

# Camouflage in predators

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## ABSTRACT

Camouflage – adaptations that prevent detection and/or recognition – is a key example of evolution by natural selection, making it a primary focus in evolutionary ecology and animal behaviour. Most work has focused on camouflage as an anti-predator adaptation. However, predators also display specific colours, patterns and behaviours that reduce visual detection or recognition to facilitate predation. To date, very little attention has been given to predatory camouflage strategies. Although many of the same principles of camouflage studied in prey translate to predators, differences between the two groups (in motility, relative size, and control over the time and place of predation attempts) may alter selection pressures for certain visual and behavioural traits. This makes many predatory camouflage techniques unique and rarely documented. Recently, new technologies have emerged that provide a greater opportunity to carry out research on natural predator–prey interactions. Here we review work on the camouflage strategies used by pursuit and ambush predators to evade detection and recognition by prey, as well as looking at how work on prey camouflage can be applied to predators in order to understand how and why specific predatory camouflage strategies may have evolved. We highlight that a shift is needed in camouflage research focus, as this field has comparatively neglected camouflage in predators, and offer suggestions for future work that would help to improve our understanding of camouflage.

*Key words:* camouflage, crypsis, predation, behaviour, movement, mimicry, evolution

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## I. INTRODUCTION

Animal camouflage is a morphological adaptation which describes all forms of concealment that hinder detection and recognition (Merilaita & Stevens, 2011). Predation, a biological interaction in which one organism kills another for food, is likely to be one of the strongest selective forces in nature. Camouflage is often considered a critical component of both prey and predator survival strategies (Cott, 1940; Endler, 1981; Stevens & Merilaita, 2009; Ruxton, Sherratt & Speed, 2004).

Although camouflage is used as an umbrella term to describe all strategies that prevent detection and recognition, there are many different ways in which organisms can conceal themselves. The most commonly documented is crypsis: adaptations involving body colouration that delay detection (Endler, 1978; Merilaita & Stevens, 2011; Merilaita, Scott-Samuel & Cuthill, 2017; Ruxton *et al.*, 2004). There are many forms of crypsis, the best known being background-matching whereby an organism matches the colour and pattern of their surroundings (Stuart-Fox, Moussalli & Whiting, 2008; Merilaita & Stevens, 2011; Ruxton & Stevens, 2015; Kang, Kim & Jang, 2016). Others include: disruptive colouration, where an organism displays a highly contrasting colour pattern in order to break up their body outline (Cuthill *et al.*, 2005; Schaefer & Stobbe, 2006; Stevens & Cuthill, 2006); self-shadow concealment (Wilkinson & Sherratt, 2008; Kelley & Merilaita, 2015; Caro, 2016), in which colour patterns (normally a dark upper surface colour and a pale underside) reduce detection by subverting variation in shadowing that is used to separate objects visually from their background (Chapman, Kaufman & Chapman, 1994; Stauffer, Hale & Seltzer, 1999); transparency (Mackie & Mackie, 1967; Johnsen, 2001); silvering/mirrors (Denton, 1970, 1971) and self-decoration (Allgaier, 2007; Yanes *et al.*, 2009).

Despite camouflage research predominantly focusing on the efficacy of crypsis strategies, there are many other forms of camouflage that do not prevent initial detection. They instead interfere with an organism's cognitive processes rather than sensory processes, in order to reduce recognition or capture success. Examples include masquerade, in which the organism resembles another object (Endler, 1981; Allen & Cooper, 1985; Edmunds, 1990; Skelhorn *et al.*, 2010), dazzle camouflage, in which detection occurs but colour patterns or movement confuse the detector as to the animal's speed and direction (Thayer, 1909; Jackson, Ingram & Campbell, 1976; Behrens, 1999; Stevens, Yule & Ruxton, 2008), and mimicry, in which one organism appears similar to another organism in order to deceive an observer (Wickler, 1968; Edmunds, 1974; Smith & Harper, 1995). By adopting a mimetic phenotype an organism will alter the selection pressures on the model they are mimicking. By contrast, masquerading organisms will have no effect on their model (Skelhorn, Rowland & Ruxton, 2009).

As predator-prey relationships are a substantial component of all biological communities, and the adaptations that

arise are key examples of evolution by natural selection (Wallace, 1889; Poulton, 1890; Cott, 1940), camouflage as an anti-predator strategy is heavily documented in the literature. Many predators also display specific colours, patterns and behaviours that appear to reduce visual detection or recognition to improve prey-capture success. Although some predator systems have been analysed, less attention has been given overall to predatory camouflage strategies, likely a result of increased challenges when monitoring predatory behaviour. The territories of large predators span wide geographical areas, making observations of natural predation events difficult, and their large size means handling can impose a risk to the investigator. Most predation events are hard to predict, as some predatory strategies are only expressed at the onset of an attack. It can also be difficult to identify whether a particular trait has evolved to reduce detection by prey or detection by another predator, as non-apex predators will operate under both selection pressures. Despite these challenges, camouflage in predators is important to document. Although many of the same principles studied in prey, such as minimising detection and or recognition, also apply to predators, the purpose of camouflage in predators is to gain close proximity to prey. Pursuit and ambush predation use different strategies to achieve this goal, giving rise to a variety of unique adaptations. Predators are also generally larger than their prey. Although research on the role of size on camouflage is limited, it has been established that larger organisms are more conspicuous in comparison to small organisms (Main, 1987), meaning that predators must evolve ways in which to remain camouflaged despite their size. Finally, as predators are at liberty to choose when and where to attack their prey, they only need to avoid detection during these specific times and locations. By contrast, prey species need to maintain camouflage more consistently as they have a limited ability to predict the presence of a threat. This enables predators to fine-tune their camouflage strategy to specific situations, unlike prey which have to achieve successful camouflage over a range of contexts. These differences between predators and prey may alter the selection pressures for certain visual and behavioural traits, making many predatory camouflage strategies unique.

This review analyses anti-detection and anti-recognition strategies in ambush and pursuit predators, focusing on the differences and similarities between the selection pressures they face, and how these contrast with those experienced by prey. The diversity of camouflage strategies in predators highlights the importance of minimising detection by prey. As some predatory taxa display camouflage strategies not observed in prey, a new focus on predators is warranted to gain a greater understanding of how and why these traits evolve and are selected for in predators.

## II. AMBUSH PREDATORS

There has been extensive research on animal camouflage showing that the efficacy of mechanisms such as

background-matching (Endler, 1981; Cuthill *et al.*, 2005), disruptive colouration, masquerade and self-shadowing (Ruxton *et al.*, 2004), rely largely on the organism (and the background against which it is seen) remaining stationary (Poulton, 1890; Cott, 1940; Heatwole, 1968; Zhang & Richardson, 2007). Lower levels of activity in camouflaged organisms decrease their probability of detection (Endler, 1978; Ioannou & Krause, 2009), with some authors even stating that moving organisms cannot be camouflaged (Regan & Beverley, 1984; Ioannou & Krause, 2009; Lui *et al.*, 2012; Yin *et al.*, 2015; Sokolov *et al.*, 2018).

Ambush predators are organisms that 'sit and wait' until mobile prey are within close proximity before they attack. This predatory strategy minimises movement by the predator, reducing the likelihood of detection by prey, and allows the predator to attack at close range, improving its chance of success (Elliott, McTaggart Cowan & Holling, 1977; Moore & Biewener, 2015). However, this strategy can be disadvantageous as sit-and-wait predators will have lower prey-encounter rates than those that actively seek out prey (MacArthur & Pianka, 1966) and prey are able to scrutinise areas that might contain danger and subsequently change their trajectory if a predator is present. One solution is for predators to use shelter to actively hide from prey. This is observed in trapdoor spiders (family Ctenizidae) (Leroy, 2003) and the zebra mantis shrimp (*Lysiosquillina maculata*) which usually ambush prey at night from burrows (DeVries, Murphy & Patek, 2012). Others have hypothesised that predators such as tigers (*Panthera tigris*) and leopards (*Panthera pardus*) primarily choose areas with high tree densities to provide concealment from prey (Karanth & Sunquist, 2000). However, while this might reduce the risk of detection by approaching prey, physical cover also could reduce the predator's ability to detect and track prey, whilst acting as a barrier that makes the final capture more difficult. Thus, hiding behind physical features is likely only practised by a minority of specialist ambush predators.

It is perhaps because of these challenges that effective camouflage is employed by many ambush predators. Ambush predators are known to use mimetic phenotypes to mislead potential prey (Wickler, 1968; Ruxton *et al.*, 2004) or cryptic phenotypes to reduce initial detection, both of which ensure that prey move to within striking range.

### (1) Aggressive crypsis

As stated in Section I, one of the best-studied forms of camouflage is background-matching. Its success as a mechanism to avoid detection by predators or prey is dependent on the interaction between body colouration, the organism's environment, and the observer's visual system (Merilaita, Tuomi & Jormalainen, 1999; Stevens & Merilaita, 2009). Some examples of background-matching in predators appear to be used solely in order to reduce detection by prey. For example, the levant green lizard (*Lacerta media israelica*) has a bright green colouration that is thought to function as camouflage in green vegetation (Disi *et al.*, 2001). However, when

evading its own predators, the lizard resides in environments that do not provide a background match (such as burrows and deadwood), suggesting that the background-matching phenotype evolved only to improve prey-capture success (Loos *et al.*, 2011).

In non-apex predators, crypsis strategies have two functions: to allow sufficient proximity to the prey to enable a successful attack, and to reduce detection by their own predators. This dual function can be seen in many species of jumping spider (Oxford & Gillespie, 1998; Théry & Casas, 2002), which display clear specialisations in phenotypic appearance according to their preferred environment (Cumming & Wesolowska, 2004). Robledo-Ospina *et al.* (2017) observed and compared cryptic strategies in two genera of jumping spider (*Anasaitis* and *Ilargus*). Although both achieved a close colour match to leaf litter from the perspective of both prey and predators, *Anasaitis* spp. display highly contrasting stripes and a closer colour match to understorey foliage compared to *Ilargus* spp. As understorey foliage represents a highly heterogeneous background that is difficult to colour-match, crypsis *via* disruptive colouration rather than background-matching is likely to benefit species that occupy this habitat. Furthermore, disruptive colouration is less background dependent, allowing predators to use a greater number of hunting locations. This suggests that the crypsis type adopted is likely driven most strongly by the location in which the predator forages. Camouflage *via* either background-matching or a striking disruptive colouration is also known in the wobbegong sharks (family Orectolobidae) (Compagno, Dando & Fowler, 2005; Huvneers, 2007). A disruptive phenotype is achieved by a series of narrow longitudinal flaps of skin along the side of the body that break up the body outline, together with a spotted body pattern (Huvneers, 2007). This cryptic camouflage allows ambush predation of a diverse range of prey (Ceccarelli & Williamson, 2012). Successful disruptive patterning is also known in species of orb-web spiders. Bright yellow banding on the dorsal abdominal surface of the orb-web spider *Argiope keyserlingi* was found to have a cryptic function *via* disruptive colouration (Hoese *et al.*, 2006).

Some predators have a flexible cryptic phenotype in which they can change their appearance in order to achieve a closer colour match to their background. For example, crab spiders (family Thomisidae) are able to change colour to match that of the specific flowers on which they hunt, to reduce detection by their hymenopteran prey and predators (Brechtbuhl, Casas & Bacher, 2010). Théry *et al.* (2005) compared the chromatic contrast of a number of spiders and flowers to the detection thresholds of the spider's prey (hymenoptera) and predators (passerine birds), finding that in both visual systems, the individual spider was able to match the precise colour of the flower.

As well as background-matching *via* colour change, some crab spiders use aggressive crypsis through decorative behaviour. The crab spiders *Stephanopis scabra* and *S. cambridgei* have a high density of setae and tubercles on the body surface that facilitate attachment of pieces of tree bark as decoration

(Gawryszewski, 2014). Individuals with attached bark debris were observed on bark with darker colours and individuals without debris were found on lighter-coloured bark, in both cases improving background-matching camouflage.

Previous studies have shown that the effectiveness of background-matching and disruptive colouration is environment dependent (Price *et al.*, 2019). Thus, these strategies may not be suitable for predators that capture prey in a diverse range of habitat types. Transparency can be a successful form of camouflage that is less environmentally dependent (Johnsen, 2001). This strategy has been documented mainly in prey organisms in pelagic environments, possibly because predators have a greater reliance on tissues such as muscle that are difficult to make transparent (McFall-Ngai & Montgomery, 1990; Herring, Dilly & Cope, 2002). Ingested prey will also increase predator visibility, as has been shown for transparent predatory *Chaoborus* sp. larvae (Giguère & Northcote, 1987). The siphonophores *Agalma okeni* and *Athorybia rosacea* are highly transparent (background-matching), but they also have nematocyst batteries which are not transparent and instead mimic the appearance (aggressive mimicry) of a copepod and a larval fish, respectively. It is hypothesised that potential prey are attracted to these mimetic parts (Purcell, 1980; Mackie, Pugh & Purcell, 1987), allowing successful ambush by the siphonophores.

## (2) Aggressive masquerade

A ‘wolf in sheep’s clothing’ is an idiom used to describe dangerous individuals that appear harmless. This concept – termed ‘masquerade’ – has been applied to predators that mimic an object in their environment to facilitate misidentification by prey (Skelhorn *et al.*, 2010). For example, the predatory orb-web spider *Cyclosa ginnaga* adds a white disc-shaped silk decoration to its web upon which it positions itself to resemble a bird dropping (Skelhorn, 2015). This strategy could have an anti-predatory function for the spider in addition to concealment from its own prey (Liu *et al.*, 2014). Similarly, the South American fish *Monocirrhus polyacanthus* resembles a floating dead leaf as it approaches its prey (Cott, 1940). Although this body morphology, colour pattern and behaviour are likely used to facilitate predation (Catarino & Zuanon, 2010), it is unknown whether it also provides protection from predators.

Masquerade *via* decoration will have associated costs: decoration adds mass and hence may limit locomotory ability, making it most effective in predators that are predominantly stationary. For example, assassin bugs of the genera *Paredocla* and *Acanthaspis* cover their body with exoskeletons of their ant prey, dust, sand and soil particles using a sticky secretion as glue, to produce a protective ‘backpack’. The layer of dust has been shown to act as a chemical masquerade, specifically reducing the probability of detection by their prey, and the ant exoskeletons have been shown to reduce the risk of predation, as well as facilitating prey capture (Brandt & Mahsberg, 2002). This masquerade allows them to remain

undetected until their prey is close enough for a successful attack. They then inject them with saliva which causes instant paralysis. Prey that survive the initial attack will not be able to flee, meaning that if the decoration limits their mobility, it is unlikely to impede prey-capture rate in this predator.

In the examples described above, the success of the masquerading phenotype is dependent on the surrounding environment. Some other ambush predators use a form of masquerade that reduces recognition in a range of environments. Death feigning, well documented as an anti-predator strategy by prey, has also been observed in predators. This behaviour is common amongst cichlid fish species (Conkel, 1993; Tobler, 2005). McKaye (1981) reported that the predatory cichlid *Haplochromis livingstoni* masquerades as a dead fish by lying on its side semi-buried in the sand in order to ambush prey. Another predatory species of cichlid, *Nimbochromis livingstonii*, matches the colour patterns of a fish in the early stages of decay in order to attract small scavenging fishes which attempt to feed on the corpse (McKaye, 1981). Field observations have also reported this behaviour in the comb grouper (*Mycteroperca acutirostris*) (Gibran, 2004).

Many species of frogfish are able to adopt a variety of phenotypes that allow them to masquerade in different environments. The striated frogfish (*Antennarius striatus*) has at least four distinct colour phases that allow it to masquerade as algae or as three different colours of sponge (Pietsch & Grobecker, 1987). They change in colour as they move to different habitats, improving the efficiency of the masquerade.

## (3) Aggressive mimicry

Aggressive mimicry is a strategy in which a predator (the ‘mimic’) simulates the properties of a ‘model’ to dupe potential prey (the ‘receiver’) in order to increase their foraging success (Wickler, 1968; Pasteur, 1982). This deceptive strategy is known in a variety of organisms including plants (Schiestel *et al.*, 2003), invertebrates and vertebrates (Pough, 1988; Sazima, 2002; Randall, 2005) and involves a variety of sensory modalities.

As highlighted above, ambush predators are predicted to have lower prey-encounter rates than active foragers (MacArthur & Pianka, 1966) since they must wait until prey are in close proximity before they can attack. Perhaps because of this, many ambush predators display a behavioural, physical or chemical lure to attract their prey. Many aggressive mimics produce a generalised lure that mimics a broad class of model. However, as there is likely to be strong selection for lure effectiveness, natural selection has given rise to lures that are species specific and exquisitely finely tuned.

### (a) Aggressive mimicry without a lure

Many aggressive mimics have evolved a particular phenotype that allows them to approach or co-exist with their prey (Poulton, 1890). One well-known example is in the blue-striped fangblenny (*Plagiotremus rhinorhynchus*), which visually

mimics juvenile blue-streaked cleaner wrasses (*Labroides dimidiatus*), allowing it to approach and feed off the scales of fishes at cleaning stations (Cheney & Côté, 2005).

Some organisms are able to combine multiple sensory modalities to increase the efficiency of aggressive mimicry. For example, common cuckoos (*Cuculus canorus*) are nest parasites that lay eggs that match the colour and pattern of their host's eggs (Honza *et al.*, 2014; Li *et al.*, 2016) to minimise the likelihood of host detection. After hatching, the nestlings also mimic the begging sounds and behaviour of the host brood (Davies, Kilner & Noble, 1998; Stoddard & Stevens, 2010). Similarly, the nestlings of the Horsfield's bronze cuckoo (*Chalcites basalis*) resemble the host nestlings both acoustically and visually (Langmore *et al.*, 2008, 2011). Another example of aggressive mimicry involving multiple sensory modalities is provided by the zone-tailed hawk (*Buteo albonotatus*), which has a clear resemblance with the turkey vulture (*Cathartes aura*). The prey of the zone-tail hawk are not preyed by turkey vultures, making the vulture a suitable model. Zone-tailed hawks resemble turkey vultures in shape, colour and flight behaviour, unlike other members of their genus. Although the hawk is smaller than the vulture, they both fly at high altitudes which may make it difficult for prey to judge their size accurately. This example of aggressive mimicry has been suggested primarily to assist prey capture rather than provide a protective function (Willis, 1963). Similarly, it has been suggested that the bird-eating bicolored hawk (*Accipiter bicolor pileatus*) is an aggressive mimic of the rufous-thighed kite (*Harpagus diodon*) that preys on insects and lizards (Cabanne & Roesler, 2007), but the evidence for this remains inconclusive (Amadon, 1961).

#### (b) Aggressive mimicry using a generalised lure

One of the best examples of generalised aggressive mimicry is provided by the anglerfish (*Lophius piscatorius*), which is a large deep-water fish that preys on small predatory fish that, in turn, prey on small invertebrates. Anglerfish possess a number of spines that extend in front of the mouth and move to mimic the behaviour of these invertebrate prey while it remains stationary (Wilson, 1937; Pietsch & Grobecker, 1978). The behaviour mimicked is a generic behaviour displayed by multiple invertebrate prey.

Similarly, the Australian crab spider (*Thomisus spectabilis*) has an ultraviolet (UV)-reflecting white carapace that makes it conspicuous when sitting on UV-absorbing white flowers (Heiling, Herberstein & Chittka, 2003). This colour contrast has been shown to be conspicuous to a variety of hymenopteran prey, which appear to be attracted to the UV patterning (Heiling *et al.*, 2003, 2005a, b).

Many species of frogfish also use a generalised lure. Although frogfish species minimise detection through masquerade (see Section II.2), many also use a mimetic lure to entice prey to within striking distance. The shape and size of the lure are species specific. The lure of the hispid frogfish (*Antennarius hispidus*) resembles a tube worm, that of the warty frogfish (*A. maculatus*) resembles a small fish (Pietsch &

Grobecker, 1987), while that of the striated frogfish (*A. striatus*) resembles a bioluminescent worm (Brauer & Hobbs, 2016). The frogfish manipulates the lure in ways that simulate the natural swimming movements of the model. However, despite each species displaying a unique lure, Pietsch & Grobecker (1987) found that the lures each attract a diverse variety of prey.

#### (c) Aggressive mimicry using a specialised lure

Although there are many types of specialised aggressive mimicry, perhaps the best documented is sexual mimicry in which a predator uses a signal that mimics one sex of a specific prey species as a lure to attract (usually male) prey. For example, the firefly *Photuris versicolor* lures male *Photinus* spp. fireflies by mimicking the flashing courtship displays of the female. These flash-reply signals have a species-specific timing in relation to the courted male (Lloyd, 1975, 1984) and observational data have shown that *Photuris versicolor* is able to mimic up to 11 species-specific female 'replies'. The genera *Photuris* and *Photinus* are closely related, which perhaps explains the origin of their mimicry.

Species-specific signalling does not require close phylogenetic relatedness. Marshall & Hill (2009) found that the predatory katydid *Chlorobalius leucoviridis* can attract male cicadas (family Cicadidae) by imitating the species-specific wing-flick replies of sexually receptive female cicadas. This aggressive mimicry is achieved both acoustically with terminal clicks, and visually by using synchronised body jerks. Interestingly, the katydids can mimic a variety of species-specific cicada songs which the predator has not encountered previously. Marshall & Hill (2009) proposed that this ability to mimic a broad range of songs has developed in *C. leucoviridis* by exploiting the general design elements common in the songs of many acoustically signalling insects that use duets in pair formation.

The use of chemical signalling as a lure has also been documented in aggressive mimicry systems. Female bolas spiders (*Mastophora cornigera*) attract male moth prey by mimicking three female moth sex pheromones [(Z)-9-tetradecenyl acetate, (Z)-9-tetradecenal, and (Z)-11-hexadecenal] (Stowe, Tumlinson & Heath, 1987). The spiders prey on male moths of at least 19 species. As a single blend of sex pheromone compounds is unlikely to attract all 19 moth species, Stowe *et al.* (1987) suggested that individual spiders may produce different blends of compounds to attract specific subsets of prey. This would be an interesting avenue of research in terms of the evolution of specialised chemical mimicry.

Specialised nutritional mimicry has also been documented, in which a predator mimics the prey species of the predator they are trying to capture. For example, some snakes remain predominantly motionless in a coiled position while moving their tails in short 'vermiform' movements that resemble prey animals. Glaudas & Alexander (2017) showed that puff adders (*Bitis arietans*) discriminate between prey organisms and use specialised caudal luring behaviour only against specific targets such as bufonid toads that prey on

small moving objects. This clearly demonstrates that the signal can be specialised according to the environmental context in which it is deployed.

### III. PURSUIT PREDATORS

One of the most common strategies of predation is pursuit. Pursuit is any strategy that allows the predator to move closer to its target. A predator may move towards prey rapidly by chasing, or may approach stealthily until they are close enough to strike [stalking (Sunquist & Sunquist, 1989; Caro & FitzGibbon, 1992)]. If the predator can reduce the prey's ability to detect and/or identify it as a threat, this could allow a closer approach before the prey can deploy active counter-measures (such as fleeing).

However, previous studies show that movement tends to break down camouflage (Scott-Samuel *et al.*, 2011) as movement produces a contrasting image against a stationary background (retinal slip) (Julesz, 1971; Regan & Beverley, 1984; Rushton, Bradshaw & Warren, 2007; Yin *et al.*, 2015; Mely *et al.*, 2016) or reduces background-matching when organisms move between environments. As pursuit predators rely on movement, they are likely to be at high risk of detection.

Additionally, the natural environment also contains moving elements. The physical movement of objects in the wind (Ord *et al.*, 2007; Peters, Hemmi & Zeil, 2007; New & Peters, 2010; Ryerson, 2017), underwater currents (Shohet *et al.*, 2006), and dynamic patterns of light (Endler, 1993; Endler & Théry, 1996) will affect a stationary predator's ability to remain undetected. Although pursuit predators may be able to minimise detection by moving slowly towards prey, successful capture may rely on a final high-speed attack. Predators are thus likely to experience a trade-off between the ability to go undetected and movement that allows successful prey capture. It is of interest, therefore, to consider how camouflage can be achieved in moving organisms in dynamic environments (Rushton *et al.*, 2007; Hall *et al.*, 2013).

#### (1) Dynamic crypsis via background-matching

The efficiency of many cryptic strategies relies on minimal movement against an unchanging background. Camouflage through background-matching will clearly be reduced in dynamic individuals, although slow movement may minimise the detectability of actively moving individuals with a background-matching phenotype. Cephalopods have been used as model organisms for analysing dynamic camouflaging as they can assess complex visual scenes and produce a body pattern that matches their surroundings (Zylinski, Osorio & Shohet, 2009). This background-matching is achieved by chromatophores – cytoplasmic sacs of pigments controlled by motor neurons attached to radial muscles (Marshall & Messenger, 1996; Mäthger & Hanlon, 2006;

Barbosa *et al.*, 2012) – and it allows cephalopod predators to achieve successful camouflage in a vast number of different locations (Shohet *et al.*, 2006; Zylinski *et al.*, 2009). For example, the mimetic octopus (*Thaumoctopus mimicus*) adopts a brown background-matching colouration when foraging for prey at low speeds. However, when moving faster, to capture moving prey or to escape their own predators, they adopt a body form that mimics other organisms in their environment, such as swimming flatfish (*Zebrias* spp.), lionfish (*Pterois* spp.) or banded sea snakes (*Laticauda* spp.). This switch in strategy is likely due to the limited success of background-matching when the organism is moving rapidly over a range of environments. An *in situ* behavioural experiment using video and image analysis (Josef *et al.*, 2015) showed that, when moving between a black and grey background, the cuttlefish (*Sepia officinalis*) changed their reflectance gradually in a sigmoidal manner to match the approaching background. To do this, *S. officinalis* must estimate the time it will take to reach a new background and the reflectance of the approaching background, allowing it to maintain background-matching camouflage during active pursuit of prey. The authors also found that the gradual change occurred primarily after the individual had moved onto the new background, meaning that there was a short period where crypsis was compromised. Although this suggests that dynamic camouflage requires time to integrate visual input and respond accordingly, in most natural environments clear transitions between two backgrounds are rare, meaning that a gradual change may not provide a disadvantage to these individuals in the wild.

Although background-matching may be less able to reduce detection in moving individuals, this strategy may still be favoured over other forms of crypsis. Zylinski *et al.* (2009) compared cuttlefish body patterns used during movement or when static against two background types, one of which promoted a low-contrast mottled pattern and the other a high-contrast disruptive pattern. Their results showed that high-contrast body patterns were not used during motion as these increased detection against a background of small, moving particles in coastal waters. Thus, for moving cuttlefish, a background-matching low-contrast pattern was more effective than disruptive crypsis.

#### (2) Dynamic crypsis via disruptive colouration

Crypsis via disruptive patterning is common across a wide range of taxa. This reduces detection by breaking up the body outline (Merilaita, 1998). Allen *et al.* (2011) investigated background-matching patterns in felids and found that the spotted pattern of the cheetah (*Acinonyx jubatus*), serval (*Caracal serval*) and black-footed cat (*Felis nigripes*) contrasts greatly with their open habitat. They suggested that this pattern reduces detection by prey via disruption. Snow leopards (*Panthera unica*) display disruptive colouration with a white coat patterned with irregular dark grey rosettes and spots. The resulting coat, with highly contrasting patches of colour, breaks up

the body outline to achieve camouflage in their mountain environment (McCarthy & Chapron, 2003).

Disruptive colouration provides concealment from prey when predators are stationary, moving slowly (stalking) or moving quickly (chasing). Highly contrasting and disruptive patterns have also been shown to alter an observer's perception of the speed and trajectory of moving objects (Thayer, 1909; Stevens *et al.*, 2008; Scott-Samuel *et al.*, 2011; Hughes, Troscianko & Stevens, 2014; Hall *et al.*, 2016; Hogan, Cuthill & Scott-Samuel, 2017). This has been described as 'motion dazzle' camouflage (Hogan, Cuthill & Scott-Samuel, 2016*a, b*). For example, Scott-Samuel *et al.* (2011) showed that dazzle-patterned objects can be perceived as moving more slowly than plain objects. This has also been tested with predatory mantids, showing that prey with narrow stripes are harder for mantids to detect than those with a background-matching pattern. This is thought to be because a striped pattern blurs into a single colour when prey are in motion, allowing them to blend into the background (Umeton *et al.*, 2019). By contrast, prey with a background-matching phenotype containing dark and light areas become more conspicuous when moving. Such patterns require a faster movement speed before they appear a uniform colour, compared with a narrow-stripe pattern. It is therefore likely that predators with disruptive patterns could achieve benefits both by minimising detection and by disrupting speed perception (Stevens *et al.*, 2008, 2011; Scott-Samuel *et al.*, 2011; Hughes *et al.*, 2014; Hämäläinen *et al.*, 2015; Hughes, Magor-Elliott & Stevens, 2015). By reducing the ability of prey to detect the direction or speed of an attack, disruptive phenotypes will minimise the ability of prey to escape successfully. Supporting evidence for this idea has been provided by Santer, (2013) using locust prey and a series of digital patterns to simulate the approach of a predator from distances ranging from 0.07 to 10 m away. Locusts have a pair of descending contralateral movement detector (DCMD) neurons allowing them to respond rapidly to objects moving towards them. Santer (2013) showed that high-contrast patterns produce a weak DCMD response in the locust, leading to delayed escape behaviour. This suggests that predators with high-contrast colour patterns may be at an advantage as this phenotype will minimise detection by prey. Similar tests carried out on humans tasked with targeting moving digital images (Troscianko *et al.*, 2008) found that organisms with conspicuous patterns (such as stripes and zigzags) were more difficult to capture than uniformly coloured individuals (Stevens *et al.*, 2008; Hughes *et al.*, 2014).

The complexity of motion-dazzle camouflage increases for animals that live in groups. Group membership and group movement is seen widely throughout the animal kingdom (Krause & Ruxton, 2002). Although this behaviour has been documented as an anti-predator strategy (Stevens *et al.*, 2011), some predators also move as a group to hunt and capture prey (Bednarz, 1988; Packer & Ruttan, 1988; Creel & Creel, 1995; Kitchen & Packer, 1999). Although group hunting may increase the size of prey that can be subdued or reduce levels of kleptoparasitism (Carbone, DuToit &

Gordon, 1997), group movement has also been shown to reduce the ability of an observer to track moving individuals: 'the confusion effect' (Krakauer, 1995). The confusion effect coupled with a disruptive phenotype could provide a selective advantage in group-living predators. For example, Hogan *et al.* (2017) found that artificial prey targets with stripes parallel to their direction of movement impeded the tracking of one target among many, and that this effect interacted positively with increases in group size. This process could benefit group-hunting predators, such as the spotted hyena (*Crocuta crocuta*) (Watts & Holekamp, 2007), by reducing the ability of prey to determine predator trajectories successfully, thus increasing the likelihood of interception. Despite this, for predators to capture prey they need to identify, target and pursue a single individual. By contrast, prey only need to detect a generic predator to initiate anti-predator behaviours. Thus, selection pressures for tracking individuals within a group are likely to be stronger in predators than in prey.

### (3) Motion masquerade

The motion of background elements is universal in natural environments, both randomly or in a directed fashion (e.g. moving water, wind motion of leaves or the movement of other organisms). Ease of detection in an environment is affected by the signal-to-noise ratio (SNR). SNR is a balance between useful and irrelevant information where the signal is the target and the noise involves all factors that interfere with the target's detection and identification (Merilaita *et al.*, 2017). As a result, for prey to locate a moving predator they must discriminate between predator movement (dynamic signal) and irrelevant moving objects in the environment (dynamic noise).

Light movement in the environment affects camouflage in terrestrial and aquatic predators. In aquatic ecosystems, light will pass through the surface of the water and refract. This, coupled with moving ripples or waves, leads to rapid changes in the areas that are exposed to light (Lock & Andrews, 1992; Swirski *et al.*, 2009), potentially revealing the location of camouflaged organisms. Light is thus a source of visual noise that can affect detection (Ortolani & Caro, 1996; Ortolani, 1999; Allen *et al.*, 2011; Merilaita *et al.*, 2017). Selection for a phenotype that minimises the effects of light was hypothesised by Merilaita & Stevens *et al.* (2011), who suggested that dwarf whales (*Kogia sima*) and minke whales (*Balaenoptera acutorostrata*) have undulating dorsoventral contrasting-colouration stripes in order to background-match changing light conditions. Similarly, analyses by Ortolani & Caro (1996), Ortolani (1999) and Allen *et al.* (2011) showed that predatory cats living in forested environments are more likely to have complex colour patterns than those in open habitats. These closed environments have more irregular and complex elements, dense vegetation and high levels of light dappling, which produce high-contrast shadows (Endler, 1993). The observed coat patterns consequently mimic the effects of light dappling and shadow

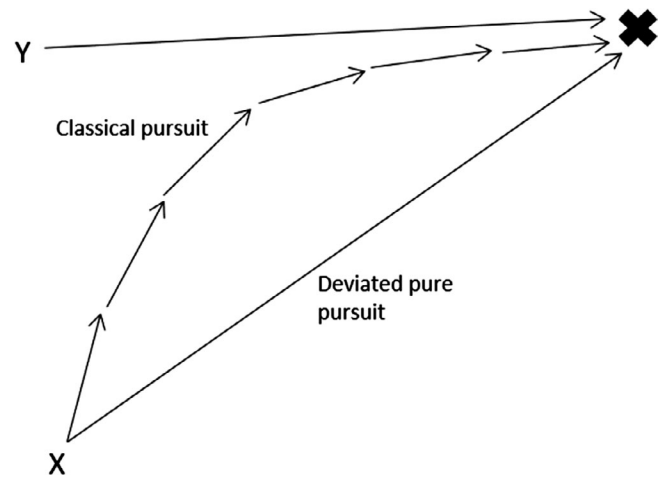
production, potentially reducing detection of moving predators by prey, although this has yet to be demonstrated.

Most documented responses to variation in light to reduce detection are behavioural. One study on the behaviour of the white shark (*Carcharodon carcharias*) found that they position themselves along an east–west axis from morning to afternoon on sunny days to keep the sun behind them while they are hunting, as this will reduce detection by exploiting surface sun glare (Heveneers *et al.*, 2015). This strategy both reduces the amount of direct sunlight in the eyes of the predator and illuminates the prey they are trying to catch. Further studies on this species showed that attack frequencies on Cape fur seals (*Arctocephalus pusillus*) are highest at high lunar and low sunlight illumination (Fallows, Fallows & Hammerschlag, 2016). Both situations will produce a silhouette of their prey at the water surface whilst the sharks remain camouflaged against dark water.

#### (4) Motion camouflage

Intercepting a moving target relies on a predator modifying its trajectory by anticipating the movement of their prey (Anderson & McOwan, 2003a). The optimal path for the predator is thus not always the one that directs the predator to the current location of the prey, but rather towards a potential interception point of their two future trajectories. Some organisms capture prey *via* classical pursuit, in which the predator directly follows the path of the moving prey (Kramer, 2001) (Fig. 1). However, this is only possible if the predator is faster than its prey (Moore & Biewener, 2015). An alternative is to follow a trajectory that can be predicted by the proportional navigation model, the basis of which follows the ‘constant bearing, decreasing range’ (CBDR) or ‘deviated pure pursuit’ concept (Fig. 1). In this strategy, the predator will move in a straight line, maintaining a constant bearing relative to a predicted intercept position with the moving prey while closing the distance between them, eventually to intercept it (Murtaugh & Criel, 1966) (Fig. 1). To use this method successfully, capture requires the pursuing individual to predict the intersection of its own trajectory with that of the target. Robots with biologically plausible inputs have successfully carried out deviated pure pursuit without the entire trajectory being known at the onset (Rañó & Iglesias, 2016) and computation modelling studies have shown that organisms can successfully intercept moving targets *via* CBDR by predicting trajectories (Anderson & McOwan, 2003b). This method of target interception has been demonstrated in dogs (Shaffer *et al.*, 2004), teleost fish (Lanchester & Mark, 1975), bats (Ghose *et al.*, 2006) and humans (Fajen & Warren, 2004).

Predators must also be able to manoeuvre towards a moving target whilst minimising their own probability of detection. Motion camouflage may use the CBDR concept whilst minimising detection by using the perceived motion of elements in the optic field. Mizutani, Chahl & Srinivasan (2003, p. 604) describe motion camouflage as when “one animal (the shadower) moves in such a way as to



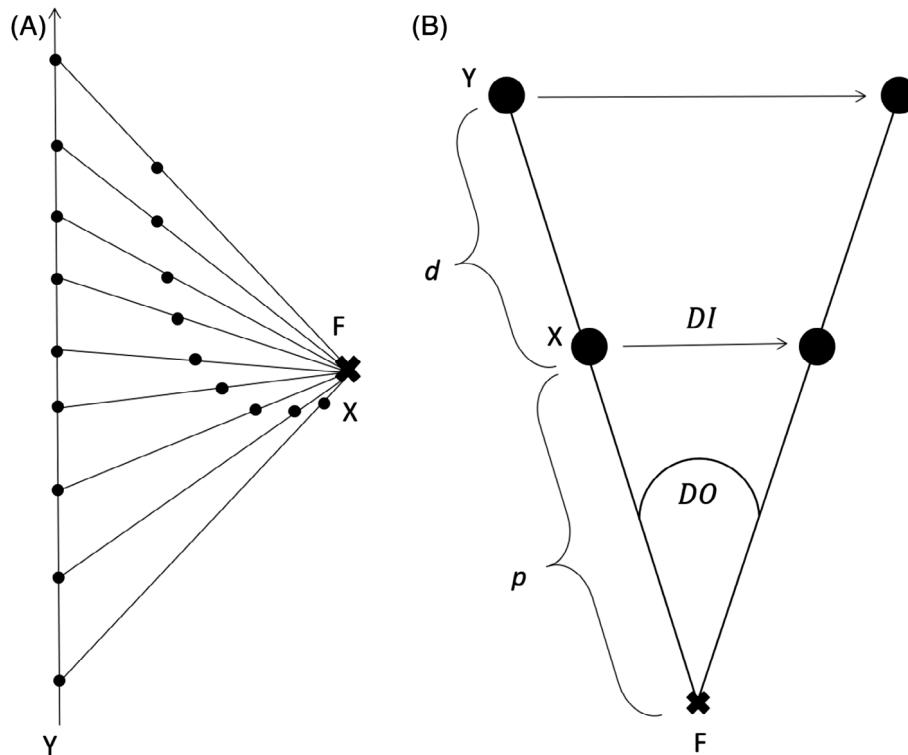
**Fig 1** Illustration of two forms of predator pursuit. X is the starting point of the predator; Y is the starting point of the prey; both are moving to the right of the page. Classical pursuit is where the predator directly follows the position of the moving prey. Deviated pure pursuit is where the predator moves in a direction that maintains a constant angle to the final intercept position of the target. This follows the constant bearing, decreasing range (CBDR) principle and the success of this strategy will be facilitated by motion camouflage (see Fig. 2).

produce the same image motion on the retina of another animal (the shadowee) as would a stationary object in the environment.” This could allow successful concealment against both homogenous and structured backgrounds (Srinivasan & Davey, 1995) and data show that motion camouflage *via* this mechanism can result in a more energy- and time-efficient pursuit path compared to classical pursuit (Glendinning, 2004; Troscianko *et al.*, 2008).

Srinivasan & Davey (1995) have proposed a series of algorithms to describe motion-camouflage trajectories. The predator chooses a particular object or some point to use as a ‘fixed point’ (F; see Fig. 2A). If the predator moves along a line connecting F and the prey (the ‘camouflage constraint line’; see Fig. 2A), this will create the impression that the predator is stationary at F as the prey will perceive no lateral motion (retinal slip) as the predator approaches (Troscianko *et al.*, 2008). For example, if the predator starts its approach towards the prey in front of a rock, by maintaining a position directly between the rock and the current position of the prey, the optic flow of the predator projected onto the retina of the prey would mean the predator would appear to be stationary against the rock (Anderson & McOwan, 2003b). By using this strategy, motion camouflage could conceal the predator’s movement (Srinivasan & Davey, 1995). Although the predator will appear to increase in size, this change in size will be hard to detect, allowing the predator to close its distance to the prey (Anderson & McOwan, 2002).

This method can also allow a predator to appear as a stationary landmark without the presence of an object to use as a fixed point as long as the predator remains on the camouflage constraint line. If the predator can estimate distance  $p$  from any fixed point F and distance  $d$  from the prey (see





**Fig 2** Illustration of motion camouflage. (A) Trajectories of a predator (X) and prey (Y). This motion trajectory gives the impression that predator X is a stationary object at point F, behind the actual position of the predator. (B) In order to appear consistently at the initial position of pursuit (F), the predator must calculate the angle  $DO$  and adjust its lateral movement by distance  $DI$  by estimating its distance from F ( $p$ ) and its distance from the prey ( $d$ ). Figures adapted from Srinivasan & Davey (1995).

Fig. 2B), it can camouflage its motion by (i) always viewing the prey frontally, (ii) pointing radially away from F, and (iii) making appropriate changes in angle  $DO$  and distance  $DI$  (Fig. 2B). To carry out this method of motion camouflage successfully both  $DI$  and  $DO$  must be estimated accurately, requiring the predator to be able to make rapid predictions regarding future prey movements. Two- and three-dimensional computer simulations have shown that artificial predators can approach prey successfully by predicting their future movements using simple input data (Anderson & McOwan, 2003b), thus achieving motion camouflage by appearing to remain stationary. Srinivasan & Davey (1995) tested their model using data collected by Collett & Land (1978) on hoverfly (family Syrphidae) mating flight paths and found that they moved such that the shadower's motion was along the camouflage line, providing evidence that these algorithms are applicable to biological systems.

Motion camouflage behaviour may be particularly applicable to dragonflies as they have a highly sophisticated neural circuit that allows detection of moving objects against a moving background (Mizutani *et al.*, 2003). Recent data show that falcons (*Falco* spp.) also use cues from prey movement to determine flight direction. Video data showed that falcons approach prey at a constant angle, following a flight path that fits the predictions of motion camouflage behaviour (Kane & Zamani, 2014).

The successful use of motion camouflage dictates that a predator is constrained to move along the camouflage

constraint line (Fig. 2). Although this does not mean that the predator will reach the prey in the shortest time, it does allow the predator to approach without detection. However, pursuit that costs the predator more time and/or energy will reduce the net worth of the prey, thus potentially reducing the motivation of the predator to initiate an attack (Krebs, 1980). Furthermore, over evolutionary timescales natural selection may have led prey to adopt unpredictable trajectories to make it more difficult for a predator to move along the camouflage constraint line. Srinivasan & Davey (1995) emphasise that their model is based on many simplifying assumptions that may only apply under certain circumstances due to the complexity of predator–prey interactions (Curio, 1976). Such models may provide insights into other motion camouflage mechanisms, and perhaps facilitate the development of new military or security applications.

#### IV. FACTORS AFFECTING THE EVOLUTION OF CAMOUFLAGE STRATEGIES IN PREDATORS

##### (1) Time of attack

The unpredictability of predatory attacks means that prey should benefit from continual expression of traits that reduce detection by predators. As pursuit predators determine the onset of an attack, unlike in prey, there will be less selection

for a continuously camouflaged phenotype. Thus, behavioural camouflage techniques that minimise movement detection are likely to be selected for in pursuit predators, with strategies which rely on continuous background-matching being less common, since camouflage is not necessary during non-hunting periods. Despite this prediction, cryptic camouflage is observed in pursuit predators, suggesting it does provide a benefit in some species. However, whether this is to facilitate prey capture or an adaptation against their own predators remains unclear.

In aggressive mimicry and cryptic strategies, predators can show finely tuned traits that may maximise their chances of successful ambush, such as species-specific deceptive signals or accurate cryptic or masquerading phenotypes (Nelson, Garnett & Evans, 2010; Bartos, Szczepko & Stanska, 2013). Jackson & Wilcox (1993) showed that web-invading jumping spiders (*Portia* spp.) display an array of different deceptive signals and monitor feedback from their spider prey. Following such feedback, the predator produces only the signal that elicited a positive response. By using this method, the spider can identify species-specific signals with which to fine-tune its aggressive mimicry in order to capture a diverse range of prey. By contrast, prey organisms can only anticipate the risk of predation to a degree, and have limited control over what type of predator attacks them and when. This means that prey need to retain a wide range of defensive traits to protect them from many types of predator, and over a range of different environmental contexts.

## (2) Size

Predators must be large and strong enough to subdue their prey, particularly when the prey are mobile and able to flee. Previous studies have shown that size can affect detectability even when stationary, with larger animals being more easily detected (Mänd, Tammaru & Mappes, 2007; Rimmel & Tammaru, 2009; Karpestam, Merilaita & Forsman, 2014) and hence it may be harder for larger organisms to achieve effective camouflage. For example, Cuadrado, Martin & Lopez (2001) investigated the cryptic success of chameleons (*Chamaeleo chamaeleon*) by investigating detection rate by predators in relation to size and background in photographs and in the field. The probability of detection was size dependent, with detection time significantly shorter for larger chameleons. As well as affecting detection, body size influenced the distance from an approaching predator at which the chameleons initiated escape. Smaller individuals allowed closer approach distances than larger individuals (Cuadrado *et al.*, 2001). Similar size-dependent retreat behaviour has been recorded in other prey species (Heatwole, 1968; Burger & Gochfeld, 1990; Martín & Lopez, 1995).

We can subsequently hypothesise that detection of movement in pursuit predators is likely to be size dependent, with larger predators potentially having to initiate an attack when they are further away. However, the effects of size on

camouflage in predators still await experimental investigation, making it an important avenue for future research.

The success of motion-dazzle camouflage is also likely to be affected by size. Murali & Kodandaramaiah (2016) investigated the effect of stripe patterns and size on attack rates in lizards. They found that the presence of a longitudinal stripe redirected attacks to the lizard's tail by exploiting the motion-dazzle effect. In later work, Murali & Kodandaramaiah (2018) also demonstrated that this benefit was greater for shorter lizards. As a relationship between body size and the effects of patterning has also been found in snakes (Allen *et al.*, 2013), it was hypothesised that smaller prey animals benefit more from the known effects of high-contrast patterns on perceived speed and motion dazzle (Hall *et al.*, 2016; Murali & Kodandaramaiah, 2016). As larger organisms have reduced manoeuvrability (Webb, 1983), it is possible that increasing body size reduces the selective advantage of this type of camouflage; indeed, in the absence of erratic movements, this form of camouflage could make them more conspicuous (Hogan *et al.*, 2016b). Conceivably therefore, predator size also could be a factor influencing the evolution of camouflage strategies in pursuit predators.

Camouflage strategies found in ambush predators are also affected by size. For organisms that use aggressive mimicry or aggressive masquerade, their body size and shape will determine which models they can successfully resemble. For aggressive mimics that use a lure resembling the prey or opposite sex of the prey, the size of the predator will potentially impact the success of the mimetic phenotype. Evidence for this can be seen in organisms that display 'transformation mimicry'; wherein they change to mimic different models during their life, in tandem with changes in body size and shape. For example, the mantis species *Mantoida maya* mimics an ant species when young and small, and a species of wasp when it is older and larger (Jackson & Drummond, 1974).

## (3) Prey

Broom & Ruxton (2005) hypothesised that two optimal prey strategies are likely to occur: prey will either flee immediately when the predator is detected (before the predator has begun an attack) or will only flee in response to a direct attack. Although their model focuses on optimal strategies for prey, it can be used to investigate the circumstances under which certain pursuit predation strategies may be selected. For example, the relative frequency with which these strategies are used depends on a range of different conditions. The strategy of fleeing as soon as a predator becomes visible is associated with slow predator search speed, low energetic cost to running in prey, large advantages to prey if they are the first to move, limited ability by prey to detect the predator at a distance, high ability to detect prey by the predator, and high probability that the predator will be successful if a chase occurs. Under these conditions, therefore, there may be selection for predators to evolve strategies such as motion masquerade or crypsis to minimise the likelihood that prey will flee before the predator has initiated a chase. By contrast,

where prey only flee in response to a direct attack, motion camouflage or motion dazzle may be selected for, as this will reduce the ability of prey to detect the true speed, direction or trajectory of a direct attack. However, such predictions remain speculative. Future research modelling optimal predator strategies is needed to understand how prey drive the evolution of camouflage in pursuit predators.

Prey group size is also likely to affect selection on pursuit predators that rely on delayed detection by prey. As prey group size increases, the probability of predator detection increases (Pulliam, 1973; Elgar & Catterall, 1981) due to the benefits of shared vigilance. As a result, predators that target group-living prey will be under stronger selection to minimise detection before initiating pursuit (Kenward, 1978; Fitzgibbon, 1989). In addition to increased prey vigilance, large group sizes could reduce predator success by a greater confusion effect of more moving targets, thereby reducing a predator's ability to track one individual successfully (Krakauer, 1995). It is likely, therefore, that predators hunting group-living prey will be under strong selection for strategies that aid successful interception and the ability to track specific individuals in a moving group.

Defensive mimicry has been the subject of much research. The two best-known examples are Batesian mimicry, in which palatable mimics resemble unpalatable models (Bates, 1862; Lea & Turner, 1972), and Müllerian mimicry, in which multiple unpalatable species converge on a specific colour pattern to enhance the value of the aposematic signal of unpalatability (Müller, 1879). Both types of mimicry are subject to frequency-dependent selection. As a Batesian mimic becomes more common in the population, the fitness of this phenotype decreases as predators are more likely to correctly identify that they are palatable. For Müllerian mimics, as mimic frequency increases the fitness of the phenotype will increase as their predators will correctly identify particular mimics and learn to avoid them (Cheney & Côté, 2005). Ings & Chittka (2009) found that bumblebees exposed to a random mixture of yellow and white flowers, in which some of the yellow flowers contained 'robotic' crab spiders, learned to avoid the yellow flowers regardless of whether the crab spider was present.

Although learnt avoidance is seen in aggressive mimics, it will not affect them in the same way as defensive mimics. As signal-based aggressive mimics use models that benefit prey organisms, a prey organism that learns to avoid a potential mate or food item will have lower survival or reproduction. Thus, the selection pressures for learnt avoidance are likely to differ in aggressive mimicry systems. This has been observed in the bluestriped fangblenny/juvenile cleaner wrasse aggressive mimicry system (see Sections II.3a). Cleaner fish display mutualistic relationships with many reef fish species, benefiting their clients by removing parasites and dead skin, which they use as a food source. By mimicking them, the fangblenny is able to reach close proximity with the reef fish, but then attacks them by biting off pieces of their flesh (Johnson & Hull, 2006). Côté & Cheney (2007)

experimentally varied the parasite load in staghorn damselfish (*Amblyglyphidodon curacao*) and observed changes in foraging success of an aggressive mimic (the bluestriped fangblenny) of the bluestreak cleaner wrasse. When parasite loads were increased, the attack success of the fangblennies also increased as there was a greater cost to the damselfish from avoiding cleaning stations. Thus, we can hypothesise that there will be selection on prey to detect signals associated with predators, however this will be offset by the potential loss of feeding or breeding opportunities.

The costs associated with learned avoidance are likely to differ depending on whether the predator uses aggressive mimicry, aggressive masquerade or aggressive crypsis. There is likely to be a lower cost associated with avoiding objects or other organisms used in aggressive masquerade/crypsis than with avoiding food or a potential mate to minimise predation risk. As a result, learned avoidance may evolve more easily in response to some types of crypsis in comparison to others.

Attack success in ambush predation depends on a number of variables including habitat structure (Whittingham & Evans, 2004) and prey group size (Fitzgibbon, 1989; Devereux *et al.*, 2006). However, when prey misidentify a mimetic sit-and-wait predator as an unthreatening model – and the predator is then successful – the prey organism does not survive. This potentially means that there will be strong selection for avoidance behaviour in prey over evolutionary timescales. Future research should focus on how the type of aggressive mimicry affects the evolution of avoidance behaviour as well as investigating long-term changes in aggressive mimicry systems.

The selection pressures driving aggressive mimicry, aggressive masquerade or aggressive crypsis are likely to involve context- and prey-dependent trade-offs. For example, lure-based aggressive mimicry reduces predator energy expenditure as it relies on manipulating prey to approach. However, prey scrutiny is likely to be higher, as the signal draws attention to the location of the predator. By contrast, in aggressive masquerade, crypsis or mimicry without a lure, prey are not actively attracted towards the predator, making them less likely to be identified, although the prey-encounter rate will also be lower. As a result, the best strategy for an ambush predator is likely to be affected by prey type. Predators that catch many different types of prey may be more likely to use aggressive masquerade or crypsis, to maximise their ability to be inconspicuous. Specific aggressive mimicry is likely to be more beneficial when a predator is limited to specific prey types.

In lure-based aggressive mimicry, the two most common types of lure are sexual or nutritional. Although there has been limited focus on predators, we can analyse preferences for certain types of lure in other biological systems, such as pollination. Orchids provide an example of deceptive flowers, with around one-third of all species offering no rewards to pollinators (Jersakova, Johnson & Kindlmann, 2006), instead attracting them by using food or sexual deception (Dafni, 1983; Nilsson, 1983; Fritz, 1990; Schiestl, 2005). Nectar production is energetically expensive (Southwick,

1984) so adaptations that allow pollination without having to provide a reward may be under positive selection. The same argument can be applied to predators: any trait that increases predator–prey encounter rate while minimising costs such as energy expenditure could be subject to positive selection, as seen in the evolution of lures.

Different lures may have different associated costs, affecting their evolution. In ambush predator–prey systems, the success of a signal is likely to be prey dependent. Nutritional lures may be selected in predators that prey on organisms that have a low abundance or low diversity of food sources, and hence a higher cost to avoidance behaviour. Reproductive lures may only be effective at certain times of the year where the mimicked species breeds seasonally (Tauber, Tauber & Masaki, 1986). There is also some evidence for learned avoidance towards sexual mimics (DeJager & Ellis, 2014), and that learning capacity is influenced by the ratio of models to mimics (Ferdy *et al.*, 1998). Subsequently, as described above for Batesian mimicry, this system will be frequency dependent.

#### (4) Environment

Phenotypic trade-offs in pursuit predators are likely to affect the selection for certain camouflage strategies. There are documented cases of trade-offs between a camouflaged appearance and a different colour pattern with another primary function (e.g. thermoregulation or sexual signalling) (Stuart-Fox *et al.*, 2008). Although such trade-offs have only been investigated to date in prey (Norris & Milstead, 1967; Hemmi *et al.*, 2006), there is no reason to suggest that pursuit predators would not be subject to similar trade-offs. If a camouflaged phenotype disadvantages a predator in some way (whether thermoregulatory or sexually), selection is likely to lead to strategies that are only expressed under specific circumstances (e.g. motion camouflage, motion masquerade and dynamic crypsis). It could be hypothesised that where predators receive a benefit from conspicuous colours or patterns (e.g. in sexual selection), they may be under strong selection for disruptive phenotypes, to allow distortion of speed and direction estimation by prey while still conferring mating success.

One of the defining features of mimicry is that the mimic affects the selection pressures experienced by the model and *vice versa*. Thus model frequency will affect the evolution of mimetic phenotypes in ambush predators. There is only limited work on how frequency dependence affects the evolution of aggressive mimicry systems (Davies, 2000; Kunze & Gumbert, 2001). One interesting series of investigations involves the bluestriped fangblenny and the juvenile cleaner wrasse (see Sections II.3a and IV.3) (Randall, Allen & Steene, 1997; Côté & Cheney, 2004, 2007; Cheney & Côté, 2005). Cheney & Côté (2005) showed that this mimicry system was affected by the relative frequencies of the mimic, the model and the potential victims. The number of successful attacks was higher when the predatory mimics were relatively rare compared to their mutualistic model, as this

minimised learnt avoidance by reef fish. Mimic success also increased with the population density of other fish on the reef, suggesting that ‘victim’ frequency dependence could affect the evolution of aggressive mimicry. Further investigations into the selective forces underlying aggressive mimicry systems will help us to understand the mechanisms behind their maintenance.

A predator’s position in the food chain may also drive different selection for camouflage strategies. Non-apex predators are themselves subject to predation, leading to selection for anti-predator adaptations. For example, apex predators may be more likely to evolve motion camouflage as they are not under selection for camouflage other than during an attack. By contrast, predators lower in the food chain may be under selection for strategies that reduce detection by their own predators (e.g. crypsis or masquerade). This could include the expression of different behaviours depending on whether they are actively trying to capture prey or to avoid predation. Similarly in many s, an odour is released to mimic a model chemically as well as visually (Haynes *et al.*, 2002). This may have the disadvantage of alerting the mimic’s own predators and may be selected against in non-apex ambush predators.

Although an interesting avenue for future research would be to investigate the relationship between a predator’s position in the food chain and their camouflage strategy, distinguishing whether strategies have evolved in order to minimise predator detection or increase prey capture may be challenging. Recently, new technologies such as drones and biologging have emerged that allow continuous observations of wild predators over large spatial and temporal scales (Wich & Koh, 2018), and effective monitoring in the laboratory using camera equipment and virtual or robotic prey. For example, Ioannou *et al.* (2019) used simulations of virtual prey with real predators in order to assess differential predation risk experienced by individuals within a group depending on their social role. Similarly, Pietsch & Grobecker (1990) analysed the biomechanics of feeding in three species of frogfish (*A. striatus*, *A. hispidus* and *A. maculatus*) by integrating frame-by-frame analysis of high-speed film with anatomical analysis of the bones, muscles and ligaments in the head.

## V. CONCLUSIONS

(1) Although camouflage is predominantly thought of as an anti-predator defence mechanism, many unique strategies are also observed in predators, and those expressed in both groups are likely to be driven by different selective forces.

(2) In ambush predators, three main strategies have evolved that act to minimise the prey’s ability to detect or identify the predator before an attack: aggressive mimicry (which may involve a generalised or specialised lure), aggressive masquerade, and aggressive crypsis. In pursuit predators, four main strategies have evolved that minimise the

prey's ability to detect or identify the predator: motion camouflage, motion masquerade and dynamic crypsis *via* background-matching or disruptive camouflage.

(3) Two evolutionary explanations for camouflage differences between predators and prey are the ability of predators to control when an attack occurs, and size differences between the two groups. There is a case for these being key drivers in the evolution of unique predatory camouflage strategies, however, few studies have addressed this and it remains an avenue for future research.

(4) Based on data in other biological systems, the camouflage strategy a predator adopts is likely to be affected by both their prey and their environment. Future research should shift towards applying empirical and theoretical frameworks to how these driving forces lead to the evolution of different predatory camouflage strategies. In particular, focus should be given to understanding how the position of a predator in the food chain impacts the camouflage strategy they use, as this will provide information not only on why a trait has evolved, but also on whether camouflage is used differently when avoiding or initiating an attack.

(5) The evolutionary forces driving camouflage in predators have received little attention. The development of new technologies is opening up avenues for future research projects on predators, and we hope that this review will stimulate interest in this area.

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