

Realised hypothetical phenotypes and the adaptive value of Batesian mimicry



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Abstract

Batesian mimicry occurs when a harmless or palatable species has evolved to resemble certain traits presented by a harmful or unpalatable model, therefore gaining protection, and avoiding predation from potential predators. A common example studied throughout the literature is the harmless hoverfly mimicking the harmful, vibrant, stinging wasp. Differing species of hoverflies resemble their unpalatable model to differing degrees, creating a range of imperfect to perfect mimics. We tested the 'Eye of the Beholder' hypothesis, suggesting that the most important predators of the hoverfly have different sensory and cognitive abilities to those of a human. Consequently, the mimics that are viewed as inaccurate by humans may actually be perceived as accurate to varying predators, thus gaining protection. To further investigate this, during this study, species of praying mantises (*Creobroter yunnan*) and jumping spiders (*Phidippus regius*) were presented with 3D printed models of wasps, imperfect hoverfly mimics and non-mimicking flies. Individuals were randomly assigned a 'punishing' 3D model and were threatened with the model if an attack was made, training the individuals to avoid their respective 'punishing' model. Both the praying mantises and the jumping spiders were able to significantly differentiate between all three 3D printed models, with the jumping spiders attacking the intermediate hoverfly model faster. Thus, in this study, we show that different vertebrate predators can both distinguish between the models and their mimics, but respond to the mimic differently, with the mantises taking longer to attack. Overall, the results found provide support for the 'Eye of the beholder' hypothesis, suggesting that imperfect mimics are perceived differently by different predators, and are not in fact imperfect to the important predators.

Introduction

Mimicry occurs when one species, the mimic, has adapted to copy distinctive features of another, the model, due to the selective benefits of replicating and displaying these similar features (Mallet and Joron, 1999; Forbes, 2011; Kikuchi and Pfennig, 2013). Mimetic signals can target a variety of senses, and can be visual (Londoño, García and Sánchez Martínez, 2015; Stanger-Hall and Lloyd, 2015; de Jager and Peakall, 2016), acoustic (Barbero *et al.*, 2009; Moore and Hassall, 2016), chemical (Schiestl and Johnson, 2013), or behavioural (Penney *et al.*, 2014; Kitamura and Imafuku, 2015). In previous studies, it has been assumed that mimics should continue to experience selection to resemble their model to the closest possible degree (Sherratt, Speed and Ruxton, 2004). This therefore increases the likelihood that the mimic is able to gain the benefits associated with the act of mimicking, with the largest benefit usually being increased protection from predation that the species would have otherwise encountered.

Throughout ecological systems, there are numerous types of mimicking phenomena that have been acknowledged, however only a few have been investigated in detail. In particular, when looking specifically at defensive mimicry, the mimicking organisms are able to avoid harmful and potentially fatal encounters by deceiving and warning any predators. By resembling an unpalatable or harmful species, predators perceive the mimic as the harmful model therefore reducing the rate of attack.

One key example of this is Müllerian mimicry (Müller, 1879). The hypothesis proposed by Müller suggested that multiple unpalatable species evolve together to display similar warning colourations or signals. This therefore reduces the mortality an individual species is exposed to when training predators to avoid them, as the two species are able to share the burden (Sherratt, 2008; Stoddard, 2012). An example demonstrating this form of mimicry can be found in both the unpalatable lycid

beetles (*Calopteron terminale*) and the lichen moths (*Lycomorpha pholus*), which both display vivid markings on their wings of highly contrasting black and orange.

A second example, which will be the main focus of this study, is Batesian mimicry (Bates, 1862). Batesian mimicry occurs when a harmless or palatable species has evolved to mimic an unpalatable or unprofitable model, therefore resultantly gaining the same protection from predation as the undesirable model due to predator deception (Stoddard, 2012).

Aposematism

Physical resemblance is a key feature of visual mimicry. However, in order for this type of mimicry to occur, there is usually a distinctive visual feature that mimics are able to replicate. The colour patterns found on many animals are incredibly important to their survival, with many individuals, for example, relying on camouflage to escape predation. Aposematic species, instead of utilising colour patterns to camouflage and blend into their surroundings, create vivid, conspicuous warning signals (Mappes, Marples and Endler, 2005). These vibrant patterns alert potential predators to a secondary defence that typically renders prey unprofitable, such as a toxin or poison. There are examples of this throughout the animal kingdom. One particular example is the blue poison dart frog (*Dendrobates tinctorius azureus*), which is a vibrant shade of blue, directly contrasting with the dull green and brown tones of its natural habitat (Meshaka *et al.*, 2022). This colourful, physical, phenotype acts as a signal, alerting predators of the deadly toxin that they would ingest, should they attack the frog. Warning colourations act as a successful primary defence for aposematic species, as the colouration is often displayed in permanent features, such as fur, feathers, or scales. This type of warning signal is advantageous, as individuals do not have to detect the presence of a predator in order to defend themselves (Ruxton, Sherratt and Speed, 2019).

Batesian Mimicry

Although aposematism is seen in a large number of species, certain species display warning colouration or other conspicuous signals, without actually possessing a secondary defence mechanism. It is often the case that these species are mimicking a true aposematic species. Batesian mimicry was primarily defined by Bates (1862) and occurs when a relatively rare, palatable species gains a degree of protection due to closely resembling an abundant unpalatable model (Gilbert, 2005). The Batesian mimic is able to gain a certain level of protection from predators as it resembles the unprofitable model enough that the potential predator is unable to distinguish between the model and the mimic. As the mimic is often less abundant than the model, a potential predator tends to encounter the harmful models more frequently than the mimics. It is due to this that predators associate the copied feature of the model with an unpleasant and/or unprofitable experience, leading them to actively avoid both the model and the mimic, so as not to risk consuming the harmful species. This form of mimicry can be heavily dependent on the frequency of the mimic. Should the mimic increase in abundance, and the population levels are higher than that of the model, it is thought the mimic could lose its mimetic protection as the predator may encounter the palatable mimic more frequently than the harmful model (Gilbert, 2005).

If disruptive selection were to occur within the model population, it would be disadvantageous for both the models and the mimics within the system. If a new morph of the model evolved, the warning colourations would be novel and therefore potential predators would not identify individuals as inedible (Gilbert, 2005). Although it is often the case that Batesian mimicry is dependent on the frequency of the individuals involved, there is the possibility that the model is so highly noxious and/or threatening that predators have learned to strongly avoid both the mimics and the models, regardless of mimic frequency, in order to avoid the potential high level of danger (Finkbeiner *et al.*, 2018).

Imperfect Mimicry

Although it was initially thought that the more perfect the mimetic resemblance, the higher the level of protection, it is often the case that many Batesian mimics are not in fact perfect, (Sherratt, 2002; Gilbert, 2005), with some being incredibly inaccurate (Getty, 1987). For example, mimetic spiders within the genus *Cosmophasis* are associated with *Polyrhachis* ants, displaying a slight physical resemblance (Edmunds, 2006). However, although, from the human eye, they are clearly distinguishable from their models, the spiders are still able to gain protection from predation. The presence and evolution of these imperfect mimics still remains a slight mystery, as with all other things in nature, it is expected that natural selection should favour the more perfect mimicry, with imperfect mimics suffering the costs of conspicuousness without the benefit of fooling predators.

Various hypotheses have been proposed as to how this imperfect mimicry has evolved. All the proposed hypotheses can be sorted into three groups, depending on whether the primary focus of the hypothesis is the predator, the mimic, or the model (Kikuchi and Pfennig, 2013). The following hypotheses proposed specifically involve predator perception and how variation among predators may play a role in explaining the evolution of imperfect mimicry. It is worth noting that although all the hypotheses proposed are separate, they are not mutually exclusive from one another (Sherratt and Peet-Paré, 2017).

One hypothesis to explain the evolution of imperfect mimicry which focuses on the predator is known as the 'relaxed selection hypothesis' (Kikuchi and Pfennig, 2013). This hypothesis assumes that imperfect mimicry reflects a lack of selection, where certain imperfect mimics have equal fitness to their model as predators do not discriminate between the two. This is predicted on the belief that, when both models and mimics share signal dimensions, it is impossible for signal receivers to distinguish between them perfectly. This occurs because the selection pressure is

reduced closer to mimetic perfection as the mimic evolves toward the model's physical phenotype (Duncan and Sheppard, 1965; Sherratt, 2001, 2002). Predators or 'signal receivers' must therefore balance correctly accepting mimics against mistakenly accepting models (Sherratt, 2001, 2002).

In order to further explain this theory, others have used the signal detection theory within mathematical models (Oaten, Pearce and Smyth, 1975). The signal detection theory itself is used to optimise correct responses to varying signals and minimise any errors that may occur. Studies that have utilised the theory to suggest that predators should select a phenotypic threshold that guarantees a positive average payoff if they accept all individuals that fall on one side of that threshold (Oaten, Pearce and Smyth, 1975; Getty, 1985; Sherratt, 2001) (See fig 1). The specific threshold will vary, depending on three key factors: the costs of selecting a model, the benefits of choosing a mimic and the relative abundance of the two (Sherratt and Beatty, 2003; Lindström *et al.*, 2004). When models are particularly aversive or abundant, or mimics are relatively profitless or rare, a smaller percentage of the mimic population is attacked, with the threshold moving away from the mean model phenotype. It is due to this that selection for mimicry is weaker and the attack threshold is lower, therefore resulting in a wide range of mimic phenotypes near the phenotype of the model that have relatively equal fitness (Kikuchi and Pfennig, 2013).

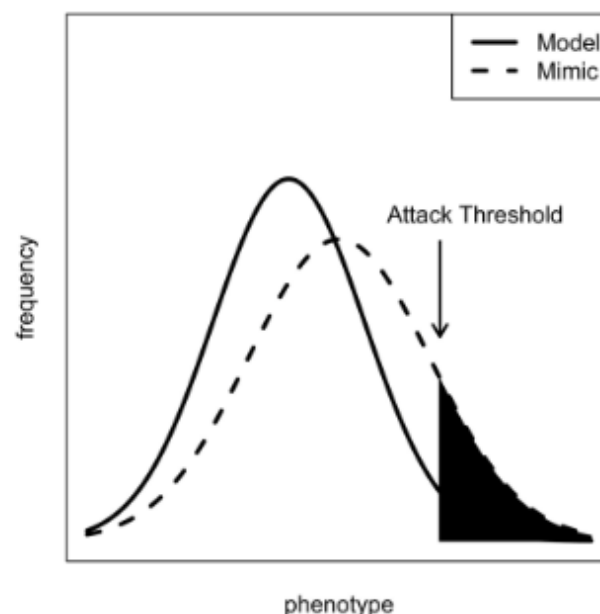


Figure 1: Threshold for selecting imperfect mimics when their phenotypic distribution differs from that of their models (Kikuchi and Pfennig, 2013).

Many studies have tested the relaxed selection hypothesis, primarily observing the response of animals or humans to artificial prey items (Schmidt, 1958; Caley and Schluter, 2003; McGuire *et al.*, 2006). One specific study, led by Harper and Pfennig (2007), looked at the precision of coral snake (*Micrurus fulvius*) mimicry by scarlet king snakes (*Lampropeltis elapsoides*) in relation to model abundance. When free-ranging natural predators were offered varying mimics in a geographical location where model abundance was lowest, it was found that predators only avoided the most accurate mimics. However, when predators were offered mimics in the centre of the model's geographical range, they attacked both perfect and imperfect mimics equally frequently. This study therefore supports the relaxed selection hypothesis, as the scarlet king snakes with the highest mimetic accuracy persist on the edge of the coral snake's natural range, where the model abundance is lowest, whilst imperfect mimics are able to thrive in the centre of the model's geographical range, where abundance is highest.

A second hypothesis that is often referenced is the 'multiple models hypothesis'. This particular theory was hypothesised by Edmunds (2000), and states that 'if mimics spatially occur over a large geographical area, it is likely that the same area contains a large number of potential models. Selection will therefore favour those individuals that imprecisely resemble many different species of models, or those with an intermediate physical phenotype, over those that precisely resemble only one model'. Therefore, if there are multiple models present and different predators have learned to avoid different, respective models, the intermediate or 'imperfect' mimics may gain more protection from a larger number of potential predators as they resemble more than one harmful model. Sherratt (2002) applied a mathematical framework to explore this idea. He assumed that both model and mimic phenotypes vary continuously and used signal detection theory to determine how predators set the optimal threshold for attacking prey. He found that when multiple sympatric models exist, mimicking species either evolve to accurately mimic one of them or produce an intermediate physical phenotype, depending on the similarity of the original models and whether

the models' own phenotypes are similar enough to confuse potential predators. However, when the models are allopatric, mimics with an intermediate physical phenotype are always favoured by selection, although it is often the case that the intermediate phenotype is weighted more towards one model than directly in the middle of the two (Penney *et al.*, 2012).

Several studies have observed that individuals of certain species are able to mimic more than one model (Mallet and Joron, 1999; O'Donnell and Joyce, 1999; Norman, Finn and Tregenza, 2001), with one particular example being the viceroy butterfly (*Limenitis Archippus*) mimicking the unpalatable monarch butterfly (*Danaus plexippus*), the queen butterfly (*Danaus gilippus*) and the soldier butterfly (*Danaus eresimus*) (Coles and Waldbauer, 2002). However, not many experiments have been carried out to actually test the multiple models hypothesis, with those that have been undertaken not fully supporting the theory. One particular study looked at poor hoverfly mimics and potential multiple bee and wasp models leading to intermediate mimics (Penney *et al.*, 2012). There was no evidence found for intermediate phenotypes between multiple models for the poor hoverfly mimics, suggesting that the multiple models hypothesis could not explain the evolution of imperfect mimicry within that particular system.

A third hypothesis as to why imperfect mimicry exists is the multiple predators hypothesis (Pekár *et al.*, 2011). This specific hypothesis differs from the multiple models hypothesis by focusing on the avoidance of predation by specialist predators. Mimics are likely to be targeted by more than one predator in the wild and this hypothesis focuses on the differing levels of selection produced as a result. Although many species are deemed to be highly suitable models as targets for Batesian mimicry, as their distinctive features provide a high level of protection, the models themselves are not completely shielded from predation. It is often the case that aposematic species are targeted by specialist predators that have evolved to attack and consume specific, usually unprofitable prey (Katsuyuki, Keiichi and Mitsutaka, 2002). If a mimic were to evolve to perfectly resemble the desired

model, it would gain full protection from many generalist predators. However, by perfectly resembling the aposematic model, the mimics become targeted by the specialist predators, reducing the evolutionary value of mimicking the model. This could explain why intermediate or imperfect mimics exist. By not fully accurately resembling the model, mimics deter the specialist predators from attacking, as they are able to distinguish between the model and the mimic. However, the mimics resemble the model enough to confuse the generalist predators, generating protection from them. As the generalist predators have a larger number of prey types to distinguish between, and also a larger selection of prey to choose from, the imperfect mimics display close enough resemblance to the aposematic model for a generalist predator to deem an attack not worthwhile, with the potential danger outweighing the potential reward. In order to test this hypothesis, Pekár et al., (2011) tested whether myrmecomorphic spiders (*Liophrurillus flavitarsis*, *Phrurolithus festivus* and *Micaria sociabilis*) were perceived as their models by two distinctive predators. The results highlighted that model-specialised predators attacked mimics significantly less frequently than the ant models, with less accurate mimics evading capture more frequently than the more accurate mimics. Conversely, when looking at the spider-specific predator, both models and mimics were rarely captured, highlighting that mimicking spiders gained protection (Pekár et al., 2011).

A final hypothesis worth noting is the 'eye of the beholder hypothesis' (Cuthill and Bennett, 1993). This hypothesis suggests that in some predator-prey interactions, imperfect mimicry does not exist. Instead, any visual imperfections are detected solely by human perception. Whilst we, as humans, are able to easily distinguish between mimic and model, the intended natural predator's perception of the mimics can differ greatly. Therefore, it has been suggested that apparent inconsistencies between models and mimics are indistinguishable to specific predators, meaning that imperfect mimics actually appear as accurate mimics to their intended receivers (Sherratt and Peet-Paré, 2017). One of the earliest studies to test the eye of the beholder theory used pigeons (*Columba livia*) as an avian predator, and their responses to wasps and hoverfly mimics (Dittrich et al., 1993). The

pigeons were first trained to discriminate between photographic slides of wasps and non-mimetic hoverflies, before being offered slides of a range of mimetic hoverflies. In order to objectify and measure the range of similarity between the hoverfly species and the wasps, an image processing program was utilised, generating individual percentages for how similar the colour pattern of each mimicking hoverfly was to the model wasp. The study itself concluded that pigeon attack rates declined in a sigmoidal pattern as the mimetic accuracy increased. More specifically, the mimetic hoverflies with a 50% similarity match or higher to the model wasp obtained the full benefit of accurate mimicry, with the pigeons actively avoiding them. A second mimicry system that has been observed for evidence in support of the eye of the beholder hypothesis is the mimicking of coral snakes by scarlet king snakes (Harper and Pfennig, 2007). The scarlet king snakes have evolved to display the same colours (red, yellow, and black) as the coral snakes, with both species having their markings arranged in rings. Studies have suggested that the relative proportion of the individual colours is under strong selection (Harper and Pfennig, 2007), as is the distinctive ringed patterns (Kikuchi and Pfennig, 2010). However, the order in which the colours are displayed differs between the two snakes, suggesting that the selection pressure is lower for this particular feature. Humans are able to distinguish between the mimic and the model fairly easily because of the difference in the order in which the colours are displayed, but for other predators that may not be the case, resulting in reduced selection pressure for mimetic accuracy in this respect.

Hoverfly Mimicry

Hoverflies are an excellent example of Batesian mimicry, with the harmless flies mimicking the vibrant colours and phenotypic features of stinging Hymenoptera. However, they are also a good example of imperfect mimicry. Whilst some hoverflies display an incredibly accurate resemblance to their various, respective wasp models, such as *Sericomyia silentis*, *Syrphus ribesii*, and *Episyrphus balteatus* (Taylor, Reader and Gilbert, 2016), others are exceptionally poor mimics yet still manage

to avoid predation and persist, for instance, *Melangyna labiatarum* and *Sphaerophoria scripta* (Taylor, Reader and Gilbert, 2016). Previous studies have been undertaken looking at this particular model-mimic complex (Dittrich *et al.*, 1993; Allen, Raison and Weale, 1998; O'Donnell and Joyce, 1999; Gilbert, 2005; Edmunds and Reader, 2014). One study by Penney *et al.*, (2012) focused on 35 different hoverfly species, looking at their abundance and recorded locations, along with individual photographs, to discern relevant phenotypic characters, including antenna length, abdomen length and abdomen colouration. Using all these data, three hypotheses to explain the persistence of imperfect mimicry were assessed and rejected. Firstly, looking at the specific phenotypic characters, it was concluded that avian rankings of mimetic fidelity displayed by the hoverflies positively correlated with human rankings, alongside the morphometric ratings calculated using a computer program. This suggested that imperfect mimicry in the hoverflies studies is not just an illusion resulting from the peculiarities of human perception. The abundance and location data collected were utilised to assess the multiple model hypothesis (Edmunds, 2000). It was found that, when mapped out in a multidimensional morpho-space, none of the mimicking hoverfly species overlapped with more than one model species. This led to the suggestion that for the particular hoverfly species observed, the multiple models hypothesis was not supported.

A second study of imperfect mimicry in hoverflies, by Bain *et al.*, (2007), focused more on the individual features mimicked by the hoverflies, assessing the rate of attack. Within this study, pigeons, previously trained to differentiate between wasps and non-mimetic flies, were offered images of increasingly accurate hoverfly mimics. In order to assess the pigeons' perception of the hoverflies' mimetic accuracy, the peck rates of the pigeons were recorded. An empirical model was then used to identify any specific features that the pigeons may have used to assess if an image was a threat or not. Overall, antennal length was a feature most commonly used to discriminate between mimetic flies and the model wasps. However, for each individual hoverfly species, a

different set of phenotypic features were important for predicting the number of pecks from each individual pigeon in order to obtain a reward.

The eye of the beholder hypothesis is thought to be a plausible explanation for the evolution of imperfect mimicry in hoverflies, with many studies finding supporting evidence (Cuthill and Bennett, 1993; Dittrich *et al.*, 1993; Taylor, Reader and Gilbert, 2016). When proposing the eye of the beholder hypothesis, Cuthill and Bennett (1993) made particular reference to hoverflies and their wasp mimicry. It was suggested that the lack of mimetic accuracy displayed by 'poor' mimics, is solely perceived that way due to human observation and our particular visual abilities (Cuthill and Bennett, 1993). It is possible that the mimics humans deem to be inaccurate could potentially be highly accurate when encountered by a predator with different cognitive and sensory capabilities (Taylor, Reader and Gilbert, 2016).

This Study

Given that the eye of the beholder hypothesis is a plausible, but mostly untested explanation for the evolution of the imperfect mimicry displayed by hoverflies, the focus of this study was placed on the hoverfly and wasp mimicry complex, looking specifically at the morphological differences between the imperfect mimics and their respective models. We examined the responses of different, non-avian predators to wasp models and their respective imperfect, hoverfly mimics. The aim therefore, was to assess how the responses differed between different predators and different models, investigating as to whether the eye of the beholder hypothesis is a plausible explanation for the evolution of imperfect hoverfly mimicry.

Although many studies have been undertaken on this complex in particular, the majority of experiments have focused on either avian predators (Mostler, 1935; Dittrich *et al.*, 1993; Ham *et al.*,

2006) or other vertebrates' perception (Nonacs, 1985; Hetz and Slobodchikoff, 1988; Osorio, Mikló and Gonda, 1999). Avian predation has been seen as an important component of the hoverfly and wasp mimicry complex, with early experiments demonstrating that the avian predators have the ability to select for Batesian mimicry but are also not easily fooled by imperfect mimics (Mostler, 1935). With many birds able to distinguish between certain mimics and their respective model, many mimetic hoverfly species do not appear to gain a great level of protection from avian predators as a result of their resemblance to their wasp model (Dlussky, 1984). However, birds are not the sole predators of mimetic hoverflies, with many invertebrate predators also attacking them (Howarth and Edmunds, 2000).

Currently there is an underrepresentation of invertebrate predators and their perception of imperfect mimicry, specifically within studies of the hoverfly-wasp complex. Many invertebrates play an important role within the hoverfly-wasp complex, acting as prominent predators of both, and therefore influencing the evolution of the mimicry. This lack of representation also reflects a wider issue in that invertebrate predator behaviour towards prey in general is poorly understood, with the small number of studies highlighting that (Gelperin, 1968; Berenbaum and Miliczky, 1984; Dejean, 1988; Morris and Reader, 2016). For instance, Dejean (1988) found that the hunting worker ants of the species *Odontomachus troglodytes* learned to avoid the larvae of an African chrysomelid beetle that displayed warning colouration, and was able to retain this learned behaviour for up to 28 days. Therefore, due to the current limited literature, in order to represent an invertebrate predatory response, species of jumping spider (*Phidippus regius*) and praying mantises (*Creobroter yunnan*) were used within this study.

Species of praying mantises can be found throughout many different biomes, with each having access to a wide variety of prey. Smaller species of praying manties, such as *Creobroter yunnan*, eat many different types of insects, including crickets, grasshoppers, butterflies, moths, spiders, and

beetles (Gelperin, 1968). Larger species of mantis can also be capable of attacking larger prey, with some consuming small birds and fish (Nyffeler, Maxwell and Remsen, 2017). When attacking prey items, the feeding behaviour of many praying mantises typically involves a period of time where the individual visually searches for prey, a slow approach towards the selected prey, followed by an extremely fast grasping movement of the front legs, leading to ingestion (Gelperin, 1968). Similarly to praying mantises, jumping spiders also have a very varied diet, consuming invertebrates such as fruit flies, crickets, butterflies, moths, mealworms and other spiders (Jackson and Pollard, 1996). Jumping spiders also follow a similar hunting strategy to the praying mantises, with their behaviour being divided into four stages, orientating, pursuing, crouching, and jumping (Drees, 1952), with the final stage resulting in the prey item being grasped within the spider's forelimbs (Forster, 1977). As praying mantises and jumping spiders are deemed generalist species, with both consuming a large proportion and range of invertebrates within their diet, it was reasoned that both the mantises and the spiders would be good representatives for general invertebrate predators within this study.

A novel technique used within this study was the use of 3D printed models. In most other studies which have sought to explore the significance of variation in mimetic accuracy, predators have been presented with either 2D images of real wasps and hoverflies (Dittrich *et al.*, 1993; Penney *et al.*, 2012) or simple, crude models (Rashed *et al.*, 2005; Aslam, Nedvěd and Sam, 2020). By using 3D models of both the flies and the wasps, it creates a closer representation to what invertebrate predators of the hoverflies would find in the natural world, without using real specimens. The models used within this study were created using photographs of captured invertebrates to create accurate 3D printed models of wasps, non-mimetic hoverflies and mimetic hoverflies. The novel use of 3D printed models in this study is advantageous due to the presentation of realistic phenotypes, rather than coloured representative, shapeless objects.

In order to assess the invertebrate predator response to the hoverfly–wasp mimicry complex, 3D printed models of wasps, non-mimicking hoverflies, and mimicking hoverflies were presented to laboratory-reared praying mantises and jumping spiders. Firstly, 3D printed models of wasps and non-mimicking flies were presented to each predator, with the aim to characterise any innate preferences or biases for one model over another. Secondly, predators were trained to avoid attacking either a wasp or a fly 3D model by associating them with a punishment. It was hypothesised that as the number of previous punishments increased, the individuals would learn to avoid the ‘threatening’ prey, showing a reduced attack rate and/or increased time taken to attack the punishing model. Finally, an intermediate mimetic hoverfly 3D printed model was introduced, each individual was presented with this hoverfly 3D model, with the aim to assess whether the intermediate physical phenotype resembled their respective punishing model enough to be treated as a potential threat, therefore gaining protection from predation. Within this study, an ‘intermediate mimic’ was deemed to be a species of hoverfly displaying a physical phenotype halfway between a wasp and a non-mimetic fly.

Methods

Predatory Invertebrates

In order to observe the predatory response and attack rate towards various, physically different models, species of both praying mantises and jumping spiders were used as the invertebrate predators within this study. For the praying mantises, *Creobroter yunnan* was used, a species originating in South-eastern China, now distributed throughout Asia (Yager, 1996). Once fully grown, female individuals range between 5cm and 5.5cm, with males slightly smaller, at 4cm to 4.5cm. For the current study, mantises were obtained from an online pet supplier (thespidershop.co.uk), as third or fourth instar nymphs, averaging 2.5 cm in length. By the end of data collection, the mantises were all adults with an average prothorax length of 4 cm. Due to the size of the mantises at the start of data collection, individuals were unable to be accurately sexed and therefore the experiments did not distinguish between sexes. When housing individuals, the mantises were raised in transparent plastic enclosures (10 cm x 15 cm x 7 cm) with a perforated lid, individually to prevent aggression. They were kept at a constant temperature of 27°C, with each being misted daily to maintain a constant level of humidity. Each individual was fed once every 4 to 6 days, initially with live mealworms, the quantity increasing as the mantises increased in size, then with a live cricket towards the end of data collection. No data collection occurred the day after feeding to ensure the mantises were hungry enough to want to attack the models.

There were two types of spiders used for the jumping spiders, *Phidippus regius* 'Rastafari', the Blue Mountain jumping spider, and *Phidippus regius* 'Apalachicola'. *Phidippus regius* is commonly found in South-eastern US and throughout the West Indies, with the Blue Mountain jumping spider located specifically in the Blue Mountain range within Jamaica. The spiders were also obtained from an

online pet supplier (thespidershop.co.uk) and used for a previous study. When used for this study, all the spiders were fully grown, with *P. regius* Rastafari averaging a body length of 12 mm and *P. regius* Apalachicola averaging 20 mm. Similarly to the praying mantises, all the spiders were kept in individual enclosures in order to prevent individuals from mating and attacking one another. The enclosures used to house the spiders were identical to the ones used for the mantises, also with a constant room temperature of 27°C and daily water misting. The feeding schedule of the spiders was slightly different to the mantises, with a live cricket being offered to the spiders once a week, with two consecutive days following where no data were recorded.

3D Printed Models

I presented life-size full-colour 3D printed models, accurately representing both models and mimics, to the mantises and spiders. To create the 3D printed models, specimens of wasps (*Vespula vulgaris*), non-mimetic flies (*Mesembrina meridiana*) and mimetic hoverflies (*Syrphus ribesii*) were collected. These specimens were collected, and the 3D models created, as part of a larger study, led by Christopher Taylor, University of Nottingham. The collected specimens were individually pinned with the anterior-posterior axis aligned vertically, allowing photographs to be taken. Photographs were taken at 12 horizontal levels, with three photos being taken at differing angles, resulting in a total of 36 levels. Accurate 3D models were then reconstructed using 3DSOM software (Pro version 5) and Blender software (2.91) was used to edit the 3D shapes before printing commenced. When editing, the minimum thickness of wings were set to 0.4mm and both the legs and antennae were set to a minimum of 0.6mm. The wings themselves were assigned a flat colour of 50% grey as printing with translucent plastic was not possible. Regarding the colour palette of the 3D printed models, using blender software, body colours were segmented into either

uniform black or yellow patches, with the specific colour being assigned using the median colour values for the vertices in each corresponding patch. The 3D printed models were then built using HP Jet Fusion 580 3D printer (originating in the United States of America) (See fig. 2). When printed, the models were attached to a base, in order to maintain stability during printing. The base was then removed from each model using a scalpel before any trials commenced.



Figure 2: 3D printed models of *Mesembrina meridiana* (Left), *Syrphus ribesii* (Centre) and *Vespa vulgaris* (Right), prior to being removed from the base plate.

Experimental Arena

Models were presented to spiders and mantises individually, in an experimental arena (See fig. 3) consisting of 6 parts: the arena enclosure, a one-way mirror, the desired 3D model, a motor, a connected fishing wire with a counterweight and a computer programmed to generate movement of the attached 3D printed model. The arena enclosure was an opaque plastic box, measuring 11 cm x 26 cm x 7 cm. The opaque sides and one-way mirror lid ensured the invertebrate inside the enclosure was not distracted by external movement and focused solely on the model being

presented. In order to present the 3D printed models, a small loop of fine fishing wire was attached to the thorax of each model, to which a small metal hook was attached. A line of fishing wire was then threaded through the metal hook, and also through two holes in the walls on either side of the enclosure, elevating the model in the centre of the arena.

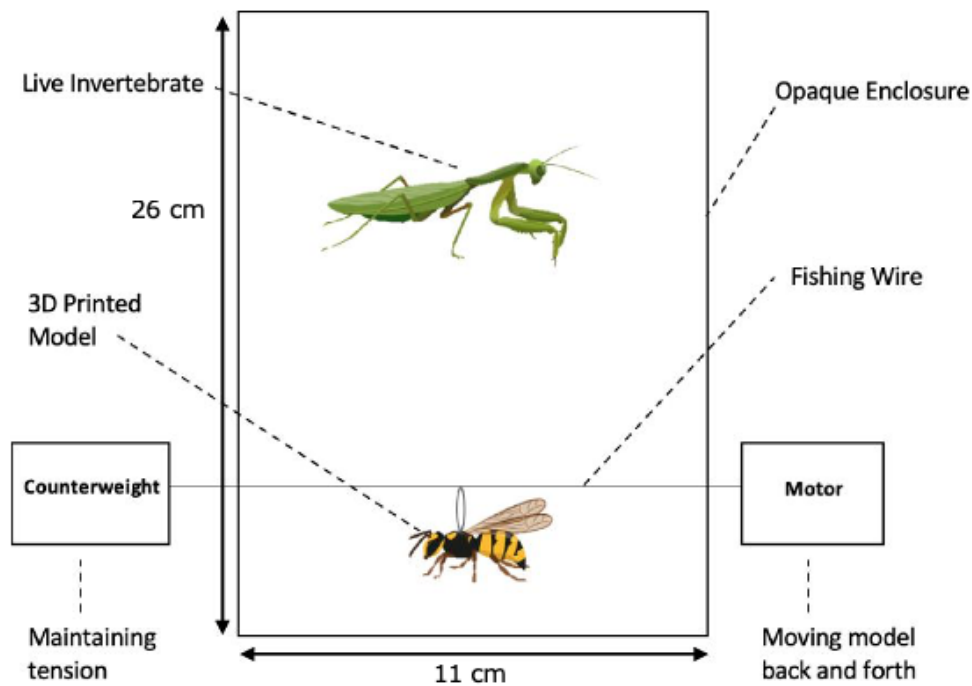


Figure 3: The apparatus used to observe the responses of both jumping spiders and praying mantises to varying 3D printed models (see text), with models and invertebrates not shown to scale.

On one end of the fishing wire a counterweight was added, in order to maintain tension and keep the model elevated. A motor was attached on the other end of the fishing wire, along with a single-board microcontroller (A000052), produced by Arduino (originating in Italy), programmed to generate movement of the motor at full speed (approximately 1cm per sec) in bursts of variable duration (randomly selected between 1-2 sec), interspersed with pauses of variable duration (randomly selected between 0-1 sec). The spinning of the motor moved the fishing wire jerkily

across the centre of the arena in view of the predator, for a randomised length of time between 1 and 5 seconds, at which point the direction of travel was reversed.

Innate Response

The untrained and innate response of the praying mantises to the non-mimic fly (*Mesembrina meridiana*) and the true wasp (*Vespula vulgaris*) was the first set of data to be recorded. For one trial, an individual mantis was first placed inside the arena and left to acclimatise to the enclosure for a total of 2 minutes. Prior to placing the praying mantis in the arena, the selected 3D model was attached to the fishing wire on one side of the arena. When the acclimation period had ended, the motor was started, moving the model backwards and forwards, mimicking flight, in front of the mantis. During pilot trials, both the mantises and the jumping spiders displayed no reaction towards the model when stationary and only responded once movement was initiated. This therefore led to the start of the trial being timed from the moment the motor was switched on. The time taken for the individual mantis to attack the model was then recorded, with it also being noted if no attack occurred at all. If an individual had not attacked the model after 120 seconds, the response of 'no attack' was recorded and the trial stopped. This period of time was selected as during pilot trials, no attacks were made after 115 seconds, with trials being run for up to 3 minutes.

Within this study, for a strike to classify as an 'attack', the individual mantis had to strike the model with its front legs, making clear contact by either hitting or holding onto the model. A total of six trials was undertaken in a random order for each individual mantis, three using the non-mimicking fly model, and the other 3 using the true wasp model. Overall, 15 mantises were used within the experiment, resulting in a total of 83 individual trials. Each individual underwent the 6 trials, with the exception of 1, which died during data collection. Consequently, the data collected from their limited trials were removed prior to data analysis, therefore resulting in 14 individuals being included in the

analysis. The innate response of the jumping spiders was not recorded during this study, as during the time of the initial data collection, the jumping spiders were being utilised for a separate study. When the jumping spiders became available, they had already been exposed to a number of training trials with the same 3D models, within the separate study and therefore their innate response could not be recorded within these experiments.

Learned Response

Both the spiders and the mantises were used during this section of data collection. In order to test for a learned response to a punishment associated with a particular model, equal numbers of individuals were randomly assigned either the wasp (*Vespula vulgaris*) or the non-mimic fly (*Mesembrina meridiana*) as a punishing treatment. In the punishing treatment, if an individual attacked the model, an identical model, attached to a metal rod, was pushed repeatedly towards the individual in a threatening way. When pushed towards the individual, the model was held at least 1 cm from its face, preventing direct injuries. The model was continually pushed towards the mantis or spider in this manner for 10 seconds. This treatment was accepted to be threatening towards both the mantises and the spiders due to the responses it produced. Each individual responded in a similar way, by firstly dropping the model, if it hadn't been released previously, then quickly retreating, evading the threatening treatment.

For the praying mantises, a total of seven trials were undertaken, with each individual receiving four punishing treatments and three non-punishing treatments. Every individual received their respective punishing model on the first trial, with the treatments received thereafter being in random order. At the start of data collection for the taught response of the mantises, a total of 10 individuals were used in the first trial. During the data collection for the subsequent trials, two individuals died. Consequently, any data collected from these two individuals were removed before analysis.

When presenting and analysing data, for the innate response, the trial number was used as one of the independent variables. However, during this section of data collection, this was changed to the number of previous punishments. This was due to the fact that the question we were asking focused on the predator's attack time after increasing numbers of punishments, and as the model presentation order had been randomised for each individual, on a specific trial, each mantis had received differing numbers of previous punishments.

As the spiders had been used previously in a similar study using the same models, each individual had already been assigned a punishing model and had already received three previous punishments, in the same manner as this study. A total of seven jumping spiders were subjected to a further five trials, with three punishing treatments and two non-punishing treatments, resulting in six punishing treatments in total, when including the previous study. Similarly to the praying mantises, on the first trial, each individual was presented with their punishing model, with the subsequent trials presented in a random order. The arena set-up and data collection was the same as for the innate trials, with the time taken for an individual to attack being recorded. However, during this section of data collection, the length of an individual trial was increased to 180 seconds before a 'no attack' response was recorded. This was increased, to allow for a potentially delayed attack due to a learned behaviour.

Intermediate Mimetic Response

In order to test responses towards mimetic, physical phenotypes, a 3D printed model of a mimetic hoverfly was introduced to the methodology. The hoverfly model was of *Syrphus ribesii*, a species which is considered to be a moderately accurate wasp mimic, easily distinguishable to the human eye, but deceiving to other predatory species (Edmunds, 2000). The models were presented to both

the mantises and the spiders in the same manner as previous sections, with the time taken for an individual to attack being recorded. The praying mantises underwent eight trials for each individual, consisting of four hoverfly trials, two with their respective punishment treatment and two with their non-punishment trials, with the punishment trials still resulting in the punishment if the model was attacked. All the individual mantises received their models in the same order: Mimic, Punishment, Mimic, Non-punishment, Mimic, Punishment, Mimic and then finally Non-Punishment. During data collection a total of 5 mantises were used, as unfortunately in between the taught and intermediate responses, a number of mantises died. The punishing models previously assigned to the remaining mantises remained even, with 3 mantises being punished with the non-mimicking fly model and 2 mantises being punished with the wasp. As the 3D models were presented in the same order for each individual, when analysing and presenting the data, the trial number was used, rather than the number of previous punishments.

The data collection for the spiders followed a similar methodology to the mantises; however, each individual was only subjected to five trials, due to time constraints. Each individual received three Mimic trials, one Punishment trial and one Non-punishment trial. The order of the trials, like the mantises, was the same for each individual, following the sequence of: Mimic, Punishment, Mimic, Non-punishment and then Mimic. When collecting data for the intermediate response, a total of seven spiders were used with each one undergoing all of the five individual trials.

Experimental Overview

Table 1: Experimental overview detailing each individual experiment

Experiment	Predator	Predator Sample Size	Type of Stimuli	Number of Trials
Innate Response	Praying Mantis (<i>Creabroter yunnan</i>)	12	Non-Mimietic Fly True Wasp	6
Learned Response	Praying Mantis (<i>Creabroter yunnan</i>)	8	Non-Mimietic Fly True Wasp	7
Learned Response	Jumping Spider (<i>Phidippus regius</i>)	7	Non-Mimietic Fly True Wasp	5
Intermediate Response	Praying Mantis (<i>Creabroter yunnan</i>)	5	Moderate Wasp Mimic Non-Mimietic Fly True Wasp	8
Intermediate Response	Jumping Spider (<i>Phidippus regius</i>)	7	Moderate Wasp Mimic Non-Mimietic Fly True Wasp	5

Statistical Analysis

For each response, for both the spiders and the praying mantises, generalised linear mixed models were created in R version 4.1.1 (R Core Team (2022). R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.). For the mean minimum adequate models, I compared the fit of all possible combinations of predictor variables using AIC values. Models were narrowed down to those with a difference of less than 2 from the lowest AIC value, and then the simplest such model (with the fewest terms) was selected as the most parsimonious. When analysing data, all the experiments regarding the time taken to attack a model had a Poisson error structure applied to them. When plotting and examining the histograms of the residuals found in the proposed models, the outputs appeared to fit an approximate normal distribution. The exception to this being the initial innate response experiment, recording the frequency of attacks, which was analysed using binomial distribution. Before simplification, all models included the same independent variables, treating 'individuals' as a random effect. For the

experiments in both the learned response and the intermediate mimetic response, an interaction term was introduced, between whether the model presented was a punishing model and how many punishments had previously been experienced.

Results

Innate Response

Overall, a total of 60 trials resulted in attacks out of the 82, involving both the wasp and the non-mimetic fly models. The model wasp was attacked more frequently, with 32 of the 41 trials resulting in attacks, whilst the non-mimetic fly model was attacked at a slightly lower frequency of 28 out of the 41 trials (See Fig. 4). The best fitting statistical model required no simplification, with all variables remaining in the model (See appendix Table 1). There was no significant difference between the number of attacks on the model wasps and the number of attacks on the model non-mimicking flies (log odds = 0.608, 95% confidence interval = (-0.48, 1.69)).

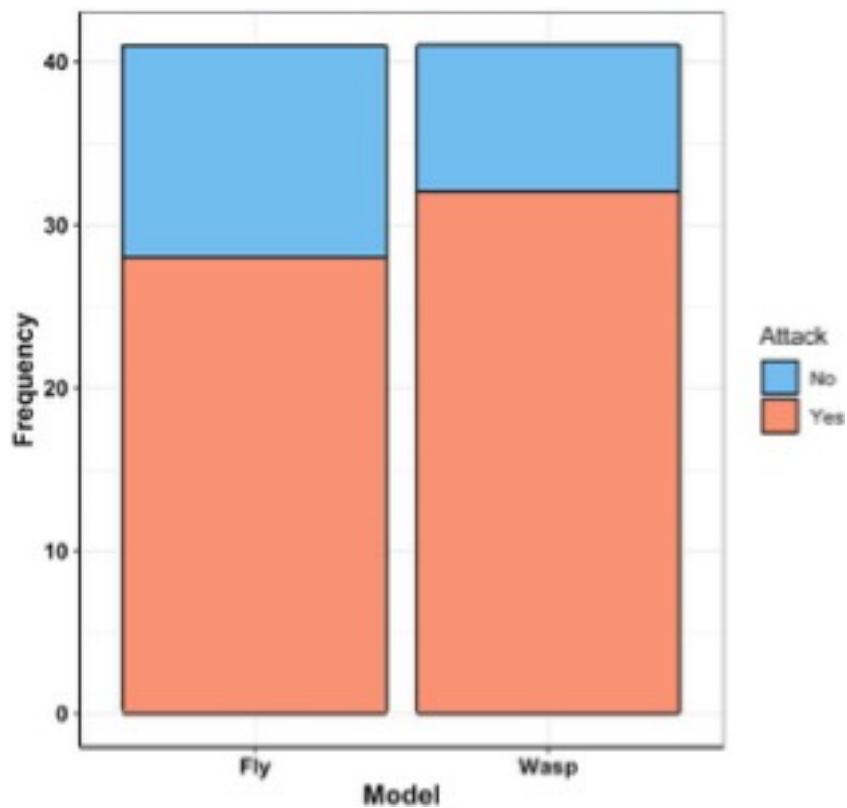


Figure 4: The total frequency of attacks (red) and non-attacks (blue) by individual praying mantises on 3D printed models of wasps (*Vespula vulgaris*) and non-mimetic flies (*Mesembrina meridiana*).

When looking specifically at the time taken to attack, the data were taken directly from the previous innate response data, however only using the trials where an attack was made. The time taken for the individual mantises to attack the model of the wasp was slightly faster, with an average time of 26.76 seconds, whereas the average time taken to attack the non-mimicking fly model was slightly longer at 29.37 seconds. (See Fig 5). In order to find the best fitting model, all potential models were compared. Two models were generated, differing by 2 in the AIC values; Consequently, the original, with the lower value, was accepted (see appendix Table 2). The time taken for an individual to attack a wasp model was significantly higher than the time taken for an individual to attack a non-mimicking fly model (log odds = -0.103, 95% confidence interval = (-0.192, -0.0128)).

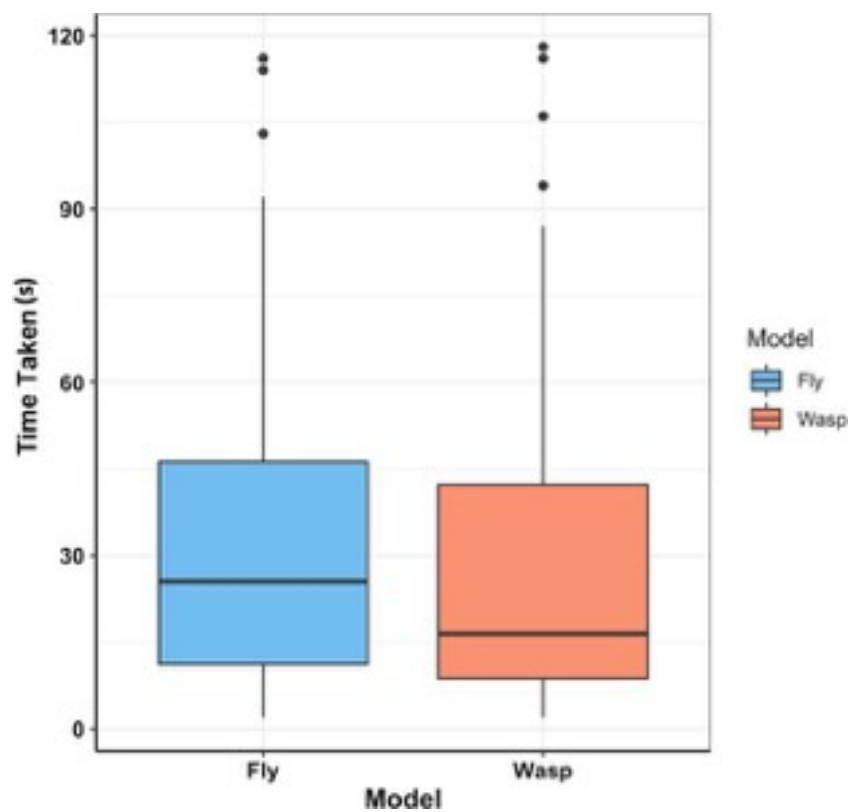


Figure 5: The time taken for individual praying mantis to attack 3D printed models of wasps (*Vespula vulgaris*) (red) and non-mimetic flies (*Mesembrina meridiana*) (blue).

Learned Response

Praying Mantis

During the learned response trials, out of the total 56 trials, 52 resulted in attacks with only 4 receiving no attacks. Consequently, no analysis was undertaken on the comparison between the number of attacks versus no-attacks.

Towards the start of data collection, the average time taken to attack each respective model was below 25 seconds (See Fig 6). As the number of previous punishments increased, the average time taken to attack the punishing model also increased, with individuals taking longer to attack. Conversely, the time taken to attack the non-punishing model remained low as the number of previous punishments increased, with the average time taken to attack still remaining below 25 seconds by the end of data collection (See Fig. 6).

When comparing the two, the best fitting model included the independent variables of the individual mantises and the interaction between whether the model presented was a punishing model and how many punishments have previously been experienced (See appendix Table 3). The time taken to attack the punishing models was significantly longer than the time taken to attack the non-punishing models (log odds = -0.351, 95% confidence interval = (-0.54, -0.159). This significant difference suggests that the individual mantises were able to distinguish between the two different models, with the delayed attack times on the punishing model also suggesting the mantises were learning which particular model resulted in a punishment if attacked.

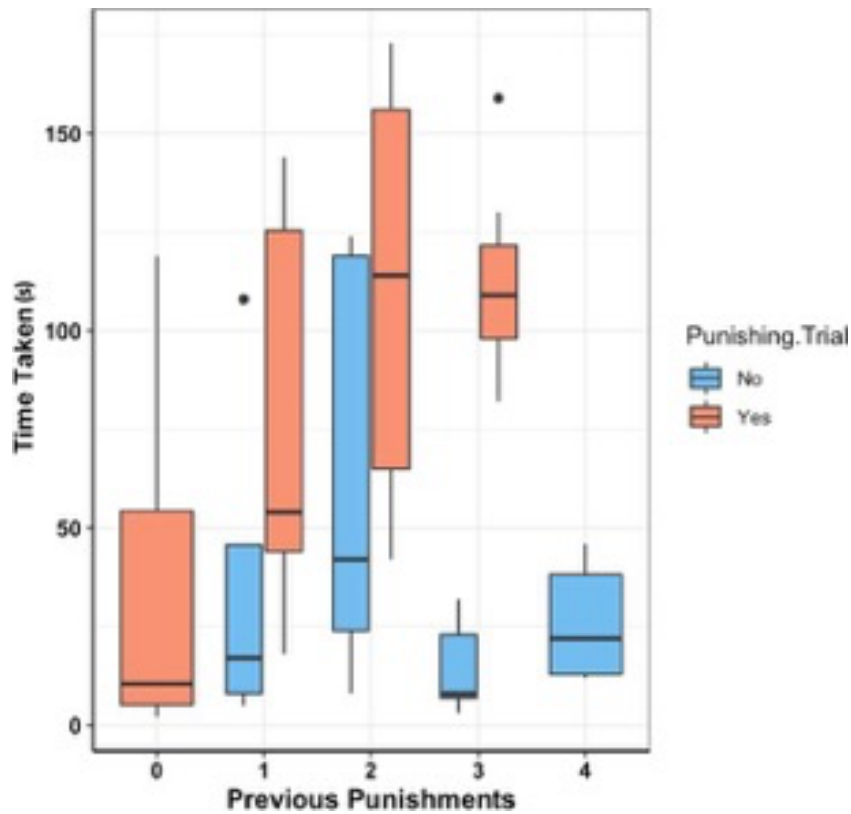


Figure 6: The time taken for individual praying mantises to attack their respective punishing models (Red) or non-punishing models (Blue), with the number of previous punishments increasing.

Jumping Spiders

Similarly to the learned responses from the praying mantises, out of the 35 trials, only four received no attacks, with the remaining 31 trials resulting in an attack. Consequently, no data analysis was undertaken on the probability of attack.

As the jumping spiders had previously been used in other experiments, the individual spiders had already experienced previous training. Consequently, at the start of the experiment, the average time for an individual to attack a punishing model was above 75 seconds, considerably longer than

the time taken to attack the non-punishing model which was below 25 seconds. The time taken to attack the punishing model continued to increase as the number of previous punishments increased, following a similar trend to the praying mantises (See Fig. 7). The trend for the time taken to attack the non-punishing model also followed a similar trend to the praying mantises. The average time taken to attack the non-punishing models all remained below 25 seconds, with the jumping spiders readily attacking the 3D models as the number of previous punishments increased.

To analyse the learned response of the jumping spiders, the best fitting model included the independent variables of the individual mantises and the interaction between whether the model presented was a punishing model and how many punishments have previously been experienced. Although the model selected did not have the lowest AIC value, the delta value was still below 2. The selected model also still included the interaction between the number of previous punishments and whether or not it was a punishing trial, whereas the model with the lowest AIC value did not (See Appendix Table 4). By the end of the punishing trials, the time taken to attack the punishing models was significantly longer than the time taken to attack the non-punishing models (log odds = 2.71, 95% confidence interval = (1.76, 3.66). The significant difference between the two highlights the difference in latency to attack between the punishing models and the non-punishing models, emphasising the fact that the spiders were able to distinguish between the two models and were also learning which model generated a punishing response, should it be attacked.

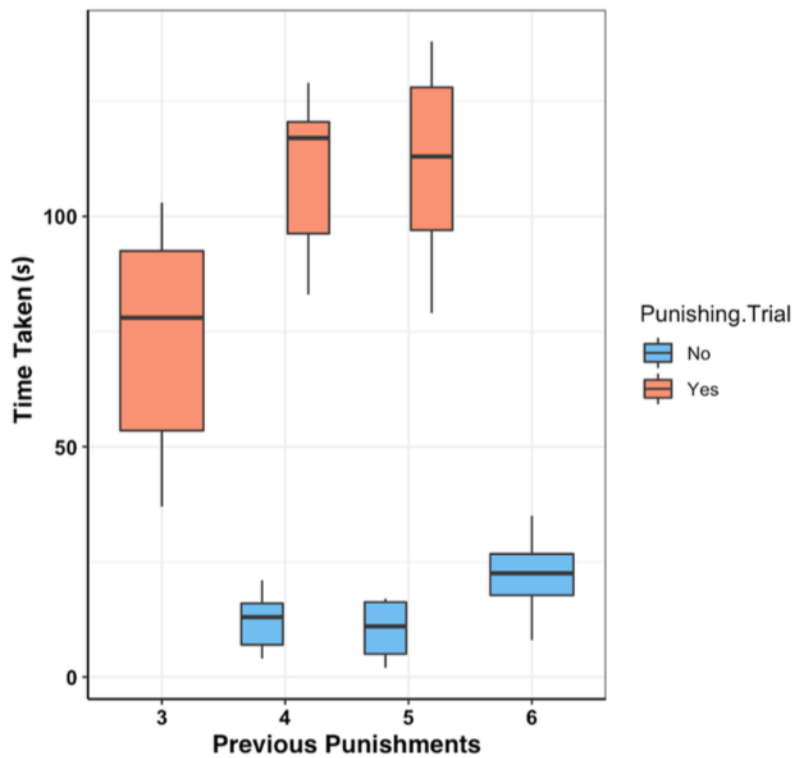


Figure 7: The time taken for individual jumping spiders to attack their respective punishing models (Red) or non-punishing models (Blue), with the number of previous punishments increasing.

Intermediate Mimetic Response

Praying Mantis

During the intermediate mimetic response experiment, a total of 40 trials were undertaken with the praying mantises. Out of the 40 trials, 35 resulted in an attack, with only five trials having no attacks. Consequently, no data analysis was carried out on the probability of an attack.

When looking at the two non-punishment trials undertaken during the intermediate mimetic response experiment, the responses were very similar to those recorded during the learned response trials, with the average time taken to attack remaining fast and constant, below 30 seconds (See Fig. 8). Conversely, the two punishment trials had a much higher average time taken to attack, as seen previously seen in the learned response trials. However, rather than continuing to increase in time, as seen in the trend displayed during previous experiments, the two trials produced similar response times, just below 125 seconds. During these trials, the 'intermediate' mimicking hoverfly was introduced. The praying mantises were hesitant to attack the intermediate model, with the average time taken to attack being slightly shorter than the response to the punishing models. This response remained consistent, with the average time taken to attack remaining between 80 and 110 seconds as the number of trials and previous punishments increased.

After testing the fit of the original model, the best fitting model included the random effect of the individual, the model type, and the trial number (See appendix Table 5). A significant difference was found between the time taken to attack the intermediate model and the time taken to attack the non-punishing model (log odds = -1.40, 95% confidence interval = (-1.26, -1.54). Although the average time taken to attack the intermediate model across all the trials was close to the time taken to attack the punishing model, a significant difference was also found between the two, with the time taken to attack the punishing model being significantly longer (log odds = 0.243, 95% confidence interval = (0.159, 0.326). The significant differences found between the intermediate mimicking model and both the respective punishing and non-punishing model suggests that the praying mantises were able to distinguish between the three different models. However, as seen in figure 7, the mantises, on average, had a higher latency to attack the intermediate model, potentially initially regarding it as possible threat and therefore taking longer to decide whether or not it was safe to attack.

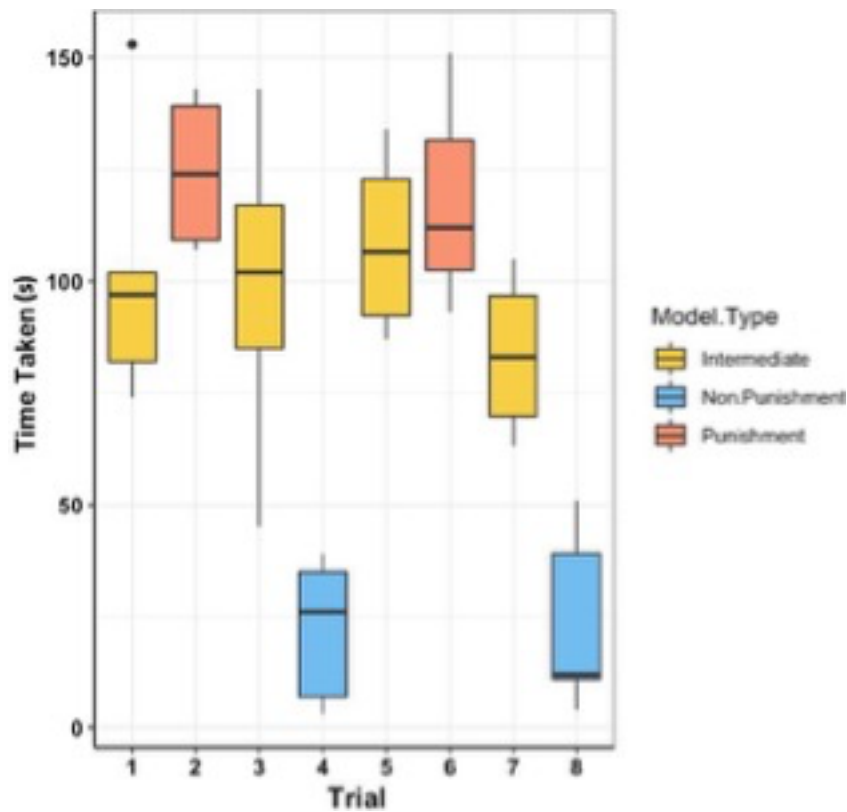


Figure 8: The time taken for individual praying mantises to attack their respective punishing models (Red), non-punishing models (Blue), and an intermediate model (yellow).

Jumping Spiders

Out of the total 35 trials, attacks were made in 33, with only two resulting in no-attacks. Consequently, as in previous experiments, no data analysis was presented on this particular variable.

As seen in the learned response trials, the time taken to attack the punishing model was above 100 seconds, with the spiders continuing the trend of a long latency to attack (See Fig. 9). It is also worth noting that the two 'no-attacks' recorded during this experiment occurred during the punishing model trial, suggesting the continued learning of the spiders to be wary of the punishing model. The

jumping spiders response towards the non-punishing model was also similar to the response observed during the learned response trials, with the time taken to attack being comparatively low at an average of 9.4 seconds. The response of the jumping spiders towards the intermediate mimicking model was different to that of the praying mantises. The spiders attacked the intermediate model much faster than the praying mantises on average, with the time taken to attack being closer to the that of the non-punishing model than the punishing model. These attack times also remained similar, with median values remaining between 20 and 30 seconds, and slowly decreasing through the trials as the average time taken to attack the intermediate model continued to get gradually faster.

After simplification, the best fitting model included the individual as the random effect, along with the model type and the interaction between model type and trial number as the independent variables (See appendix Table 6). When focusing on the difference between the jumping spiders' responses to the intermediate mimicking model and the punishment model, a significant difference was found, with the time taken to attack the punishing model being significantly higher (log odds = 1.39, 95% confidence interval = (1.25, 1.53). Although the time taken to attack the non-punishing model was very close to the time taken to attack the intermediate mimicking model, a significant difference was also found, with the time taken to attack the non-punishing model being significantly faster (log odds = -0.85, 95% confidence interval = (-1.121, -0.59). As seen with the two significant differences, the spiders were able to distinguish between the three models, similarly to the praying mantises. However, unlike the mantises, it appeared the spiders were able to ascertain the intermediate mimicking model was not a threat comparatively quickly. Although, they still took slightly longer to attack the intermediate model than their respective punishing model.

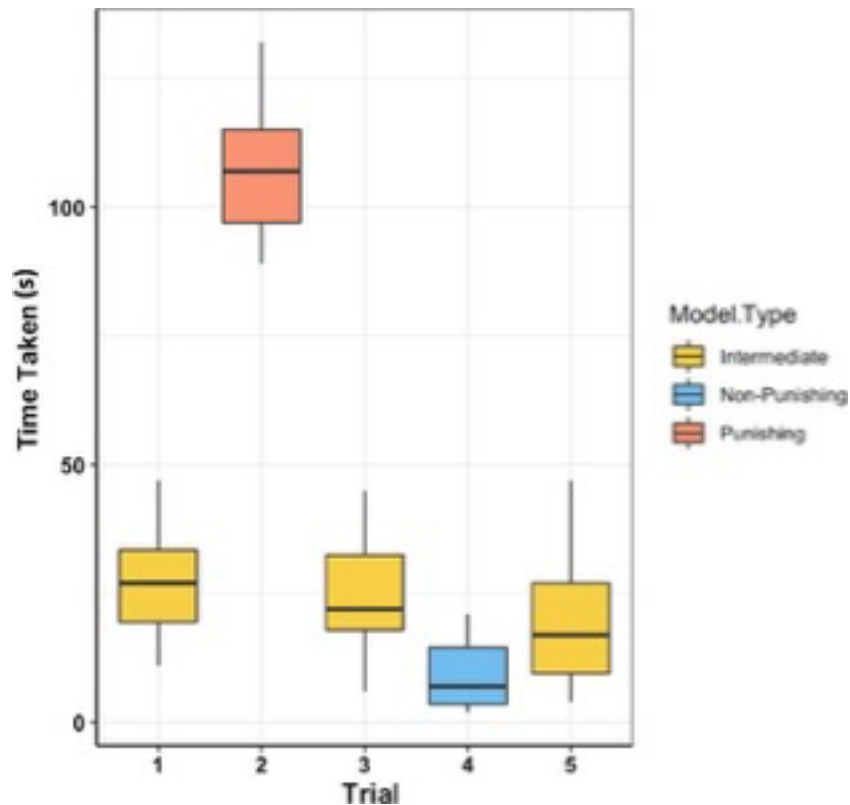


Figure 9: The time taken for individual jumping spiders to attack their respective punishing models (Red), non-punishing models (Blue), and an intermediate model (yellow).

When comparing both the praying mantises and the jumping spiders, they had differing responses to the mimicking hoverfly model. On average, the praying mantises took longer than the spiders to attack the hoverfly model, with the time taken to attack being almost as long as the time taken to attack the punishing model. In contrast, the time taken for the jumping spiders to attack the hoverfly model was much closer to the response time towards the non-punishing model. As the time taken to attack the imperfect model was still significantly different, this suggests that the spiders were able to distinguish between the model of the imperfect mimic and both the wasp and the fly, acting as the respective non-punishing model. However, the spiders were able to decide much faster that the hoverfly model was not a threat, with the average response times being almost as fast as the time taken to attack the non-punishing models. No statistical analysis was undertaken comparing the

two, as they were not directly comparable, due to the difference between the methods in data collection.

Discussion

The experiments undertaken within this study tested the responses of two taxonomically well-separated invertebrate predators to 3D printed models of individuals within the hoverfly-wasp mimicry complex. The results show that the jumping spiders and the praying mantises are able to perceive the difference between models of a wasp and of a non-mimic fly, at least after learning to associate one model type with punishment. There was limited evidence of an innate difference in responses to the two models in mantises: whilst they were no more likely to attack wasp models, they did attack them slightly more rapidly. When they were trained to associate a model with punishment, the time taken by both species of invertebrate predator to attack the punishing model gradually increased with the number of previous punishments, such that the difference in responses to the two models amongst experienced individuals was very large. This suggests that each individual learned the consequences of attacking a punishing model, utilising the differing features of the 3D models to distinguish between the two. When comparing the learned responses of the mantises to that of the spiders, there was a difference between the two. The praying mantises seemed to generalise their learned responses to the hoverfly mimic, which was attacked less rapidly than the non-punishing model, thus treating it as a potential threat. Conversely, this generalisation was much weaker in the spiders, which appeared to be much more capable of distinguishing between the three different models, attacking the mimic almost as readily as the respective non-punishing model.

The learned responses of jumping spiders and praying mantises to 3D models are consistent with previous studies showing the capacity for learning in both taxa (Maldonado, 1972; Maldonado, Jaffé and Baldérrama, 1979; Nakamura and Yamashita, 2000; Skow and Jakob, 2006; VanderSal and Hebets, 2007; Liedtke and Schneider, 2014; de Agrò, Regolin and Moretto, 2017; Carle *et al.*, 2018).

For the learned response of praying mantises, Maldonado (1972) used a similar technique, presenting each individual with a star or a fly. This particular study differed from our own, as the praying mantises were prevented from attacking a specific model, rather than punishing any attempted attacks, as was done within this study. Similar to our findings, the time spent before an attempted attack gradually increased with the number of trials, also leading to a reduction in the amplitude of head movements, with individuals learning not to attack the unrewarding offering. The learning of jumping spiders in relation to prey avoidance has also been studied in previous papers, with findings showing similar results to our own. Skow and Jakob (2006) demonstrated that jumping spiders could be trained to avoid aposematic, distasteful milkweed bugs (*Oncopeltus fasciatus*). Spiders were offered, in turn, both the aposematic milkweed bugs along with appetising crickets. During the first trial, the spiders readily attacked the milkweed bugs, but after eight trials stopped attacking altogether, as they learned to avoid the unpalatable offering. A similar response was also seen within our data, with the jumping spiders having a higher latency to attack the punishing and threatening prey. It is possible that with further trials the spiders may have followed a similar trend to what Skow and Jakob (2006) found, eventually learning to stop attacking the punishing 3D models all together.

As 'sit and wait' predators, both jumping spiders and praying mantises often have to rely on deciphering multiple sensory cues before deciding whether a prey item is palatable (Prudic, Skemp and Papaj, 2007). Ramesh et al., (2016) observed the differential response of praying mantises to ant-mimicking spider. After presenting the praying mantises with both a palatable, non-mimicking spider (*Epocilla aurantiaca* and *Plexippus petersi*) and an unpalatable carpenter ant (*Camponotus sericeus*), the mantises were then presented with a jumping spider that mimics carpenter ants (*Myrmarachne sp.*) and their responses recorded. Similarly to the results found within this study, the mantises were able to distinguish between all three species, with the percentage of approaches differing significantly between each. It was also found that whilst the mantises readily attacked the

non-mimic spiders, they rarely attacked the mimic spiders, concluding that the mantises were duped by the *Myrmarachne*'s ant-like resemblance, a trend also found within our own results.

A few studies have also been undertaken on the response of jumping spiders towards Batesian mimics (Cutler, 1991; Nelson and Jackson, 2006; Durkee, Weiss and Uma, 2011; Huang *et al.*, 2011). Nelson and Jackson (2006) focused on a mimicry system, whereby the unpalatable models were ants (*Formicidae*), and both the mimics and the predators were jumping spiders (*Salticidae*). The predatory jumping spiders were presented with a variety of dead arthropods mounted in a life-like posture, with the opportunity to either approach the prey item or enter an empty chamber. These arthropods included ants and ant mimics, alongside an array of non-ant-like species. Similarly to our own findings, the jumping spiders were able to differentiate between the individual arthropods, avoiding the unpalatable ants, but approaching the palatable and non-harmful prey more readily. Within our own study, similar responses were observed, with the jumping spiders appearing to correctly identify the mimicking hoverfly models as non-threatening. It is possible that the predatory jumping spiders were able to visually distinguish between the punishing models and the mimicking hoverfly models quickly, due to their highly acute vision, as observed and described in previous studies (Jackson and Blest, 1982; Cerveira, Jackson and Nelson, 2019).

During the mimic response trials, the mantises and the spiders had differing responses to the mimicking hoverfly model. Overall, the mantises took longer than the spiders to attack the hoverfly model, with the time taken to attack almost being as long as the time taken to attack the punishing model. This suggests that the mantises perceived the hoverfly model as more of a potential threat than the non-mimetic fly, taking more time to decide it was safe to attack. The response of the spiders contrasted with this, with the average attack time being closer to the response time of the non-punishing model. This therefore suggests that the spiders were able to distinguish between the

three models faster and were consequently able to attack the hoverfly model in a much shorter period of time.

The difference in eyesight between the two invertebrates could be a potential factor as to why the jumping spiders were able to distinguish between a threat and a non-threat faster than the praying mantises. Although, no study has been undertaken directly comparing the eyesight of the two differing taxa. Praying mantises possess binocular vision, with the field of view of the two forward facing foveas overlapping by a substantial amount (Rossel, 1986). This therefore allows a praying mantis to perceive a single three-dimensional image of its surroundings, whilst observing excellent depth perception. However, Nityananda et al., (2018) observed that praying mantises only excel at depth perception when their prey item is moving. Rather than comparing luminance in the two eyes' images directly, as is seen within vertebrates, praying mantises look for regions in the images where luminance is changing, with this change occurring due to an object moving. Luminance contrast refers to the difference in the amount of light reflected from an object and its background (Cohen, Wyszecki and Stiles, 1968). Although praying mantises are excellent at perceiving depth, there is existing physiological and molecular data that suggests they have very limited or no colour vision (Sontag, 1971; Rossel, 1979; Towner and Gärtner, 1994). Chromatic contrast, also known as colour contrast, alongside luminance is a key characteristic of visually deterring aposematic species (Sherratt, Speed and Ruxton, 2004). The colour schemes of many aposematic species usually include hues of red, yellow or orange, vivid colours that contrast with the green and brown hues of many terrestrial environments (Aslam, Nedvěd and Sam, 2020). The vivid nature of many aposematic species not only creates chromatic contrast, but also luminance contrast due to the display of significant brightness when compared to the background (Sherratt, Speed and Ruxton, 2004). As praying mantises have little to no colour vision, they therefore must heavily rely on luminance contrast for recognising visual warning colourations from unpalatable and mimetic prey, alongside prey detection (Prudic, Skemp and Papaj, 2007).

Most spiders have simple eyes and poorly developed vision, however jumping spiders differ from most and are seen to have highly acute vision (Drees, 1952). Unlike praying mantises, jumping spiders have 4 pairs of eyes, with one pair functioning as the primary pair and the other three pairs functioning as secondary (Land, 1969). The antero-median eyes, or principal eyes, are responsible for acute vision, with the three other pairs acting primarily as movement detectors. The lens system and structure of the antero-median eyes is incredibly complex, distinguishing this pair of eyes from the rest. The retina is tiered, with light passing through 4 distinct layers before reaching the retina (Williams and Meintyre, 1980). The presence of these layers alongside a second diffracting lens provides jumping spiders with extraordinary resolving power within their primary eyes. The retina within the antero-median eyes also provides jumping spiders with the ability to see colour, with sensitivity ranging from red to ultraviolet (Peaslee and Wilson, 1989). The ability to see colour is incredibly important for the jumping spiders, not only is it useful for predation, but salticids are often very colourful, with colourful markings playing a large role within courtship and reproduction (Richman and Jackson, 1992). As jumping spiders are able to see colour along a large spectrum, they are able to see the vivid colours of the warning signals displayed by aposematic, unpalatable and mimetic prey, distinguishing their abilities from the praying mantises'.

Although neither the jumping spiders nor the praying mantises treated the hoverfly model exactly the same as the punishing model, they also did not instantly regard it as a non-punishing model. If responses to real hoverflies in the wild were the same, the extra time taken to assess and attack the imperfect mimic could be crucial to the individual hoverfly's survival. The presence of imperfect mimicry could lead to a higher latency of attack by the potential predator, due to the presence of a potential threat. This would therefore allow the hoverfly to gain enough time to fly away and escape, highlighting the possibility that mimicry is adaptive. Without the imperfect mimicry, it is

possible that the predator would instantly regard the hoverfly as a palatable prey item, leading to a much faster and higher attack rate.

Despite the wealth of literature on hoverfly mimicry, very few studies have looked predator responses to the hoverfly-wasp mimicry complex, let alone used invertebrates to do so. In the most relevant experimental study of predator responses to hoverfly mimicry, Dittrich et al., (1993) used retired racing pigeons (*Columba livia*) as the selected predator. This particular paper followed a similar methodology to this study, measuring the similarity perceived by pigeons between the unpalatable wasp and various different species of hoverfly mimics. The primary aim of this study was to observe how easily the pigeons were able to distinguish between mimics and wasps. This would therefore give insight as to how visual perception in other birds might shape selection on mimicry in the wild. In order to test this, the pigeons were trained to peck a computer screen when presented with a rewarding image of a true fly, with the number of subsequent pecks being recorded. After using an image processing technique to create a measurement of the objective similarity between the hoverfly mimics and the wasps, it was demonstrated that the pigeons ranked the hoverfly mimics in a fairly similar way to the human rankings, with a higher number of pecks equaling a higher certainty of reward. The number of pecks reduced, as the objective similarity between the non-profitable wasp and the hoverfly mimic increased. However, it was noted that initially, many of the hoverflies were regarded as a potential threat, with the pigeons behaving as if they were the wasp photographs. Very similar findings were observed within our own data, with both the praying mantises and the jumping spiders initially treating the intermediate model as the punishing model, generating a delayed response time. It is also worth noting, the pigeons ranked the two most common hoverflies (*Syrphus ribesii* and *Episyrphus balteatus*) as very similar to wasps. To the human eye, these mimetic hoverflies were deemed to be poor mimics with a clear distinction between them and their model wasp. With the models utilised in this study, the hoverfly 3D model is easily distinguishable to the human eye from both the wasp and the non-mimic fly models. Similarly to the

study undertaken by Dittrich et al., (1993), the results found within this study suggest that non-human predators may perceive, what we as humans deem 'imperfect' mimicry as relatively accurate, therefore supporting the eye of the beholder hypothesis theorised by Cuthill and Bennett (1993). The differing responses found in this study to the imperfect mimics by the praying mantises and the jumping spiders also suggests that imperfect mimics may be perceived as differing levels of mimetic accuracy by different potential predators, further supporting the eye of the beholder hypothesis.

Although this study was successful in addressing the intended aims, there were a few limitations associated with data collection. It is worth noting, that the models utilised within the study, although created using photographs of live models, are still inanimate objects. This therefore allowed us to study the response of the predators to the morphological aspects of the models, ensuring the responses observed by the predators were solely due to the physical differences between models. However, not every characteristic present in real insects, such as movement or sound, were tested. There is limited evidence of both behavioural mimicry (Golding, Ennos and Edmunds, 2001; Penney *et al.*, 2014) and acoustic mimicry (Rashed *et al.*, 2009; Moore and Hassall, 2016) in hoverflies, which suggests that other sensory modalities may be important. For example, one study led by Golding, Ennos and Edmunds (2001) compared the movement of hoverflies mimics to their model honeybees, finding that the flight behaviour of a specific mimic (*Eristalis tenax*) was closer to the behaviour of the potential honeybee model, than that of other related flies. These other characteristics could be introduced into the methodology, by creating a more complex movement set up, to more accurately mimic hoverfly flight, or by introducing a speaker, playing different recordings of the relevant wasp mimics.

The evolution and persistence of imperfect mimics within the animal kingdom still generates a large number of questions. In order to further uncover the cause of their evolution, additional studies

could be undertaken. Future studies could continue to utilise the creation of the 3D printed models, following a similar methodology to this study. More detailed models could be created, producing a larger number of imperfect mimics, each with a different level of mimetic accuracy focusing more on the gradient of the poor mimicking hoverfly to the more accurate mimicking hoverfly. This could then be used to assess the point at which the predator perceives a 3D hoverfly model as indistinguishable from a hymenopteran model, or the point at which it is instantly perceived as palatable, with no hesitation. Similarly to observing the full range of the mimetic accuracy, 3D printed models of hoverflies could be created, with a singular trait, such as wing size, antenna length or colour pattern being altered. A similar study was undertaken in this manner by Rilling, Mittelstaedt and Roeder (1959), where artificial dummies were offered to praying mantises where a characteristic such as body shape or the number of antennae differed with each model. This had the aim of ascertaining what specific features the mantises used to assess the palatability of a prey item. A second avenue of enquiry could be the observation of a larger variety of predatory species. Currently, the majority of studies have utilised birds such as pigeons (*Columba livia*) or great tits (*Parus major*) to assess the success of an imperfect hoverfly mimic. Within this study, two different invertebrate species were used, with each having a different response to the hoverfly mimic. In order to diversify the predatory response, and further assess whether the eye of the beholder hypothesis is a possible explanation to the evolution of imperfect mimicry, a wider variety of predatory species could be observed, investigating different predatory responses to varying degrees of mimetic accuracy.

In conclusion, we demonstrated that both praying mantises and jumping spiders are able to differentiate between two distinctive models, whilst delaying an attack on a punishing model due to a learned response. It was also demonstrated that whilst the invertebrate predators could also differentiate between the intermediate mimicking model and both a non-punishing model and punishing model, a different response was recorded for each invertebrate. The jumping spiders

determined the intermediate model as non-threatening and attacked much faster than the praying mantises, suggesting that the differing sensory abilities possessed by each predatory invertebrate altered the time it took to assess the threat of the model. This therefore supports the eye of the beholder hypothesis, with both the praying mantises and the jumping spiders appearing to perceive the intermediate hoverfly mimic as differing levels of mimetic perfection.

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Appendix

Comparison of Potential Models

Innate Response

Probability of Attack

Table 1. A comparison of the fit of all the possible combinations of predictor variables for the probability of attack. Model 1 variables include the model type and the fixed variable of each individual. Model 2 variables only included the fixed variable of each individual.

	df	AIC	BIC	Deviance
Model 2	2	96.141	100.95	92.141
Model 1	3	96.912	104.13	90.912

Time Taken to Attack

Table 2. A comparison of the fit of all the possible combinations of predictor variables for the time taken to attack during the innate response. Model 1 variables include the model type and the fixed variable of each individual. Model 2 variables only included the fixed variable of each individual.

	df	AIC	BIC	Deviance
Model 2	2	1537.9	1542.1	1533.9
Model 1	3	1534.9	1528.9	1528.9

Learned Response

Praying Mantises

Table 3. A comparison of the fit of all the possible combinations of predictor variables for the time taken for praying mantises to attack during the learned response.

	(Intercept)	Previous Punishments	Punishing Model	Punishing Trial	Previous Punishments: Punishing Trial	df	AICc	Delta
Model 14	4.095	-0.2513		+	+	5	1172.9	0.00
Model 16	4.113	-0.2513	+	+	+	6	1175.5	2.55
Model 6	2.823	0.2114		+		4	1437.3	264.36
Model 8	2.858	0.2114	+	+		5	1439.7	266.77
Model 5	3.444			+		3	1606.5	433.59
Model 7	3.462		+	+		4	1608.8	435.00
Model 1	4.063					2	2144.3	971.37
Model 2	4.076	-0.006395				3	2146.3	973.41
Model 3	4.049		+			3	2146.5	973.62
Model 4	4.061	-0.0064	+			4	2148.7	975.75

Jumping Spiders

Table 4. A comparison of the fit of all the possible combinations of predictor variables for the time taken for jumping spiders to attack during the learned response.

	(Intercept)	Previous Punishments	Punishing Model	Punishing Trial	Previous Punishments: Punishing Trial	df	AICc	Delta
Model 6	1.603	0.2158		+		4	350.4	0.00
Model 14	1.041	0.3259		+	+	5	351.6	1.18
Model 8	1.565	0.2162	+	+		5	352.3	1.83
Model 16	1.025	0.3222	+	+	+	6	353.8	3.36
Model 5	2.680			+		3	403.7	53.23
Model 7	2.642		+	+		4	405.7	55.24
Model 2	5.098	-0.2369				3	1245.1	894.65
Model 4	5.089	-0.2369	+			4	1247.7	897.29
Model 1	4.100					2	1334.8	984.41
Model 3	4.113		+			3	1337.3	986.85

Intermediate Mimetic Response

Praying Mantis

Table 5. A comparison of the fit of all the possible combinations of predictor variables for the time taken for praying mantises to attack during the intermediate mimetic response.

	(Intercept)	Model Type	Punishing Model	Trial	Model Type: Trial	df	AICc	Delta
Model 6	4.666	+		-0.02603		5	455.4	0.00
Model 8	4.645	+	+	-0.02609		6	458.1	2.79
Model 14	4.662	+		-0.02506	+	7	459.2	3.82
Model 2	4.571	+				4	461.1	5.79
Model 16	4.640	+	+	-0.02514	+	8	462.4	7.07
Model 4	4.553	+	+			5	463.8	8.43
Model 5	4.830			-0.107		3	1068.4	1068.40
Model 7	4.813		+	-0.107		4	1070.8	615.49
Model 1	4.390					2	1236.4	781.09
Model 3	4.385		+			3	1238.8	783.48

Jumping Spiders

Table 6. A comparison of the fit of all the possible combinations of predictor variables for the time taken for jumping spiders to attack during the intermediate mimetic response.

	(Intercept)	Model Type	Punishing Model	Trial	Model Type: Trial	df	AICc	Delta
Model 6	3.389	+		-0.07438		5	364.6	0.00
Model 14	3.389	+		-0.07438	+	5	364.6	0.00
Model 8	3.339	+	+	-0.7438		6	367.1	2.53
Model 16	3.339	+	+	-0.07438	+	6	367.1	2.53
Model 2	3.173	+				4	369.2	4.63
Model 4	3.124	+	+			5	371.6	6.95
Model 7	3.930		+	-0.2764		4	866.0	501.43
Model 5	4.194			-0.2765		3	866.5	501.94
Model 3	3.137		+			3	1029.7	665.14
Model 1	3.422					2	1030.6	665.98