What is known and what is not yet known about deflection of the point of a predator's attack

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Abstract

Deflection occurs in predator-prey interactions where prey possess traits that influence the position of the predator's initial contact with the prey's body in a way that enhances the prey's probability of survival when attacked. As an anti-predatory defence occurring late in the sequence of an attack, deflection is an understudied but fascinating strategy involving a range of unusual adaptations in diverse prey species. Deflective traits have been postulated to be important to the defensive strategies of a range of organisms, but while evidence for its existence is quite variable among groups, we argue that previous research neglects some promising taxa. As a defence, deflection will probably play a crucial role in the behavioural ecology and evolution of both prey species and their predators; as such it warrants greater interest from zoologists. Here, we first summarise what is known about deflection from the current literature. We next offer predictions about the co-evolutionary possibilities surrounding deflection, based on the benefits and costs experienced by prey and their predators. Finally, we outline the most interesting outstanding avenues for future research in the field of deflection and make novel suggestions as to how they could be usefully explored.

Keywords

Adaptations – Anti-predatory defence – Autotomy – Deflection – Eyespots – Perceptual exploitation – Predator-prey interactions

Introduction

Predation is a fundamental influence on the lives of wild animals as it can affect key factors that contribute to overall fitness such as feeding, breeding, and often direct mortality. Because of this, predation has served as a significant selection pressure on prey species over the course of evolutionary time, and the anti-predatory prey defences that have developed in response to such a pressure are crucial to many aspects of behavioural ecology. Anti-predatory defences can take the form of morphological, physiological, chemical and behavioural adaptations and, in part due to this variety and complexity, have been intensively studied. The predation process can often usefully be broken down into a sequence of stages, beginning with a prey individual and a predator individual being in proximity, and leading through detection, identification, reducing separation, contacting, subduing and finally consuming (Endler 1991; Caro 2005). Many studies focus on anti-predatory defences deployed early on in this predation sequence, such that they help the prey to avoid detection by the predator; this includes defence strategies such as camouflage. However, very late-acting anti-predatory defences are much more neglected. The predator that manages to make physical contact with its prey need not inevitably achieve successful predation – many prey possess traits that make subduing and/or consumption difficult for their predator. One key factor affecting predator success in these late stages of an attack is where on the prey's body contact is made. Fascinatingly, some prey species have evolved traits that influence the position of the initial contact of a predator with the prey's body in a way that enhances the likelihood of prey surviving an attack; these traits are known as 'deflective traits'.

As an anti-predatory strategy, deflection may involve biasing the point of attack to parts of the prey's body that are difficult to grasp or parts that can be broken off without causing catastrophic damage to the prey. For chemically-defended prey it may involve biasing the point of attack to allow the predator to accurately evaluate these defences without damaging the prey. With or without chemical defence, deflection can involve the employment of specialised behaviours, morphological structures, pigmentation and other appearance traits, or combinations thereof. Within the overall umbrella of deflection, distractive markings that draw a predator's attention away from distinctive features and divertive markings that manipulate where a predator directs its attack are both suggested to effectively bias predator attacks towards body regions that facilitate prey escape or reduce prey mortality (Kjernsmo & Merilaita 2013; Stevens et al. 2013; Kjernsmo et al. 2016; Merilaita et al. 2017).

Deflection has been postulated to occur in a sparse and eclectic range of organisms, and the evidence for its existence is quite variable among taxa. The benefit of the deflection strategy to all types of prey is normally considered to be an increased likelihood of escaping the attack, and so this main benefit to the prey comes at a cost to the predator. However, for chemically-defended prey, both predator and prey may benefit if the predator's point of contact is biased to positions on the prey's body that allow the predator to accurately assess these defences, and subsequently abandon the dangerous attack, without incurring significant damage to the prey.

Importantly, there are two conceptually-different mechanisms by which a predator's point of attack might be influenced by prey appearance: perceptual exploitation and mimicry. In perceptual exploitation, a predator's point of attack can be drawn to particular body areas due to them stimulating its senses more than other areas, through being the most conspicuous or salient parts. In contrast, the mechanism of mimicry fools the cognitive systems of the predator, drawing its attack to, for example, a false head structure, due to the predator misidentifying a different part of the body as the part it intended to attack. However, in situations where deflection by mimicry is occurring, deflection through perceptual exploitation was a likely precursor to those predator-prey interactions. Indeed, we feel that perceptual exploitation as a mechanism makes fewer assumptions about the cognitive complexity in the decision-making processes of the predator and find it the more parsimonious explanation of observed deflection than specific mimicry, which requires us to assume misidentification on behalf of the predator. Of course, perceptual exploitation and mimicry need not be viewed as dichotomous, but are best seen as descriptions of ends of a continuum of a cognitive underpinning of behaviour; Schaefer & Ruxton (2010) discuss these concepts in greater detail.

Whichever cognitive mechanisms are involved in its success, it is clear how deflection may offer great benefits to a prey individual during potentially fatal encounters with predators. In this review, we first hope to summarise the most interesting findings about deflection that are safe to conclude from the current literature; we divide this summary into two main sections, looking first at which taxa utilise deflection as an anti-predatory strategy and by what mechanisms, and then turning to explore the related costs, benefits, and trade-offs experienced by prey. After this, we make some predictions about the co-evolutionary possibilities surrounding the development of the deflection strategy based on the benefits and costs experienced by both prey and their predators. We then outline what we believe should be explored next in the field of deflection, for example studies concerning more promising taxa and deflection in chemically-defended prey, and how scientists may go about researching these new avenues through the use of new technologies and comparisons across ontogeny, populations, and species.

Which taxa deflect their predators' attacks and by what mechanisms do they achieve deflection?

Deflection has been reported to occur in a range of taxa but, most famously, there is abundant evidence from laboratory and field studies that behavioural and appearance traits in lizards with tails that can be broken off (autotomy) have been selected to bias predator strikes towards this tail (see Bateman & Fleming (2009) for an insightful review of lizard caudal autotomy). While in some species, such as butterflies (as will be discussed later), deflection is debated, lizard tails that can be non-fatally detached are an unambiguous case of deflection. Such tails are often conspicuously-coloured relative to the rest of the lizard's body and typical substrates, and the effect of such distinctively coloured tails is often enhanced by dramatic tail-waving behaviours that draw further attention to them. Cooper, Caffrey & Vitt (1985) and Cooper & Vitt (1991) demonstrated clearly, in experiments with predatory snakes, that the appearance of tails can have a deflective effect; increasing the chance of the predator grasping the lizard by the tail and increasing the probability of the lizard's escape from the predator's grasp following autotomy. In the case of these autotomic lizard tails, the predator retains the nutritionally-valuable tail and so its motivation to pursue the rest of the lizard may be reduced, enabling the prey to escape alive and relatively unharmed. As a useful escape strategy, lizards can drop their tails when the risk of predation is much higher than the cost of fleeing and so allow predators to come closer when tails are intact (Downes & Shine 2001; Domínguez-López et al. 2015).

Alongside some lizards, the strategy of deflection has also been suggested to occur in many invertebrates (in which autotomy is common) and in the morphology of some butterflies, fish, tadpoles, and even weasels. The potential deflecting effect of eyespots in butterflies and moths is perhaps the most intensively studied example. Some forms of eyespot patterning on adult lepidopteran wings seem to have the potential to influence the point of attack by birds (Stevens 2005; Vallin et al. 2011; Kodandaramaiah et al. 2013; Pinheiro et al. 2014). Often eyespots are present on the periphery of butterfly wings rather than close to the body and it is suggested that deflecting a predator's point of attack to the margins of wings in this way could benefit a butterfly if the edges of its wings could be broken off in an attack without causing it catastrophic damage (Hill & Vaca 2004; Olofsson et al. 2010, 2013). Ambient light conditions also appear to interact with the natural appearance of butterflies in a way that impacts the effectiveness of deflection. Olofsson et al. (2010) suggest that the increased salience of eyespots relative to the rest of woodland brown butterflies' bodies (*Lapinga achine*) mean that the eyespots are preferentially attacked by blue tits (*Cyanistes caeruleus*) under low light intensities with accentuated UV levels. Attacks not focussed on the head often seem directed at peripheral eyespot markings on butterfly wings, and the deflective effect of eyespots has been suggested to be effective independent of background (Olofsson et al. 2013).

Most field studies on lepidopteran deflection hinge on assumptions about the ease with which wing damage from different sources can be differentiated and that species or morphs with different eyespots are exposed to the same frequency of predatory attacks. These assumptions are not easy to investigate. Laboratory studies have begun to investigate the strength required to damage different areas of some butterfly wings, but while current observations support deflection theory – as there appears to be less prey investment in wing strength at areas with patterns predicted to be the targets of attacks (Hill & Vaca 2004) – further studies should evaluate whether this effect is found consistently across a range of species. A further issue for the case of deflection via eyespots in lepidopterans is that several studies have found no support for the theory that eyespot patterning causes predators to misdirect their attacks (Lyytinen et al. 2003, 2004; Vlieger & Brakefield 2007), and even in some supporting studies the majority of predators are not deceived by eyespots (Olofsson et al. 2013) or require particular lighting conditions to be deceived (Olofsson et al. 2010). Because of such complications, it is difficult to conclude that lepidopteran eyespots have an adaptive deflective defence function against predation.

Perhaps a more convincing case for deflection in adult lepidopterans lies in the occurrence of traits strongly suggestive of the 'false-head' mechanism in many Lycaenid butterflies (see Stevens 2005 and references therein). Deflection through misleading predators as to the position of an animal's head is the most plausible explanation for false-head traits, especially in the case of false antennae. Several studies support the effectiveness of false head features – including behaviours that apparently mimic antennal movement (López-Palafox et al. 2015) – at deflecting attacks and increasing prey escape likelihood (Wourms & Wasserman 1985; Sourakov 2013). A recent study by Bartos & Minias (2016) provides the first experimental evidence of the effectiveness of false heads in moving prey. They examined the reactions of the jumping spider *Yllenus arenarius* (Araneae, Salticidae) to various virtual prey varying in: the number of head-indicating details, the position of these details in relation to the direction of motion, the local motion of legs, and the presence of horizontal motion. The findings suggest that the spiders used both the direction of the prey's motion and the complexity of head-indicating details when making decisions regarding the direction of their predatory strikes. In stationary prey simple head-indicating patterns efficiently redirected attacks and, interestingly, when the pattern and motion cues provided contradictory information about true head position the spiders attacked prey’s trailing end more often the more details were placed there, visually inspecting both body ends of their prey before attacking. Cordero (2001) suggests that false heads may offer anti-predatory defence through fooling predators that attempt surprise attacks by approaching from the rear such that prey can escape before contact. However, this lack of contact defies our definition of deflection, and we are more inclined to trust in Robbins' (1981) hypothesis that butterflies can break free and escape after being grabbed in the false head region, as this is what Sourakov (2013) suggests from his staged attacks by a spider and in observations of damage to the wings of wild-caught individuals. However, despite the potential deflective advantage of false heads, few lepidopteran species exhibit these features.

Fascinatingly, yellow-lipped sea krait (*Laticauda colubrine*) snakes may also use a combined behavioural and morphological variation on the ‘false-head’ deflection strategy. Rasmussen & Elmberg (2009) report that when these sea snakes are foraging they twist their tail so as to apparently mimic their head; the movement and posture of the tail here, alongside the head-reminiscent patterning and colouration lead the authors to hypothesise that this is a “concerted behavioural–morphological adaptation”. We would be interested in any future studies exploring how effective the apparent false-head behaviour in sea snakes is in deflecting the attacks of predators.

Eyespot, or ‘ocelli’, dark spot patterns on the posterior end of many tropical fish have also been proposed to serve a deflective function. However, direct evidence for this is limited, with a couple of supporting studies, relying on artificial eyespot patterning, failing to provide detailed methods or results (McPhail 1977; Dale & Pappantoniou 1986). Considering what little empirical field work exists, Winemiller's (1990) two-species comparison of sympatric cichlids varying in patterning and apparent fin damage does not actually shed light on the potential deflective function of eyespots due to the considerable differences in these species’ behaviour and ecology, and Gagliano's (2008) study found no differential survivorship on the basis of natural variation in size of the eyespot on juveniles of the coral reef fish *Pomacentrus amboinsis*. As in butterflies, deflection is less clearly utilised as an anti-predatory defence; potential issues for evidencing deflection in these taxa are discussed further in our section concerning outstanding questions. More recently, however, Kjernsmo & Merilaita (2013) found that with artificial prey and predator-naive three-spined sticklebacks (*Gasterosteus aculeatus*), prey eyespots smaller than the predator fish’s own eye very effectively deflected the attacks of sticklebacks. These same authors have since found that mimicry of predators’ eyes through eyespot patterning can be key in evoking hesitation in attacks, as well as deflecting them, because predators associate those eyelike displays with their own enemies (Kjernsmo & Merilaita 2017). Marks of different shapes – including eyespots and eye stripes – seem to differ in their effectiveness at deflecting predators (Kjernsmo et al. 2016), and undoubtedly we will learn more about the anti-predatory influence of fish patterning in future studies.

Perhaps more convincingly, for now, tadpoles often have patterning on their tail that has long been suggested to have a deflective function. Touchon & Warkentin (2008) reared tadpoles of the neotropical treefrog *Dendropsophus ebraccatus* subject to cues from either predatory fish, from predatory dragonfly nymphs, or under control conditions. They found that tadpoles reared with dragonfly nymph cues developed larger and redder tails than controls, while those reared with fish cues had shallower achromatic tails compared to controls. These cue-dependent developmental differences are probably adaptive because while fish are long-range cruising predators, against which crypsis is the best defence, dragonfly larvae are ambush predators, for which deflection may be more effective. Deflection is probably a more effective defence against dragonfly larvae because (unlike fish) the dragonfly has little ability to pursue the tadpole through open water after a failed attack. When exposing tadpole models to a live predatory dragonfly larvae, Van Buskirk et al. (2004) found that models with bold and dark colouration on the tail were struck significantly more often on the tail than on the head or body than models with less patterning on the tail. Previously, Van Buskirk et al. (2003) demonstrated that live *Rana temporaria* tadpoles were around three times more likely to survive attacks to the tail by dragonfly larvae compared to attacks directed to the body. When viewed collectively, these studies considerably strengthen the evidence for deflection of predatory attacks by tadpole tail traits.

Considering mammals, little work has investigated the possibility of deflection as an anti-predatory defence, perhaps due to the relative lack of distinct, conspicuous regions of patterning in this taxa. However, one intriguing suggestion concerns the black tips of some weasels' tails. Powell (1982) hypothesised that the black tip on the tail of a stoat (*Mustela erminea*) acted to draw attacks from potential avian predators towards the tail, which is a smaller target than the stoat's body and more easily missed by the predator. He further hypothesised that least weasels (*Mustela nivalis*), being smaller than stoats and having shorter tails, do not have a black tip to their tail because this would be too close to the body to provide any deflective advantage. These hypotheses were tested using captive hawks attacking target models of similar sizes to stoats and least weasels with either: entirely white colouration, white with a black tip to the tail, or white with a black band pattern on the body. Of the larger, more stoat-like, long-tailed targets, hawks were much more likely to miss the model with the black tail tip than the ones with no black tip or a black band on the body. Conversely, for the smaller, more weasel-like, short-tailed models, hawks were much more likely to miss the entirely white model than either of the other two. This is an interesting potential case of deflection in the mammals and, while very different from the false head and false eye structures suggested in many insects and fish, Powell proposes that the contrasting colour of tail tips may be enough of a mimic to achieve the same results as an accurate false eye.

Despite the eclectic group of taxa deflection has been proposed to occur in, it certainly appears to be much less commonly observed than other anti-predatory traits such as crypsis or mimicry, although no data explicitly confirm this yet. We suspect that this apparent paucity of natural deflection examples is not due to neglect or oversight by researchers but, instead, a genuine reflection of its rarity. As a defensive strategy, deflection will most obviously be successful in mobile prey that have the ability to escape their predator (or prey that can otherwise mount an effective defence, or is taste-rejected by predators), even after contact between the two has been initiated, and that feature at least some body parts that are highly resistant to – or tolerant of – damage inflected by contact with a predator. We suspect that taxa that meet both these requirements will be relatively uncommon. Future observations of deflection in new taxa may strengthen this prediction and, equally, this prediction may explain why deflection is proving difficult to unambiguously identify in butterflies and fish; this is discussed in more detail later.

What are the costs, benefits, and trade-offs of deflection to prey?

Considering first the deflective use of autotomic tails in lizards, despite the obvious defensive benefit, the resulting escape unavoidably comes at a cost. In many lizards, the tail acts as a fat store and so the loss of this fat store may make an individual more at risk from starvation (McConnachie & Whiting 2003; Gillis & Higham 2016). However, the distribution of energy reserves in species showing autotomy may mean that caudal fat storage does not always come into conflict with tail loss (Chapple & Swain 2002). A lizard’s tail also has other functions, such as balance (Ballinger 1973; Gillis et al. 2009; Libby et al. 2012; Gillis & Higham 2016) and thermoregulation (Martin & Salvador 1993), and so tail loss comes with a number of costs alongside loss of fat store and a predator avoidance mechanism. Fundamentally, caudal autotomy may alter an animal's morphology such that its mass and mass distribution are affected, influencing locomotor activities often critical for survival and reproduction (see Bateman & Fleming (2009) and Gillis & Higham 2016 and references therein). However, costs to autotomy vary with species and context and some lizards do not appear to experience certain costs (e.g. some species do not appear to experience a trade-off between tail autotomy and thermoregulation; e.g. Herczeg et al. 2004; Bateman & Fleming 2009; Zamora-Camacho et al. 2015). Several studies appear to show that energetic and locomotor costs of autotomy are not necessarily high in several reptile species (Guohua et al. 2012), but some suggest that more proximal autotomy occurring in the wild is likely to have greater associated costs (Lin et al. 2006; Sun et al. 2009).

Forfeiture of the tail can also negatively affect future foraging, as autotomized salamanders have been found to have a significantly greater latency to strike at prey and to make fewer predatory strikes than intact salamanders (Gildemeister et al. 2017). The Chinese skink *Eumeces chinensis*, as an example, also seems to experience reduced sprint speed following experimental tail removal (Lin et al. 2006). Interestingly, sprint speed may be affected by tail autotomy differentially between the sexes of some species, as Anderson et al. (2012) found that tailless males in the lizard *Uta stansburiana* appear to maintain high speeds compared to females. Anderson et al. suggest that this is possibly due to males' greater conspicuousness, ascribable to sexual dimorphism and behaviour, as well as their need to retain their territories from rivals.

After autotomy, a lizard must invest in re-growing the tail, and until regrowth is complete this anti-predator technique is unavailable to the individual concerned. Autotomy of the whole tail has been shown in some species to affect microhabitat selection, with tailless lizards favouring more closed habitats where predator avoidance is expected to be more efficient (Bateman & Fleming 2009; García-Muñoz et al. 2011). In salamanders that strategically lose their tails, however, tail loss has recently been found to have little effect on jump characteristics, suggesting that preservation of jumping as an escape tactic following forfeiture of the tail may reduce the cost of losing a predator avoidance mechanism (Hessel et al. 2017). Salamanders and lizards surviving an attack have, though, been found to experience altered exploratory movements, escape distance, and temperature preferences (Bateman & Fleming 2009; Bliss & Cecala 2017). A preference for warmer microenvironments might accelerate tail regeneration (Bliss & Cecala 2017). Although it is well known that lizards can regrow their tails, the structure of the regrown tail is characteristically different from the original and it is possible that this structural change has a long-term effect on the vulnerability of the lizard to predators – or some other cost – even after the tail has regrown (Foster et al. 2015; Gillis & Higham 2016). During tail regeneration, digestive performance can also be affected, as protein income needs to be maximised (Sagonas et al. 2017). However, despite initial costs of reduced survival rate associated with autotomy, tailless lizards' mortality risk does return to baseline following tail regrowth (Lin et al. 2017). Apparent changes in feeding rate and digestive efficiency are again, though, inconsistent costs across autotomotizable reptiles and can depend somewhat on associated behavioural responses (Bateman & Fleming 2009). Experimental removal of tails in the many-lined sun skink (*Mabuya multifasciata*) did not cause greater food intake, apparent digestive coefficient or assimilation efficiency compared to tailed controls in Sun et al.'s (2009) study; however, as touched upon earlier, skinks collected in the field were found to experience tail breaks more frequently in the proximal portion of the tail, suggesting to the authors that caudal autotomy occurring in nature may more often incur substantial energetic and locomotor costs.

Alongside costs relating to tail loss, there is also probably to be a cost in increased conspicuousness to predators associated with bright tail colouration (see Husak et al. (2006) for empirical support). Probably due to this, not all lizard species show autotomy and associated coloration and tail-waving behaviours that probably cause predators to deflect their point of attack towards the tail. Additionally, in those species that do show brightly coloured detachable tails, this colouration is commonly lost over ontogeny (see Bateman & Fleming (2009) and references therein); older, larger individuals probably possess a greater ability to outrun or outfight predators, thus shifting the trade-off in the costs and benefits of alternative strategies away from autotomy. The work of Telemeco, Baird & Shine (2011) supports this idea of a trade-off between strategies, as they found that skink hatchlings with less ability to run fast when exposed to a predatory threat were more likely to use tail-waving behaviours. In a 2017 study, Starostová, Gvoždík & Kratochvíl found that in juvenile males of the Madagascar ground gecko (*Paroedura picta*) tail regeneration had a negligible influence on metabolic rate; this suggests to the authors that fast-growing juveniles with unrestricted food can largely compensate for costs of tail loss and regeneration in their somatic growth, without significant metabolic costs.

Juvenile lizards may also depend more on deflection than adults due to their differing foraging styles; juveniles may be more commonly active foragers while larger adults switch to a more sit-and-wait foraging style, for which cryptic colouration may be more effective than conspicuous deflective colouration. The effectiveness of cryptic colouration is often compromised by movement and as conspicuous colouration is lost over ontogeny, so too are any associated waving or eye-catching behaviours (Hawlena 2009). This again suggests that colouration and behaviour work synergistically in deflective defence, but that the costs of such traits begin to outweigh the benefits as individuals develop. There are also probably costs associated with autotomy that are paid even when the ability is not used, such that the physiological and behavioural traits are selected against where predation is reduced (Cooper & Peréz-Mellado 2004). However, this suggestion warrants further investigation with useful quantification of predation pressures and, indeed, other factors such as intraspecific competition (Itescu et al. 2017) and predator diversity may impose differing selection on autotomy.

An obvious potential drawback to brightly-coloured deflective signals is increased detection by predators. However, Cooper & Vitt's (1991) model exploring this possibility suggested that, actually, even if deflective markings cause an increase in the rate at which their bearer is attacked, this does not necessarily mean that such markings will not be selected for overall. Deflective signals can still be selected for, providing their enhancement of probability of escape from an attack is sufficient to compensate for the potential cost of increased detection.

Beyond lizards alone, in all taxa that utilise deflection as an anti-predatory defence, one would expect that related morphologies carry associated costs. However, currently we know of no empirical demonstration of this. Further, this does not always seem to be the case: as in Vallin et al.'s study (2011) involving blue tits attacking artificial prey, birds took longer to attack prey when the background closely matched the colour of the prey than when a contrasting background was used, regardless of the presence or size of eyespots; here, deflective traits appear not to impose a cost on prey that are also selected to be cryptic for defence. In some species there may also be significant production costs associated with deflective traits. Although Gagliano (2008) found no evidence for an anti-predatory function of eyespots in *Pomacentrus ambionensis* fish, she found that laboratory-reared individuals developed smaller eyespots compared to their wild counterparts. From this, she speculated that the difference was not due to dietary differences but, instead, that there was a cost to eyespot production that juveniles should be selected to avoid in the absence of potential agonists through reduced investment in eyespot production. In this vein, Touchon & Warkentin (2008) found that tadpoles exposed to cues from dragonfly larvae predators developed larger, more colourful tails, but that these changes came at a cost of reduced body size.

An interesting avenue of study that may uncover more about the costs and benefits of deflection in different situations would be how ecology may affect the effectiveness of deflective traits; few studies have explored this to our knowledge. Since deflection relies on the predator's visual representation of the prey, Olofsson et al. (2010) usefully explored the effect of ambient light levels on deflection induced by butterfly wing patterning. They found that the deflective function of eyespots was highly dependent on the light environment, functioning most effectively under low light intensities with UV wavelengths. The benefit deflection offers to prey individuals and the costs of conspicuous patterning could therefore depend on the time of day; the deflective traits are likely adaptive to the time of day butterflies experience greater predation. Additionally, it has recently been reported that the shades of blue colour in the tails of juvenile *Plestiodon latiscutatus* lizards vary across island populations with different predator assemblages (Kuriyama et al. 2016). Kuriyama et al. (2016) found that tail colouration varied with the colour vision of specific predators. Vivid blue reflectance occurred in communities with either weasel or snake predators (both groups of which can detect blue wavelengths), while UV reflectance was much higher in populations with only snake predators (snakes can detect UV, but weasels cannot). Cryptic brown lizard tails occurred independently on islands where birds were the primary predators, probably because birds have keen visual acuity and so a cryptic phenotype may be more advantageous. This adaptation of different levels of tail conspicuousness indicates a deflective function of the tails against specific predators. Greater costs would be experienced when facing the 'wrong' predators, but the benefits of deflection against the 'correct' predators make the specialisation worthwhile in environments where the 'correct' predators are the primary ones. No doubt ecology will influence the costs and benefits of deflective traits in other ways, which should be explored in further research, but in turn deflective traits have probably influenced the development and evolution of predator traits and behaviours too, and we now turn to consider possible co-evolutionary influences of deflection as an anti-predatory strategy.

Co-evolutionary predictions

Given that deflective traits induce predators to attack specific parts of a prey individual's body in a way that reduces the probability of successful capture, it seems important to consider why predators 'allow' themselves to be deflected when it costs them prey items. Firstly, it is important to consider whether deflection is always truly costly to the predator. In the case of chemically-defended prey, touched upon earlier, it may be that deflection to areas of prey body that enhance the ease of taste rejection will benefit the predator as well as the prey. This is a speculative idea without solid empirical underpinning, though, and in most cases deflection should be costly to predators and therefore selected against. However, predators of reptiles with autotomizable tails do not necessarily experience strong selection against being deflected as they do end up with a substantial and often very nutritional meal from the tail, particularly as tails are often used as fat stores. To us, it seems possible that where deflection is linked with autotomy, prey may experience selection to make the 'consolation prize' of the autotomized body part sufficiently valuable to prevent predators being selected to stop responding to deflective traits. From this 'consolation-prize' hypothesis, we might speculate that sometimes autotomy would occur nearer to the prey's body than the predator's point of contact with the tail in order to offer a higher reward to predators for allowing prey escape; this is yet to be empirically explored.

Where prey are not chemically-defended or able to autotomize body parts, we expect that deflection is costly to predators and should be subject to counter-selection to ignore the deflective traits. The continued application of deflection as an anti-predatory defence in wild situations suggests that the deflected predator has not experienced this strong counter-selection; from this, we predict that deflection occurs because of a lack of co-evolution with the prey type. Therefore, specialist predators should be less easily fooled by deflective markings, whereas generalist predators will experience costs of "falling for the trick" of deflection as a by-product of having evolved to be able to handle diverse prey types. Given sufficient practice, predators may be able to learn to ignore deflective traits, and thus deflective traits may be less common in species that have life-history traits that would allow predators repeated experience of being deflected within a concentrated time interval, such as aggregating in groups. This suggestion is based on the assumption that predators habituate, such that with increased exposure to deflective markings their probability of being fooled declines. This habituation has been demonstrated repeatedly for startle signals (Vaughan 1983;

Schlenoff 1985; Bates & Fenton 1990; Ingalls 1993; Dookie et al. 2017), where an undefended prey individual stimulates the sensory system of its predator such that the predator breaks off or delays its attack in some way, but has not yet been explored for deflective signals. However, we can imagine how false heads have the potential to offer continued benefits against even specialist predators. If the prey is fleet and the predator must strike at any discovered individual quickly, then the time may not be available for even experienced specialist predators to reliably differentiate between the real and false heads.

The evolutionary or behavioural restriction of some predators' ability to counteract deflective traits may have an important impact on aspects of both deflective traits and the life-history of prey. For example, a generalist predator may find deflective marking difficult to combat in one infrequently-encountered species if similar visual cues are useful when attacking a different frequently-encountered species. This argument may provide a theoretical framework for exploring why some styles of signal will be more effective at deflecting than others. It also raises the testable hypothesis that prey that use deflective signals will generally not be the main prey of predatory species that they successfully deflect, and that the success of deflection will be affected by predator exposure to other prey types. We consider deflection to involve some sensory and/or cognitive traits in the predator that are retained despite the costs to the predator associated with deflection. These sensory and/or cognitive traits may be retained either because they exploit some constraint of the sensory system, or because there is counter-selection because changes that reduce the risk of deflection in this context have a greater cost to the predator than the benefit of reduced deflection. These costs might manifest themselves as a reduced ability to capture other prey, or detect other valuable resources, or detect its own predators. Again, empirical investigation is needed to explore the fundamental idea that deflection only occurs because a similar response to similar cues benefits the predator in another context. Identifying all the potentially relevant contexts for any given predator would certainly be challenging, but this idea is so fundamental to the concept of deflection, that we feel deeper exploration is warranted. Much of this argument is analogous to the importance of frequency-dependence inherent in the success of Batesian mimicry, and consideration of the extensive empirical literature on that subject (Brower 1960; Huheey 1980; Nonacs 1985; Lindström et al. 1997, 2004; Pfennig et al. 2001; Edmunds & Reader 2014) may provide a useful guide when designing studies on deflection.

Other outstanding questions

One key suggestion we have for the study of deflection is that research should re-focus on more promising taxa. Deflection is probably rarer than other anti-predatory defences, occurring – by our definition – only in taxa that are mobile enough to escape their predator even after contact between the two has been initiated, and feature at least some body parts that are highly resistant to, or tolerant of, damage inflicted by contact with a predator. The clearest evidence we currently have regarding deflection comes from the colouration and behaviour of the tails of lizards that can show autotomy. Autotomy occurs across a wide spectrum of animals: reptiles, salamanders, both terrestrial and sea slugs, octopuses, crabs, brittle stars, lobsters and spiders (see Fleming, Muller & Bateman (2007) for distribution among invertebrates). In animals with the ability to break off body parts, there would be a strong benefit to deflecting attacks towards these regions, hence we would not be surprised to find that there are further examples of deflective traits associated with autotomy. However, much historical interest in deflection has focussed on butterflies and fish and, given that evidence for its importance in these taxa has not strengthened in recent years (see immediately below for further discussion on this), we feel it may be time for research to shift away to more promising groups.

One reason deflection may be less clear in butterfly and fish species is that momentary release by a predator often cannot be converted into a longer-term escape, as their predators are typically birds or other fish that are characteristically mobile themselves. Exceptions to this may be where freshwater or coral reef fish have access to nearby refuges, or in complex vegetation where butterflies may be able to escape by dropping to the ground if the vegetative structure makes it inefficient for a bird to attempt to search for it. Further to the difficulties of proving deflection in these taxa, though, are phylogenetic studies which fail to support a defensive function to eyespots in Lepidoptera (Kodandaramaiah 2009; Shirai et al. 2012) or butterflyfish (Kelley et al. 2013); eyespots have evolved independently multiple times and their number has both increased and decreased in lineages over time. However, Olofsson et al. (2010) suggest that previous studies may have found little evidence for a deflective function in butterfly eyespots because the deflective ability is highly dependent on the ambient light environment. Further research using light more carefully calibrated to match naturally-occurring light spectra could be valuable for the case of deflection in butterflies, as would studies resolving previous assumptions. If it can be demonstrated, for example, that evidence of failed predatory attack can be reliably obtained from inspection of captured butterflies, then a capture-mark-recapture experiment may be of value where the size and or number of contrasting spots on the periphery of wings of a species are manipulated. Such manipulation would resolve concerns about confounding effects of varying exposure to predation, provided it could be convincingly argued that the nature of the change in appearance caused by different types of markings might influence the point of attacks but would not influence the rates at which attacks occur.

The strongest wild evidence for deflection comes from autotomic lizards' tails, and there are certainly non-trivial ethical and practical challenges in exploring anti-predatory traits manipulatively in vertebrates. We therefore fully recommend exploiting artificial model prey when studying the traits that may cause deflection of predators. Currently, though, understanding of deflection is limited by the fact that empirical research is dominated by laboratory studies; we lack a clear, simple and effective methodology for detecting deflection occurring with wild-living predators. However, new technologies offer the potential to evaluate the importance of deflection in the field. Examples of this involve miniature cameras on-board predators, and robotic prey that are able to mimic not just the pigmentation but the movement of prey and log the part of their body that first experiences contact with predators.

We also think that the use of deflection in chemically-defended prey should be further explored. In caterpillars, for example, markings are often considered to have a startling effect (possibly even involving mimicry of snakes), but Hossie & Sherratt (2012) provide some evidence, from models exposed to free-living birds, that some spot markings may influence the point of birds' attacks on a caterpillar's body. While, on its own, this sort of deflection is unlikely to increase the likelihood of the caterpillar's escape, it may be that this deflection changes the position in which the caterpillar is taken into the mouth of a bird, influencing the ability of the bird to detect chemical defences deployed by the caterpillar and, thus, increasing the chance of prey survival through taste rejection by the predator (an idea first suggested by Blest (1957) in relation to eyespots in Papilionid caterpillars, possibly directing attacks towards their defensive organ - the osmeterium). Alternatively, or additionally, deflection may direct the point of attack to areas of the body that are more resistant to damage incurred prior to taste-rejection or that damage in some areas of the body can be more easily tolerated than in others. Deflection working to enhance taste-rejection in this synergistic way may induce a predator to voluntarily release prey and would mean that the predator has no motivation to repeat any attack. This idea has been the subject of repeated speculation, for example in relation to the brightly-coloured papillae of some sea slugs (Edmunds 1966, 1974), but has not been subject to scientific testing. We think that empirical evaluation of the survival and growth of chemically-defended invertebrates following handling and rejection by predators could be of great value to the study of both deflection and the evolution of chemical defences and associated signalling.

There seems to be evidence that predators can be deflected to areas of the body where physical damage caused by contact by the predator is less costly to the prey. It is theoretically possible that deflection could also benefit the prey if it were directed to parts of the body (e.g. an armoured carapace) where the predator's grasp is less likely to cause any damage at all, but this remains a speculative idea. Similarly, it seems plausible - but has yet to be demonstrated - that predators could be deflected to body parts that are harder to grasp and make subduing the prey less effective even in the absence of autotomy.

For all uses of deflection, the longer-term costs and benefits should be further explored in different taxa, at different stages of ontogeny, and in the context of different environmental cues. As an example, tadpole tails present an attractive group for exploring the costs of deflection. Touchon & Warkentin (2008) found that tadpoles exposed to cues from dragonfly larvae predators develop a larger, more colourful tail, but that these changes came at a cost of reduced body size. Quantifying the costs and benefits more fully could be very useful. It would also be interesting to explore whether this induced defence affects the timing or size at metamorphosis, and how effective the induced change is in affecting survival rate in as close to a natural environment as possible. While tadpoles can survive some attacks by dragonfly larvae especially when grabbed by the tail (Van Buskirk et al. 2003) and tail-damaged larvae can readily be found (Blair & Wassersug 2000), the longer-term fortunes of surviving tadpoles remain ripe for exploration. The ecological influence of predatory threats could also be further explored in tadpoles that experience predation from both relatively immobile dragonfly larvae and relatively mobile fish; we would welcome systematic comparison of variation in tail morphology between populations of tadpoles exposed to different relative threats from these two groups.

More generally, the use of comparisons across populations, species or ontogeny in the presence or prominence of putative deflective markings is, at present, greatly hampered by the potential for these markings to sometimes fulfil other (perhaps simultaneous) functions. In fish, for example, alongside anti-predatory deflection eyespots have been suggested to: mislead predators as to the prey's direction (Meadows 1993), make fish appear more fearsome by apparently displaying an animal with a greater distance between its 'eyes' (Karplus & Algom 2010), encourage potential prey to inspect an individual (Paxton et al. 1994), help with species recognition (Uiblein & Nielsen 2005), or mediate within-species social interactions (Gagliano 2008). Again, tadpoles may be the preferred taxa in which to separate out some potential functions of markings. Identification of specific features of such markings that are effective in deflection of predators, probably through laboratory experiments, would be very beneficial in allowing comparative work to focus particularly on these features. For example, using models of tadpoles it should be possible to identify the specific traits that seem effective against ambushing dragonfly larvae through deflection. From this, it should be possible to test how closely these traits correspond to morphological changes caused by exposure to cues associated with this particular predator in the laboratory in different species. It should also be possible to predict, and then test, the relative effectiveness of different morphs, or different species, of tadpole in terms of these trait values.

Cross-species comparisons could also develop our understanding of deflection in less-studied taxa. Following Powell's (1982) suggestion of weasels' tails serving a deflective defence from avian predators, we would welcome a cross-species comparison among mammals to explore whether there were any morphological or ecological variables that could be related to contrastingly-coloured tail tips. Powell's hypothesis predicts that contrasting tips would be more prevalent in species with longer tails and in those facing greatest predation pressure, and this could be relatively simple to explore. It would also be valuable to expand Olofsson et al.'s (2010) work to explore further how variation in natural lighting conditions affects deflection in taxa other than butterflies, such as mammals. Anecdotally, it appears to us that the contrasting tip to the tail of, for example, the red fox (*Vulpes vulpes*) is much more salient when the animal is viewed under low-light conditions.

Comparisons among species and phylogeny may also expand understanding of the evolution of traits associated with deflection. In lizards with autotomizable tails, for example, the results of Cooper & Vitt's (1991) modelling suggests that tail autotomy – and perhaps associated tail-waving behaviours – probably developed before the conspicuous colouration of these body parts in some species; this could be explored in a comparative survey across the reptiles. In lizards it has also been suggested that 'redirection' may work in combination with deflective autotomy in lizards, such that longitudinal-striped patterns on anterior body parts may redirect attacks towards less vulnerable posterior parts during motion, for example, the autotomous tail (Murali & Kodandaramaiah 2016); further study separating out functions, probably with models, could shed light on the relative role of 'redirection' in body patterns.

Finally, we feel that it is important not to rule out the role of other senses in deflection's anti-predatory function. While this review and the currently available literature almost exclusively deal with situations where it is assumed that the predator's visual sense is the key sensory system involved in determining the point of attack, we can think of no physical reason why deflection must be confined to this modality. A fascinating study on luna moths (*Actias luna*) has recently shown that, in predator-prey interactions with big brown bats (*Eptesicus fuscus*), luna moths generate an acoustic diversion with spinning hindwing tails to deflect echolocating bat attacks away from their body and toward these nonessential tail appendages (Barber et al. 2015). Barber et al. (2015) show that moths with intact hindwing tails experience a survival advantage of ~47% relative to artificially-tailless individuals, demonstrating the effectiveness of this acoustic deflection at enhancing prey survival. We suspect that many more cases of deflection in modalities other than vision await discovery, and we look forward to research exploring instances where the sound, smell, or perhaps even texture of a prey individual advantageously influences the position of the initial contact of a predator with the prey.

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