Antipredator defences in motion: animals reduce predation risks by concealing or misleading motion signals

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ABSTRACT

Motion is a crucial part of the natural world, yet our understanding of how animals avoid predation whilst moving remains rather limited. Although several theories have been

proposed for how antipredator defence may be facilitated during motion, there is often a lack of supporting empirical evidence, or conflicting findings. Furthermore, many studies have shown that motion often 'breaks' camouflage, as sudden movement can be detected even before an individual is recognised. Whilst some static camouflage strategies may conceal moving animals to a certain extent, more emphasis should be given to other modes of camouflage and related defences in the context of motion (e.g. flicker fusion camouflage, active motion camouflage, motion dazzle, and protean motion). Furthermore, when motion is involved, defence strategies are not necessarily limited to concealment. An animal can also rely on motion to mislead predators with regards to its trajectory, location, size, colour pattern, or even identity. In this review, we discuss the various underlying antipredator strategies and the mechanisms through which they may be linked to motion, conceptualising existing empirical and theoretical studies from two perspectives – concealing and misleading effects. We also highlight gaps in our understanding of these antipredator strategies, and suggest possible methodologies for experimental designs/test subjects (i.e. prey and/or predators) and future research directions.

Key words: antipredation, behaviour, camouflage, crypsis, motion.

CONTENTS

I. INTRODUCTION

Animals are often faced with the need to move in order to survive, whether for food, travelling to new environments, searching for potential mates, or escaping from potential predators. Motion is prevalent in the natural environment, such as the rustling of leaves in the wind or the flowing of water in a stream. Although motion is such a crucial part of the natural world, there remain significant gaps in our understanding of how animals employ various antipredator defences, including camouflage whilst moving. Camouflage refers to the adaptations of organisms that reduce their probability of detection and/or recognition by others (Stevens & Merilaita, 2011; Skelhorn & Rowe, 2015; Pembury Smith & Ruxton, 2020). Whilst camouflage in stationary animals is a well-studied topic, there remain conflicting ideas as to its efficacy when motion is involved. Many theories and hypotheses facilitating motion and camouflage have been proposed, with multiple studies lending support for camouflage in motion (Poulton, 1890; Thayer, 1909; Cott, 1940; Brattstrom, 1955; Wickler, 1968; Jackson, Ingram III & Campbell, 1976; Pough, 1976; Brodie III, 1992, 2010*a*,*b*; King, 1992; Shine & Madsen, 1994; Lindell & Forsman, 1996; Titcomb, Kikuchi & Pfennig, 2014; Umeton *et al.*, 2019). However, many prior studies only provided

75 correlational associations of an animal's colour patterns to its behaviour (Jackson *et al.*, 1976,
76 Pough, 1976; Brodie III, 1989, 1992; King, 1992; Lindell & Forsman, 1996), with empirical
77 evidence corresponding to outcomes (e.g. detection or recognition by observers) remaining
78 limited to date. The mechanisms involved have also often been unclear. Furthermore, many
79 studies have shown otherwise – that motion 'breaks' camouflage, as abrupt movements can
80 draw attention and be detected easily even before the animal is recognised (Bauwens &
81 Thoen, 1981; Regan & Beverley, 1984; Cicerone & Hoffman, 1997; Broom & Ruxton, 2005;
82 Rushton, Bradshaw & Warren, 2007; Ioannou & Krause, 2009; Yin *et al.*, 2015). For
83 instance, the outlines of animals relying on background matching [i.e. similarity in
84 appearance of an individual to its surrounding environment (Stevens & Merilaita, 2011;
85 Michalis *et al.*, 2017)] may become more visible against spatially patterned backgrounds
86 when they start moving (Hall *et al.*, 2013). However, motion is inevitable, as animals must
87 move to forage for food or find mates.

88 Although motion can aid detection, recent studies have shown that motion does not
89 necessarily lead to identification (Cuadrado, Martín & López, 2001; Hall *et al.*, 2013;
90 Umeton, Read & Rowe, 2017; Brunyé *et al.*, 2019; Smart, Cuthill & Scott-Samuel, 2020).
91 Unless it is already detected, an individual – whether a prey avoiding its predators or a
92 predator approaching prey – usually moves first in the observer's peripheral vision, rather
93 than the central field of vision (Smart *et al.*, 2020). Motion in the observer's peripheral vision
94 can often go unnoticed if the animal pauses and becomes cryptic again after moving
95 (Carrasco, 2011; Smart *et al.*, 2020). Although the topic of motion and antipredator defence is
96 garnering more interest recently, empirical studies investigating this relationship remain
97 scarce. Most studies have applied the principles and mechanisms of crypsis to animals in
98 motion (Cuthill, Matchette & Scott-Samuel, 2019). Research into crypsis has primarily
99 focused on morphological aspects of the animal, which are often linked to the observer's

perception, visual attention, and cognition (Endler, 1978; Cuthill, 2019; Troscianko *et al.*, 2021), although there have also been a variety of studies into how camouflage is facilitated by behaviour (Stevens & Ruxton, 2019). In contrast to stationary objects, patterns and markings in motion can alter perceptions of a target's speed, shape, size and relative position (Brattstrom, 1955; Jackson *et al.*, 1976; Bechtel, 1978; Brodie III, 1989; Scott-Samuel *et al.*, 2011; von Helversen, Schooler & Czienskowski, 2013; Umeton *et al.*, 2019). Contrasting lines on the body of animals can function as flash or dazzle marks which may confuse an approaching predator that might misjudge the speed or direction of the prey's escape (Cott, 1940; Brattstrom, 1955; Wickler, 1968; Jackson *et al.*, 1976; Edmunds, 2008; Stevens, Yule & Ruxton, 2008; Scott-Samuel *et al.*, 2011; Stevens *et al.*, 2011; Rojas, Devillechabrolle & Endler, 2014; Hämäläinen *et al.*, 2015; Hughes *et al.*, 2017).

Crypsis may be an effective strategy for individuals in motion to avoid predation to a certain degree. However, the behaviour of animals – how they may move to avoid detection and/or capture – also needs to be considered. In fact, some animals have evolved highly specialised morphology and/or behaviour to avoid predation whilst moving, such as the swaying motions of mantids and lizards to resemble wind-blown vegetation (Gans, 1967; Watanabe & Yano, 2009; Ramos & Peters, 2021), or deimatic displays by mountain katytids (Umbers, Lehtonen & Mappes, 2015; Umbers & Mappes, 2015). Strategies involving animal behaviour, such as motion dazzle, protean motion and flash colouration have been shown to serve as forms of distraction in various animals, ranging from butterflies to lizards, as well as hindering human observers' responses to artificial targets (Blest, 1957; Wickler, 1968; Papageorgis, 1975; Vallin *et al.*, 2005; Stevens *et al.*, 2008; Murali & Kodandaramaiah, 2016; Halperin, Carmel & Hawlena, 2017; Ruxton *et al.*, 2019). Although concealment in the form of camouflage may seem to be the best form of protection against predation, it may be sufficient for animals to mislead the predator and escape capture. Therefore, only focusing on

125 the concept of camouflage is too restrictive when we consider how animals avoid predation
126 whilst in motion. However, the behavioural aspects of animals needing to mislead predators
127 are usually overlooked in antipredation studies, or not measured directly and manipulated
128 (Brodie III, 1989, 1992; Shine & Madsen, 1994; Kelley & Kelley, 2014; de Alcantara Viana
129 *et al.*, 2022; Franklin, 2022). The lack of empirical research is unsurprising since the
130 component of motion adds an additional layer of complexity that is difficult to measure. Even
131 in camouflage research that considers behaviour, studies have focused on behaviour that
132 allow animals to select appropriate resting backgrounds to remain motionless, with a range of
133 work carried out on animals (e.g. Milne & Milne, 1952; Eterovick, Figueira & Vasconcellos-
134 Neto, 1997; Merilaita & Lind, 2005; Schaefer & Stobbe, 2006; Webster *et al.*, 2009; Xiao &
135 Cuthill, 2016; Merilaita, Scott-Samuel & Cuthill, 2017;Stevens & Ruxton, 2019).
136 Herein, we provide a review of the various underlying mechanisms involved in
137 facilitating antipredator defence while moving and classify them into two categories –
138 concealing and misleading motion signals (Table 1, Fig. 1). Although we have separated
139 these mechanisms to facilitate our discussion, we emphasise that certain strategies may
140 concurrently employ mechanisms from both categories. To increase the chances of survival
141 further, animals may simultaneously rely on multiple defence mechanisms to protect
142 themselves when moving (Edmunds, 1974; Endler, 1978, 1981; Stevens *et al.*, 2008; Hall *et*
143 *al.*, 2017; Ruxton *et al.*, 2019). We acknowledge that debates persist regarding the
144 terminologies used for the proposed antipredator strategies over time (see Scott-Samuel *et al.*,
145 2023). However, for the purposes of this review, we will refrain from dwelling extensively on
146 this aspect, but rather focus our discussions on the mechanisms involved, as well as gaps in
147 our understanding regarding antipredation and motion.

II. CONCEALING MOTION SIGNALS

If an animal moves sufficiently rapidly, it can exploit the predator's visual constraints and escape detection. Whilst several studies support this notion (e.g. Pough, 1976; Jackson *et al.*, 1976; Brodie III, 1992; Stevens *et al.*, 2008; Brunyé *et al.*, 2019; Smart *et al.*, 2020), the camouflaging effectiveness of an animal's appearance in motion depends on how they move. In addition to moving speed, other factors include the physiology and morphology of the animal, the visual systems of predators, as well as habitat complexity. For instance, the patterns and markings of an animal can alter perceptions of the individual's speed, shape, size, and relative position (Scott-Samuel *et al.*, 2011; von Helversen *et al.*, 2013; Umeton *et al.*, 2019). In fact, patterns may enhance concealment depending on the direction of motion change, as well as how they are perceived by predators, which in turn involves parameters such as visual acuity, contrast and light sensitivity, and spatial and resolving power of the predators (Bruce, Green & Georgeson, 2003; Land, 2014). Changeable or variable body colouration, including iridescence and colour changes at a cellular level [such as in cephalopods (Mäthger & Hanlon, 2007; Akkaynak *et al.*, 2013)], as well as the presence of independent movements of coloured body parts such as the tentacles of cephalopods (Bruce *et al*., 2003; Robison *et al.*, 2003; Land, 2014), can lend animals greater flexibility in movement while avoiding predation. In much the same way that many animals rely on body patterns and colouration to distract seekers from accurately discerning their body shapes and movement, environmental complexities could also distort visual acuity and speed perception. A plain individual moving against a plain background may appear to be stationary, but if the same individual moves against a patterned background its movement would become more apparent (Bonnet, 1984). Separately, greater environmental complexity can potentially reduce prey detectability as well as hinder mobility by the predator. In this section, we discuss how animals rely on the above factors to conceal motion signals through two perspectives which

differ in terms of the detectability of an animal in motion: (*i*) preventing detection of the animal (i.e. camouflage), and thus its movement; or (*ii*) preventing detection of movement only. Regarding the first perspective, an animal that remains camouflaged when moving should be able to escape detection, and thus predation, most effectively. Conversely, the second perspective may be more effective from a predator's point of view: prey may only detect the approaching predator when it is too late.

(1) Flicker fusion camouflage effect

The flicker fusion camouflage effect was first observed subjectively from field observations of snakes, where their crossbands were reported to blur into a uniform colour when they moved, and an abrupt cessation of movement rendered them discernible from their background (Table 1; Jackson *et al.*, 1976; Pough, 1976). In addition, correlational studies on snakes found that bands or zig-zag patterns were associated with higher survivability compared to monomorphic snakes, thereby lending indirect support for the flicker fusion camouflage effect (Shine & Madsen, 1994; Lindell & Forsman, 1996). The blurring effect occurs when an individual moves at speeds surpassing the critical flicker fusion frequency (i.e. the threshold of resolving rapid stimulus change, CFF) of the observer (Table 1). Possible reasons for this camouflaging effect include (*i*) the observer's continued search for the path of movement even after the target has stopped moving, or (*ii*) that the abrupt shift from being uniformly coloured to a patterned appearance allows the target to become cryptic against its surrounding environment (Pough, 1976; Titcomb *et al.*, 2014; Umeton *et al.*, 2017). In addition to being a camouflage strategy, the abrupt change in appearance may also cause the predator to hesitate (similar to the mechanism behind flash behaviour), thus providing the prey with an opportunity to escape (Umeton *et al.*, 2017). These different reasons thus suggest a variety of mechanisms through which the flicker fusion camouflage

198 effect may hinder prey capture, with camouflage being the most relevant effect from the
199 blurring illusion.
200 Studies of flicker fusion camouflage using natural predator–prey systems are
201 challenging and thus rare, and until recently the phenomenon was little more than an idea.
202 Although highly contrasting patterns are prevalent in many animals in the natural world
203 (Cott, 1940; Jackson *et al.*, 1976; Ruxton, 2002; Stevens & Merilaita, 2011; Allen *et al.*,
204 2013, 2020; Barnett *et al.*, 2017), it is unknown if the colour patterns of these animals are
205 associated with flicker fusion camouflage, and how this strategy works in evading natural
206 predators remains unexplored. Perceived changes in colouration through the blurring of
207 banded patterns of coral snake mimics (*Lampropeltis* sp.) were predicted to exceed the flicker
208 fusion frequency of diurnal birds (Titcomb *et al.*, 2014). The flicker fusion effect was also
209 observed in the zig-zag patterns of the European viper *Vipera berus* (Valkonen *et al.*, 2020),
210 though this study focused more on the cryptic effects of patterns, rather than the blurring
211 illusion brought about by motion of the vipers. Some of the first evidence for this mechanism
212 was tested in the praying mantis (*Sphodromantis lineola*), where computer-generated moving
213 prey with narrow stripes perpendicular to the direction of motion were harder to detect
214 compared to wide-striped or even background-matching prey (Umeton *et al.*, 2019).
215 For flicker fusion camouflage to be effective, factors involving (1) prey (e.g. prey
216 colour patterns, temporal pattern of speed and direction), (2) predator vision, and (3)
217 environmental conditions (e.g. lighting and visual background complexity) need to be
218 considered. Prey patterns – such as bands– should exhibit a pronounced perpendicular
219 orientation to the direction of motion for blurring to occur. For ease of reference, these
220 patterns are hereafter referred to as bands. In addition, the animal needs to move at a certain
221 speed to create the blurring illusion and optimise the effects of flicker fusion camouflage.
222 More importantly, the effectiveness of this mechanism relies heavily on a predator's visual

223 capabilities. Bands possess light and dark elements, which alternate when the animal moves
224 across the predator's field of view. The light and dark elements of banded patterns need to
225 alternate fast enough (i.e. temporal frequency) such that they exceed the CFF of the predator
226 and appear blurred (Umeton *et al.*, 2017). A higher spatial frequency pattern, which involves
227 the number of pattern cycles (i.e. the number of alternating light and dark elements) per
228 degree of visual angle, also increases the effectiveness of blurring (Umeton *et al.*, 2017).
229 Thus, individuals with finer bands should blend into the background more easily than those
230 with thicker bands, thereby potentially reducing detection through this mechanism (Barnett *et*
231 *al.*, 2017; Umeton *et al.*, 2017). In addition, patterns that appear to be blurred to one predator
232 visual system may remain visible to another predator visual system with higher spatio-
233 temporal acuity. Even for predators with similar visual acuities, the distance at which they
234 can recognise and attack prey may differ. Furthermore, viewing conditions of moving prey,
235 including the distance between predator and prey, as well as light intensity, greatly influences
236 the effectiveness of flicker fusion camouflage (Titcomb *et al.*, 2014; Umeton *et al.*, 2017).
237 More specifically, flicker fusion camouflage should occur more effectively in lower light
238 conditions, and when the predator is further away from the moving prey. Thus, studies
239 exploring the mechanisms that underpin the prevention of prey capture, and how these
240 mechanisms are linked to specific features of target appearance would be valuable.
241 Arguably, the biggest shortcoming of flicker fusion camouflage is the lack of
242 evidence that animals in nature move fast enough to exceed the CFF of an observers. It is
243 debatable as to how often this strategy could occur when prey face predators with relatively
244 high flicker fusion vision, such as birds (Jones, Pierce Jr & Ward, 2007). Furthermore,
245 blurring may not occur if the predator tracks the target, such as with head movements or
246 actual pursuit. As many predators will track the movement of their prey (Umeton *et al.*,
247 2017), it is harder for prey to blend into the background. The first step to determine the

248 ecological relevance of flicker fusion camouflage is to measure the potential predator's
249 critical flicker fusion frequency and to determine if the frequency of pattern alternations in
250 moving prey exceeds that threshold. The flicker fusion frequency threshold has been
251 determined in various animals, including several species of birds, reptiles, fishes, and insects
252 (Woo *et al.*, 2009; Lisney *et al.*, 2012; Inger *et al.*, 2014; Kalinoski *et al.*, 2014; Chatterjee *et*
253 *al.*, 2020; Potier *et al.*, 2020). These flicker fusion frequency thresholds, coupled with
254 information such as prey band width, prey moving speed, predator viewing distance and
255 lighting conditions, would be valuable inferences for how successfully the blurring effect
256 may occur when natural predator–prey experiments remain difficult to conduct.
257 With banded patterns ubiquitous across diverse taxa such as mammals, reptiles, and
258 insects (Cott, 1940; Jackson *et al.*, 1976; Ruxton, 2002; Stevens & Merilaita, 2011; Barnett *et*
259 *al.*, 2017), flicker fusion camouflage may be a more common antipredator strategy than
260 previously thought. Although we have focused our discussions on the camouflaging
261 effectiveness of bands, some animals such as snakes may possess both bands and longitudinal
262 stripes (i.e. patterns with a pronounced parallel orientation to the direction of motion), which
263 may serve as an additional layer of protection in the form of predator redirection (see Motion
264 Dazzle section) (Jackson *et al.*, 1976; Pough, 1976; Brodie III, 1992, 1993). We can start by
265 investigating flicker fusion camouflage in relevant, better-studied animal groups, such as
266 snakes and lizards. Testing the relevance of flicker fusion camouflage using natural predator–
267 prey systems will be difficult, especially since motion is a vital component involved and
268 methodological advancements will be required. While computer-generated stimuli are now
269 widely used in behavioural studies, present-day technology may be unable to recreate moving
270 bands that appear to be sufficiently fluid to the observer at high speeds. More specifically, the
271 refresh rate for current computer screens may not be high enough to exceed animals with
272 high critical flicker fusion frequency, such as birds (Jones *et al.*, 2007). Future research on

flicker fusion camouflage can first begin with a hybrid methodology involving live predators with prey lures, robots or 3D-printed stimuli attached to electromechanical devices to control motion. To determine accurately if patterned prey escape predator detection at high speeds, retina-tracking systems or algorithms can be used. Such systems, whilst still limited, have already been adapted for invertebrates, such as jumping spiders (see Jakob *et al.*, 2018). Comparative studies of selected taxa with relevant patterns would also provide insights into the evolutionary selection pressures on the flicker fusion camouflage strategy.

(2) Active motion camouflage

Active motion camouflage (i.e. motion camouflage or constant absolute target direction; Ghose *et al.*, 2006) can be executed with manoeuvres such that the image produced by a moving individual (i.e. the shadower) on the retina of the observer (i.e. the shadowee) is the same as that produced if the shadower was stationary at a fixed point (Table 1; Srinivasan & Davey, 1995; Glendinning, 2004; Reddy, Justh & Krishnaprasad, 2006). Thus, this strategy involves a certain degree of 'fixed retinal effect'. For instance, hoverflies (*Syritta pipiens*) were observed to rely on this stealth strategy when mating (Srinivasan & Davey, 1995). To conceal motion, the shadower would move along a camouflage constraint line, which connects the shadower to its shadowee, and this is possible through two mechanisms (Srinivasan & Davey, 1995). First, the shadower selects a visible landmark and continually moves towards its shadowee along the camouflage constraint line, thus creating the impression that it is stationary (Collett & Land, 1975; Srinivasan & Davey, 1995). Second, whilst moving towards its shadowee, the shadower is in a constant frontal or radial position from the shadowee (Collett & Land, 1975; Srinivasan & Davey, 1995). Thus, with the perceived lack of change in the position of the shadower, the moving shadower would appear to be stationary to the shadowee.

298 Active motion camouflage is more effective when the shadower moves at a slower
299 rate compared to its shadowee (Glendinning, 2004). The shadower can pursue the shadowee
300 from a greater range of angles that are equidistant (Glendinning, 2004). Active motion
301 camouflage can also remain effective even when the shadowee's speed and trajectory become
302 unpredictable (Srinivasan & Davey, 1995). Since this strategy assumes that the shadower
303 adopts the optimal direction of movement to appear stationary to the shadowee, a predator
304 that adopts active motion camouflage is likely to specialise on certain prey species. Since this
305 is likely to be a species-specific strategy, there is an added challenge of identifying the
306 predator–prey system. Since the effectiveness of this strategy hinges on whether apparent
307 motion can be perceived, the shadowee (or prey) should ideally possess weak depth
308 perceptions and looming (i.e. rapidly approaching or expanding) cues (Srinivasan & Davey,
309 1995). This is crucial as looming tends to generate escape responses in some species (Chan &
310 Gabbiani, 2013; Yilmaz & Meister, 2013), which would make active pursuit of prey difficult.
311 A shadowee that has difficulty resolving the motions of the shadower at a distance would be
312 ideal for active motion camouflage to work. Some exploration of this strategy has been
313 conducted in the field, on dragonflies, bats and falcons (Mizutani, Chahl & Srinivasan, 2003;
314 Ghose *et al.*, 2006; Reddy *et al.*, 2006; Kane & Zamani, 2014). An insect predator, the
315 dragonfly *Hemianax papuensis*, was observed to conceal its movements during territorial
316 aerial interactions (Mizutani *et al.*, 2003). Other predators that are known to stalk prey (i.e.
317 approach in a stealthy manner), such as felines, may potentially rely on motion camouflage,
318 although this remains untested. While active motion camouflage has primarily been discussed
319 in the context of active pursuit, it is possible for the shadower to utilise both stalking and
320 hunting at varied paces and momentum, so as to reduce the chances of detection by the
321 shadowee. Separately, humans were shown to be susceptible to active motion camouflage in
322 computer simulations (Anderson & McOwan, 2003). There is an increasing interest in the

application of active motion camouflage in the military, such as for missile guidance, surveillance, and in aerial drones (Justh & Krishnaprasad, 2006; Mischiati & Krishnaprasad, 2011; Savkin & Huang, 2020).

Although limited, the studies discussed above have provided evidence regarding the mechanism of active motion camouflage and proved its effectiveness. However, the degree of accuracy associated with shadowing an unsuspecting shadowee is a challenging aspect of this strategy. One difficulty associated with conducting such research is determining whether the animal relied on active motion camouflage specifically, or if its trajectory was random. Recently, there has been increasing interest in developing motion-tracking algorithms to analyse behaviour across various systems (Pérez-Escudero *et al.*, 2014; Rasch, Shi & Ji, 2016; Mathis *et al.*, 2018; Nath *et al.*, 2019; Walter & Couzin, 2021). Although these algorithms may be more suited to laboratory-based conditions, they have greatly improved the accuracy in quantifying animal motion and can be valuable in analysing the pursuer's direction of motion in relation to prey. Field studies can instead utilise trail-tracking systems involving tracking collars and tags, or even mounted global positioning system (GPS) cameras (e.g. Kane & Zamani, 2014; Kane, Fulton & Rosenthal, 2015) to analyse the predator's direction of motion in relation to its prey. Further exploration is necessary to understand (*i*) how animals utilise this strategy in nature, (*ii*) the factors influencing its effectiveness, such as environmental complexity and habitat type, and (*iii*) how widespread this strategy is.

III. MISLEADING MOTION SIGNALS

Whilst escaping detection entirely may be the most effective form of antipredator defence, animals need only to mislead or confuse potential predators to avoid capture most of the time. Like concealing motion signals, an animal's morphology plays an important role in

misleading predators. Animals with striped or zig-zag patterns, for instance, can confuse the predators' perception of their trajectory and speed when they move fast enough. Animals aimed at misdirecting the attention of predators through their motion (i.e. motion masqueraders) need to resemble an object and its associated motion as closely as possible to mislead predators from detecting them. Animals utilising flash colouration possess conspicuous, hidden colours that are revealed when they escape from predators. However, unlike strategies that are aimed at concealing motion, in this section we focus on how animals move to evade capture despite having been detected by potential predators. These strategies are aimed at confusing potential predators with regards to their speed, trajectory, and location.

(1) Motion masquerade

We classify motion masquerade as both concealing and misleading signals (Fig. 1) and propose two mechanisms which are not necessarily mutually exclusive: (1) motion masqueraders may mislead predators to misclassify them as uninteresting objects; and (2) motion masqueraders may conceal themselves from predators through a resemblance to the movement patterns of surrounding elements (Table 1). Rather than exploiting primarily sensory processes (i.e. detectability), masquerade primarily exploits the observer's cognitive senses to misdirect the predator from accurately tracking the animal (Endler, 1981; Skelhorn, Rowland & Ruxton, 2010; Skelhorn, 2015). The mechanism associated with concealment may have different levels of effectiveness depending on the motion type: (1) motion created to match that of surrounding elements; or (2) motion when the animal is moving from one location to another. The benefits of concealment for motion type 1, whilst not a primary function of masquerade as defined by Endler (1981) and Skelhorn *et al.* (2010), may serve as an additional layer of antipredator defence for motion masqueraders. Motion masqueraders

positioned against a background of other similar elements that are moving (e.g. a stick insect amidst sticks swaying in the wind) may be more difficult to detect when they adopt a similar pattern of motion (Fleishman, 1992; Eckert & Zeil, 2001; Skelhorn *et al.*, 2010). Thus, motion masqueraders may benefit from crypsis in avoiding being detected in the first instance, and subsequently from masquerade if the first line of defence fails. For motion type 2, the degree of movement resemblance to the model element can affect recognition by potential predators, since such movements may inevitably differ from that of the imitated element (e.g. a stick insect in motion may differ from that of a stationary wind-blown stick). Crypsis strategies, such as background matching, may play an important role in concealment and reducing detection by potential predators instead. Thus, it would be valuable to isolate various aspects of environmental motion and associate it to the masquerader's movement (see Eckert & Zeil, 2001). Research in environmental motion using three-dimensional (3D) animated environmental reconstructions, models for quantifying environmental signals and noise, and motion-tracking algorithms have been conducted using lizards as the model subject (Ord *et al.*, 2007; Peters, Hemmi & Zeil, 2007, 2008; Ramos & Peters, 2017; Bian *et al.*, 2018, 2021). For instance, plant motion was quantified using gradient detector models to compare potential differences with the motion generated by motion masqueraders (Peters, Clifford & Evans, 2002; Ramos & Peters, 2017). Bian *et al.* (2021) used habitat models based on field surveys to reconstruct virtual, 3D habitats and quantify various environmental parameters including motion, which will be useful in understanding the interactions between a 'masquerader' and its environment.

For motion masquerade to be effective, the individual needs to generate movement similar to that of the natural environment (Fleishman, 1985; Bian, Elgar & Peters, 2016; Bian *et al.*, 2018). Motion masquerade can thus create misleading motion signals or distort perceived speeds to potential predators (Peters *et al.*, 2007; Merilaita *et al.*, 2017). Motion is

prevalent in the natural environment (hereafter termed 'environmental motion'), such as the movement of leaves in the wind, or the flowing of water in a stream. An animal mimicking such environmental motion may be able to trick predators and prey into perceiving it as inanimate. A well-studied environmental motion associated with this strategy is that of windy conditions, where the masquerading animal sways in a manner similar to that of moving, uninteresting object such as a stem or leaf in the environment. For instance, the sinusoidal oscillation of neotropical vine snakes (*Oxybelis aeneus*) resembles that of wind-blown vegetation (Fleishman, 1985). The gliding membranes of the Bornean gliding lizard (*Draco cornutus*) have also been reported to closely resemble the colours of fallen leaves in the same habitat (Klomp *et al.*, 2014). As the gliding membranes were reported to not be used in communication, Klomp *et al.* (2014) proposed that this resemblance may aid the lizard in being perceived as a falling leaf when it glides. Stick insects and mantids sway during windy conditions to appear as vegetation displaced by the wind (Watanabe & Yano, 2009, 2013; Bian *et al.*, 2016). In fact, mantid activity and swaying behaviour increased with surrounding wind velocity (Watanabe & Yano, 2009). Whilst swaying behaviour was shown to reduce detection rates significantly in mantids (Watanabe & Yano, 2009), there remain limited studies investigating the survival advantages attributed to motion masquerade to date.

Since motion masqueraders need to conform to the environmental motion they are mimicking, this raises the question of how they can travel efficiently from one place to another, and what trade-offs exist for them. Some attempts at understanding this question have been made. Motion-masquerading animals usually appear cryptic to the observer and adopt behavioural adaptations to resemble environmental motion. Animals observed to sway like wind-blown leaves tend to move in a slow or jerky manner (Edmunds & Brunner, 1999; Watanabe & Yano, 2013). When the wind stimuli ended, motion-masquerading mantids that were cryptically approaching prey would pause in motion (Watanabe & Yano, 2009). As

423 animals will need to evaluate trade-offs on the risks of detection *versus* opportunity costs of
424 mate or food location, this may not be an all-or-nothing scenario. For instance, Pohl *et al.*
425 (2022) suggest that stick insects may adopt swaying to provide concealment in intervals,
426 between riskier revealing behaviours such as exploration. Such behavioural changes indicate
427 the need for specialised adaptations to detect and adjust to surrounding changes. Mantids, for
428 example, have wind-sensitive sensory hairs on their posterior appendages (cerci) (Triblehorn
429 *et al.*, 2008). Adaptations, such as cerci, may be important in enhancing the accuracy of the
430 masquerader's resemblance to wind-blown leaves as the masqueraders would be more
431 attuned to changes in the surroundings. Animals lacking such adaptations may be less
432 convincing to the observer when the stimuli change.

433 Swaying and oscillating motion have been mainly reported in reptiles and insects
434 (Gans, 1967; Bassler & Pflüger, 1979; Fleishman, 1985; LeGros, 2017). Evaluating how such
435 behavioural adaptations (e.g. swaying and oscillating motion) are associated with antipredator
436 defence and prey acquisition can be the next stages of study. Apart from the movement of
437 vegetation because of wind, other forms of environmental motion may also be exploited in
438 motion masquerade, such as aquatic animals masquerading as drifting leaf litter or debris
439 along river streams. Motion masquerade in the aquatic environment has been proposed in
440 several species of fish (e.g. *Canthidermis maculata*, *Monocirrhus polyacanthus* and *Platax*
441 sp.) masquerading as drifting debris such as leaves or pebbles (Randall & Randall, 1960;
442 Sazima *et al.*, 2006; Sato, Sakai & Kuwamura, 2022). However, these studies were of an
443 observational nature, and the effectiveness of such behaviour in avoiding detection and/or
444 predation remains untested.

445 The effectiveness of motion masquerade depends on how a potential predator
446 perceives the prey, and this is often tricky to disentangle. We suggest potential experiments to
447 tease apart the mechanisms – concealing and misleading – involved in motion masquerade.

448 Skelhorn *et al.* (2010) highlighted how predator experience and environmental background
449 influences the efficacy of this strategy. Whilst some evidence indicates how motion aids the
450 survival of motion masqueraders (Watanabe & Yano, 2009), manipulating predator
451 experience may help us understand whether the predator misidentifies the prey or simply is
452 unable to detect it. To examine how a motion masquerader can be concealed when travelling
453 from one location to another (i.e. motion type 2), the masquerader could be manipulated
454 together with its background, and its detection by the predator quantified. In the presence of
455 similarly moving background elements, if motion masquerade serves to conceal prey, the
456 predator should detect the prey once the prey or the background elements cease motion. By
457 contrast, if misidentification, rather than concealment, occurred, cessation of motion should
458 result in prey detection, but not recognition as an interesting (edible) object. We will thus
459 expect a similar response from the predator to both prey and background elements upon a
460 cessation of motion.
461
462 **(2) Motion dazzle**
463 Motion dazzle employs patterns that impair the accurate perception of a target's speed or
464 trajectory (Table 1; Stevens, 2007; Hämäläinen *et al.*, 2015; Hughes *et al.*, 2017; Merilaita *et*
465 *al.*, 2017). Recently, Scott-Samuel *et al.* (2023) proposed an expansion of the definition to
466 include the impairment of range perception as an additional effect of motion dazzle. Whilst
467 not empirically tested, dazzle patterns may distort the size of a target, which may in turn
468 affect estimations of its distance from the predator (Scott-Samuel, 2023). Size distortion
469 would also influence perceptions of the moving speed of the target: smaller targets may
470 appear to move faster (Brown, 1931; Scott-Samuel, 2023). Motion dazzle differs from flicker
471 fusion camouflage in that, rather than blurring into the surrounding background, parts of the
472 animal employing motion dazzle remain visible to potential predators. Dazzle colour patterns

473 are conceptually assumed to be used by various species of mammals, snakes, lizards, fishes
474 and some invertebrates (Jackson *et al.*, 1976; Brodie III, 1992; Hawlena *et al.*, 2006; Stevens
475 *et al.*, 2011; Halperin *et al.*, 2017; Murali & Kodandaramaiah, 2018). Flying insects, being
476 able to move across the visual fields of potential predators rapidly, may potentially benefit
477 greatly from motion dazzle if they possess dazzle patterns, although this has yet to be
478 empirically studied (Ruxton *et al.*, 2019). Phylogenetic comparative analyses on snakes,
479 lizards and bovids have drawn associations between striped body patterns and fleeing as an
480 antipredator strategy (Allen *et al.*, 2013; Halperin *et al.*, 2017; Murali, Merilaita &
481 Kodandaramaiah, 2018; Yu *et al.*, 2022). Striped patterns (i.e. longitudinal stripes) on snakes
482 may make it difficult for the seeker to track them, as well as drawing attention away from
483 their trajectory (Brattstrom, 1955; Jackson *et al.*, 1976; Bechtel, 1978; Brodie III, 1989,1992;
484 Allen *et al.*, 2013). Longitudinal stripes have been observed in shorter and smaller lizards and
485 snakes, suggesting that the effectiveness of such striped patterns may be negatively
486 associated with body length (Allen *et al.*, 2013; Murali & Kodandaramaiah, 2018).
487 Furthermore, such longitudinal stripes may allow the animal to appear to be stationary as it
488 escapes. The longitudinal stripes may remain roughly constant in the predator's retinas when
489 the animal moves, thus allowing its movement to be seemingly camouflaged. While not
490 empirically tested, the stripes on the head of small felines or badgers could potentially act as
491 retinal focal points for prey, thereby effectively camouflaging the felines' movement when
492 they stalk the prey. Animal patterns have also been associated with movement behaviour,
493 such as in lizards (Halperin *et al.*, 2017) – striped lizards tend to be more mobile than cryptic
494 lizards as they may rely on motion dazzle to enhance survival. Experiments showed that
495 longitudinally striped virtual lizard prey were perceived to be moving more slowly than their
496 actual speed, resulting in more attacks on the hind regions of targets (Murali &
497 Kodandaramaiah, 2016). However, how natural predators perceive live lizards with such

498 longitudinally striped patterns in motion remains untested. Nevertheless, these results may
499 explain the differently marked torsos *versus* expendable body parts (e.g. tails) of such
500 animals, if it leads to more attacks that miss vital body parts (Murali & Kodandaramaiah,
501 2016). In this aspect, motion dazzle works similarly to attack deflection, which refers to the
502 use of defensive features (e.g. eyespots) and behaviours (e.g. tail-shedding or autotomy) that
503 enhance the survivability of the animal (Wickler, 1968; Stevens, 2005; Kodandaramaiah,
504 2011; Quicke, 2017; Ruxton *et al.*, 2019).

505 The effectiveness of motion dazzle has been observed in several computer-based
506 experiments involving human observers, where contrasting patterns hindered capture of the
507 target (Stevens *et al.*, 2008, 2011; Scott-Samuel *et al.*, 2011; Hughes, Troscianko & Stevens,
508 2014; Hughes, Magor-Elliott & Stevens, 2015; Hogan, Scott-Samuel & Cuthill, 2016). These
509 studies showed that targets with monochrome stripes and zig-zagged markings were captured
510 less than uniformly white or background matching targets (Stevens *et al.*, 2011; Hughes *et*
511 *al.*, 2014; Hogan *et al.*, 2016). However, the effectiveness of this antipredator strategy can be
512 subtle and affected by pattern aspects such as stripe frequency, contrast, orientation,
513 luminosity, as well as background texture and complexity (Thompson, 1982; Stevens *et al.*,
514 2008, 2011; von Helversen *et al.*, 2013; Hughes *et al.*, 2017). The effectiveness of various
515 stripe orientations has been met with contradictory reports depending on how the target
516 moves, or how the observer captures the target (e.g. von Helversen *et al.*, 2013; Hughes *et al.*,
517 2015; Kodandaramaiah *et al.*, 2020). There is some support in research on snakes, where
518 differences in behavioural strategies were observed amongst differently patterned snakes –
519 snakes with longitudinal stripes were more commonly associated with flight while snakes
520 with bands or blotches were observed to rely on crypsis and aggressive defence tactics
521 (Jackson *et al.*, 1976; Brodie III, 1989, 1992). Additionally, when coupled with the confusion
522 effect (i.e. the use of distractors/grouping to reduce capture rates), motion dazzle further

523 reduced capture rates (Hogan *et al.*, 2016). However, when variations in speed are involved,
524 striped stimuli are more easily detectable even when in a group (Hogan, Cuthill & Scott-
525 Samuel, 2017). Whilst varied speeds may be detrimental to motion dazzle, it would be
526 valuable to determine if variations in speed, coupled with variations in trajectory (i.e. protean
527 motion), would achieve the same effect.

528 Empirical studies investigating motion dazzle are limited and dominated by
529 experiments with human observers and artificial targets and patterns. With motion as a factor,
530 field studies using live animals are challenging and limited. Hämäläinen *et al.* (2015) found
531 that striped moving prey were harder to capture compared to uniformly brown moving prey
532 for wild great tits (*Parus major*), while Santer (2013) showed that contrasting patterns
533 affected looming motion perception in locusts (*Schistocerca gregaria* Forskål). Studies
534 involving human observers have explored the effects of speed, pattern contrast, and
535 orientation on motion dazzle, although further investigations are required to draw concrete
536 conclusions (Scott-Samuel *et al.*, 2011; Hogan *et al.*, 2016, 2017). The effectiveness of
537 motion dazzle is likely to be predator specific, since visual illusions are perceived differently
538 across species (Eagleman, 2001; Kelley & Kelley, 2014). Thus, to draw ecologically relevant
539 conclusions and understand the mechanisms behind motion dazzle better, more research
540 needs to be conducted on natural predator–prey systems. Several major gaps remain to be
541 investigated with regards to motion dazzle and its potential functions in nature: (*i*) what types
542 of naturally occurring markings are most effective, and do they provide an advantage over
543 uniform appearances; (*ii*) what predator–prey systems, and associated animal behaviours,
544 operate in motion dazzle; and (*iii*) what survival advantage does motion dazzle provide?
545

(3) Protean motion

First proposed by Chance & Russell (1959), the erratic movement (i.e. zig-zagging, bouncing, spinning, or tail flips) associated with protean motion is a commonly observed defence tactic for a variety of animals, especially in situations with limited hiding space (Table 1; Humphries & Driver, 1970; Chai & Srygley, 1990; Yager, May & Fenton, 1990; Jackson, Rowe & Wilcox, 1993; Edut & Eilam, 2004; Bilecenoğlu, 2005; Garde *et al.*, 2021). Prey with greater path complexity can confuse and disorient predators, thereby reducing the accuracy of capture (Humphries & Driver, 1967, 1970; Driver & Humphries, 1970; Edut & Eilam, 2004; Jones, Jackson & Ruxton, 2011; Kane *et al.*, 2015; Scott-Samuel *et al.*, 2015; Clemente & Wilson, 2016; Richardson *et al.*, 2018). Furthermore, unpredictable prey movement can limit the scope of predator learning and adaptation, since the predator is unable to predict the future positions of protean-moving prey (Murali & Kodandaramaiah, 2020).

While it is not always feasible, increasing the speed of prey is often associated with reduced capture rates, as prey at a constant speed are easier for predators to detect and track (Stevens *et al.*, 2008; Brunyé *et al.*, 2019). Conversely, a predator scanning the environment with a fluctuating focal point may likely overlook prey adopting protean motion. Therefore, prey only need to vary their speed and/or trajectory, rather than move at high speeds, to be energetically efficient (Moore *et al.*, 2017; Wilson *et al.*, 2018). Besides considering the movement of the prey, the effectiveness of protean motion may be influenced by environmental complexity – a more heterogeneous environment may be more suitable for this strategy compared to a uniform/homogeneous environment.

Although protean motion has been observed in a wide variety of animals, empirical research on the effectiveness of protean motion to reduce predation using natural predator–prey systems remains limited to date. Body size may be a factor influencing the effectiveness

of protean motion – a smaller animal may be able to move in a faster and more erratic manner than a larger animal, as the latter may not be able to change trajectory and velocity as efficiently (Martín & López, 1995; Hedenström & Rosén, 2001). Although body mass may influence escape behaviour in prey (e.g. evasiveness, angle and speed of escape), it may not necessarily affect escape ability adversely (Pérez-Tris, Díaz & Tellería, 2004; Walters *et al.*, 2017). However, there are no studies evaluating the effects of prey size on protean motion to date. Video recordings of predator–prey interactions (see Edut & Eilam, 2004) could be the first step to understanding how unpredictable motion aids in evading capture. Apart from prey speed and trajectory, factors such as predator speed and manoeuvrability can also influence prey capture (Clemente & Wilson, 2016). The effectiveness of protean motion may also differ depending on the predators' approach to the prey. For instance, an ambush predator may be less likely to adjust and modify their trajectory and tactics rapidly, compared to a pursuit predator (Szopa-Comley & Ioannou, 2022). Furthermore, unpredictable motion may be more effective during initial attempts to escape, as the predator may adapt to the prey's path after a certain period. Thus, factors such as distance of the predator to prey, as well as duration of predator–prey interactions, need to be considered. As predator–prey interactions often vary in the natural world, evaluating how these factors influence the effectiveness of protean motion can be challenging. Szopa-Comley & Ioannou (2022) recently developed robot-controlled prey to investigate how unpredictability influences prey capture in the blue acara cichlid (*Andinoacara pulcher*). The ability to manipulate prey movements will allow us to understand how live predators respond to unpredictability in prey motion.

There may be synergies between protean movement and other antipredation strategies. For instance, butterflies possessing both light and dark colouration (e.g. *Heliconius* sp.) may confuse predators and avoid detection by flying across regions of different light

intensity in rapid succession (Thayer, 1909; Papageorgis, 1975). Whilst not empirically tested, these butterflies may be adopting both protean motion through erratic movement and flash colouration by changes in conspicuousness. For instance, dark colours on the butterflies would appear to be hidden in regions of low-light intensity, which would become exposed when butterflies move to regions of high light intensity. Recent studies have also provided evidence on how antidetection strategies, such as dynamic flash colouration and the confusion effect, benefit more from erratic movement alone in monochrome, computer-generated prey (Scott-Samuel *et al.*, 2015; Murali & Kodandaramaiah, 2020). Animals adopting motion dazzle may additionally benefit from the unpredictable nature of protean motion as it further reduces predators' ability to predict prey trajectory. These in turn raise the following questions: (*i*) which strategy evolved first, i.e. is protean motion a derived strategy; (*ii*) if protean motion is a derived strategy, do animals adopting motion dazzle always evolve protean motion; and, more importantly, (*iii*) to reconstruct the evolutionary selection pressures, which clade(s) of animals are likely to rely on protean motion as an antipredator strategy?

(4) Flash behaviour

Flash behaviour has been broadly used to describe any display of conspicuous signals, such as colour patterns or noise, which are normally hidden at rest (Table 1; Cott, 1940; Edmunds, 1974, 2008). Deimatic behaviour (also referred to as startle display), which involves the element of surprise and potentially intimidation (Table 1; Crane, 1952; Maldonado, 1970; Edmunds, 1974), has often been confused with flash behaviour. More recently, however, the notion of deimatic behaviour being distinct from flash behaviour is becoming more popular, and deimatic behaviour has been discussed in great detail in several recent reviews (Umbers *et al.*, 2015, 2017; Ruxton *et al.*, 2019; Caro & Koneru, 2021; Drinkwater *et al.*, 2022). We

thus focus on flash behaviour in this section. As the effects of hidden colouration have received greater attention compared to other forms of hidden behaviour, we primarily focus our discussion on flash colouration in this section. Nonetheless, there is a need to place greater emphasis on understanding the effects of hidden signals involving other sensory modes, which have received scant attention to date. Flash behaviour has been postulated to occur across diverse taxa ranging from mammals, such as deer and birds, to cephalopods, fishes, frogs, lizards and arthropods, including butterflies, moths, grasshoppers, and spiders (Cott, 1940; Anonymous, 1945; Blest, 1957; Edmunds, 1974, 2008; Papageorgis, 1975; Sheppard *et al.*, 1985; Chai, 1986; Caro *et al.*, 1995; Hanlon & Messenger, 1996). For instance, grasshoppers tend to stridulate when they move and predators following the stridulations may be unable to find them when the noise ceases as the grasshoppers stop moving (Edmunds, 1974, 2008).

Misleading motion signals followed by crypsis is one of the mechanisms of flash behaviour. At rest, the animal would appear to be cryptic against its surroundings, thereby emphasising the conspicuousness of hidden signals and creating a greater element of surprise when it starts moving. The display of a conspicuous signal (e.g. colouration or sound) occurring before or as the prey moves, is followed by a sudden cessation of movement and reversion back to crypsis (e.g. masking of conspicuous colouration or cessation of sound), thus rendering the prey difficult to locate (Cott, 1940; Edmunds, 1974, 2008). The predator may assume that the prey has a conspicuous appearance and would continue the search for the conspicuous features of the prey when the signals are hidden (Cott, 1940; Edmunds, 1974; Martin *et al.*, 2022). Factors such as prey body size (Bae *et al.*, 2019; Caro, Raees & Stankowich, 2020; Emberts *et al.*, 2020) and the distance between prey and predator (Loeffler-Henry, Kang & Sherratt, 2021) can influence the efficacy of flash behaviour. For instance, contrasting colour patterns that may be effective in flash behaviour were associated

with larger body size in some insect groups (Kang, Zahiri & Sherratt, 2017; Loeffler-Henry, Kang & Sherratt, 2019; Caro *et al*., 2020). A greater escape distance between the prey and its predator improves survivorship as the predator is less likely to observe the prey's cryptic appearance at rest (Loeffler-Henry *et al.*, 2021).

Another mechanism associated with flash behaviour is the use of misleading motion signals that confuse the predator (i.e. dynamic flash colouration): differential colour change achieved through movement, reduces capture rates by misrepresenting the trajectory or location of the prey (Edmunds, 2008; Murali, 2018). For instance, black-tailed jackrabbits (*Lepus californicus*) exhibit different ear-flashing behaviour in rapid succession (Kamler & Ballard, 2006). Flash colouration in this aspect has been observed in fish, birds, and butterflies (Young, 1971; Brooke, 1998; Murali, Kumari & Kodandaramaiah, 2019). Dynamic flash colouration can also involve the use of iridescence (i.e. visually striking colours that appears to be different depending on the illumination angle), which has received much attention (see Fox & Vevers, 1960; Fox, 1976; Srinivasarao, 1999; Berthier, 2007; Doucet & Meadows, 2009; Seago *et al.*, 2009; Pike, 2015). Changes in colouration due to iridescence can hinder the ability of predators to locate the prey accurately and thus reduce prey capture rates (Pike, 2015). Such dynamic colour change is also shown to be enhanced with protean motion (Murali & Kodandaramaiah, 2020).

Flash and deimatic behaviour affect predators differently, even though the outcome may be the same – avoiding capture. While flash behaviour confuses the predator through misleading motion signals, deimatic behaviour involves the element of surprise. Unlike flash behaviour, deimatic behaviour does not impair the predator's ability to track prey as the signals can remain conspicuous after exposure (Loeffler-Henry *et al.*, 2018; Kim *et al.*, 2020; Drinkwater *et al.*, 2022). Furthermore, deimatic behaviour does not necessarily involve the exposure of a previously hidden colour signal (Ruxton *et al.*, 2019; Drinkwater *et al.*, 2022).

While flash behaviour involves the element of motion to mislead predators, deimatic behaviour can occur regardless of whether the prey is stationary or moving (Olofsson *et al.*, 2012; Umbers *et al.*, 2017). Animals relying on deimatic signals do not necessarily have to flee and may continue signalling in their spot until the predator leaves or stops its attack (Ruxton *et al.*, 2019; Caro & Koneru, 2021). This means that deimatic behaviour does not require longer escape distances to enhance survivorship and may require lower energetic costs than flash behaviour. However, since deimatic behaviour works more effectively on naïve predators to elicit a startle effect, continuous displays or signals may incur high energetic costs (Umbers *et al.*, 2017, 2019; Ruxton *et al.*, 2019; Kim *et al.*, 2020). Whilst flash and deimatic behaviour are now regarded as distinct, these strategies may occur simultaneously or sequentially as part of a multifaceted antipredator defence (Cott, 1940; Edmunds, 1974; Kim *et al.*, 2020; Drinkwater *et al.*, 2022).

There remains some doubt as to whether flash behaviour can mislead predators into assuming the animal is unprofitable and thus deter pursuit. By signalling its awareness or unprofitability of capture, prey may discourage predators from initiating an attack (Hasson, 1991; Caro, 1995). Prey unprofitability as a form of pursuit deterrence may be related to other strategies involving warning signals to approaching predators, such as deimatic behaviour and aposematism (i.e. displays that denote toxicity or unpalatability; Umbers *et al.*, 2015). Hidden signals, such as tail-flashing in deer and various birds, were shown to be effective forms of pursuit deterrence (Edmunds, 1974; Randler, 2016; Peltier, Wilson & Godard, 2019; Ramesh & Lima, 2019). Another form of pursuit deterrent signal known as stotting (i.e. a type of jumping behaviour more commonly observed in various species of ungulates; Walther, 1969) may also elicit a startle response in predators (Caro, 1986), Whilst not empirically tested, the combined effects of tail-flashing and stotting in some species of deer, for instance, may enhance the survivability of the animal. However, whether these

signals are associated with deimatic or flash behaviour remains untested, therefore making it difficult to tease the strategies apart. Kim *et al.* (2020) have recently shown that both flashing and deimatic prey benefit from being identified as unprofitable. Teasing apart the evolutionary drivers shaping warning signals is an important next step to understand the importance of flash (and deimatic) behaviour as an antipredator defence. In amphibians, the evolution of cryptic to aposematic colours involves hidden colour signals as an intermediate stage (Loeffler-Henry, Kang & Sherratt, 2023).

Understanding the underlying mechanisms behind flash behaviour is complicated because it is difficult to measure accurately the intended effect on the displayer's behaviour. As flash behaviour may be effective as an antipredator strategy through several mechanisms simultaneously, it may be difficult to tease the mechanisms apart. Recently, Sherratt & Loeffler-Henry (2022) proposed a Bayesian model to assess how animals rely on flash behaviour in avoiding predation. Predictions of the model include: a predator will spend more time searching for the prey if it believes the prey is hiding there; prey with greater conspicuity in flash behaviour while appearing well camouflaged at rest will avoid predation more effectively; and flash behaviour works more effectively for predators without knowledge of the prey's appearance at rest (Sherratt & Loeffler-Henry, 2022). However, there remains a need for the development of new methodologies (see Sherratt & Loeffler-Henry, 2022) to facilitate empirical investigations and better understand the mechanisms behind flash behaviour within ecologically relevant contexts. Some major gaps remain to be addressed: (*i*) are hidden signals exposed by motion (i.e. flash behaviour) or the approaching predator to induce a startle effect (i.e. deimatic behaviour); (*ii*) what are the various antipredation mechanisms involving hidden signals; and (*iii*) how do warning signals (i.e. aposematism, flash and deimatic behaviour) work in association in the natural world?

(5) Behavioural mimicry

Mimicry is a topic that has received much debate over the years, with several proposed definitions (Bates, 1862; Müller, 1878; Cott, 1940; Wickler, 1968; Edmunds, 1974; Wiens, 1978; Vane-Wright, 1980; Endler, 1981; Robinson, 1981; Pasteur, 1982; Grim, 2013; Dalziell *et al.*, 2015). Nonetheless, the general concept of mimicry involves the resemblance of an animal (i.e. the mimic) to another (i.e. the model), such that a third party (e.g. a predator) may misclassify the mimic as the model. To date, several mimicry categories exist depending on the relationship between the predator and prey, with Batesian and Müllerian mimicry being regarded as the extreme ends of the protective (or defensive) spectrum of mimicry (Table 1; Bates, 1862; Müller, 1878). Batesian and Müllerian mimicry have been shown to involve behavioural mimicry (Mallet & Gilbert, 1995; Srygley, 1999*a*, 2004; Howarth, Edmunds & Gilbert, 2004). However, behavioural mimicry has generally received little attention, with a greater focus on arthropods such as butterflies, hoverflies, moths, and spiders (Table 1; Edmunds, 1974; Srygley, 1994, 1999*b*; Brower, 1995; Golding, Ennos & Edmunds, 2001; Howarth *et al.*, 2004; Nelson, Li & Jackson, 2006; Kitamura & Imafuku, 2010; Penney *et al.*, 2014; Skowron Volponi *et al.*, 2018). Although the term 'locomotive mimicry' has been used interchangeably with 'behavioural mimicry', we here define 'locomotive mimicry' as mimicry involved in moving from one location to another and regard it as a subset of behavioural mimicry.

Locomotive mimicry was first described in the butterfly genus *Heliconius* (Srygley, 1994). In general, palatable butterflies (i.e. mimics) tend to fly in a rapid, erratic manner to avoid capture while unpalatable butterflies (i.e. models) typically move more slowly to highlight their conspicuousness and advertise their unpalatability (Fisher, 1958; Turner, 1984; Chai, 1986; Chai & Srygley, 1990; Srygley & Chai, 1990; Srygley, 1994). For mimicry to be more effective, Srygley (1994) assumed that palatable *Heliconius* mimics should evolve their

746 wing morphology and flight patterns to resemble their models better while balancing the
747 costs of avoiding predation. However, there is some debate regarding the proposed
748 mechanism behind locomotive mimicry as previous studies have not accounted for
749 phylogenetic relationships (Brower, 1995). Furthermore, the costs involved in resembling the
750 flight patterns of unpalatable models may outweigh the benefits involved – the slow mimetic
751 flight of palatable butterflies may hinder their ability to escape pursuit by predators (Srygley
752 & Chai, 1990). In fact, palatable mimetic butterflies tend to consume more energy than
753 unpalatable models when mimicking their flight patterns (Srygley, 2004).
754 Myrmecomorphy, a well-known form of mimicry, refers to the morphological and
755 behavioural resemblance of ants (Donisthorpe, 1927; Mclver & Stonedahl, 1993; Cushing,
756 1997). Ants serve as a good model as they are aggressive, possess various offensive tactics to
757 attack as a collective, and produce defensive secretions (Hölldobler & Wilson, 1990). While
758 the morphological aspects of ant mimicry are relatively well-studied, there are limited
759 empirical studies of the behavioural component of mimicry (Nelson & Card, 2016; Shamble
760 *et al.*, 2017). Myrmecomorphy in spiders is relatively common, with hundreds of ant-
761 mimicking spider species recorded (Mclver & Stonedahl, 1993; Cushing, 1997). Spider
762 myrmecomorphs tend to move in an erratic, zig-zag fashion similar to ants, and also wave
763 their front legs to resemble antennae (Jackson, 1986; Reiskind, 1977; Mclver & Stonedahl,
764 1993). Interestingly, Shamble *et al.* (2017) showed that, instead of moving on six legs, spider
765 myrmecomorphs typically move on all eight legs and only waved their front legs while
766 stationary. Some spider myrmecomorphs are known to adopt aggressive mimicry, which
767 involves the predator resembling its prey (Wickler, 1968; Mclver & Stonedahl, 1993;
768 Cushing, 1997). However, whether these ant-mimics also rely on Batesian or Müllerian
769 mimicry has received some debate (Cushing, 1997). Due to the lack of evidence indicating
770 the unpalatability of spider myrmecomorphs, it is unlikely that spiders adopt Müllerian

771 mimicry (Cushing, 1997). As many predators are specialised at capturing ants as prey, there
772 is doubt as to the level of protection gained from resembling ants (Brignoli, 1984). On the
773 other hand, since spider myrmecomorphs tend to escape from potential threats in a manner
774 unlike ants, which tend to respond aggressively, resembling ants may potentially still confer
775 survival benefits (Edmunds, 1978).

776 The accuracy of a mimic's resemblance to its model may influence the effectiveness
777 of behavioural mimicry. Behavioural mimicry was previously assumed to enhance the
778 deceptive effectiveness of inaccurate morphological (i.e. based on colour patterns) mimicry
779 (Howarth *et al*., 2004; Pekár & Jarab, 2011; Pekár *et al*., 2011). For instance, a few species of
780 spider myrmecomorphs with inaccurate morphological resemblance to ant models may rely
781 on behavioural resemblance, such as moving speed, to improve overall mimetic accuracy
782 (Pekár & Jarab, 2011). Furthermore, despite having inaccurate morphological and
783 behavioural resemblance to the model, the mimics are shown to be easily confused with their
784 models during locomotion (Golding *et al.*, 2001; Pekár & Jarab, 2011). Additionally,
785 continuous movement may make it difficult for predators to assess the mimic's morphology
786 (Pekár & Jarab, 2011). Thus, behavioural mimicry may be more suited to models that rely
787 heavily on locomotion. While generally regarded as a secondary form of defence, chemical
788 (or olfactory) mimicry should also be considered, especially since it can enhance the
789 effectiveness of behavioural or morphological mimicry (Dettner & Liepert, 1994). However,
790 further investigations are needed to explore how chemical and behavioural mimicry can work
791 in tandem to increase the survivability of the animal. The relative importance of mimicry
792 across different modalities will also be dependent on the sensory systems of the receivers.
793 Behavioural mimicry may also potentially offset the costs required by morphological
794 mimicry, such as changes in body plan to resemble the model, and therefore improve overall

795 resemblance. However, McLean & Herberstein (2021) found no correlation between moving
796 speed and morphological resemblance in spider myrmecomorphs.
797 Rather than considering the interactions between behavioural and morphological
798 mimicry, the effectiveness of mimicry may instead be more dependent on the amount of
799 information received by the predator: a mimic's resemblance to its model may be more
800 effective if the predator has received limited information (i.e. information limitation
801 hypothesis; McLean & Herberstein, 2021). Recent studies have also shown otherwise – while
802 accurate morphological mimics can be accurate behavioural mimics, accurate behavioural
803 mimics do not necessarily have to be accurate morphologically (Ceccarelli, 2008; Penney *et*
804 *al.*, 2014). For mimic–model systems involving active models, such as ants, the element of
805 behavioural mimicry may potentially be more important than the mimic's visual appearance
806 (Ceccarelli, 2008). An alternative hypothesis has been proposed – mutualistic deceptive
807 mimicry, which refers to various similar-looking mimics occurring in the same environment
808 using different escape tactics to confuse a common predator (Loeffler-Henry & Sherratt,
809 2021). This primarily aims to confuse the predator from employing the appropriate capture
810 tactic and, thus, benefits the co-mimics (Loeffler-Henry & Sherratt, 2021). However, further
811 empirical studies are needed to test this hypothesis.
812 With advances in technology, it is now possible to quantify behavioural resemblance
813 from the perspectives of natural predators using more objective tools to assess behaviour
814 instead of relying on human judgement, which can be skewed (Howarth *et al.*, 2004). For
815 instance, motion-tracking algorithms and software can be useful, especially in providing
816 more detailed information related to the mimic's behaviour and its accuracy to the model.
817 Skowron Volponi *et al.* (2018) found evidence supporting behavioural mimicry in clearwing
818 moths by digitising their flight trajectories. However, understanding how motion and
819 mimicry interact to deceive predators in the natural world remains a challenge. Empirical

820 studies in more animal systems are sorely needed to better understand the ecological
821 relevance of behavioural mimicry as a form of antipredator defence. Furthermore, although
822 we have focused on the interactions between morphological and behavioural resemblance in
823 this section, how behavioural mimicry interacts with other aspects of mimicry, such as
824 chemicals and texture, remains a major gap in our understanding of mimicry.
825
826 **IV. FUTURE WORK**
827 We highlighted several antipredator strategies that animals may adopt whilst in motion, and
828 how preventing detection and capture can be linked to various aspects of motion. Throughout
829 this review, we provided specific suggestions for further studies. Although the topic of
830 antipredator defence and motion are receiving increasing attention, there remain many gaps
831 that need to be filled. Here, we highlight five main questions in our understanding of
832 antipredator defences and motion: (1) how widespread are these antipredator defence
833 strategies in the natural world; (2) what are the patterns and markings that are most effective
834 in avoiding predation while moving and what are the mechanisms used; (3) how does habitat
835 structure and complexity influence the effectiveness of these strategies; (4) what are the
836 various selection pressures that have shaped animals in avoiding predation whilst moving,
837 and why have some species adopted one strategy over another; and (5) how can mechanisms
838 involved in antipredator defences and motion be teased apart, and how do these mechanisms
839 interact with each other to improve survivability?
840 Regarding how widespread the antipredator defences in motion discussed herein are,
841 there is a need to conduct more empirical studies across more animals in the natural world.
842 The lack of natural predator–prey studies remains one major recurring gap for most, if not all,
843 of the antipredator defences discussed in this review. Studies manipulating either the prey
844 (e.g. Umeton *et al.*, 2019) or the predator (e.g. Hall *et al.*, 2013) are a first step, but future

studies should use ecologically relevant subjects. Whilst studies relying on computer simulations and human observers test proof-of-concept of many potential strategies, the effectiveness of these strategies in the natural world are often inferred, rather than directly quantified. Furthermore, in the presence of motion, camouflage primarily aims to exploit potential predators' visual systems and perceptions. As many animals have different visual systems from humans, even our closest relatives the chimpanzees, (Fagot & Tomonaga, 1999; Pene, Muramatsu & Matsuzawa, 2020), results based on subjective human perceptions inevitably make it difficult to infer the effectiveness of camouflage for moving prey in natural predator–prey systems. Stimuli that appear to be highly cryptic to humans may be glaringly obvious to other visual systems. Minute differences in visual acuity of the observer may significantly influence the prey animal's survival in the real world. Admittedly, studies involving natural predator–prey systems are difficult, especially since technological advancements are required to quantify the effectiveness of antipredation strategies involving motion. Even though this issue has been raised repeatedly (e.g. Merilaita, Lyytinen & Mappes, 2001; Troscianko, Skelhorn & Stevens, 2017; Price *et al.*, 2019; de Alcantara Viana *et al.*, 2022), there are still gaps in our understanding of antipredator defences and, in particular, their relationships with motion.

Understanding which patterns and markings give animals a survival advantage over others remains a key study area for antipredator defences and motion. Crucially, we need to understand the mechanisms through which strategies work, to be able to understand the prevalence of phenotypes in nature that may be involved. We highlighted the relevance of potentially contrasting patterns (i.e. stripes, zig-zags, and flash colours) when motion is involved. The strategies discussed in this review employ different mechanisms compared to those that are effective for stationary animals (such as background matching, disruptive colouration). However, it is possible that patterns effective in camouflaging stationary

animals against one predator species may also effectively conceal them against other predator species when they are moving. For instance, as various studies investigating motion dazzle have reported conflicting results on the effectiveness of pattern orientation in relation to motion (von Helversen *et al.*, 2013; Hughes *et al.*, 2015; Kodandaramaiah *et al.*, 2020), it is highly likely that different pattern orientations are more effective against different predator taxa. Furthermore, differences in patterns and markings may be associated with behavioural differences, although this hypothesis remains untested. For instance, pattern variation in aposematic frogs is associated with differences in movement and behaviour – frogs with elongated patterns tend to move linearly and quickly while those with interrupted patterns tend to move slowly and adopt unpredictable trajectories (Rojas *et al.*, 2014). Further empirical experiments are required to verify such associations.

With habitat complexity known to be a major determinant of the detectability of stationary, camouflaged targets, environmental background features such as luminance, contrast, hue, texture, and motion patterns may also play important roles in minimising a moving individual's probability of standing out (Brown, 1931; Merilaita, Tuomi & Jormalainen, 1999; Blakemore & Snowden, 2000; Merilaita *et al.*, 2001; Butler & Gillings, 2004; Xiao & Cuthill, 2016). The influence of environmental conditions on the effectiveness of conspicuous patterns and flash markings may also play an important role in concealing or misleading the animals' signals in motion. Since motion perception declines with reduced light intensity (Bruce *et al.*, 2003; Land, 2014), antipredation strategies, such as flicker fusion camouflage, should work more effectively in low-light conditions. Animals employing flicker fusion camouflage or motion dazzle (e.g. some species of snakes; Clarke, Chopko & Mackessy, 1996; Lillywhite & Brischoux, 2012) also tend to dwell in low-light habitats. For motion masquerade, the structure and complexity of the environment may also impact the degree of motion matching needed for the masquerader to be successful. Thus, how

environmental luminance or habitat complexity influences the detectability of motion signals and, therefore, the effectiveness of antipredation strategies, remains unexplored.

To date, little remains known about the various selection pressures that have shaped how animals avoid predation whilst moving. Nonetheless, increasing interest in this area has allowed us to glean some understanding regarding the potential pressures influencing antipredation and motion (Ruxton *et al.*, 2019). Halperin *et al.* (2017) showed how potential motion dazzle colouration in lizards is related to foraging patterns, while Loeffler-Henry *et al.* (2019) drew links between the evolution of flash markings and prey body size. Although several studies provided evidence for size-related antipredation strategies, more emphasis was placed on stationary individuals rather than motion. Cryptic colouration, for instance, has been suggested to be more effective in smaller individuals while conspicuous colouration is often associated with larger individuals instead (Cott, 1940; Hagman & Forsman, 2003). It would thus be valuable to determine if the association of animal size with conspicuous colouration still holds true when motion is involved. A major question is why some animals have adopted one strategy, or a combination of them, over another. Phylogenetically controlled comparative studies assessing ecological correlates of specific strategies may help to answer this question and provide predictions to be tested in experimental studies.

With the myriad factors involved, it is difficult to disentangle the mechanisms involved in the detection and perception of animals in motion. For the purposes of this review, we discussed possible strategies that animals rely on to camouflage or avoid predation whilst moving. However, animals can simultaneously rely on multiple camouflage strategies to improve their survival chances when moving. For instance, a striped prey relying on motion dazzle may further confuse the seeker from accurately predicting its trajectory if it is moving in a group (Hogan *et al.*, 2016). Furthermore, as some antipredator defence strategies involving motion can be similar, it is possible that the mechanisms have some

overlaps. An animal with hidden colouration, for example, may use both flash and deimatic behaviour to improve its survivability against predators. As we glean more information on the mechanisms and factors influencing antipredator defence strategies in motion, understanding how these strategies interact to enhance the animal's odds of survival should be the next focus of study.

V. CONCLUSIONS

(1) The belief that movement can 'break' camouflage is over-simplified and various morphological and behavioural antipredator strategies may work synergistically to avoid capture. Various antipredator strategies aimed at concealing or misleading motion signals have been proposed, although empirical tests remain limited to date.

(2) Animals can conceal their motion through the strategic use of morphology or behaviour. Patterns appearing to be conspicuous when the animal is at rest may blur into the background when the animals move quickly enough. Through active motion camouflage, an animal can also move in a manner such that it appears to be stationary to the observer.

(3) Animals may create misleading motion signals to confuse or deceive the predator regarding its speed, trajectory, and position. This can be achieved through patterns – cryptic or conspicuous – as well as motion (protean and dazzle motion).

(4) Studies involving motion and antipredator defence remain limited, especially in ecologically relevant predator–prey systems. This is unsurprising as studies examining motion, patterns and perception are challenging. However, an increasing interest in this area, coupled with advancements in technology, could provide more insights into the mechanisms and potential selection pressures involved.

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Figure legend

Fig. 1. Two categories of antipredator defence mechanisms – concealing and misleading motion signals – used to reduce the risk of predation whilst moving. Top left to right: the banded krait *Bungarus fasciatus* which uses the flicker fusion camouflage effect; the cosmet moth *Ressia* sp. which spins when it lands to cause motion dazzle; the spider *Argiope versicolor* which uses protean motion in web bouncing. Bottom left to right: active motion camouflage is adopted by dragonflies such as *Neurothemis fluctuans*; motion masquerade is used by the dragon mantid *Stenophylla* sp., here outlined in grey as we propose that motion masquerade includes both concealing and misleading signals; behavioural mimicry of an ant-mimicking salticid *Toxeus maxillosus*; flash behaviour of the phasmid *Marmessoidea rosea*; Image credits: Mohammad Azlin bin Sani, Eunice Jingmei Tan and Daiqin Li.