties of begging signals for communication with the parents, aside from any effect on predators. Further, the suggested reduced localizability of the signals has not been demonstrated empirically. In a comparative study, Haskell (1999) found that ground-nesting warblers had higher frequency begging calls than tree-nesting species. In experiments with loudspeakers in dummy nests, they demonstrated that the calls of tree-nesters produced higher predation rates (than those of ground-nesters) when played on the ground, but that the calls of ground nesters did not increase predation risk (compared with tree-nesters) when played in dummy nests in the trees. Briskie *et al.* (1999) studied a 24-species community of breeding passerines, measuring egg loss from predation and recording begging calls. Controlling for phylogeny, they found a relationship where species with higher predation rate had calls of higher frequency and lower amplitude. Their interpretation is that louder and lower frequency calls aid in soliciting food from parents but impose greater likelihood of attacking predators. Those species whose nest site, time of breeding or parental activity increases predation rate will feel greater selection pressure to reduce the detectability and locatability of calls. Variation in calling between chicks in the same nest has commonly been reported, and exploration of whether it can be related to within-nest chick selection by predators would be very valuable. However, for all the intense interest there has been in potential predation costs of begging calls; definitive empirical evidence of such a cost in a natural system remains very scant (Moreno-Rueda 2007), and thus we are some distance away from being sure that any nestling call can usefully and accurately be described as more acoustically cryptic than another.

With vision, detection and localization generally happen simultaneously; when an item is visually detected, the detector generally also gains accurate information as to the direction and range of the detected item. This can be much less the case for detection through sound, where the processes of detection and localization can be distinct. That is, a predator may detect the sound characteristics that inform it that prey is nearby, combined with no or poor information of the direction in which the prey lies or the distance away. Although it is common in the literature to find claims that some type of calls are selected for poor localizability by enemies, this assertion is generally not fully tested, and is based on the identification of signal properties that are considered to make localization less easy. This is however currently far from a good understanding of what such signal properties might be in particular cases or as a generality. The warnings of the very careful study of Klump & Shalter (1984) that ‘crude differentiation between localizable and non-localizable signals is not possible, and the localizability of particular sounds varies between species’ are not always heeded. In some cases the question of detectability may render the problem of localizability unimportant. What can be said with certainty is that there are no universally effective signal properties that render a signal difficult to localize, rather the localizability of a signal will vary dramatically according to the relative positioning of sender and receiver, the physiology of the receiver and the local acoustic and physical environments. Further the relative directions that signaller and receiver are facing may impact on both detectability and localizability. We would expect acoustic signallers in general to face towards intended receivers and away from potential directions of unintended receivers (Witkin 1977; Klump & Shalter 1984). The extensive work on the great-tit–sparrowhawk system by Klump & Shalter (1984) suggests that the high frequency ‘seeet’ calls of the tit has low detectability by the sparrowhawk, perhaps being undetectable beyond approximately 10 m, whereas it may be detectable to the intended receivers (conspecifics) up to 40 m distant (Klump *et al.* 1986). The ‘seeet’ call is only used when the sparrowhawk is distant, in contrast to other calls that can be detected at greater distances and do not show differential detection distances between tits and sparrowhawk (Klump *et al.* 1986). Thus, it does seem reasonable on the basis of our current understanding to describe these calls as cryptic.

Wilson & Hare (2006) demonstrate that Richardson’s ground squirrel (*Spermophilus richardsonii*) gives different alarm calls according to the distance to the stimulus: using more ultrasonic (to humans) calls when the stimulus is further away. Compared with the alternative call, these ultrasonic calls are less easily detected by both the ground squirrels and likely predators. Hence the authors suggest that the squirrels switch to the ultrasonic call when predators are distant because it is possible in this situation to contact conspecifics (albeit with reduced effectiveness: compared with the alternative audible call) without alerting the predator to the existence and position of the caller. When the predator is close, the caller will attract the predator’s attention no matter which call it adopts, and so the call that most effectively warns conspecifics is adopted. If this interpretation is correct, then the ultrasonic call can be considered acoustically cryptic.

A particularly satisfying study is that of the calling by katydid insects that are predated by bats, as reported by Belwood & Morris (1987). In a cross-species comparison, they show that species in a habitat where bat predation was common spent less time producing mate-attraction noises (termed singing) than species in a nearby habitat without bats. The one species from the bat-vulnerable habitat that sang for a high proportion of time specialized in singing from a particularly spiny plant that offered excellent protection from bats. In cage experiments, the authors further demonstrated that bats took longer to locate infrequent callers and entirely failed to locate silent insects. Although this study demonstrates conclusively that call production is modulated in accordance with control of predation risk, whether it is best described as hiding or ‘crypsis’, according to my definitions in the introduction, is less clear. I would describe complete cessation of calls as hiding. If bats spend some time attempting to locate an insect (equivalent to several inter-call intervals), then reduction in calling rate might usefully be described as crypsis if the longer inter-call interval disrupts localization. Alternatively if bats simply pounce on any insects that reveal their position with a call when the bat happens to be passing close by, then reduction in call frequency might more usefully be described as hiding. In the first case, protection from predation occurs because the prey’s rate of detection per unit time decreases, but the prey is always at some risk, whereas in the second case, the fraction of time when detection is possible at all is decreased. This discussion illustrated that, just as visual crypsis, evaluation of whether a specific trait is cryptic or not is a function of the ecology of the viewer as well as the focal organism.

Morisaka & Connor (2007) argue that selection pressure from predation by killer whales (*Orcinus orca*) has caused changes in the echolocation and communication systems of certain other marine mammals, such that the sounds emitted are more difficult for killer whales to detect. Although it is difficult to prove the link with killer whales definitively, Morisaka & Connor (2007) marshal all the available evidence and argue that the 'acoustic crypsis' explanation seems more plausible than any alternative explanation for variation in noise produced by different species. Of course, crypsis can work for predators too, and killer whales that specialize on mammals appear to make sounds differently from those specialising in fish, and this has been argued to make the killers less easily detected by their prey (Barrett-Lennard *et al.* 1996; Deecke *et al.* 2005).

Co-evolution of moths and echolocating bats has been much studied, and certain noise production by moths has been described as functioning to 'enhance crypsis'. However, this term is not helpful since there is no suggestion that this noise disguises the presence of the prey, but rather may startle or confuse the bat or mislead it as to the direction or identification of the prey (Ratcliffe & Fullard 2005; Barber & Conner 2006). If the noise production by the moths does act to mislead the bats as to the position of the moth, then (by my definition) I would consider this to be crypsis. However, evidence for this specific mechanism is currently inconclusive. We might also expect adaptations (perhaps in frequencies used and/or intensity) in the echolocating bats to minimize the ease with which prey can detect them and take evasive measures. This has been much less investigated, but see Miller & Surlykke (2001) for a thoughtful discussion of the issues involved.

In a laboratory experiment, it has been demonstrated that birds feeding alone respond to higher levels of background noise by increasing visual monitoring for predators (Quinn *et al.* 2006). It would be interesting to explore whether in any natural systems predators exploit high levels of background noise to mask noise of their approach by specifically biasing their predation to times or places when background noise is higher.

In sum, although conclusive evidence can be difficult to obtain, there currently exists highly suggestive evidence of acoustic crypsis in a small number of different systems. Evaluation of this evidence highlights an important difference between visual crypsis, and crypsis in other sensory modalities (including sound). With vision (in species with a complex eye), if a viewer detects the existence of an object, it also simultaneously obtains good information as to the position of that object. With sound, the processes of detection and location are less tightly bound, and the listener may detect that a specific object is in the local vicinity without simultaneously obtaining accurate information as to its specific location.

3. OLFACTION

There are many examples, particularly among insects, of what I would term chemical mimicry, where one species (or sex) chemically disguises itself as another; this is well summarized in the review by Dettner & Liepert (1994). However I would follow Dettner & Liepert (1994) and Portugal & Trigo (2005) and consider this separate from the crypsis that is the focus of this article. Mimicry involves being misidentified but being treated as a specific entity of interest, whereas crypsis involves a failure to detect that the camouflaged individual is a distinct entity or failure to locate the individual. For mimicry the model with which the mimic has been misidentified can be identified in principle at least, whereas this is not so for crypsis. Note that some other authors use these terms entirely differently, defining chemical mimicry as misidentification caused by internally synthesized chemicals and chemical camouflage to involve essentially the same outcome (misidentification, not failure to detect as an interesting entity) when arising from sequestering of chemicals from the environment (e.g. Akino *et al.* 1999).

Some authors define chemical insignificance as a lack of odours. This is the typical state of callow social insects, in marked contrast to the adults that take on the signature chemical composition of their colony, and maintain acceptance in the colony because of this. As Lenoir *et al.* (2001) discuss, obligate social parasites are odourless at the time of usurpation, and may remain in this state or develop the chemical signature that allows them to mimic adult colony members. It is not currently clear whether this lack of chemicals causes the intruders to be passed over as a part of the fabric of the nest (chemical crypsis) or misidentified as callows (chemical mimicry). Lambardi *et al.* (2007) lean towards the former, concluding from their study that 'a chemically insignificant cuticular hydrocarbon profile therefore seems adaptive because it enables the tiny ants to merge with the background nest material', but evidence that they are not misidentified as callow ants is missing from their study.

Akino *et al.* (2004) present a particularly impressive study of chemical background matching by caterpillars of *Biston robustum*. Visually these caterpillars look similar to the twigs of the plants, so that they are commonly found. However, visual masquerade of twigs would not protect them from predatory ants, which primary detect and locate prey olfactorally. Despite this, ants were observed to repeatedly walk over the caterpillars without attacking them, even after antennal contact. This was considered to be because the caterpillars' cuticular chemicals resembled those of the twigs of the food plant. When caterpillars were transplanted to a food plant of a different species, they were readily attacked by ants. This vulnerability lasted only until the next moult, with cuticular chemicals after moult resembling the new food plant (but only if the caterpillar had been allowed to feed on it, demonstrating that the protection is food derived). This moult 'corrected' not only the chemical signature of the caterpillars but also their appearance. One particularly interesting aspect to this is that the caterpillars eat leaves, and leaves have a similar but identifiably different chemical signature to twigs of the same plants, yet the caterpillars more closely resembled the twigs than the leaves. Thus, here we have fine-tuned, flexible chemical defence combined with visual masquerade.

There is an important issue here as to whether this combination of chemicals is best seen as crypsis or masquerade. My feeling is that twigs are commonplace on the plants on which the predator–prey interactions take place, and are often huge in scale compared with ants and not of interest to ants as entities. For this combination of reasons, I think the chemical adaptation of the caterpillars can more usefully be seen as crypsis by background matching than masquerading. However, this viewpoint rests on an untested assumption that ants do not form cognitive images of twigs as entities that could act as models in a masquerade system; this is only my assumption, without empirical evidence.

Portugal & Trigo (2005) presented an essentially similar demonstration for the larvae of another butterfly species, *Mechanitis polymnia*. Again the ants were seen to walk over this larva and ignore it on its normal host plant, but to readily attack individuals transplanted to another plant in a laboratory study. Further when the (freeze-dried) larvae of another butterfly (*Spodoptera frugipera*) were placed on the normal host plant of *M. polymnia*, they were attacked readily, but when coated in the cuticular lipids of *M. polymnia* they were done not. The fact that protection only occurs when on the appropriate plant is suggestive of the fact that this must be explained by chemical crypsis on the plant, rather than any inherent repellency of the chemicals that should work regardless of context. Further, the difference in the effect of plant on attack rate could not be explained by changes in behaviour or in chemical signature, because the caterpillars were freeze dried before being randomized to one plant or the other.

Chemical communication can be very important to the ecologies of herbivorous insects, and predators are well known to cue on the aggregation or sexual chemical emissions of such taxa. In a series of papers culminating in Raffa *et al.* (2007), Kenneth Raffa and colleagues have studied the chemical interactions of bark beetles and their predators. This work does point to aspects of the chemical signals of one bark beetle in particular (*Ips pini*) whose signals seem to have been selected to reduce (but not eliminate) detectability by predators. The pheromone mixture emitted by individuals of this species in a particular area seems to be intermediate between the mixtures such that different predators are most effective at detecting. Further, an additive that boosts the detectability of the cocktail to conspecifics but not predators appears only to be added in times of the season and geographical locations when predation risk is high. Further, in elaborate transplantation experiments (e.g. Raffa & Dahlsen 1995), it has been demonstrated that there is regional variation in the chemical mix issued by individuals of this species, and that predators from a given locality are more able to detect and locate individuals from distant populations than from the same locality as the predators. Taken together this evidence seems highly suggestive of selection pressure on chemical communication signals to reduce detection and/or location by predator, i.e. of chemical crypsis.

Fishlyn & Phillips (1980) present evidence that is highly suggestive of chemical crypsis in a marine context, although the evidence is not quite as compelling as the caterpillar examples discussed above. The limpet *Notoacmea palacea* that feeds on the marine angiosperm (surfgrass) *Phyllospadix* would appear to be vulnerable to attack by sea stars. However a field study reported this species to be taken much less by sea stars than its abundance relative to other gastropods would predict. Twenty natural encounters between this gastropod and sea stars were observed, in each case the sea star did not attack the limpet: 'the sea star usually continues without pause to crawl over the limpet. The sea star does not recoil from the limpet, nor does it attack it. The sea star seems simply to have not detected the limpet'. Biochemical assays demonstrated that the limpet's shell (but not its flesh) contains appreciable quantities of flavonoids present in the surfgrass on which it feeds. The authors speculate that this is likely to function as chemical camouflage rather than as an aversant. They argue that the lack of observed avoidance by the potential predator and the presence of the chemical in the shell but not the flesh are consistent with this interpretation. The limpet responds to the sea star by withdrawing its body parts and clamping its shell down firmly on the plant blade. Although the authors argue that this is consistent with chemical crypsis (to me), it is not inconsistent with toxic defence held in the shell but not the flesh. Nonetheless, Fishlyn & Phillips (1980) do present a very suggestive case for chemical camouflage in this system, and further work is definitely warranted.

A particularly interesting example of apparent olfactory crypsis is the switch in preen wax associated with breeding recorded in several ground-nesting birds (Reneerkens *et al.* 2005). Normal waxes are replaced by less volatile ones. This change occurs prior to the onset of breeding and continues into incubation (suggesting olfactory camouflage rather than a sexual signal, for example). Further, in species where only the female incubates, the male does not show this change in wax composition. An experiment with a single dog provides some evidence that the breeding-related waxes are more difficult to detect than the normal waxes in an abstract situation. These promising results very much warrant further investigation in a more realistic setting, if possible with natural predators.

Hudson *et al.* (1992) provide good evidence for a parasite-induced increase in the scent produced by grouse in such a way as to increase vulnerability to mammalian predators (the ultimate hosts of the parasites concerned). Grouse treated with an anthelmintic drug were less easily found by dogs trained to hunt by scent than control birds. Although this does not demonstrate that unparasitized grouse have particularly effective chemical camouflage, it does highlight that the parasite can increase the chemical conspicuousness of the host, and further investigation is warranted, again (if possible) using natural predators.

Thus, at present we have very few examples of chemical crypsis. However, olfaction is an important means of food finding in both air and water. Further, for herbivores, consumption of their host plant may naturally provide them with the chemicals required to reproduce the plant's chemical signature. For these reasons, I suspect that the current small number of examples of chemical crypsis is likely to creep remorselessly upwards as more scientists become aware of the phenomenon. But (as discussed previously) whether an insect matches the chemical signature of its host plant is best considered as an example of crypsis or masquerade depends on the cognitive functioning of the detecting organism, and is currently far from being empirically resolved in any particular case.

4. ELECTRICITY

Electric fields can only be detected in water rather than in air. This is because air is 2×10^7 times more resistant to electrical flow than water, and the power of an electrical signal varies linearly with the inverse of such resistance (Denny 1993). Many cartilaginous fishes have sensors that can detect changes in electric fields, so do some bony fishes (Collins & Whitehead 2004). Such sensors have been reported in a few amphibians and even fewer aquatic-foraging mammals (such as the platypus; Manger & Pettigre 1995), but not in any invertebrates. Electric sensing can be passive, detecting the changes in electric fields caused by the movement of nearby animals, or active when so-called weakly electric fish produce an electric field around them and detect changes in that field caused by nearby objects with different electric conductivity to water. Either way, Denny (1993) suggests that the power available for detection declines with distance from the source to the power negative six, and thus electric senses only work at a range of a few (or at most a few tens of) centimetres (see also Knudsen 1975; Haine *et al.* 2001). Although injured animals are likely to produce more powerful electric fields than the uninjured, Denny (1993) suggests that this will only increase detection range by a factor of approximately 2.

Although electric senses only work at a very short range, they can be very effective at detecting nearby objects and countermeasures may be difficult to implement. Electric senses appear to be effective at discovering animals buried in the benthos (Kalmijn 1971). The electric sense (unlike visual sensing) can detect individuals that are completely covered in substrate. The substrate will distort the electric field of a weakly electric fish swimming just above the benthos. Anything buried in the substrate with a different electric conductivity to the substrate will cause a different distortion that can be detected and investigated by the fish. It is not physically possible to change the structure of a living tissue for it to be a good match to the background substrate in electric conductivity; hence something akin to background matching in the visual modality is not possible. Even if the conductivity of the animal were altered to be different from a fish, to be as a buried stone or wooden fragment say, this would not offer much protection, since such distracters may be so uncommon that it is not overly expensive for the fish to investigate anything out of the ordinary that it detects in the substrate. By similar reasoning, something akin to disruptive coloration, or masquerade, would not be effective in providing protection from electric sense. Ahlborn (2004) suggested that human divers working in a metal cage to protect them from sharks may gain extra protection through the cage acting as a Faraday cage blocking electric signals as well as through the intended physical barrier. While this is intriguing, a cage that successfully blocks all electric signals from within would probably require too fine a mesh size to be useful.

An electric field is produced by any movement of an animal: a muscle contraction moves ions and so sets up an electric field that could potentially be detected by a predator at a close range (Denny 1993). Clearly, there is some protection from moving as little as possible so as to reduce this effect, or from staying close to another moving organism or a number of moving organisms that are not attractive to the predators so that their electric field serves to mask the prey's own field. Lightning strikes produce huge electrical discharges that serve as noise that may be able to interfere with electrical detectors even hundreds of kilometres away from the electrical storm. Hopkins (1973) suggested that electric fish produced discharges that did not contrast with lightning noise, which he suggested might be useful in allowing predatory electric fish to approach their prey undetected. This electric background matching has not however been rigorously demonstrated, and the relatively short range of the signals generated by such fish may mean that disregard of the contrast to background electric noise, the predator cannot be detected by its prey until it is only a few body lengths away. Lastly, because electric detection only works at a short range, hiding in a crevice or other structure that does not allow the predator to approach closely can prevent the predator from being able to detect the prey at all in this sense.

Fish that use electric signals in their own navigation, prey detection and sexual signalling may be vulnerable to eavesdropping by predators. In a series of papers culminating in Stoddard & Markham (2008), it has been demonstrated that those electric fish that appear to be most at risk from electroreceptive predators have characteristically higher frequency electric discharges that are suggested to be less detectable to their predators. Further, these authors argue that some of these fish show what they call a 'signal cloaking' adaptation, where the spatiotemporal distribution of electric production by the fish is such that low-frequency parts of heterogeneous local electric fields cancel each other out at a distance of more than a few centimetres. Further, in laboratory experiments electric fields of this nature aroused less interest from elector-sensitive fish than analogous fields without the correct characteristics for effective cloaking. This suggests that the output of some electric fish may have evolved to reduce ease of detection by predators. Although logistically (and potentially ethically) challenging, this interesting body of work is now at a stage where exploration of predator responses in the wild or in realistic captive conditions would be very much worthwhile.

5. DETECTION OF BULK FLUID MOVEMENTS: WAKE FOLLOWING

It has recently been experimentally demonstrated that the predacious, nocturnal European catfish (*Silurus glanis*) could track piscine prey over distances of 55 prey body lengths using wakes that were up to 10 s old (Pohlmann *et al.* 2001). The authors further argued that the conditions in their experimental tanks (with reflection of waves from the sides of the tank) were not conducive to wake following, and based also on work by Hanke *et al.* (2000) on the wake of a goldfish (*Carassius auratus*), speculated that fish should be able to derive directional information from wakes as old as 60 s. In a follow-up study, Pohlmann *et al.* (2004) demonstrated that this wake following relied on detection of hydrodynamic disturbance through the lateral line, rather than olfactory cues. Wake following may be widespread among predators that hunt in darkness (including the deep ocean) and in murky waters, and has also been demonstrated in harbour seals (*Phoca vitulina*) (Schulte-Pelkum *et al.* 2007). It may often be the case that prey cannot take action in response to detecting a nearby predator to avoid wake following, since wake following predators will generally attack from behind and detection may thus be difficult, and even if detection occurs, a fish that has stopped moving at this point will still have a wake leading towards it. However, it may be that there are particular modes of swimming and/or morphological adaptations that make wake following more challenging, if such adaptations lead to a reduction in the age of wakes that can be detected, then this could be seen as a form of crypsis, but currently there is no evidence for counter-adaptations to wake following predators.

6. SUBSTRATE VIBRATIONS

Mechanical vibratory signals of the substrate are used in mate finding and courtship in many insect species. Zuk *et al.* (2001) demonstrated that the cricket *Teleogryllus oceanicus* living on pacific islands has longer pulses to their songs that mainland Australian population, interpreted as a response to lower predation on the islands. Previous work by this group (Zuk *et al.* 1998) had demonstrated that crickets that produced longer pulses were more readily detected and found by parasites. This suggests that the vibratory signals of mainland species might have been selected for increased crypsis, but more work would be required to strengthen this case.

Pit-building antlion (*Euroleon nostras*) larvae have been demonstrated to be able to detect nearby prey before they fall into the pit through detection of vibratory signals carried through the sandy substrate (Devetak *et al.* 2007). This presumably allows the larva to prime itself for potential arrival of prey at the bottom of the pit, and thus improve prey capture rates (although I have not seen any evidence of such an advantage). There is unlikely to be strong selection pressure on prey to reduce the extent of such signals; if they detect nearby pits it is much more important that they avoid falling into the pit, than that they minimize the effectiveness of these vibratory signals. Such sand-borne vibrations are also important in prey location by some nocturnal scorpions (*Paruroctonus mesaenis*; Brownell & Farley 1979). Again it may be difficult for the prey to counteract this, as they will often be unable to detect ambushing scorpions sitting stationary in the environment, and will be obliged to travel across the sand in pursuit of their own prey.

7. HEAT

Richardson & Borden (1972) suggested that the braconis parasitoid *Coeloides vancouverensis* found the location of its host, the bark beetle *Dendroctonus pseudotsugata*, through the intervening bark by detecting the heat generated by host individuals. Their evidence has since been disputed (Mills *et al.* 1991), and I am not aware of any further instances of host or prey location by local temperature. If this were a common phenomenon, then some crypsis would be achieved by inhabiting already warm microhabitats. For example, a bark beetle might gain protection by being preferentially located to parts of trees which are reliably exposed to the warming effects of direct sunlight.

8. CONCLUSION

Although other sensory modalities have not received the same attention as vision, there seems to be good evidence that crypsis can meaningfully be applied in non-visual contexts. There are important challenges ahead to understand better the mechanisms by which such crypsis is achieved, to evaluate the ecological and physiological costs of such cryptic adaptations and how cryptic adaptations in different sensory modalities (including vision) combine.

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