The Evolution of Mimicry – A Network Based Approach

Tom Wookey

(200766590)

Submitted in accordance with the requirements for the degree
Master of Science by Research

Supervisor: Christopher Hassall

Faculty of Biological Sciences

The University of Leeds

UNIVERSITY OF LEEDS

September 2019

Acknowledgements

Firstly, I would like to thank Dr Christopher Hassall for his continued support and guidance throughout this masters, helping me and providing me with invaluable pieces of advice. Additionally I would like to thank the University of Leeds for the use of the facilities. Finally I would like to Harewood house and Nicholas Dowling for the opportunity to work with the zebra finches and collect data in their aviary.

Table of Contents

List of Tables

List of Figures

Chapter 1 - The Evolution of Mimicry

1.1 Introduction

Batesian mimicry is a phenomenon by which a harmless mimic imitates the warning signal of a harmful model to avoid the costs associated with the common signal receiver (Ruxton et al., 2004). Batesian mimicry has been a fundamental cornerstone in evolutionary biology for over 150 years since its discovery in 1862 (Bates, 1862). Throughout this time, vast inroads have been made into the understanding of this complex product of natural selection. Mimicry, being a form of communication, is relayed via signalling across multiple modalities (Johnstone, 1995; Rowe, 1999; Dalziell and Welbergen, 2016). Mimicry is the process by which an individual (mimic) imitates a signal of another individual (model) resulting in a behavioural change of the signal receiver, providing the mimic with a selective advantage (Wickler, 1968). This process has been naturally refined across multiple taxa and can be seen throughout the globe in a vast array of living organisms (Dafni, 1984; Herberstein, 2011; Pfennig et al., 2015). This explosion of diversity is down to the evolutionary processes and selection pressures that have helped refine mimics, allowing them to thrive in their specific ecological environment (Mallet and Joron, 1999). The resultant characteristics of the mimic and behavioural response of the signal receiver can drive selective action, consequently leading to either evolutionary convergence or divergence amongst the mimic and model (Maynard-Smith and Harper, 2003; Stevens, 2007). Depending on the mimic, mimic fidelity can vary and multiple polymorphisms can occur in any given range. This creates a diverse fluid system between models and mimics, providing ample opportunity to explore various avenues of research within the field.

1.2 Mimicry as a Concept

Originally proposed in a predator-prey context (Figure 1), and used as an antipredator defence (Bates, 1862; Müller, 1879), Batesian mimicry can now be seen as a mechanism that has been moulded by natural selection. This mechanism from a predator-prey perspective can be to the benefit of a mimic. These benefits can ultimately improve fitness and create a selective advantage – but mimicry is not solely based upon predator-prey interactions (Thomas and Settele, 2004; Stoddard and Stevens, 2010). The two main forms of mimicry are defined as Batesian mimicry and Müllerian mimicry and can be seen as defence strategies. Both are similar concepts in that they contain a mutual predator who exerts a selection pressure on the individuals, however have minor aspects that differ. A predator within a mimetic system is one that is falsely cheated by mimetic signals and alters its behaviour, to the benefit of the mimic. Müllerian mimicry is when two or more species possess a similar warning signal along with a common trait for example unpalatability (Rothschild, 1961; Sherratt, 2008). This form of mimicry has the ability to enhance predator learning (Rowland, Hoogesteger, et al., 2010). The most well-known example can be seen in the tropic butterflies *Heliconius* who share vibrant wing colour variations and are unpalatable to predators (Benson, 1972; Flanagan et al., 2004). It is important to note, Müllerian mimicry does incorporate the fact that two or more species can converge on a shared signal and all share the same trait, which in the case of *Heliconius* butterflies is unpalatability. This convergence on a shared signal means both species equally share the costs associated with predation, especially when the predators are naïve or uneducated, meaning it is a form of mutualism (Figure 2). However recent studies have found that in certain circumstances it can be deemed parasitic depending on the defended prey (Rowland, Mappes, et al., 2010). Despite this, Müllerian mimicry has also often been referred to as an interspecific form of aposematism, due to the nature of the co-mimics (Wallace, 1882). Contrasting Müllerian mimicry is Batesian mimicry. Batesian mimicry is a form of parasitism, where the mimic benefits from the costs associated with the model. The most studied model for Batesian mimicry is the interactions between the Syrphidae family and Hymenoptera (Waldbauer, 1988; Edmunds, 2000; Howarth et al., 2004; Marchini et al., 2017). Batesian mimicry is most apparent in aposematism – animal colouration (Cuthill et al., 2017). Aposematism is a common antipredator defence mechanism and presents a warning signal as a footnote for unpalatability, across different sensory modalities (Mappes et al., 2005). The predator-prey co-evolutionary arms race has been a stable fixture in evolutionary biology and antipredator adaptations are key to the prey's survival (Endler, 1986; Dieckmann et al., 1995). Interestingly, there are additional examples of mimicry that display parasitism. The common cuckoo, *Cuculus canorus* who exhibits egg mimicry, indirectly displays parasitism resulting in brood host parental care if the egg remains undetected (Attard et al., 2017). Again, whether it is parasitic mimicry or even Müllerian mimicry, the signals emitted from the model and mimic play a vital role in both their fitness and the fitness of the signal receiver.

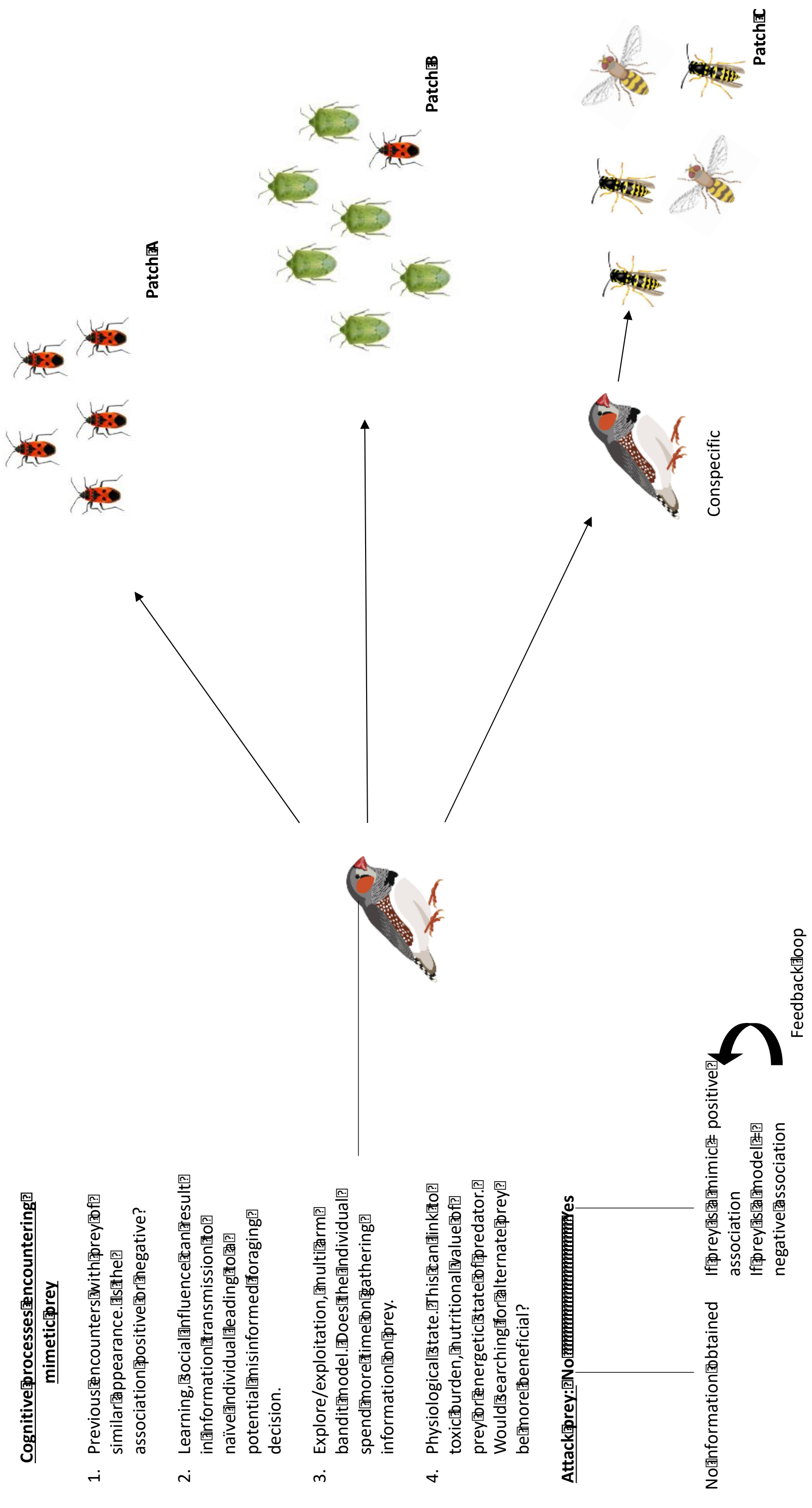


Figure 1. General overview of some factors that can influence a predator when foraging in a mimetic environment. Patch A represents an aggregation of aposematic prey. Patch B represents a mixture of aposematic and normal prey. Patch C demonstrates a mixture of models and mimics with a conspecific present, which may influence foraging decisions of the predator. All three patches can alter the cognitive processes of the predator and thus effect future foraging decisions. Zebra Finch, www.istockphoto.com. Hoverfly, www.clipground.com. Wasp, www.gograph.com. Firebug and True bug, www.uiex.com.

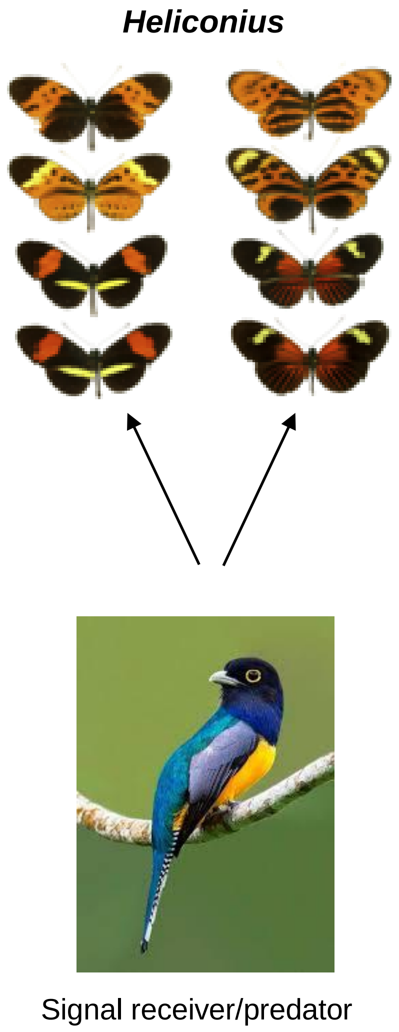


Figure 2. Mutualistic Müllerian mimicry where all harmful or unpalatable species associated with a similar warning colouration share the costs associated with the education of the signal receiver. Images represent the *Heliconius* butterflies and a possible avian predator, , *Trogon violaceus*. The top four *Heliconius* display the diversity in *H. numata*. The third row illustrates *H. melpomene*. Finally, the bottom row belongs to *H. erato*, the co-mimic of *H. melpomene*. Images: *Heliconius* butterflies, www.wikimedia.co.uk. Signal receiver, *Trogon violaceus*, www.topbirdingtours.com.

The types of signal produced from either the model or mimic can be split into honest and dishonest signalling (Guilford and Dawkins, 1991). In Batesian mimicry this is crucial as certain situations can result in high costs for the signal receiver (Lindstrom et al., 1997). For example in Figure 3, *Sericomyia silentis* (Syrphidae) displays warning colouration imitating *Vespula vulgaris* (Hymenoptera), resulting in the signal receiver potentially paying a cost for exploiting the wrong prey (Howarth and Edmunds, 2000; Golding et al., 2001).

It is ultimately up to the signal receiver to decipher if the prey is producing an honest or dishonest signal. Different factors can influence a signal receiver's behaviour when responding to a signal. For example: is the signal novel (Speed, 2000; Marples et al., 2005; Thorogood et al., 2018); has the signal receiver got a mild association between the signal and signal consequence; or has the signal receiver only encountered the signal briefly before, something that is common in foraging (Rashotte et al., 2013).

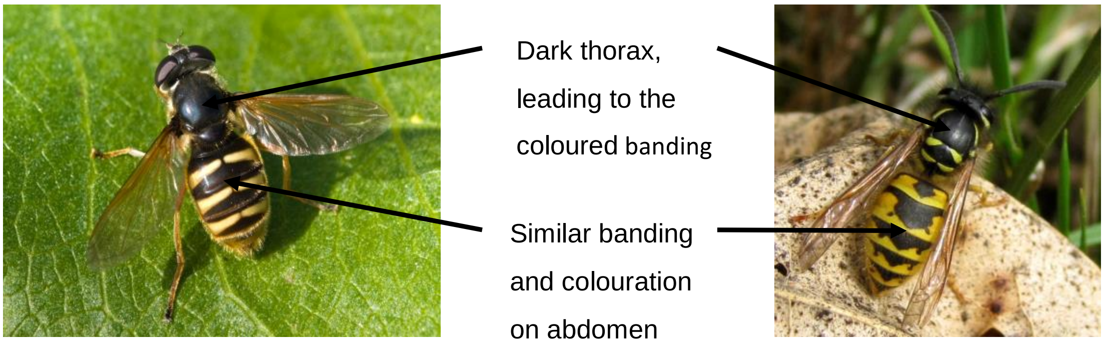


Figure 3. Batesian mimicry system illustrating the mimic, *Sericomyia silentis* (left) of the model *Vespula vulgaris* (right). Specifically, the abdomen colouration containing yellow and black banding highlighting aposematism. Images: Vespula vulgaris, www.animalphotos.me and *Sericomyia silentis*, www.wikimedia.com.

1.3 Mimicry and Learning

Learning is a fundamental part of mimicry (Ihalainen et al., 2007; Stuckert et al., 2014; Sherratt and Peet-Paré, 2017). Specific studies have considered the effects of learning on predators, and the implications of this in Batesian mimicry linking this to the evolutionary dynamics of the mimic and model (Darst and Cummings, 2006). Throughout time, natural selection has resulted in an extraordinary diversity of animals, each playing key roles in their environments. Predator-prey dynamics are a key aspect, via which natural selection acts creating a constant arms race (Brodie III and Brodie Jr, 1999). Warning colouration has evolved multiple times to educate predators about the unpalatability of prey by multi-sensory signals. Different studies have used different methods of learning and applied these to mimicry systems, such as observational learning, social learning and conditioned learning (Thorogood et al., 2018). Taking social learning in various models such as *Parus major* and conditioned learning in *Gallus gallus,* it can be observed that aspects of learning do occur in predators when foraging (Carle and Rowe, 2014). Interestingly, studies with individual birds have been carried out in detail, using demonstrators to facilitate learning (Landová et al., 2017). Much less is known regarding social interactions and group behaviours, and how they affect the learning of mimetic signals. With Batesian mimicry predominantly using warning colouration or aposematism, there is a lot of empirical evidence supporting learning in avian predators by means of association with colouration in prey (Exnerová et al., 2015; Rowland et al., 2017). The presence of learning within mimicry highlights another element which can exert selective power over the mimetic species.

1.4 The Challenges of Mimicry

Currently the two main approaches to studying mimicry involve either a theoretical approach or empirical approach. The theoretical approach follows the use of models and mathematical paradigms. Conversely, studies using an empirical approach include evidence based on observation. Both approaches have been argued to not cover sensory and taxonomic divides (Dalziell and Welbergen, 2016). With both of these frameworks in place, it can make mimicry a difficult concept to evaluate. For example, theoretical approaches may be used when investigating the effects of mimicry on population dynamics for two interacting species (Huheey, 1988). This may incorporate fixed algorithms and mathematical equations to simulate biotic factors such as breeding and mortality. Although the model may present a rough indicator for population dynamics in the context of mimicry, it may also lack the ecological context of real species interaction, something empirical approaches focus on.

When looking at the individual components of a mimicry system it is difficult to identify which aspect can be attributed to mimetic evolution. For example, a signal receiver foraging in a Batesian mimicry system has various factors to consider when selecting a prey item. If the signal receiver is at a low energy state or has a relatively high toxin burden (Barnett et al., 2012), they may reconsider expending energy on prey which may be potentially harmful, as the costs of doing so may outweigh the costs of not consuming prey at all (Smith et al., 2014). However, if the signal receiver's energy state is high and has the capacity to continue foraging, after coming across a potential noxious prey, they may also not select to do so. This can be due to additional elements, such as competition or abundance of additional prey (Brown, 1999; Valkonen et al., 2012; Carle and Rowe, 2014). Alongside the biotic factors influencing aspects of mimicry, there are abiotic factors which can contribute to multiple phenotypes, behaviours or even selection pressures (Speed and Ruxton, 2007). Abiotic factors can range from light intensity to temperature, and can have a significant impact on species. For example, light intensity can influence perception in certain species (Arenas et al., 2014), resulting in difficulty distinguishing aspects of the environment. A study by Arenas and Stevens (2017) considered signal conspicuousness of various ladybird species and how easily avian predators could recognise them. It was identified that all ladybird species, against their own background were highly conspicuous. However, the theory stipulates that changes in lighting, whether that be shade or altercations throughout the day, alters the signal receiver's perception and can influence selection (Troscianko and Stevens, 2015).

When all these componenets are implemented into a continually changing ecological environment it is difficult to identify which element or elements may hold the greatest significance on the evolutionary dynamics of a mimicry system. With each ecosystem containing complex organismal interactions and stochastic tendencies, it makes the evolution of mimicry an extremely difficult concept to study in a natural environment. However, with empirical and theoretical approaches continually being refined and improving, the gaps are slowly reducing.

1.5 Moving Forward

With so many questions still unanswered, there is opportunity to address the areas of the field that require further attention (Jamie, 2017). In Batesian mimicry, there are multiple avenues in which research could advance including: phenology and population dynamics in the context of mimicry; abiotic and biotic factors influencing the signal receiver's perception; observational learning in the context of predation on aposematic prey; spatial co-occurrence between the mimic and model and cognitive mechanisms of the signal receiver. These specific areas may also allow us to tie aspects in with Müllerian mimicry, comparing the two systems and identifying possible patterns or trends. Model species such as *Parus major, Taeniopygia guttata* and *Sturnis vulgaris* enable us to construct studies in an empirical format. Alongside these model systems, complex computer modelling programmes with the ability to emulate the environment as avian predators may perceive it, hold the key to cognitive mechanisms that occur when a signal receiver perceives a signal, and may pave the way for us to understand decisions that are made in relation to aposematic prey.

1.6 Spatial Occurrence

Across the globe many biological organisms are under geographical constraint, their range is finite and may occasionally overlap. This boundary is usually a result of biotic and abiotic factors, which play a role in habitat availability (Bacheler et al., 2009). Therefore, occurrence across a range for any organism is crucial for multiple reasons, for example: competition for mates and foraging. Mimicry in the context of spatial and temporal occurrence has been evaluated in previous work. It was found that mimics and models were likely to co-occur around the same time of year with mimics having a lower abundance (Howarth and Edmunds, 2000). This supplemented with other work on associations (Waldbauer, 1988; Hassall et al., 2018), has allowed us to conclude mimetic relationships can be influenced by variation in spatial and temporal co-occurrence. The idea that models and mimics which are approximate in relation to signal similarity co-occur within a given range is a plausible assumption. The first data chapter of this thesis will consider spatial-temporal occurrence of models and mimics and whether co-occurrence is present across a several sites in the UK, and how this may influence species that are perceived to have stronger similarity compared to others.

1.7 Conclusion

Mimicry is an extremely informative case of natural selection, that contains complex interactions between species. With multiple frameworks established which identify key concepts that all contribute to the evolution and constant adaptation of mimicry, new opportunities arise for further research. Ecological networks have been successful in the continual understanding of social networks and ecological interactions. This thesis will look to apply network theory to mimics, models and predators to evaluate some hypotheses about the evolution of mimicry which are fundamental but untested. Beginning with spatial co-occurrence, I will look to identify if high fidelity mimics and models do in fact spatially co-occur more than by chance across a given area. From here we can look to derive model-mimic relationships empirically and derive model-mimic cluster empirically. Following this, I will look to evaluate the influence of learning on a Batesian mimicry system. This will incorporate both social learning from a predator’s perspective and how this may influence the Batesian mimic’s (prey’s) perspective. Thus, by evaluating literature that has been underpinning the evolution of mimicry and Batesian mimicry, I will highlight the studies and concepts that will be most relevant to the research I look to conduct, and how these can be implemented into my studies, enhancing what we know today.

Chapter 2 - Literature Review

The evolution of Batesian mimicry has been at the forefront of evolutionary biologists minds for over 150 years. Despite inroads unveiling multiple evolutionary drivers, Batesian mimicry still requires investigation. The foundations set by previous studies allows us to build and direct research towards avenues of mimicry that have not yet been evaluated in depth. This thesis will consider different aspects of Batesian mimicry along with the processes influencing its evolution. Therefore previous studies and a wide array of literature from similar backgrounds are crucial in devising a suitable study to further advance the field of mimicry. I begin with evaluating literature on current themes within mimicry and then move onto mimetic co-occurrence, which creates a background to understanding the interaction between mimetic species across different ecological environments, and how this may link to mimicry. Following co-occurrence, I will look to unravel the use of networks on mimicry and their application to species interactions, and how these can be applied empirically. Finally, I consider previous studies which investigate the effect of learning on Batesian mimicry and how these implications may exert selection on models and mimics. Additionally, I will identify species and experimental designs previously used in studies incorporating mimicry and learning. This insight may present valuable ideas which can be integrated into my study.

2.1 Introduction

The evolution of mimicry is based on a tripartite relationship (Figure 4). This relationship is convoluted and dynamic consisting of: the model, the mimic and the signal receiver (Bates, 1862; Vane-Wright, 1980; Wickler, 2013). The mimic imitates the models warning signal in order to alter the signal receiver's behaviour, gaining a selective advantage (Figure 4). This selective advantage is dependent on a magnitude factors such as the signal receiver themselves, alternate prey and environmental conditions (Ruxton et al., 2004). Interactions between all individuals in this tripartite relationship are crucial in understanding how mimicry may have evolved and developed in this fluid system. Mimicry is diverse and abundant in a wide array of taxa. This abundance means it is a functioning process in many ecosystems and is displayed via multiple sensory modalities. Mimicry can be seen across invertebrates, from aposematic signalling to chemical mimicry (Jackson and Wilcox, 1993; Kilner and Langmore, 2011; Bocakova et al., 2016) and is also evident in vertebrates (Wüster et al., 2004; Kraemer and Adams, 2014; Pfennig et al., 2015) further highlighting its diversity. Plant mimicry has been illustrated in different contexts (Pannell and Farmer, 2016). The diversity displayed in signalling when relating to mimicry emphasises the range of diversity within different mimetic systems, and how variance occurs across each distinctive ecosystem.

Recent work within the field of mimicry has focussed on aposematism and its association to mimicry. Aposematism is a vibrant product of natural selection, which has been refined through centuries. This refinement is enhanced through the constant predator-prey co-evolutionary arms race. Aposematism is a common antipredator defence mechanism and presents a warning signal as a footnote for unpalatability, across different sensory modalities (Mappes et al., 2005). Aposematism consists of a primary and secondary defence system with the primary system comprising bright colouration, sounds or odours and the latter being chemical, behavioural or incorporating morphology (Rojas et al., 2015).

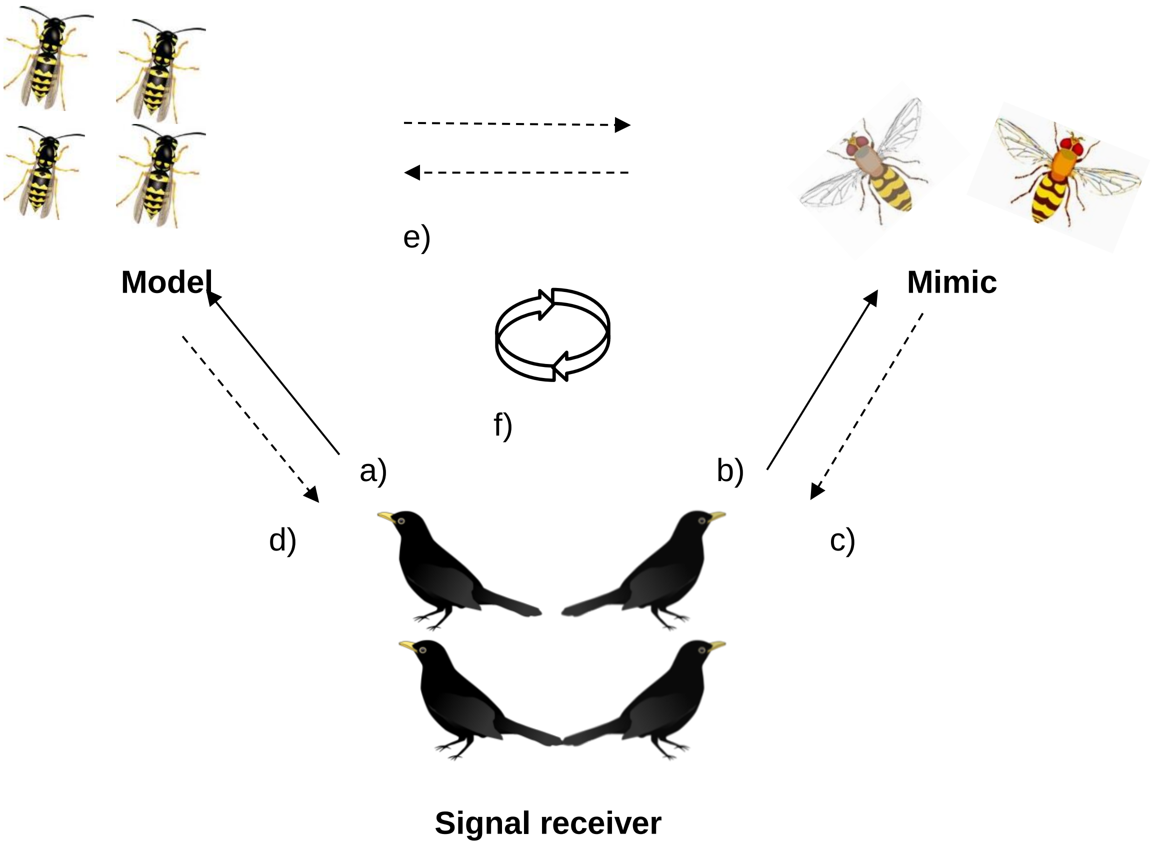


Figure 4. Functional model of a basic mimicry system, based on the common definition of mimicry. (**a**) illustrates the core requirements which are fundamental if mimicry is to evolve. The signal receiver is in receipt of a specific signal/combination of signals from the model and in response adapts its behaviour. Mimicry is then selected if the signal receiver can perceive the resemblance between the model and mimic, in context to the signal, resulting in altered behaviour benefitting the mimic (**b**). The dotted lines and unfilled shapes demonstrate supplementary interactions in the system which can promote evolutionary changes in both the mimic and model, such as the *imperfect* mimic in the figure. The model can have change imposed indirectly by the mimic, when the signal receiver alters its behaviour through interaction with the mimic (**c**)**.** The reformed behaviour of the signal receiver can result in the model altering its phenotype to either converge or diverge from that of the mimic (**d**). The direct influence of either the mimic or model is highlighted in (**e**), where both have the potential to occasionally disrupt the signalling environment for either individual resulting in a possible coevolutionary pathway (**f**). Please note the dynamics of this system are always changing and can result in the prominence of imperfect mimicry, or mimics with different forms. Figure adapted from Dalziell and Welbergen (2016). Pictures: Common blackbird, *Turdus merula*, www.openclipart.org. Hoverfly, www.clipground.com. Wasp, www.gograph.com.

Warning colouration is a diverse occurrence and is evident across multiple taxa (Maan and Cummings, 2008; Lev-yadun, 2009; Cooke et al., 2015). Across Müllerian mimicry, aposematism is exploited in a mutualistic way between equally defended species, who display similar warning colouration (Sbordoni et al., 1979; Symula et al., 2001). Alternatively Batesian mimicry demonstrates species who mimic an aposematic model in order to gain a fitness benefit. With particular species using warning colouration as a defensive mechanism, predators need to be able to identify the signals and marry their pattern with possible unpalatability.

A recent review looked into the diversity of warning signals and their composition, reiterating the fact that aposematic colouration is usually characterised by red, yellow and black and is thought to do so for different reasons (Stevens and Ruxton, 2012). Within the review different hypotheses have been suggested surrounding these aposematic colours and why they may be dominant within aposematism. First it was put forward these colours when placed against alternate backgrounds are high in contrast, facilitating detection. Additionally, these colours, when present in a varied habitat with a constant change of lighting, are resistant to both shadows and illumination alterations. This specific feature, also correlates with the colours possessing a reasonably high contrast in luminance and chromatic properties. Interestingly it was highlighted that red, yellow and black may aid camouflage when a predator is at a distance, meaning identification of the prey is restricted due to the warning signal blending with the background. This notion is labelled as “distance-dependent camouflage”. With the hypotheses above attributing a possible reason for aposematic colouration, additional studies could be utilised to assess predator foraging behaviours. Supporting some of the hypotheses, Arenas and Stevens (2017) investigated different ladybird species and how their specific phenotypes matched up against different backgrounds. It was concluded that against the species’ own background they were deemed highly conspicuous, illustrating that not all warning colouration results in camouflage (Arenas and Stevens, 2017).

Opposing the notion of aposematic significance, Wüster et al (2004) recognised the importance of specific patterns within some mimetic systems, instead of the need for bright aposematic colours to deter predators or impose learning. Imitating viper markings, plasticine snakes were placed in the field with half containing viper markings and half remaining plain. The phenotypes of the models were either grey or terracotta, which were placed against a card background or left against the environmental background. The subsequent results indicated models containing viper markings irrespective of background or colour possessed a lower attack rate. This study simulates a natural predator-prey dynamic for mimicry. However through the use of artificial prey containing a conspicuous warning colouration and using patterned prey, a diverse prey base could be studied. Incorporating an aversive compound such as Bitrex^{TM} to mimic the models unpalatability and through the use of mark-release-recapture techniques a greater level of community dynamics could be established building on Wüster et al (2004).

Particular studies have delved into the cognitive function of predators and their response to warning signals from a foraging perspective. For example, through the use of *Sturnus vulgaris* (European starlings) it was recognised that nutritional content of aposematic prey can be acknowledged via a feedback mechanism (Halpin et al., 2014). Altering the nutritional content of artificial prey demonstrated this, with a linear response to prey consumption when the nutritional content increased. Opposing this, the consumption rate decreased when the nutritional content decreased, providing significant evidence that a feedback mechanism was active within *Sturnus vulgaris*. This study opens the door to understanding cognitive recognition within foragers and the implications associated with aposematic colouration. The response throughout the study elicited by *Sturnus vulgaris* may pave the way for similar studies on alternate species to observe their behaviours when placed in similar environments. These behaviours can be used to conclude whether species' cognitive function is universal when placed in a foraging capacity amongst aposematism. Concurring with Halpin et al (2014)'s notion of predator influence on aposematic prey, analysis was carried out on the poison dart frog *Oophaga pumilio* which displays a difference in aposematic colouration between populations (Dreher et al., 2015). The investigation targeted predator attack rates against the aposematic coloured frogs. Overall there was a positive correlation between attack rates by avian predators and conspicuousness of frogs, illustrating the fact conspicuousness correctly indicates prey toxicity to predators. With warning colouration and aposematic signals varying across species and taxa, it has been found within the context of mimicry that certain species and populations can exhibit imperfect mimicry if there is opportunity for mimics to do so.

Imperfect mimicry a widely-discussed topic, has been a recent marker for the evolutionary advancements in mimicry (Sherratt, 2002; Penney et al., 2014). 11

hypotheses were recently proposed as potential theories as to how and why imperfect mimicry may arise (Kikuchi and Pfennig, 2013). For example, the relaxed selection hypotheses states that imperfect mimics gain the same level of protection from predators, despite their low mimetic fidelity. An additional study looking at morphological and genetic data for Syrphidae species concurred with the relaxed selection hypothesis as a viable cause for imperfect mimicry (Penney et al., 2012). Despite empirical evidence suggesting the relaxed selection hypothesis as a plausible theory for the cause of imperfect mimicry, there are alternate studies opposing these views. Recently the information limitation hypothesis was suggested as a cause for imperfect mimetic maintenance (Sherratt and Peet-Paré, 2017). Stating predators are not omniscient and must pay close attention to specific traits which may hold strong predictive power in relation to unpalatable prey, the information limitation hypothesis highlights the fact predators may take a general rule of thumb when dealing with aposematic prey. Opposing both theories is the idea that overshadowing and signal salience can contribute to the maintenance of imperfect mimicry (Kazemi et al., 2014). Overshadowing is a common phenomenon with compound stimuli and is present in associative learning (Mackintosh, 1976; Dickinson, 1980). The importance of overshadowing is seen when the most salient characteristic is associated with the outcome and the additional components are overlooked. Thus, the salient stimulus reaches a greater level of associative learning. Trained blue tits investigated coloured paper prey and how various trait characteristics such as shapes, colours and patterns influenced cognition (Kazemi et al., 2014). It was found colour mimics were protected just as much as models, whereas pattern and shape mimics suffered a vastly greater level of mortality. This result highlighted the idea signal salience and overshadowing on prey characteristics is prominent and can lead to altered predator foraging behaviours when coming across these salient traits. Thus the maintenance of imperfect mimicry can be sustained through predator selection. Although the empirical evidence demonstrated this, repeating a similar study in a natural environment would cement this theory as one possible cause and explanation for imperfect mimicry.

Overall there are multiple theories pinpointing imperfect mimicry and what may be responsible for its maintenance and persistence in an ecological sense. Different hypotheses may coincide to play vital roles in contributing to imperfect mimicry and the phenomenon it is today. Nevertheless, further work is needed in an empirical sense to home in on what mechanisms may be responsible for this concept, and the selection pressures placed in an open environment.

2.2 Mimicry and Co-occurrence

Models and mimics in theory are presumed to occur together across geographical regions, based on their relationship. It has been found through multiple studies that co-occurrence is an underlying feature of mimetic interactions and is important spatially although may not be as so temporally (Brodie, 1981). With models and mimics in constant competition with one another the dynamics between both are often fluid and interchangeable. Bates (1862) highlighted the possibility of co-occurrence between both models and mimics, as did Wallace (1867). Many studies have since supported this view, allowing us to evolve our perception of mimicry and thus leading us to where we are today.

Looking at the Batesian mimicry system featuring Syrphidae and Hymenoptera, much work has been carried out evaluating co-occurrence between species. It was initially stated that models and mimics of this Batesian mimicry system differ in phenology, with mimics emerging after their corresponding model. This difference in behaviour means the mimics avoid the naïve fledglings when they learn to forage (Waldbauer, 1988). Interestingly the theory itself relied on a major assumption – the birds remembered previous years' encounters with noxious models. However work since this has found individuals can reverse the learning process if the association is altered (Shettleworth, 1998). The work by Waldbauer (1988) was carried out in the USA, but a similar study assessing phenology and co-occurrence was conducted in the UK. Considering the phenology of a range of models and mimics, it was concluded that both the model and mimic are present at the same time of year and the flight season was synchronous between hoverflies and their model (Howarth and Edmunds, 2000), opposing Waldbauer (1988). In conclusion following on from Howarth and Edmunds (2000) it was found that across the three study sites in the North West, there was indication of a significant non-random pattern with 16 of 17 relationships classed as positive between the models and mimics (Howarth et al., 2004). The results indicate the mimetic breakdown across a region in the UK, however does not portray the overall picture across environmental gradients. Different regions comprise of a variety of landscapes and these will heavily influence the species present within them, for example the reduction in the *Bombus* genus with an increase in altitude (Hoiss et al., 2012). Additionally, with human practises such as beekeeping occurring throughout the UK, the aggregation of a higher abundance of models may have a significant impact on spatial and temporal occurrence of both the model and mimic. Therefore, there is room for a wider geographical study to supplement and focus on spatial and temporal co-occurrence across mimetic species and the effects of these environmental gradients and compositions.

Throughout the original study (Howarth and Edmunds, 2000) it was identified that mimics were temporally co-occurring with their models but were significantly rarer, apart from a couple of taxa. These individuals; *Helophilus*, *Syrphus* and *Eristalis* all occur at a higher rate than their model Hymenoptera, which could be attributed to the fact these taxa mimic more than one model. This perhaps suggests they gain a slightly increased rate of protection, allowing them to increase in abundance. Interestingly, a previous study highlighted the possibility that anthropogenic changes to the landscape are creating altered environments where mimicry is breaking down through a reduced need for protection (Azmeh et al., 1998). This may also account for an increase in urban mimic abundance.

Contrasting the original views presented (Waldbauer, 1988; Howarth and Edmunds, 2000) a recent study hypothesised that hoverfly mimicry systems when linked to eusocial Hymenoptera (wasp mimicry), mimic these insectivores for both defence from vertebrate predators but also their model counterparts (Boppré et al., 2017). With wasps being insectivores, there is an intraspecific form of communication (in the form of colouration) which can be hijacked. This ultimately stops wasps from attacking each other. Therefore, mimics of wasp species adopting this can co-occur with their models and gain protection from the model and predator in situ. This moot study presents a couple of complexities. Firstly, insects have never been evaluated as predators of mimetic species, although there are many in nature, no laboratory studies have been conducted. Additionally, this convoluted system of wasp recognition and mimicry requires an extensive library of species to be placed in experimental conditions. Despite the draw backs, this theory does present an alternate view on this specific mimicry system and opens the door for further analysis.

With species co-occurrence considered an underlying assumption in mimicry, in theory it can be deemed plausible that mimics can gain advantage without the presence of the model. This can be apparent when predators migrate to and from areas which possess the model (Poulton, 1909; Waldbauer, 1988; Pfennig and Mullen, 2010). Mimics can be seen to persist outside of sympatry (Mullen et al., 2008; Cheney, 2010). The Eastern coral snake (*Micrurus fulvius*) in the USA has been subject to a lot of mimetic work focussing on co-occurrence and abundance (Figure 5). A recent review incorporating this system has looked at causes and consequences of allopatric mimics and what this means for mimicry (Pfennig and Mullen, 2010). Various compelling points were mentioned within the review, attributing evolutionary and geographical reasons for occurrence of allopatric mimics (see Table 1).

This review focusses heavily on spatial co-occurrence and provides theoretical evidence that models and mimics are nearly always linked temporally despite spatial separation. An interesting point illustrated in the review is the possibility that throughout time mimetic protection could decline due to allopatric separation. This could develop through predator isolation in the allopatric regions and the lack of encounters with the models in sympatry. This subsequently can result in a model-mimic decoupling making the advantage of mimicry redundant. A similar example has been suggested in the hoverfly Batesian mimicry system, where mimics are outnumbering their models as a result of urbanisation (Azmeh et al., 1998). Additionally, it was suggested apostatic predation favours allopatric mimics, with predators selecting common phenotypes to predate (frequency based), thus the mimetic variant can pertain in the environment (Endler, 1991). Although this is not always the case, as some predators do in fact display antiapostatic predation (Lindstrom et al., 2001; Endler and Mappes, 2004).

A recent study evaluated the fidelity of coral snake mimics and their geographic distribution (Akcali and Pfennig, 2017). Interestingly the study supported Pfennig and Mullen (2010), illustrating yet again that coral snake mimicry systems are geographically diverse supporting allopatry and sympatry. However it was noted that the difference in mimetic fidelity was transcended across geographical regions with different phenotypes being found in either allopatry or sympatry. Further work will be required to try to discover the evolutionary mechanisms as to why certain mimics are able to persist in allopatry, along with Batesian mimicry maintaining away from the model.

Table 1. Selection routes for the occurrence of allopatric mimics across geographical areas (Pfennig and Mullen, 2010).

Selection route	**Description**
The mimic and the model are deemed unpalatable	• Mistaken case of Batesian mimicry not Müllerian mimicry • Identical phenotype arisen from separate convergence • Species toxicity differs across ranges
Predators occupy an innate avoidance of particular phenotypes	• Can demonstrate avoidance behaviours towards aposematic colouration • This can possibly carry through to species in allopatry
An unpalatable model and its assumed mimic may have separately converged on a phenotype which deters predators - for various selective explanations	• A phenotype which displays a warning signal for the model may infact facilitate crypsis in a mimic • Therefore, based on the environment a certain phenotype may have multiple functions, potentially allowing for this phenotypic variance to pertain in allopatry or sympatry
The convergence on a phenotype by the model and mimic for reasons other than antipredation	• In both intraspecific and interspecific competition, species may gain an advantage if competitive individuals are distracted by signals or have an innate fear of them.
Predators migrate between areas where models are abundant and areas where models are non-existent. Alternatively, predators occur through vast ranges	• Predator migration from sympatry to allopatry, so learned avoidance to specific warning colourations may hold valid.

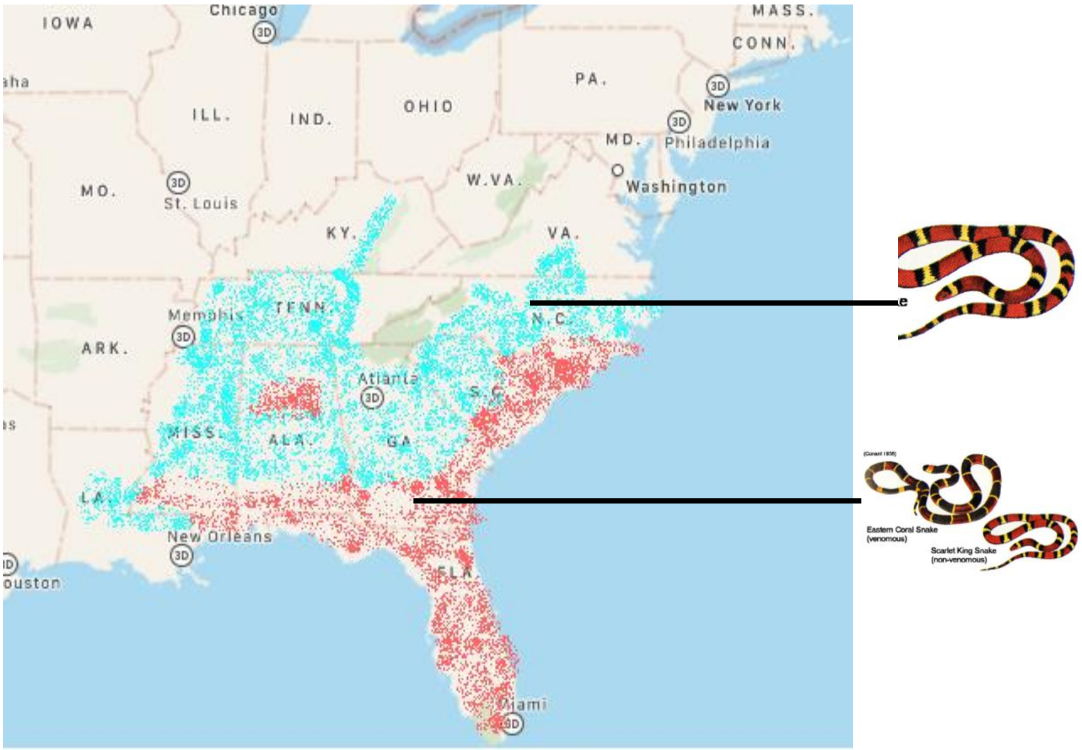


Figure 5. A map showing the allopatric and sympatric distribution of the model eastern coral snake and the non-venomous mimic scarlet kingsnake. The red range shows the model (coral snake) and its mimic (scarlet kingsnake) occurring in sympatry. However, the blue range highlights the mimic living in total allopatry. Images: coral snake and kingsnake extracted from www.petMD.com. Map taken from Apple™ maps. Figure adapted from Harper and Pfenning (2007).

Similarly to the coral snake Batesian mimicry system (Pfennig and Mullen, 2010; Akcali and Pfennig, 2017), Kristiansen et al (2018) tested admiral butterflies, both the palatable mimic and unpalatable model in North America and how both allopatry and sympatry effected survivorship and colouration. One aspect of the study identified that frequency dependant Batesian mimicry may be present between both *Adelpha californica* (the model) and *Limenitis lorquini* (the mimic), resulting in species boundaries being maintained through divergent selection. The mark-recapture study demonstrated that *L.lorquini* resided for a significantly greater period of time where the model *A.californica* was present, as opposed to where it was rare or did not occur (allopatry). Interestingly models and mimics (in rare occurrences) can occur in sympatry linking to the coral snake mimicry system, despite the difference in taxa. In the butterfly mimicry system, the mimic gains protection from the model in sympatry via mimicry. An example of this can be seen between certain Hymenoptera and Syrphidae as proposed by Boppré et al (2016).

To unveil the importance of mimetic interactions and their implications across communities, further work is required to advance our current ideology. Spatial and temporal co-occurrence has long been an extremely well-studied area in biogeography. With a deeper insight into the relationships of high fidelity model-mimic pairings and their co-occurrence, we may be able to identify multiple species interactions and how they link to their environment, thus unveiling new evolutionary mechanisms driving mimicry.

2.3 Batesian Mimicry – The Importance of Learning

Predator learning has long been a central focal point in the Batesian mimicry complex. Predators exert selective pressures on both the model and mimic acting as a selection agent influencing prey morphology (Ruxton et al., 2004; Sherratt, 2008; Ruxton et al., 2018). With predators of mimetic species continually foraging, frequent encounters with models can lead to avoidance learning towards specific phenotypes. The negative encounters with the model prey can result in an association between prey signals and unpalatability (Ham et al., 2006; Rowland et al., 2017). This learning process can subsequently result in evolutionary consequences for mimetic prey with mimics gaining a selective advantage, allowing for the specific prey signal to spread.

Studies have investigated the influence of social learning on aposematic prey (Figure 6). Across many predatory species, foraging is carried out in social groups (sociality) where communication is key. In multiple Batesian mimicry systems birds are often the fixed predator. Great tits (*Parus major*) have been at the forefront of these studies demonstrating the effect of social learning when placed in contained environments. A recent study using firebugs as aposematic prey and juvenile great tits as the predator evaluated social learning and its influence across individuals (Landová et al., 2017). The birds were placed in two separate groups (control and observed) with the observed group observing a demonstrator prior to their encounter with the firebugs, and the control having no interaction with a conspecific. Social learning was found to increase the rate of individual learning with a significant decrease in firebug mortality within the observed group. This study demonstrates a common theory that social learning has evolutionary consequences for individual predators and their aposematic prey. Despite the isolation of both the demonstrator and observer the study would be worth replicating in as close to natural conditions with a housed population of chicks or birds. From here it would be possible to identify individuals and behaviours within a group setting. Supporting the study carried out by Landová et al (2017), Thorogood et al (2018) used *P.major* as their predator and placed artificial prey with specific patterns (aposematic and cryptic prey) across the floor of an aviary. Video playback was used for the individuals as to keep demonstrator actions consistent. Again the study found significance in the fact learning can influence evolutionary trajectories for both the cryptic and aposematic prey. In conjunction with both studies a separate analysis looked into novel foraging techniques in wild birds and how the social learning could diffuse across the population (Aplin et al., 2015). Despite the study investigating foraging techniques with puzzle boxes, the consequences and learning demonstrated has implications for mimicry. With demonstrators the novel behaviour spread amongst the population, showing that through social learning new techniques were acquired.

The importance of learning in the context of mimicry is a relatively modern revelation. The predator-prey arms race has been a continuous battle between both sets of species. It is well known that predators act as a selection agent on mimicry, and their behaviours influence prey morphology (Ruxton et al., 2004; Sherratt, 2008). However, more recently it has been identified through negative encounters with prey, predators are able to associate prey signals with unpalatability (Ham et al., 2006; Darst and Cummings, 2006; Rowland et al., 2017). This in turn allows for cognitive associations to be made between the predator and their perception of the prey (Sillén-Tullberg, 1985; Kikuchi and Sherratt, 2015). This can result in different predator behaviours, which in turn can have a hand in influencing selection. After all, mimicry is a product of natural selection, and with the addition of predator learning to current evolutionary drivers in mimicry, selection is always changing. With specific warning signals, their conspicuousness can result in an accelerated learning for predators. For example, a recent study assessed the power of signal salience within a mimetic scenario (Kazemi et al., 2018). Signal salience has been attributed to lead to imperfect mimicry as well as accelerate learning in some instances (Kazemi et al., 2014; Kazemi et al., 2015). In the recent study it was found that the previous indications and hypotheses regarding salience were true. Using semi artificial prey in the form of butterfly wings and predators as wild birds it was concluded Batesian mimicry evolution can be influenced by salience when linked to learning. The black morphs were avoided at a greater rate which was thought to link to their melanism, whereas other species were unable to be distinguished by the hind wing colouration – indicating a lower salience. The findings established in the previous studies mentioned, correspond with a similar salience investigation using domestic chicks

(*Gallus gallus*). This study used different colours and patterns attached to mealworms to test the importance of specific signal features (Aronsson and Gamberale-Stille, 2008). Concurring with various other studies, the results highlighted colour was a prominent feature when learning amongst the prey types. With a lot of learning studies individuals are used, which provides an insight into social learning. However in order to gain a greater understanding of predator dynamics during foraging, as well as group learning, future studies should isolate the model-mimic characteristics and place them in an as close to natural environment as possible. Here group scenarios may be able to be used to unveil key evolutionary drivers for mimicry, unlocking potential benefits models and mimics may accrue through social learning. For example, fewer encounters may be required to educate the population, thus providing the model with a fitness benefit.

Through previous work it was identified that associative learning is predominantly at the heart of mimicry and aposematism (Skelhorn et al., 2016). This ideology is crucial when building a framework evaluating mimicry in an evolutionary sense. Associative learning is a common mechanism by which a predator may learn to avoid aposematic prey through multiple negative encounters or experiences, leading to the association of a prey's toxicity with its specific warning signal (Skelhorn and Rowe, 2006; Prudic et al., 2007). This therefore creates avoidance behaviours towards the common signal. Skelhorn et al (2016) go on to add that the salience of the prey's warning signal *should* create a lower asymptote and steeper curve when illustrated on a learning curve. This has been supported by previous work highlighting the association between the prey's toxicity and signal, leading to a steeper learning curve (Aronsson and Gamberale-Stille, 2013).

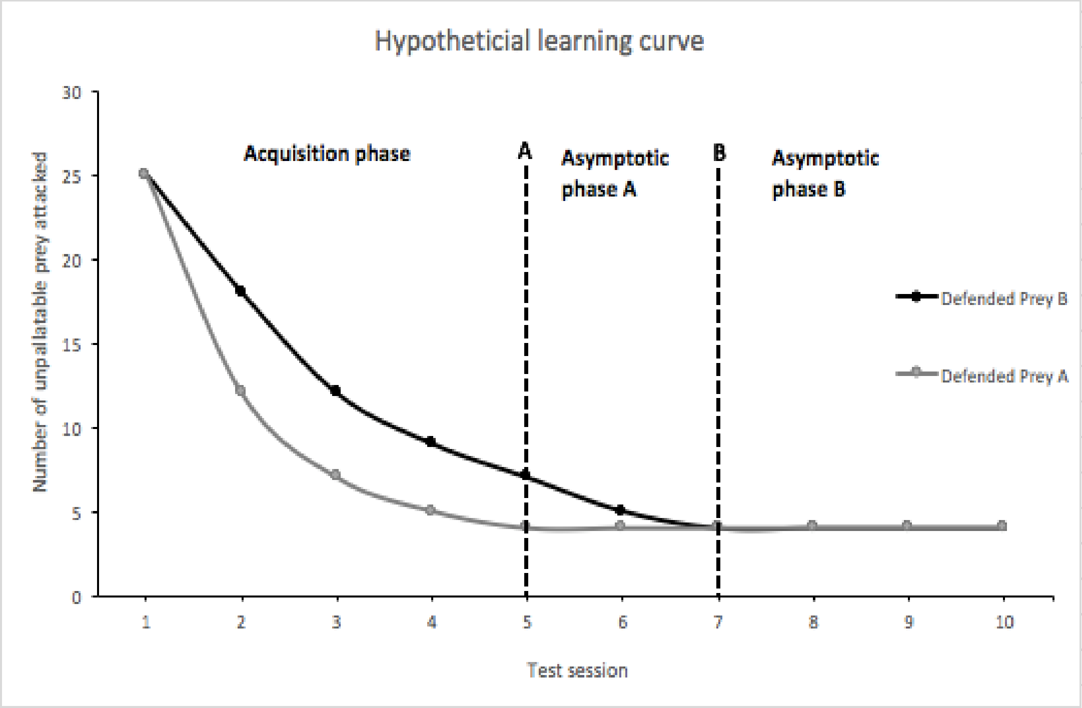


Figure 6. Graph representing a hypothetical learning curve for associative learning, and how this can be influenced by salience. In this hypothetical figure, defended prey A possesses a salient warning signal which leads to an increased speed of associative learning thus a steeper learning curve (Roper, 1993; Hauglund et al., 2006). The steeper learning curve results in the asymptotic phase occurring much earlier on. In comparison, defended prey B has a less salient warning signal, thus it takes longer for the conditioned stimulus to gain association with the unconditioned stimulus. Resultantly, this leads to the asymptotic phase occurring later. The acquisition phase is the period where the predator is learning about the prey’s warning signal and subsequently is believed to display the speed by which the association of the warning signal (conditioned stimulus) and unpalatability (unconditioned stimulus) is learned. Following the acquisition phase, comes the asymptotic phase which highlights the idea the predators have learned and the attack rate does not change. Figure adapted from Skelhorn et al (2016).

With learning being a complex cognitive function, much work is being done to understand the cognitive state of signal receivers and how this may influence selection on mimicry. This is especially important when applied to mimicry in the wild, as different foraging behaviours are crucial in the evolution of aposematic prey and mimicry.

Opposing learning within a mimetic sense is innate avoidance. Innate tendencies for predators can first of all offer protection to the predator but also influence mimetic evolution across different geographical regions to a similar degree as learning.

Through innate avoidance, imprecise mimics can be thought to often gain protection if the specific model tendencies are replicated. Supporting the theory for innate avoidance of specific mimetic morphs, a paper evaluating the experimental studies of coral snake mimicry discussed the possibility that through conflicting life history traits and ancestors inhabiting sympatric ranges, predators display a general avoidance towards ringed patterns through ancestral encounters (Brodie III and Janzen, 1995). The paper states, though there are two documented cases of innate avoidance (Smith, 1975; Smith, 1977), the species in question (Kiskadee's and motmots) share ranges with the coral snake *Micurus* thus the innate avoidance is likely towards more the pattern than colour. The paper goes on to add this could be attributed to ancestral encounters throughout history. Smith (1975) investigated the innate behaviours of motmots when faced with wooden models of snakes painted different colours, including some common aposematic warning colourations. Motmots have been known to co-occur with *Micurus* across their native range. The coloured patterns involved consisted of: green and blue, a red and yellow stripe and a red and yellow ring. Interestingly avoidance behaviour was only present when the closest replica to a snake, red and yellow ringed pattern, was presented to the motmots. The results suggests innate aversion is prominent within certain species and environments, which could also correlate to the danger of the aposematic prey. Additionally a similar study was replicated with kiskadee's (Smith, 1977) but incorporated a coral snake replica pattern, alongside a supplementary ringed pattern of red and yellow. The results confirmed an avoidance type behaviour to both the ringed patterned models suggesting a possible innate aversion to the pattern as opposed to the colour, going against Sillén-Tullberg (1985)'s study on zebra finches. The study inferred it is predominantly colour not conspicuousness that leads to innate aversion. However, as mentioned by more recent studies (Mappes and Alatalo, 1997) it can be difficult to distinguish between neophobia and innate aversion towards specific aposematic colouration, especially with test subjects that have not encountered such colours before.

Therefore, both Smith (1975; 1977)'s results do point towards a more generalized avoidance towards the pattern as opposed to the colour, as the yellow and red stripes on the model were still attacked. In conclusion, further investigations should consider adapting Smith (1975)'s study isolating both experienced wild motmots and naïve juvenile motmots, repeating the study with bi and tricoloured replicas of coral snakes with different colours to see if there is an innate tendency to avoid specific warning colourations or if the pattern is the most important feature. Comparing the analysis of juvenile naïve individuals and wild experienced individuals would allow us to identify any discrepancy between both groups.

2.4 Mimicry and Networks

Networks have been at the heart of community ecology for a vast period of time and can be seen across multiple biological systems (Proulx et al., 2005). Batesian mimicry has been a challenge for many evolutionary scientists, however with many studies unveiling new insights into this phenomenon, Batesian mimicry has now gained a greater understanding across the board. However, with mimicry influencing multiple species on not only an individual but a community level, a niche for network modelling has become apparent. Little work has been carried out to date on mimicry with the incorporation of networks.

Marchini et al (2017) recently looked at the abdomen pattern of 203 Syrphidae and 127 Vespidae to analyse the co-occurrence of their colour patterns. Through the use of classification, four thoracic segments were highlighted and given their own identification for both the Vespidae and Syrphidae group. Interestingly, two intraspecific networks were constructed illustrating the co-occurrence of specific thoracic patterns. In conclusion Marchini et al (2017) showed that between the two groups the lower abdomen contained the highest number of co-occurrences for colour pattern, whereas the thoracic segments had the highest degree of difference perhaps linking to imperfect mimicry. These networks are useful in being able to distinguish the frequency of species colour pattern across mimetic species. However, as known with mimicry, different ecological habitats contain different terrains and house different species. Therefore similar network mapping (incorporating environmental gradients) of mimetic species and their phenotypic variance across these terrains may further enhance mimetic understanding as species are distributed unevenly across geographical ranges. Despite phylogenetic networks being a recent avenue for network mapping in mimicry (Penney et al., 2012; Vršanský et al., 2018), nothing has been done on a community level incorporating ecological networks and their implications to mimicry systems.

2.5 Conclusion

With natural selection continually refining mimicry, the underlying mechanisms by which mimetic systems are influenced, are slowly becoming apparent. The understanding of species interactions within a mimicry system are crucial in pinpointing potential evolutionary drivers, which lead to a continued battle between both the model and mimic to enhance fitness. Models and mimics within a Batesian mimicry system are constantly under significant selection pressures from (more often than not) their mutual predator. The shared signal between model and mimic can be important when an experienced predator is foraging, thus meaning signal accuracy can be vital to potentially deter the predator. Despite the many components which influence mimicry, many areas remain relatively unexplored. This opportunity does lead to empirical and theoretical approaches presenting themselves. In my thesis, I will evaluate two different components of mimicry. Each component will contribute to the evolution of mimicry, hopefully paving the way for further studies to build on the basis it will present. One aspect of my study, will investigate high fidelity model and mimic co-occurrence across a vast geographical data set. The idea of species co-occurrence in a mimicry system is one of interest as this can provide an insight to species distribution and interaction. Species distribution has been a fundamental aspect of community ecology, which alongside the novel approach towards co-occurrence modelling, has the potential to create a greater understanding of various ecosystems and the roles species play within them (Cazelles et al., 2016). Supplementing the co-occurrence investigation, I will also apply network theory to Batesian mimicry which will allows us to determine clusters of models alongside meso-scale species interactions. The second component will be my study investigating the effects of social learning on novel prey items in zebra finches, *Taeniopygia guttata* within a Batesian mimicry system. Similar studies have evaluated ideas on this topic (Aplin et al., 2015; Thorogood et al., 2018). Through the use of NBDA analysis I will be able to test the spread of social information within a group, alongside the benefits accrued through social learning for models and mimics.

Chapter 3 - Batesian Mimicry: The Application of Network Theory to Model-Mimic Interactions

3.1 Abstract

Mimetic relationships that have evolved to deter predation rely upon predators encountering both the model and mimic in order to transfer learned avoidance onto the mimic. However, the nature of spatio-temporal co-occurrence of models and mimics has received little attention. Here, we test two key hypotheses: first, that models and mimics cooccur more often than would be expected by chance, and second that mimetic bipartite networks exhibit consistent structural configurations across spatial gradients. Using data on Hymenoptera (models) and Syrphidae (mimics) from a large-scale standardised survey of pollinators and biological recording schemes, we created detailed networks and graphs to illustrate mimetic interactions. We found co-occurrence did not occur more than would be expected by chance. However, it was identified that bipartite networks, alongside NMDS analysis produced empirical evidence of mimetic interaction and clustering. Complimented with the incorporation of network motifs, mimetic interactions can be analysed in a new way. With the opportunity to evaluate mimetic complexes further with new theoretical approaches, the evolutionary pathway of mimicry is slowly growing in understanding. However further work is required to unravel its origins.

3.2 Introduction

Mimicry is a complex product of natural selection, with its occurrence spanning multiple taxa (Pfennig et al., 2015; Dalziell and Welbergen, 2016). There have been many small-scale observational studies of mimicry, but few have occurred at ecologically relevant taxonomic scales. Despite these studies the evolutionary pressures that produce and drive mimetic relationships are less well described. Model-mimic interactions have been studied in depth both empirically and theoretically (Huheey, 1988; Kikuchi et al., 2015), with examples such as clay snakes being used to imitate the geographic phenotypes of the highly venomous eastern coral snake. These clay mimics were placed to test the predation rate on individuals in areas of sympatry or allopatry (Pfennig et al., 2015). Mimetic antagonistic coevolution among models and their mimics leads to a dynamic co-evolutionary system (Speed and Ruxton, 2005). For optimum species success, models would need to diverge away from the mimic, and the mimic would need to converge on the model (Jamie, 2017; Kristiansen et al., 2018). Therefore, the occurrence of models and mimics will have a positive effect on mimic fitness and a negative effect on the model.

Co-occurrence of interacting species is a widely-discussed topic (Gotelli, 2000; Davies et al., 2007; Cazelles et al., 2016). Spatiotemporal co-occurrence facilitates interactions among species (Gotelli and Graves, 1996; Horner-Devine et al., 2007), and the degree to which species cooccur can strongly influence the structure and function of ecological communities. For example, the co-occurrence of plants and pollinators has been used to infer the resilience of the community to species loss (Ballantyne et al., 2015; Beckett, 2016). Many factors can influence co-occurrence, such as abiotic and biotic factors. Bumblebees (*Bombus* spp.) are an example of a species that’s heavily influenced by both abiotic and biotic factors. With recent studies highlighting both climate change and parasitism as a key driver in both range and species decline (Kerr et al., 2015; Sirois-Delisle and Kerr, 2018). Null model analysis is a common method used to study co-occurrence with species associations being identified through non-random patterns (Ulrich and Gotelli, 2013). Positive species associations can be a result of environmental requirements that influence both species. Additionally, factors from a historic perspective, such as dispersal barriers can contribute (D’Amen et al., 2018). Specific ecological requirements of species vary and this can lead to species variation spatially. This variation, alongside allopatric speciation are only a couple of examples that can lead to negative species associations (Diamond, 1975). Null model analysis patterns are often hunted to indicate any processes that may influence community assembly.

Species aggregation can be a strong indicator of species co-occurrence. Aggregation can be a result of multiple processes such as predation or mutualism (Sih, 1984). Co-occurrence can vary from species to species and across environmental gradients. One aspect that can influence co-occurrence is community structure (Pulver et al., 2016). Community structure is defined by both species richness and species diversity. Community structure is subject to multiple biotic and abiotic factors, some of which can heavily influence the composition of the community (Dunson and Travis, 2002; Mitchell et al., 2017). Many studies apply theoretical models to community structure in order to assess different measures such as connectedness (Newman and Girvan, 2004; Proulx et al., 2005; Coyte et al., 2015). The neutral theory can be applied to community structure through its theoretical approach to community formation. The theory suggests speciation balances chance extinction, ultimately leading to the development of communities rich in equal species (Hubbell, 2001). The theory takes into account stochastic processes such as immigration from a meta community and death (Figure 7). However, it also considers species of a trophic similarity within an ecological community inhabit differences, however these differences are “neutral” to species success. Therefore, communities are not created through environmental filtering but through random walks – suggesting species inhabit areas where they end up (Hubbell, 2001).

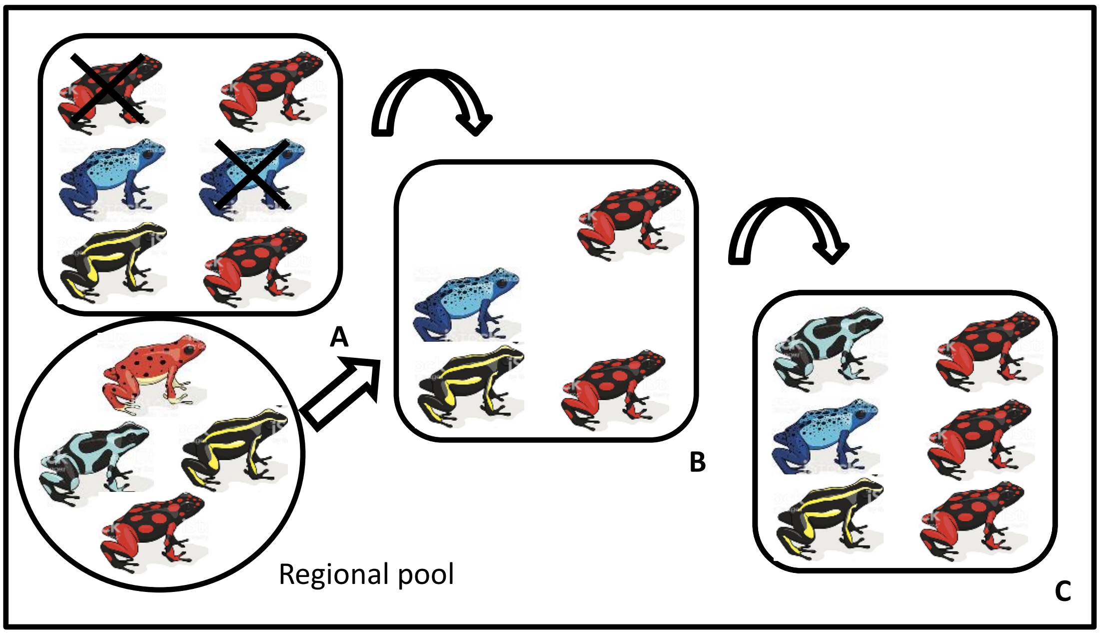


Figure 7. The neutral theory in an artificial simulation. The local community (A,B and C) contains a diverse selection of species which are present in the regional pool also (regional pool scaled down for purpose of figure). The local community undergoes random death leaving small pockets for species to migrate into (B). Through the process of dispersal species are able to inhabit the vacant areas (C). This random process can result in species from either the regional pool or local community entering the space. Within a greater context the process of speciation is possible over time. This can arise through random mutations and local extinctions with the local community able to frequently inhabit vacant sites. Adapted from (Harpole, 2010). Images: www.istock.com.

Despite co-occurrence varying across spatial gradients, mimics and models can co-occur more readily through chance. Co-occurrence can be used on an ecological scale to obtain information on networks of species interaction (Freilich et al., 2018). Despite many mimics co-occurring with their respected models in sympatry (Harper and Pfennig, 2007), mimics can persist in allopatry with examples such as the eastern coral snake in the USA (Pfennig and Mullen, 2010; Pfennig et al., 2015). Mimics require the selection agent to maintain their mimetic characteristics (Skelhorn et al., 2016). Interestingly, some migratory predators have been identified to possess the ability to demonstrate long term memory (Mappes et al., 2005). Therefore, mimics are able to persist in allopatry away from their models, through the cognitive recognition of their mutual predator (Poulton, 1909; Pfennig and Mullen, 2010). Geographical separation of models and mimics can influence selection pressures: sympatric mimic populations experience relaxed selection due to the higher abundance of models. Meanwhile allopatric mimics are attacked by predators that have less experience with the model phenotype, therefore those mimic populations require higher levels of fidelity to provoke the same response in the predator (Harper and Pfennig, 2007). The idea species in allopatry require a greater mimetic fidelity, parallels with the fact: a) models are not present in the same geographical range, therefore morphological similarity is key to fool their common predator, thus gaining the greatest fitness advantage. b) Predators display aversive behaviour towards aposematic colouration through associative learning (Kazemi et al., 2014).

Mimetic fidelity is an indicator of mimetic strength, showing the similarity between both the model and mimic (Iserbyt et al., 2011; Easley and Hassall, 2014). Harper and Pfenning (2007) demonstrated that mimetic fidelity increased depending on the ratio between models and mimics when observed across a specific site. Additionally, Iserbyt et al (2011) looked at mimetic fidelity from an intraspecific perspective, identifying fidelity increases alongside a change in the mimic-model ratio. The relationship between co-occurrence and mimetic similarity has not been tested to date, and we will be looking to see if there is a positive relationship between both high fidelity mimics and their co-occurrence.

Network theory is the application of visual and computational methods in order to characterise the relationships among a set of objects. This network provides an insight into the overall structure of the community or system whilst outlining individual interactions (Jacoby and Freeman, 2016). In the context of mimicry, network theory has very rarely been used and is untested with mimetic interactions. There are a wide array of networks that can be applied to community ecology, with these ranging from food webs through to bipartite networks. Network theory has been applied across different ecological scenarios, displaying species or individuals throughout a vast network and indicating how interactions occur (Proulx et al., 2005; Farine and Whitehead, 2015; Gosak et al., 2018). Social networks are used across a variety of species, to identify information transmission (Allen et al., 2013), or even to display social structure (Lehmann and Boesch, 2009). Bipartite networks are used to break down complex networks which possess two sets of species or organisms. The network illustrates the interaction between species or individuals, creating an overview of the community (Corso et al., 2011). Bipartite networks have been used to demonstrate pollinator species and the floral host they interact with the most, along with parasites and the species they parasitize across a community. (Poulin, 2010; Ballantyne et al., 2017).

Network motifs represent sub graphs that re-occur among networks that can vary, along with networks that can be deemed specific (Simmons et al., 2018). Network motifs are defined as: "*patterns of interactions occurring in complex networks at numbers that are significantly higher than those in randomized networks*" (Milo et al., 2002). Motifs have been suggested as a toolkit that can be used across a wide array of disciplines, from ecology to chemistry (Milo et al., 2002; Kashtan and Alon, 2005). The use of network motifs within a bipartite network display meso-scale constructs, which can be overlooked. In a typical bipartite network macro and micro scale interactions are considered, looking on a whole scale across the entire network and individual species interactions (micro scale). Recent studies have applied networks and their measurements to assess species on an ecological level. A paper looking at species' role in an oak forest found that their individual roles across the community heavily correlated to their intrinsic property (Baker et al., 2015). The study evaluated whole scale measurements such as abundance and number of interactions. However, fidelity was found to link to species' role within the community. Through the use of bipartite motifs we have access to a series of metrics that allows us to describe processes that operate at the meso-scale (Simmons et al., 2018). A recent review analysed the application of meso-scale structures of a network and how these can allow us to develop a greater understanding of the whole network (Zanin et al., 2014). Communities has been the primary focus of meso-scale structures which looks at the clustering of nodes within a network (Fortunato and Barthélemy, 2007). However motifs, recently have been considered as a useful method of obtaining additional information on communities. The subnetworks generated from bipartite motifs can tell us how often certain motifs occur across a network (Rodríguez-Rodríguez et al., 2017) to illustrate a species' role by calculating species frequency within different positions across motifs (Baker et al., 2015).

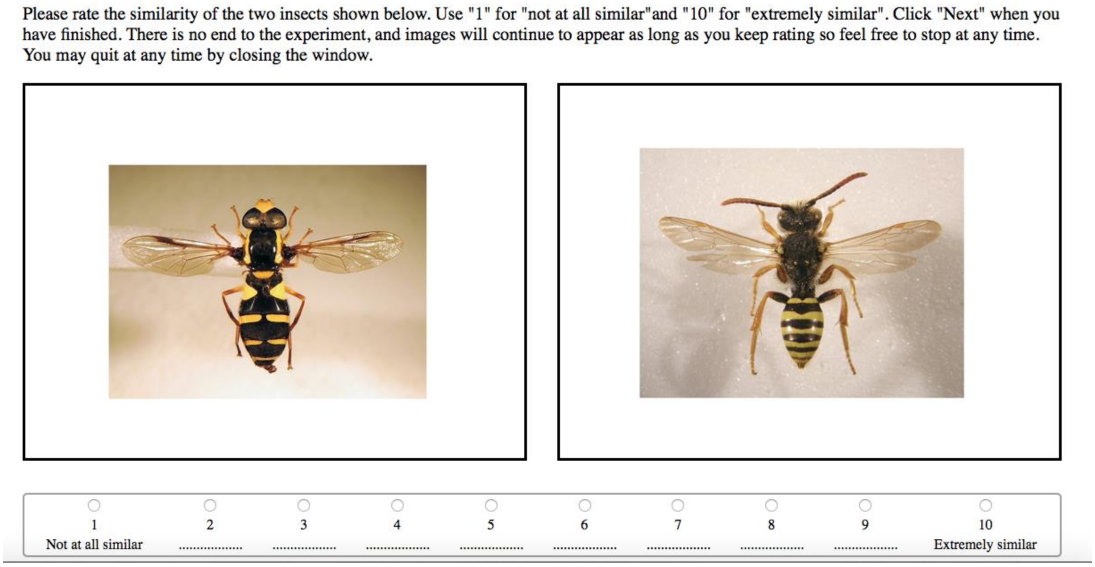
Mimetic relationships are the basis on which mimicry has been built, and are crucial to their maintenance (Ruxton et al., 2018). However, various aspects of these mimetic interactions have not been explored in detail. These range from species-species co-occurrence to wide scale community approaches to mimicry. In the recent study by Hassall et al (2018), we can see evidence of mimetic similarities being derived empirically to produce an overall matrix, identifying species similarity on a large scale. Applying such techniques across systems can lead us to understand the ecological significance of mimicry and how species, both models and mimics are influenced by their counterparts. Our application of the similarity work produced previously, has allowed us to produce empirical evidence that mimetic relationships can be derived and displayed. To build upon the knowledge we have today surrounding mimicry, we can use these mimetic interactions and apply them to multiple techniques. In a study by Penney et al (2014) a phylogenetic tree was produced for particular species of Syrphidae. These techniques alongside the knowledge of mimetic interactions can pave the way for a greater understanding of the evolutionary process that arose to form mimetic interactions.

In this study, we apply network theory and the concept of bipartite motifs to Batesian mimicry systems to explore spatiotemporal variability in model-mimic interaction networks. We derive information on model-mimic similarity based on a citizen science experiment, and combine that information with network theory and biological recording to test three key hypotheses: 1) model-mimic networks can be characterised using citizen science, (2) higher fidelity models and mimics co-occur more than by chance, and 3) meso-scale network structure varies along a spatial gradient.

3.3 Materials and Methods

3.3.1 Model-Mimic Similarity Relationships

The models and mimics used for each study were species used in a recent similarity paper (Hassall et al., 2018). Forty-two Hymenoptera species consisting of bees and wasps, along with 56 species of Syrphidae (Diptera) were selected. The species included in the study (see Appendix A) were both high in abundance and common across both the bees, wasps and ants recording scheme (BWARS) and the hoverfly recording scheme (HRS). Common species were selected based on the idea species that were more common would be more likely to co-occur with each other and hence have a mimetic relationship if they possessed similar morphologies. This study looked at mimetic networks on a community level using a citizen science experiment, www.mimicryexperiment.net. The randomly selected images (one from the Hymenoptera group and one from the Syrphidae) were presented to online human participants via a computer screen, whilst being side by side against a white background (Figure 8). Their task was to rank the species' similarity from one to ten, with ten being listed as “extremely similar” and one being listed as “not at all similar”.



Please rate the similarity of the two insects shown below. Use "1" for "not at all similar"and "10" for "extremely similar". Click "Next" when you have finished. There is no end to the experiment, and images will continue to appear as long as you keep rating so feel free to stop at any time. You may quit at any time by closing the window.

○	○	○	○	○	○	○	○	○	○
1	2	3	4	5	6	7	8	9	10
Not at all similar	....	....	....	....	....	....	....	....	Extremely similar

Figure 8. User interface for the mimetic fidelity rankings, where users had to rank randomised models and mimics based on their similarity with a score of 1-10. Image taken from www.mimicryexperiment.net.

3.3.2 Co-occurrence of High Fidelity Models and Mimics

The species used in the similarity study were again selected for the co-occurrence study. Records of the 42 Hymenoptera and 56 Syrphidae were extracted from a large dataset of standardised pollinator sampling. This project looked at pollinators and their decline across various regions in the UK. The Agriland dataset was chosen for our network based approach due to the data available, which was easy to manipulate to create a mimietic network based on the pollinators. The dataset produced a large number of networks through time and across landscapes that could be used to look at network-scale interactions in a way that has not been done before. Currently data doesn’t exist for a multi network approach within a mimietic capacity. Additionally community data for models and mimics is hard to come by with most studies relying on individual sites and often individual pairs of interacting species. Therefore the dataset available provided an opportunity to analyse mimetic species from a community perspective and see how networks could qualtitaviely provide information on mimcry. For the co-occurrence investigation, the data was collected throughout six locations in the U.K. The six locations ran along a transect starting at Ayrshire. The transect then ran through: Inverness, Yorkshire, Staffordshire, Cambridgeshire and Wiltshire. The sample regions were an area of equal size but differed in their composition. The regions were approximately 100 by 100 km grids and had 16 sites each. Sampling areas were selected to represent statistically the British countryside based on their land use, climate, natural habitats and topography. The individual pollinators were caught in pantraps across the different sites, and recorded into a vast dataset. The species caught were tested to assess co-occurrence within these sites across the UK.

3.3.4 Data

The data was analysed through the data analysis toolkit, R version 1.1.456 (R Core Team, 2018). The co-occurrence matrix was constructed to measure co-occurrence on an observed against expected occurrence for individual species. The R package vegan (Oksanen et al., 2018) was used to produce non-metric multidimensional scaling (NMDS) plots of models and mimics. The cooccur (Griffith et al., 2016) package was used to perform statistical comparisons of observed co-occurrence patterns against a null distribution to evaluate statistical significance of the pattern of models and mimics across a spatio-temporal gradient. The similarity matrix in the paper by Hassall et al (2018) and co-occurrence matrix from the Agriland analysis, were combined to create a single matrix. A customised permutation test based on a generalised mantel test was used to analyse the matrices and to see if there was any significant difference between the high-fidelity models and mimics and species which co-occurred more than by chance within the geographical range. In addition to the r packages vegan and co-occur, the package jmuOutliner (Garren, 2019) was used to carry out the customised permutation test. The bipartite (Dormann, 2011) package in r was used to create visual graphs of the similarity dataset to illustrate mimic to model connections. Finally the r package bmotif (Simmons et al., 2018) was used to analyse the motifs in a bipartite network. Network motifs focus by looking at the specific patterns networks possess that are significantly greater in number when compared to same patterns in random networks, These motifs are used to analyse the meso scale, which were suitable for this particular study due to the nature of information that can be derived from their use. The use of motifs allows us to look at multiple interactions across a community in depth, providing a greater insight into the connections between species (Figure 9). Alternatively the use of motifs could contrast the information obtained from micro (dyadic) and macro (whole network metrics) interactions. For example dyadic interactions can tell us which species are imitating which species, but these are bound to be confusion effects when models and mimics co-occur. Similarly, network scale effects can tell us about the complexity of a system and whether as a group models and mimics are more common. The real benefit of meso scale effects is that it tells us something complementary: if we have a group of similar animals (e.g 2-3 models and 2-3 mimics) then it describes the nature of the relationship among them. Do the mimics share models or the models share mimics? Are models linked indirectly through shared mimics? Bipartite analysis focuses on a community on a wider scale, with traditional research looking at small numbers of species on a much smaller scale. Both computational methods provide visual graphs that illustrate the composition of a community (Beckett, 2016). Much previous work has used bipartite networks and motifs as a source of network illustration, ranging from host-parasitioid species to the plant-pollinator species.

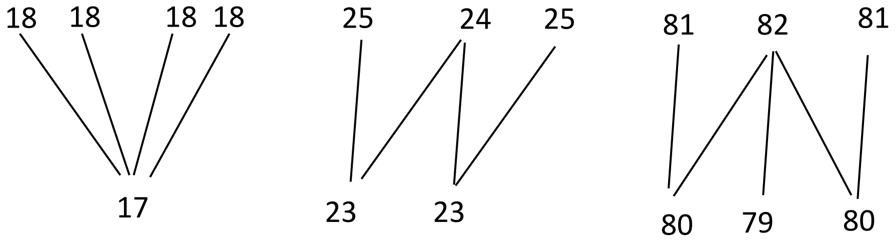


Figure 9. Bipartite motif example illustrating the visual representation of the network structures. The examples presented display common motifs across five and six node variants. These particular scenarios depict a pattern that can be followed for mimicry. In this hypothetical network, mimics would be represented by the the numbers featured on bottom of the motifs with models at the top. So the number 18 could represent different model species which are mimicked by one mimic species. When applied to literature, this overview provides a strong indication toward the multimodal hypothesis where a mimic may mimic more than one model (Edmunds, 2000). Each node on the theoretical network above illustrates a potential position for a species to occupy based on the overall bipartite network.

3.4 Results

3.4.1 Do Higher Fidelity Models and Mimics Co-occur More Than by Chance?

Based on the Agriland dataset and similarity work previously done (Hassall et al., 2018) on the 42 Hymenopteran and 56 Syrphidae, there was no significant relationship between high fidelity models and mimics and their co-occurrence. Based on the permutation test which centred around the generalised mantel test, P>0.05, 0.05 = 3136.98 and 0.95 = 4585.33 (Figure 10). Alternatively, there was no evidence to suggest that higher fidelity models and mimics co-occurred more than by chance. Based on the similarity and co-occurrence matrices (Figure 12) *Apis mellifera* and

Eristalis tenax ranked the highest across both matrices, with a mean similarity score of 5.93 and co-occurrence of 42 (44%).

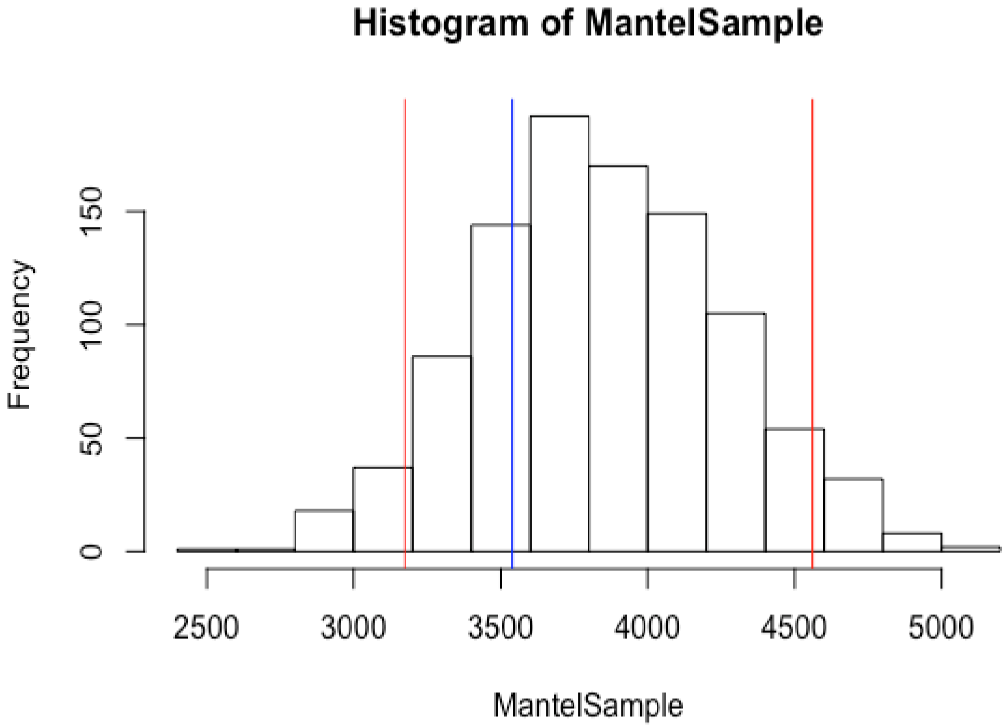


Figure 10. Mantel test for co-occurrence. Histogram of null distribution from a permutation test based on a generalised mantel test. The significance limits (red lines) at 5% and 95% have been included along with the observed value (blue line). Illustrating p>0.05.

3.4.2 Can We Derive Model-Mimic Relationships Empirically?

Across the 2,352 potential model-mimic pairwise combinations, 237 combinations were deemed suggestive of a mimetic relationship based on the assumption that a similarity score >=5 would indicate "high fidelity" pairings (Hassall et al., 2018). The 237 mimetic pairings displayed a mean 13.5% Jaccard indices overlap. The Jaccard indices overlap varied between 2.6% - 28.4% (Hassall et al., 2018). The similarity scores were ranked by human perception, however when compared to previous visual experiments using pigeons, the results correlated significantly. The use of bipartite networking can be implemented across mimetic systems and was illustrated in line with the similarity data set.

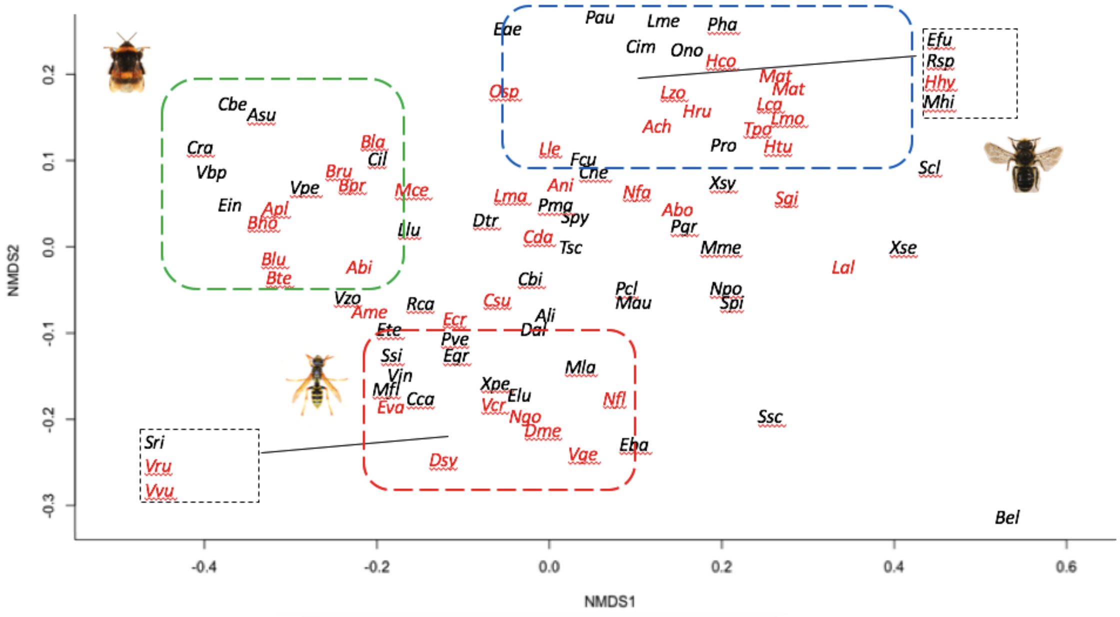


Figure 11. NMDS analysis of the 56 Syrphidae and 42 Hymenopteran from the similarity dataset, including outline of clustering for different mimetic systems. Images: Both common bee and wasp images (left handside) www.herebydesignnet. The solitary bee *Osmia spinulosa* www.flickriver.com.

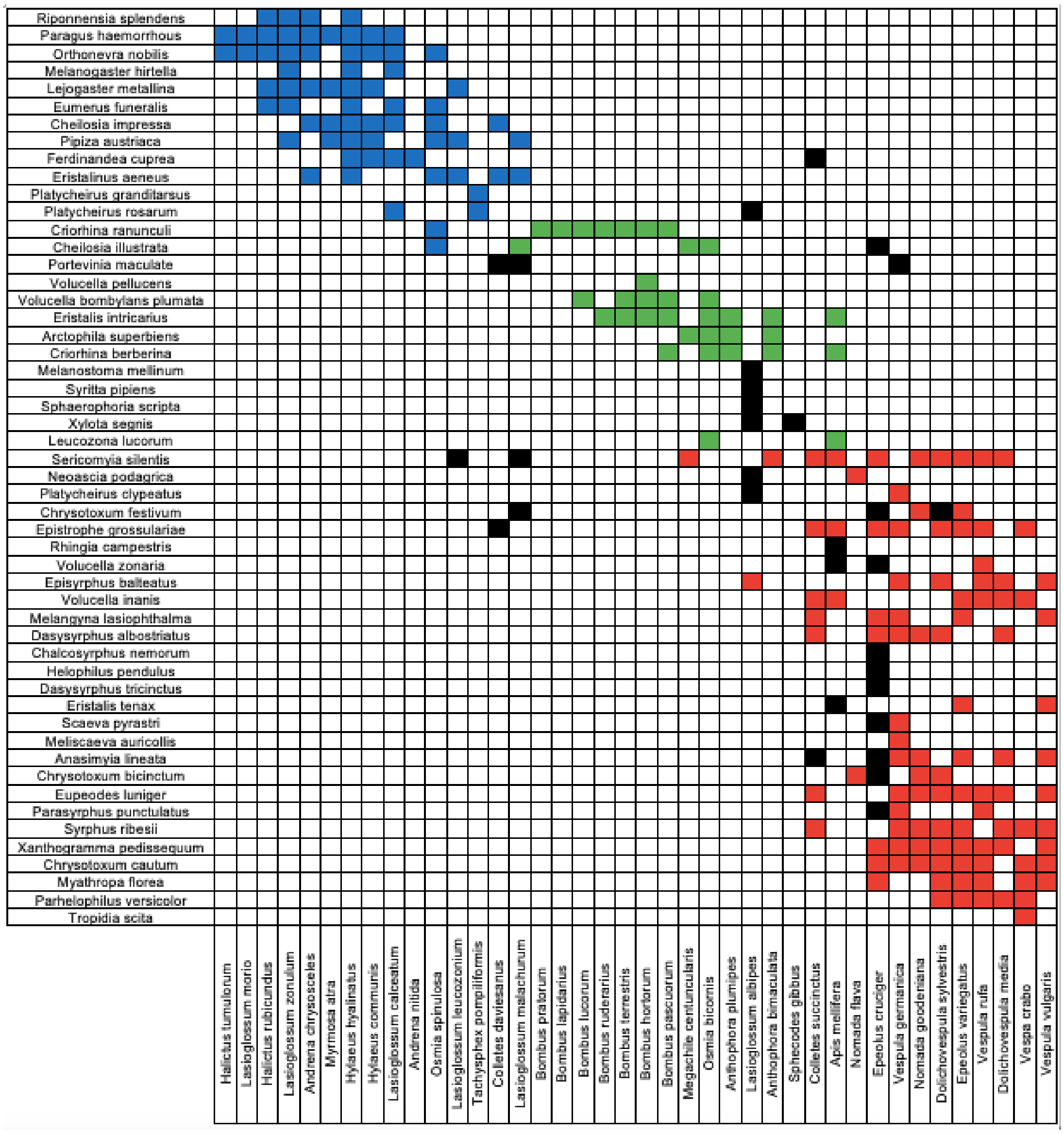


Figure 12. Grid representation of the NMDS network of models and mimics. The colours represent the different clusters as shown in Figure 10.

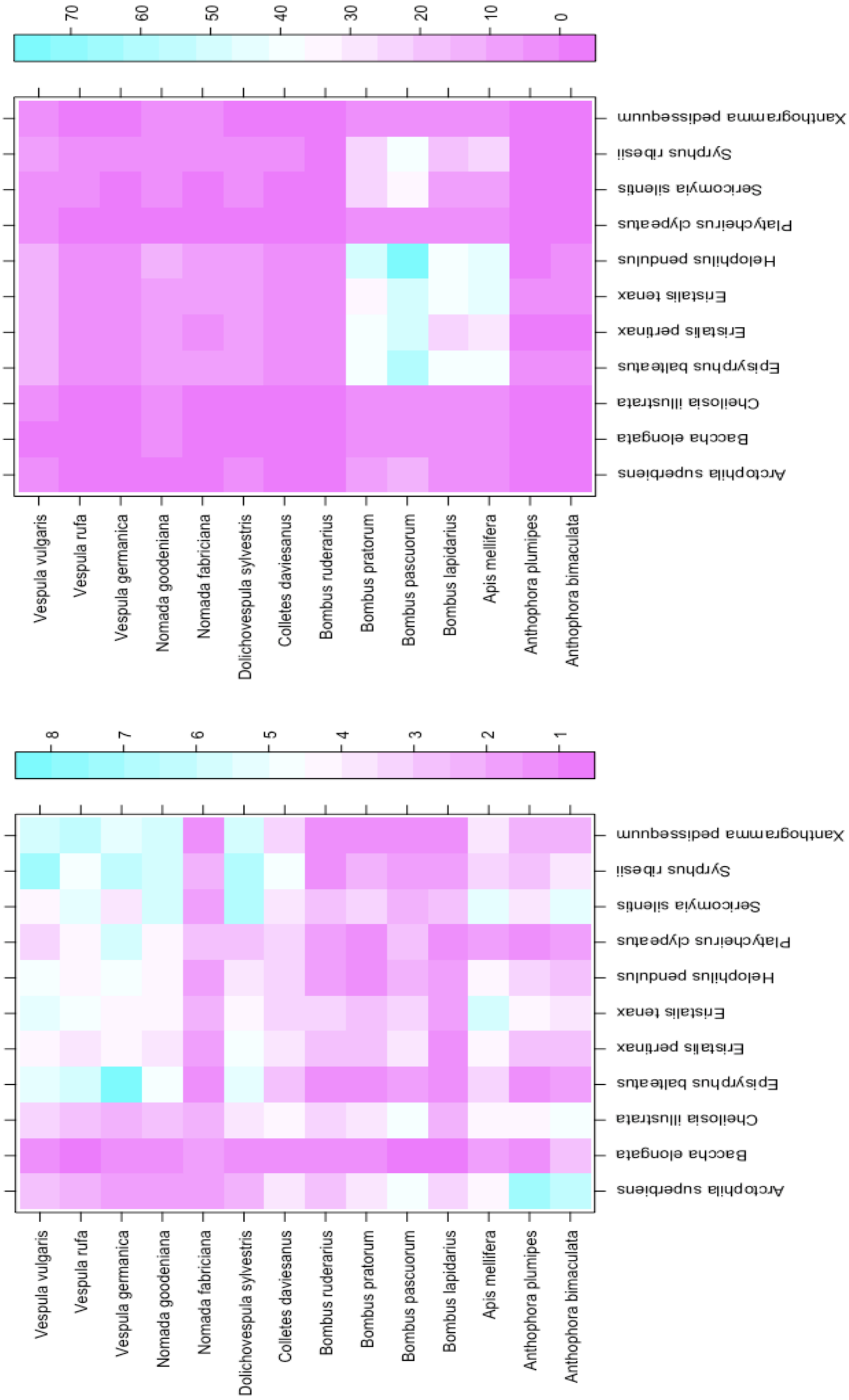


Figure 13. Similarity and co-occurrence matrix for 14 models and 11 mimics. The similarity matrix (left) shows mean similarity rating for model-mimic pairs based on the similarity paper (Hassall et al., 2018). The co-occurrence matrix (right) shows species co-occurrence across all the Agriland sites with the co-occurrence value illustrated by the key.

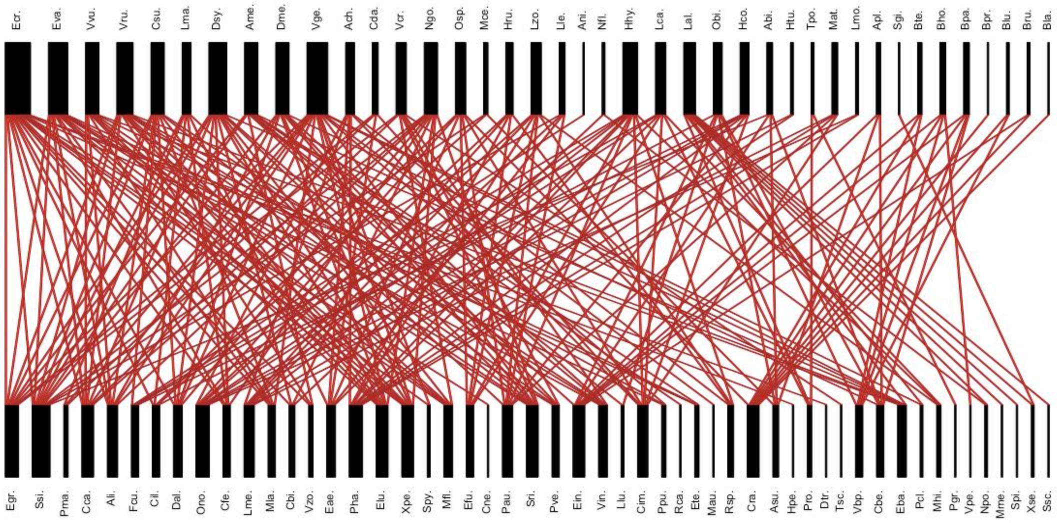


Figure 14. Bipartite network between the 56 Syrphidae and 42 Hymenoptera used in the citizen science experiment. Interactions based on mean similarity scores ranked >=5. Nodes are proportionally sized based on the number of interactions. Model species are placed on top with mimics placed below.

Figure 14 highlights a bipartite network with two levels, models (higher) and mimics (lower). The width of the node is proportional to the number of interactions with species on the opposite trophic level. Based on the individual species' morphological similarity, the bipartite network was able to distinguish species that are linked through their perceived similarity. The higher species, *Epeolus cruciger*, a cuckoo bee model interacted with 17 mimetic species whilst obtaining a similarity score >=5 for each interaction. Whereas the lower trophic species *Sericomyia silentis*, a hoverfly mimic, interacted with 12 Hymenopteran models. Figure 15 shows a bar graph highlighting the key motifs within the bipartite network. The four key motifs are classified as six mode motifs, broken down as six species per motif (illustrated by the numbers attached to each node). Key motifs were identified with the mcount feature of the bmotif package. The mcount measurement allows us to identify how often specific motifs appear within a network. The most common motif across the bipartite network was 20 which occurred 58,864 times. This particular motif contains two mimetic species and four models, with five unique positions within the motif. Motif 19, occurred 30,917 times across the network. Interestingly one specific mimic in this motif interacts with only one model, where-as the other mimic interacts with all four models. Motif 19, compared to 20, is similar but differs in unique positions and interactions amongst the models and mimics (Figure.14). One mimetic position interacts with two models, whereas the other mimetic position interacts with three models, with both mimetic positions sharing one common model. Motifs 28 and 29 occurred 47,645 and 30,599 respectively across the network. Motif 28 illustrates a six node motif with 3 models with the positions (87,88 and 89) and three mimics with the positions (83,85 and 84). The mimics in this particular motif show two mimics connected to two models and one mimic linked to one model.

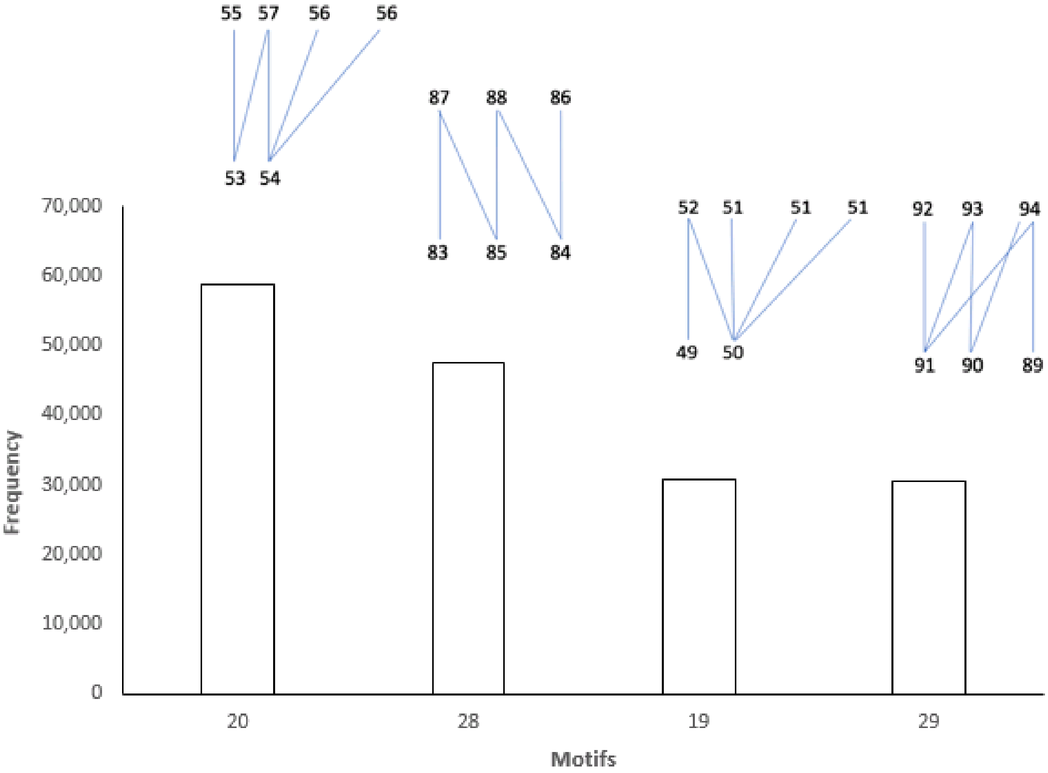


Figure 15. Bipartite motifs in order of occurrence. Frequency is based on the number of specific motifs in bipartite network (Figure 13). The small number represented at the end of the nodes, displays the position species can occupy across all 44 motifs. There are 148 positions across all 44 motifs. Motifs extracted from Simmons et al., 2018.

3.5 Discussion

3.5.1 High Fidelity Mimicry Complexes and Their Co-occurrence

This study has demonstrated that model-mimic relationships can be inferred from data drawn from human visual assessments, and that those relationships match what would be expected based on natural history observations. Bringing those mimetic relationships to bear on a largescale ecological dataset, we show that there is no evidence of statistically greater probabilities of co-occurrence in high fidelity model-mimic pairs than among other pairs of species. Finally, we discuss the potential use of bipartite motifs in understanding the structure and function of model-mimic networks.

Deriving species interactions from citizen science experiments has been successful with previous studies. In a recent review the wide scale use of citizen science is illustrated, pinpointing its importance in collecting data for multiple ecological scenarios. Ranging from seasonal phenology in insects to the migratory behaviour of birds and mimicry (Ries and Mullen, 2008; Chandler et al., 2017; Miller-Rushing et al., 2019) citizen science has contributed to vast datasets allowing studies to get meaningful results. Within a mimetic context, citizen science has allowed for the development in understanding mimetic species to species interaction. Our results through the use of citizen science demonstrate that mimetic interactions can be derived empirically and used to gain an understanding of mimetic communities. This network based overview can allow us to eventually gain an insight to the meso-scale interactions within a community alongside the model-mimic relationships and their significance to one another. An example of mimetic work with citizen science is apparent in the model-mimic fidelity work published in a recent study (Hassall et al., 2018) applying human perception to rank model-mimic similarity using a web page. The results correlated significantly with a previous experiment using pigeons as a study system when given various images of Hymenopteran models and Syrphidae mimics and their corresponding peck rate to those images (Dittrich et al., 1993). Interestingly the methodology between both Hassall et al (2018) and Dittrich et al's (1993) studies were similar in terms of presenting images of models and mimics on a screen for their subjects to rank or peck respectively.

Other studies looking at mimetic fidelity have used qualitative approaches measuring mimetic traits possessed by individuals. An experiment evaluated the distance transform method when applied to the same Batesian mimetic system and utilised the qualitative approach to deduce wasp hoverfly abdomen similarities (Taylor et al., 2013). This model-mimic fidelity comparison used the distance transform method and highlighted the level of detail the method goes into when analysing model-mimic pattern differences. When compared to the Hassall et al (2018) approach, the web based approach with human interaction can be deemed more efficient and scalable. This also has implications when applied to an ecological scenario, as it allows us to analyse data across a wide scale. Human perception has been shown to closely mirror that of avian species when tested in confined environments and compared statistically (Seddon et al., 2010; Hassall et al., 2018). Therefore, the human based ranking system used in previous studies gives us a minor insight into the potential similarities avian species would perceive. Such experiments using citizen science and a web page interface has the ability to be utilised across alternate fields. For example, in a plant pollinator context, species can be distinguished between mutant and wildtype flowers. This again has the potential to enhance ecological understanding across a wide range of disciplines.

Spatial and temporal co-occurrence has been studied in great depth across community ecology, with modelling and theoretical work at the centre of study (Cazelles et al., 2016). Within the context of mimicry little work has been carried out on co-occurrence. Co-occurrence studies have been used to test the well-known Batesian mimicry system in USA containing the venomous coral snake and its putative mimic *Lampropeltis elapsoides* (Kingsnake). Much work has been done identifying the mimic's ability to survive in allopatry and sympatry. One assumption for this was based on the predator's innate avoidance towards the model phenotype (Smith, 1975; Brodie, 1993). Despite this difference in spatial co-occurrence it has been found that the mimetic fidelity of the isolated mimic was greater in allopatry than sympatry (Akcali and Pfennig, 2014). Our results demonstrated that high fidelity models and mimics do not co-occur more than by chance ($P>0.05$), coinciding with previous results on the coral snake mimicry systems highlighting three points: 1) Spatial co-occurrence may not be a pre-requisite for Batesian mimicry 2) Similar patterns can be seen across different mimetic systems and taxa and 3) Hymenopteran mimicry complexes are fluid and can be maintained without the need for continual sympatry. However, our results suggest some mimetic species may co-occur with their models more than other mimetic pairings. For example *A.mellifera*, a common honeybee model and its mimic *E.tenax* were the only two species that seemingly co-occurred at a relatively high rate (44%) and obtained a similarity score =>5. Some species may co-occur more than others, based on their common predator (Mackenzie et al., 2004). Avian predators can cover a vast geographical range (Pfennig and Mullen, 2010) meaning mimics can gain a protective advantage through their warning colouration without being in sympatry with their model. This is possible as the predator will have encountered its unpalatable counterpart previously (Speed, 1993; Halpin et al., 2008; Skelhorn et al., 2016). Therefore, mimics and models, in theory, do not need to be placed in the same geographical area at the same time.

Inferences can be deduced from these previous studies showing that in mimetic systems, predators play a vital role in the maintenance and evolution of warning colouration, as underlined by the presence of mimics without models. Additional studies have looked at Hymenopteran and Syrphidae in relation to spatial and temporal co-occurrence. The abundance of Syrphidae mimics has been investigated in relation to behavioural mimicry and the need for their Hymenopteran model (Howarth et al., 2004). This emphasised the similarity in activity patterns for both models and mimics if the mimic was abundant. However, when the mimic was rare the daily patterns were not similar. Although our results hold no weight for temporal activity patterns, we were able to pinpoint the idea spatial and temporal co-occurrence may attribute to mimetic variation and demonstrate that Hymenopteran mimicry systems are fluid. An ecological study in the USA suggested that mimics appear after their Hymenopteran models avoiding the period when naïve fledglings begin to forage and learn (Waldbauer, 1988). This study argued the idea temporal co-occurrence was apparent in the Syrphidae Batesian mimicry system. Despite this, supplementary studies have shown models and mimics do demonstrate temporal co-occurrence being present at the same time of year with mimics being relatively rarer in abundance (Howarth and Edmunds, 2000). Supplementing our findings, and expanding on temporal and spatial co-occurrence, future work can tie in species distributions in mimetic systems and the implications of this to spatio-temporal co-occurrence, especially if there are geographical variations present in species' given ranges.

Species occurrence across a range demonstrates the species' tolerances to the physical conditions across a geographic gradient (Schowalter, 2006). Random occurrence a common ecological process for species can be attributed to metapopulations of individuals who are all able to migrate between patches. This would be a viable assumption correlating with the likelihood of predators within a mimicry system foraging between patches, thus creating a suitable range for mimicry to develop.

Hubbell (2001) stated, species can end up in their given range through random movement across the environment not through environmental filtering. From a mimetic perspective random occurrence and species distributions have been altered through anthropogenic alterations to landscapes (Azmeh et al., 1998). These changes have created urban landscapes allowing species such as *Eristalis tenax* to flourish and surpass their models in terms of individual biomass. These changes to landscapes due to human interference have been supplemented by the impact of biotic factors such as climate change (Parmesan and Yohe, 2003; Hassall et al., 2018). These stochastic forces have the potential to lead to the decoupling of species interactions in both space and time and thus have negative impacts on mimetic relationships.

The bipartite network (Figure 14) highlights the individual interaction between model and mimic species where mean similarity scores =>5. Interestingly many models (top row) had multiple interactions with mimetic species. Our results through bipartite motif analysis supported the idea specific mimics may mimic more than one model. This may support the multi-modal hypothesis to some extent highlighting mimics with multiple models (Edmunds, 2000). In a natural environment this could be a plausible assumption, with mimics dispersing across patches. Therefore, exploiting several models (even if the association may be deemed weak) would allow for a significant degree of protection from predators. This again can link to co-occurrence as mimics would not necessarily have to co-occur with a model at the same time. The metapopulations of mimics can be very dynamic (Akcali et al., 2018) with a model always being available to exploit. Despite this assumption, the multi model hypothesis has been linked predominantly with imperfect mimicry. A comprehensive analysis of multiple imperfect mimetic hypotheses did not find the multi model hypothesis as a theory that was consistent with imperfect mimicry (Penney et al., 2012). An additional explanation for the motif results observed, may link to the relaxed selection hypothesis. This has gained the most support in previous studies as the theory which fits imperfect mimicry, especially in the Hymenopteran/Syrphidae mimicry system, or has offered to play a large part in its maintenance (Holloway et al., 2002; Penney et al., 2012; Sherratt and Peet-Paré, 2017). The relaxed selection hypothesis states mimics whether accurate mimics or not, obtain the equivalent level of protection from predators (Kikuchi and Pfennig, 2013). Our results correspond with this hypothesis and can be evidenced through mimics having multiple strong interactions with models, which from a fidelity perspective, corresponds with particular mimics resembling more than one model. As ultimately the selection faced on mimics will create a spectrum of phenotypes and from a mimetic fidelity aspect, result in certain mimics being deemed similar to models to different degrees. Relaxed selection in certain environments has been hypothesised to lead to imperfect mimicry. Therefore (similar to multi modal hypothesis) can be attributed to the results found in the bipartite network.

Supplemented by motifs, a network has the potential to display key processes that occur across an ecosystem (Simmons et al., 2018). The model *E.cruciger*, a common cuckoo bee contained the most interactions within the bipartite network with 17 to corresponding mimics. With an aposematic warning colouration similar to *V.vulgaris* and multiple morphological similarities, it indicates a potential for a Müllerian relationship between *E.cruciger* and other eusocial Hymenoptera. Additionally, it highlights the possibility the model *E.cruciger* is an example of a model that has multiple mimics. Interestingly, further analysis could be used to assess the spatio and temporal occurrence of the model and how the range could affect the relationship with mimics. For example the species across the UK is commonly found in southern areas, however is predominantly scarce in northern regions (Else, 2002). On the macroscale level our results can show the overall similarity patterns of the models and mimics across the whole network, as well as individual interactions of each species. However through the use of motifs we are able to depict particular common patterns across species, for example key model-mimic associations. These associations begin to reveal key patterns. One of these can include mimetic characteristics such as species interacting with one or more models. Through further analysis we may be able adopt this approach to more complex networks and unveil a more accurate guide to model-mimic associations perhaps providing more evidence for mimetic theories and mechanisms underpinning its maintenance from an ecological perspective. The results from our study demonstrate how the use of networks and motifs can be applied to outstanding ecological questions and what information we can derive from them.

Mimetic clusters have the potential to be a useful model for the identification of different mimetic submodules across mimetic systems. This can be used when mimetic clusters are potentially scattered across a network supplementing species interaction and identifying grouping. For example Figure 11 displays the particular clusters of mimetic species. The model *C.succinctus* who is the primary host for *E.cruciger* (Kuhlmann et al., 2007) is shown to be close to its “parasite” in terms of its morphology and similarity ranking. Additionally, these clusters illustrate different mimetic modules from within the same mimetic system. Bee clusters can be identified separate to the wasp clusters and solitary bee species (with darker colouration, and smaller stature). This technique can be applied to future studies when assessing different species across a wider ecological context. The solitary cluster contains species of mimics who possess an overall slightly darker colouration along with a smaller body plan. From this we could hypothesise a possible link to the imperfect mimicry relaxed selection hypothesis (Penney et al., 2012). This cluster of “imperfect mimics” possesses a reduced selection for mimetic similarity. This colouration is viable for mimics as their small body plan, allows for the relaxed selection from predators. These models and mimics within the cluster who possess similar morphology as ranked by the citizen science experiment (Hassall et al., 2018) may create a pathway for further investigation when applying hypotheses to network modelling. The illustrated cluster follows the relaxed selection hypothesis in terms of the mimetic morphology. However, further analysis would be required to build a complete picture of Hymenopteran and Syrphidae mimicry complexes and their position within a mimetic evolutionary context.

Additionally, biotic factors can influence specific species (Lee, 1999; Louthan et al., 2015). With model and mimic phenological differences (specifically emergence) where Hymenopteran generally emerge sooner than Syrphidae (Howarth and Edmunds, 2000; Hassall et al., 2018). Naïve predators learn to avoid mimics because of previous negative interactions with models (Halpin et al., 2008; Exnerová et al., 2010) Therefore, this learned behaviour can result in the mimic gaining fitness benefits without having to co-occur with its corresponding model. In many studies, it has been found, so long as there is a boundary where both species can be found in sympatry, mimics can persist in allopatry (Pfennig and Mullen, 2010). However, further investigation would be required to observe all species present in a mimetic complex and their individual geographical ranges, to gain a further understanding. Subsequently information such as overlap, predator presence and species absence can be obtained to complement co-occurrence. A recent study by Valkonen et al., (2018) looked at the effects of human habitats on the endangered smooth snake, a mimic of venomous vipers. This study highlighted the need for mimetic systems to be protected as a whole when an endangered species is involved . With the use of network theory, this would make processes smoother and provide more information, especially based on mimetic interactions, leading to the establishment of protocols in conservation.

With co-occurrence being a relatively novel concept in mimicry, further work is required to gain a greater understanding of its significance in high fidelity mimetic complexes from an evolutionary perspective. To enhance the picture we have already, a similarity study following the same methodology as Hassall et al, 2018 could be used to look at the similarity of mimics against mimics and models against models. This would allow for a morphological comparison across each mimetic complex and allow for a greater in depth analysis of mimetic clustering. Despite this, the Agriland results have opened an interesting insight to co-occurrence in mimicry, creating a platform for future studies.

3.6 Conclusion

Our results suggest that high fidelity models and mimics co-occur more by chance. Despite this, co-occurrence still is a naïve avenue when it comes to mimicry and is very much understudied. Further work would be required to evaluate co-occurrence and its implications to the evolution of mimicry. Together with potential phylogenetic studies, we may gain a greater understanding of the evolutionary pathway for both models and mimics. Batesian mimicry evolution can benefit greatly from the use of network theory when applied in both ecological and evolutionary contexts. Our results suggest that mimetic interactions can play a key role in understanding mimetic evolution. Additionally, the discovery of empirically deriving mimetic clusters can support both individual mimetic interactions and the already present ecological understanding of mimicry. Combined, this can be used to enhance our current knowledge in the field. In summary Phylogenetics when applied alongside the network theory can drive forward our understanding of mimicry from where we are today.

Chapter 4 - The Influence on Mimicry of Information Transmission Through Social Networks

4.1 Abstract

The evolution of mimicry in nature represents one of the most famous and accessible products of natural selection. However, while we understand a great deal about the patterns that have been produced to create a high degree of resemblance, studies of the processes by which those patterns have been produced are far less common. Here, I test a novel hypothesis in mimicry theory: that information transfer through social networks can accelerate exploitation of mimics and, hence, reduce the fitness advantages to mimicking organisms. I first train a captive population of zebra finches (*Taeniopygia guttata*) to avoid foraging from a non-rewarding stimulus (the model). I then use network-based diffusion analysis (NBDA) to map the spread of feeding events on mimetic stimuli (that mimic that stimulus but are, in fact, rewarding) through the finch social network. My results indicate that social learning in zebra finches occurs between foraging associates. This finding sheds further light on the complexity of natural predator-prey systems and provides a platform for further work to enhance our knowledge on the evolutionary consequences of social learning.

4.2 Introduction

Sociality in the animal kingdom has long underpinned the evolutionary success of many species. Sociality spans multiple taxa and for many species has long been an evolutionary strategy which has been engrained into their life history. Many different species have evolved to incorporate sociality across different evolutionary timescales (Yamaguchi et al., 2004; Brady et al., 2006). Sociobiologists have identified that across different taxa, different classes of sociality can be recognised alongside different degrees of sociality. For example, in the eusocial Hymenoptera a range of social traits can be identified, from a clear caste system to a distinctive reproductive division of labour (Premnath et al., 1996), which allow the colony to run smoothly and successfully (Wilson, 1987). Vertebrates that have a degree of sociality, such as the mammalian predator the grey wolf (*Canus lupus*), lack the complexities of sociality shown by eusocial insects. Many avian and mammalian species utilise basic levels of sociality in order to increase individual fitness. These methods can range from aggregation to avoid predation to strategic hunting to increase the success rate for predators (Stander, 1992). In sum, sociality can be defined as the level to which members of a population reside in groups and work cooperatively within a social setting (Smelser and Baltes, 2001).

Sociality within populations has the implications to affect learning on an individual basis. Learning is a common process which occurs across the animal kingdom, with species acquiring or modifying new or existing information in order to successfully tackle various situations (Hilgard and Bower, 1966). Learning can be split into different types such as, observational, social and individual. Observational learning falls into the category of social learning but occurs when individuals observe and replicate others whilst retaining the information. Where by social learning is the process of learning within the presence of others (Heyes and Galef Jr., 1996). Many studies have identified learning in numerous animal taxa, from tool use in chimpanzees (*Pan trogladytes*) to local urban bird (*Parus.major* and *Parus.caeruleus*) species peeling milk bottle lids (Fisher and Hinde, 1949; Whiten et al., 2005).

One product of sociality is social learning. This process occurs in many species and has multiple functions. Social learning has many advantages, mainly reducing the time required to acquire information. Social learning is a common form of learning amongst species who interact with one another which can lead to the transfer of social information through those networks of interaction. This particular type of learning allows individuals of a species to observe or interact with other individuals, which in turn facilitates the acquisition of a skill or change in behaviour (Hoppitt and Laland, 2013) and speeds up the spread of novel behaviours and traits (Galef and Laland, 2006; Page and Ryan, 2006). This acceleration in learning has positive fitness benefits to individuals in a scope of scenarios, such as predation or foraging (Griffin, 2004; Thorogood et al., 2018). Additionally, social learning through social networks has been observed to lead to persistent culture in a non-primate species, highlighting the strength of information transmission (Aplin et al., 2015). Social networks have been used as a model to describe the spread of learning across a population, as well as quantifying the strength of individual relationships (Franz and Nunn, 2009). This approach can be used to identify the spread of novel prey avoidance or exploitation across a population. Despite social learning possessing multiple advantages, asocial learning can be more advantageous in other scenarios, such as when the information gathered is known by the individual to be reliable (Kendal et al., 2005). However, the benefits of learning socially in terms of increased rates of learning are traded off against the costs in terms of unreliable social information and the loss of time spent on individual learning (Udino et al., 2017). This tends to be related to costs associated with time when exploiting asocial information including the process of trial and error, or reliability when faced with social information (Boyd and Richerson, 1985; Rendell et al., 2011).

The process by which predators learn to exploit certain types of profitable prey is complicated by the fact that prey have evolved defensive strategies that either hinder predator learning (e.g. Batesian mimicry) or reinforce predator learning (e.g. aposematism). Aposematism is the phenomenon by which unpalatable (e.g. toxic or venomous) organisms signal their unpalatability to would-be predators in order to strengthen learned associations. The most common form of aposematism is warning signals in the appearance of conspicuous colouration. Aposematism has been a prominent feature of scientific study over the last 150 years (Wallace, 1882). By using conspicuous warning signals, prey are able to avoid and educate predators which in turn allows for the spread aposematic phenotypes (Leimar et al., 1986; Thorogood et al., 2018). The main colours associated with aposematism are usually red, yellow or white accompanying black (Cott, 1940). Understanding the evolutionary processes behind aposematism, to date, remains a difficulty to evolutionary biologists. Aposematic visual signals are characterised by certain conspicuous colours that are often more visible to predators. The enhanced conspicuousness of the warning signal also means they are able to educate the predator more readily, thereby building up an association if the predator encounters their prey (Speed and Ruxton, 2007). In many communities, aposematic prey are preyed upon by naïve predators, which in turn facilitates learning. The learning of aposematic signals educates the predator for future encounters and the negative association with the stimulus is enough to ensure continuous sampling of aposematic prey is not attempted.

Predator learning is both fluid and adaptable. The abundance of aposematic prey within a community can create a niche for ‘cheats’. The ‘cheats’, known as mimics, are a product of natural selection and throughout time have benefitted from imitating the warning signal of unpalatable prey without producing the defence that truly aposematic prey possess to gain a fitness advantage (Howarth et al., 2004; Ham et al., 2006; Kikuchi and Sherratt, 2015). Novel prey have been used in multiple studies within the field of mimicry and aposematism. Domestic chicks (*Gallus gallus*) have been presented with multiple aposematic prey (wasps) creating an aversive response (Mostler, 1935), whilst great tits (*Parus major*) have been presented with firebugs resulting in aversion also (Landová et al., 2017). Mimetic prey heavily relies on the predator’s association of a prey characteristic and previous encounters. One aspect that can mediate the predator perception of novel prey is social information. In mimicry, little work has been carried out on the social influence of predators and the impact on both models and mimics. Subsequently this influence has the potential to have evolutionary consequences. A common form of mimicry is known as Batesian mimicry (Bates, 1862). Batesian mimicry is one of the key forms of imitation in nature, whereby harmless organisms imitate the signals of defended organisms (Wickler, 1968). Müllerian mimicry is another common form of mimicry where similar phenotypes of both the model and mimic influence the signal receiver (Müller, 1879). In nearly all scenarios this form of mimicry is used to evade predation (Ruxton et al., 2004; Jamie, 2017). However, it is ultimately up to the predator or signal receiver to decide whether the model or mimic are a palatable or unpalatable meal. With learning being a vital mechanism in species’ life history, it can help guide animals across their environment influencing their foraging decisions (Zentall and Galef, 1988).

The aim of foraging is to maximise energy gain (Bergman et al., 2001; Hazen et al., 2015; Pyke, 2019), which subsequently allows individuals to carry out metabolic processes alongside their day to day activities. However, foraging is a complex process where multiple decisions are required to be made. Those decisions are generally based on i) prior experience, ii) current physiological state and iii) the environment (Schoener, 1971; Dall et al., 2005). Predators are often faced with the exploration/exploitation dilemma (Figure 16) where the individual is faced with a trade-off. This trade-off is the decision between sticking with what they know (prey type, or even a foraging patch) or expending the energy to exploit an alternate area or prey (McNamara and Houston, 1985; Sherratt, 2011; Berger-Tal et al., 2014; Raubenheimer and Simpson, 2018; Morimoto, 2019). Novel prey are a prominent feature of explore-exploitation models and can influence predator decision making, especially if they exhibit neophobia (Marples et al., 2005). Ultimately successful foraging can lead to an increase of fitness, which allows for species to thrive, and keep their genetic information within a population (Bell, 1990).

Much work has been carried out on aposematic prey and predator learning (Skelhorn et al., 2016; Landová et al., 2017). Aposematism is a term coined to describe a species with a specific warning signal, telling a predator it is toxic, unpalatable or dangerous. The warning signal is associated with the individuals unprofitability (Ref). Aposematic signals have been known to accelerate the speed of learning through associative learning in previous experiments (Sillén-Tullberg, 1985; Prudic et al., 2007; Ruxton et al., 2018). Predators when faced with aposematic prey are thought to associate aspects of the signal with the negative stimulus which presents itself in the form of toxins or pain (Maan and Cummings, 2012). A recent study investigated the importance of signal salience and how this can influence prey within the community, leading to the sustainability of intermediate aposematic colouration in alternate prey (Kazemi et al., 2014).

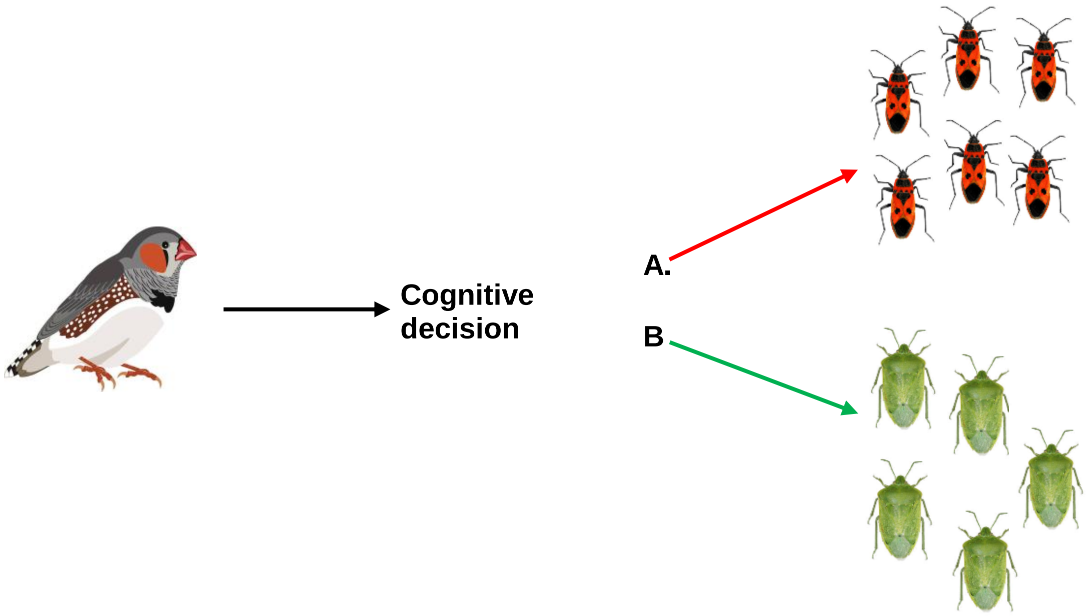


Figure 16. The multi arm bandit model (explore-exploitation) with the predator having to make adaptive foraging decisions. Figure 15A represents the novel aposematic prey, which haven't been experienced by the predator. Alternatively, Figure 15B highlights prey that is routinely consumed by the predator. Zebra finch, www.istockphoto.com. Firebug and true bug, www.ui-ex.com

Aposematism is a key component in Batesian and Müllerian mimicry and is as a product of natural selection, used predominantly in the predator-prey arms race. While direct predator learning has long been known to be central to Batesian mimicry, far less is known about how social learning contributes to predator decision making when faced with Batesian mimics.

The study system for the investigation was the zebra finch, *Taeniopygia guttata.* This species of finch is highly social often residing in groups often reaching above 150 individuals in the wild (Zann, 1996). The zebra finch is a common native species to Australia and Indonesia and is known for its adaptability across environments. Previous studies have considered the social structure of this avian species, with work identifying personality as an influencer on female dominance as well as male presence affecting group foraging decisions (Katz and Lachlan, 2003; David et al., 2011). In this study, we will look at the spread of information across a social network in response to a mimicry system. Through the use of group foraging in an aviary and artificial mimetic prey we can test a key hypothesis, 1) Different levels of social learning affect the benefits accrued by Batesian mimics.

4.3 Materials and Methods

4.3.1 Study System

The study was conducted at Harewood house bird garden, Leeds. Latitude: 53° 53' 28.79" N. Longitude: -1° 31' 25.19" W. where a captive population of zebra finch (*Taeniopygia guttata*) were housed inside an aviary (Figure 17). Each member of the population was ringed to allow for individual identification. The trials were carried out between April 2019 and June 2019 at approximately the same time during the day. The total number of individuals in the captive population exceeded 50 individuals and a social structure was present across the population, based on unpublished previous work (Rowlands, 2019), allowing us to identify the possible social influence on mimicry.

Figure 17. The side view of the three variations of phenotypes (top). The control (left), the intermediate mimic (middle) and the non-rewarding model (right). The layout of the trials with the pots on the plyboard (bottom left). The aviary where the trials took place (bottom right) with the location of the trials illustrated by A.

4.3.2 Mimicry Task

A common aposematic signal that is known to be common amongst multiple avian predators involves yellow colouration with black stripes (Mostler, 1935), as possessed by venomous species such as *Vespula vulgaris* (common wasp) and *Apis mellifera* (European honey bee). Many hoverflies (Diptera: Syrphidae) mimic this warning colouration to deter predators (Penney et al., 2012). We made use of this Batesian mimicry system by designing a task that involved empty food containers coloured yellow with black stripes (the unrewarding "model") and full food containers coloured plain yellow (the rewarding "mimic"). A third phenotype consisted of a plastic pot containing millet seed and no colouration, acting as a control (analogous to alternative prey in nature). This trio of stimuli, modified from a previous study on zebra finches (Chantal et al., 2016), was used to quantify the contribution of social learning to the fitness benefits of mimicry. This study system was adapted and based on previous studies looking at aposematism and learning in avian species (Aplin et al., 2015; Thorogood et al., 2017). The modifications to the study system in comparison to the literature ensured a free flowing ‘foraging system’ for multiple avian species across an aviary. For example including multiple wells across a plyboard floor each containing a specific phenotype. This particular task was set up so the difficulty meant some but not all the birds would solve it. Additionally the task was designed as such that the visual colour system was adapted to suit the finches.

I constructed 12 wells evenly across a wooden ply board (Figure 17) to provide a neutral background, blending into the aviary floor to avoid any aversive behaviour from the finches. Every well housed a plastic cup (dimensions: 4cm x 4cm x 4cm), with each cup representing one of the three phenotypes to simulate multiple prey species within a foraging context (see Appendix B). Four GoPro cameras were situated either side of the ply board in the same position throughout each trial. These recorded movement from each individual bird and allowed for identification when a task was solved, as well as removing the need for me to be close to the aviary where I might disturb the birds’ foraging.

The training phase of the trials comprised of six model pots and six control pots. I ran the training phase for a total of 46 trials which were 30 minutes in duration each. Each feeding event was recorded and the individual involved was identified based on their unique coloured band. If a task was solved within the 30 minutes, the pots were reset and the task continued for the remainder of the time. For each day, I calculated the proportion of zebra finches foraging on the control compared to the model pots. A proportion of 75% control solves, maintained over three consecutive days, was considered to represent the population having learned to avoid the non-rewarding model. At that point, the testing phase began where four mimetic pots, four model pots and four control pots were randomly arranged on the board. The testing phase was again run for 30 minutes per day with all feeding events recorded. The task was considered to be solved by an individual when they had removed the lid from either a model, mimic or control pot.

4.3.3 Networks and Coding

Different social networks were constructed using previous unpublished data collected on the same captive population of zebra finches (Rowlands, 2019). The study looked at social learning across the finch population and how a task solving exercise influenced the learning behaviour of the finches. The study took into account the different networks (Table 2) and how the novel behaviour spread across both an asocial network in comparison to a social network. The networks used in both my study and Rowlands (2019) focused on two forms of interaction that may influence social learning: 1) association interactions based on co-occurrence of individuals, and 2) dominance interactions based on the outcomes of agonistic encounters. These two networks were used in our study as they allowed us to see which particular network fit the social transmission model best for our mimetic solves. Overall the networks looked at which particular method of transmission would have the best fit or highest proficiency, in regards to the finch population dynamics. For example, the association matrices are measures of time spent together, which would offer additional oppurtunites to learn. Dominance matrices indicate something about the way that individuals interact – dominant individuals have been shown to learn less because they can monopolise easy resources, while less dominant individuals have to be more innovative. Overall the networks may influence learning across the finch population in different ways with the social dynamics of the finches playing a specific role. For example the dominance matrices may suggest certain individuals do not learn but faciliatate the learning of others, where as the association matrices looks at the time spent together among indviduals so points toward a co-foraging opportunity for learning. Table 2 describes the networks that were compared to see which model fit the spread of mimetic solve behaviour. The association networks were created using the data extracted from video playback, which identified which individual was responsible for solving the task (using the ringed band on the bird’s leg) and the implications of this across the social network.

The video playback analysis of the captured footage was carried out offsite with the video being transcribed into code on a Microsoft Excel spreadsheet.

Table 2. Breakdown of networks created from previous unpublished work on zebra finches to model social transmission (Rowlands, 2019).

NETWORK	TYPE OF NETWORK	HOW EACH NETWORK WAS CREATED
COMBINED ASSOCIATION MATRIX	Association	Feeder related. Linked to proportion of time individuals spent on the feeder. This was in relation to the time in feeder videos.
ACTUAL VS EXPECTED MATRIX	Association	Feeder related. Focuses on the proportion of time individuals spend together on the feeder in relation to amount of time expected together. Centred on amount individuals spent together on feeders.
OBSERVED FIGHTS MATRIX	Dominance	Dominance matrix crated through observed fights between individuals
SUM TIME DOMINANCE MATRIX	Dominance	The sum time spent on the perch (object used to measure dominance). Each bird was timed every time they visited the perch and were assigned a rank based upon their sum time.
AVERAGE TIME DOMINANCE MATRIX	Dominance	The average time spent on perch.
FIGHT SCORE MATRIX	Dominance	The fight score which has been totalled (overall). This was a measure of fights won and lost (losses subtracted from victories) leaving a specific score for each individual. This score was used to assign a rank to each bird.
NET RATE MATRIX	Dominance	Points system. Net loss or gain in respect to fights.

4.3.4 Data Analysis

Firstly, I calculated the fitness outcomes for the models, mimics and predators. A fitness score was given to all 27 individuals who solved the task. A +1 was allocated to each individual if a solve was carried out on a control or mimic in the testing phase.

Additionally, a -1 was allocated when a model solve was carried out. This allowed for an overall fitness score to be calculated for all individuals. Mortality rates were also calculated for the control, model and mimic for both the training and testing phase. This was done by calculating the number of solves of each phenotype, divided by the total trials and then multiplied by the number of pots of each type. Clopper-Pearson confidence intervals were calculated for each mortality rate.

NBDA was carried out in R 1.1.456 (R Core Team, 2018), using the packages NBDA (Hoppitt, 2019). NBDA looks at whether the occurrence of behaviours or other phenomena are random with respect to any network – based model of interaction. Specifically NBDA looks at the social network as a whole and its contribution to the spread of novel behaviours by analysing the amount of time associated individuals spend together (Allen et al., 2013). Using NBDA analysis, we were able to quantify the relative contributions of individual and social learning based on the diffusion of task solving through the population. The analysis looks in depth at the different networks and the importance of asocial and social learning throughout these networks. Order of acquisition diffusion analysis (OADA) was applied using NBDA with each of the social networks described in Table 2. The explanatory power of each network was compared to an asocial model (a uniform network) using likelihood ratio tests to test whether the social models performed better than the asocial model. Social learning parameters (s) were extracted from the models for each of the networks. These s-parameters describe the increased probability of a behaviour occurring in an individual that is connected to an educated individual compared to an individual that is not connected to an educated individual. For example, an s parameter of 2 means that being connected to an educated individual doubles your chance of expressing the behaviour compared to not being connected to the educated individual.

Each of the asocial and social models obtains an Akaike information criterion value (AICc), which is a metric used to rank the models and their fit to the diffused information transmission obtained in the network. The AICc value with the lowest score can be accredited with the best fit for the model and diffused data.

4.4 Results

Overall 92 trials including the training phase were carried out, with mimics being introduced at the beginning of the testing phase (Figure 18). Figure 18 highlights the overall solves (as a moving average) amongst the model, mimic and control pots. Forty-six trials were carried out in the training phase with the control and model pots being used. The control solve proportion across the training and testing phase remained relatively level, however the model solve proportion decreased overall across the 92 trials. Across the training phase the model pots were solved a total of 31 times (27 of those coming between trials 1-23). The control pots were solved a total of 46 times (26 of those coming between trials 1-23). Therefore trials 24-46 saw a substantial decrease in model solves (a total of four).

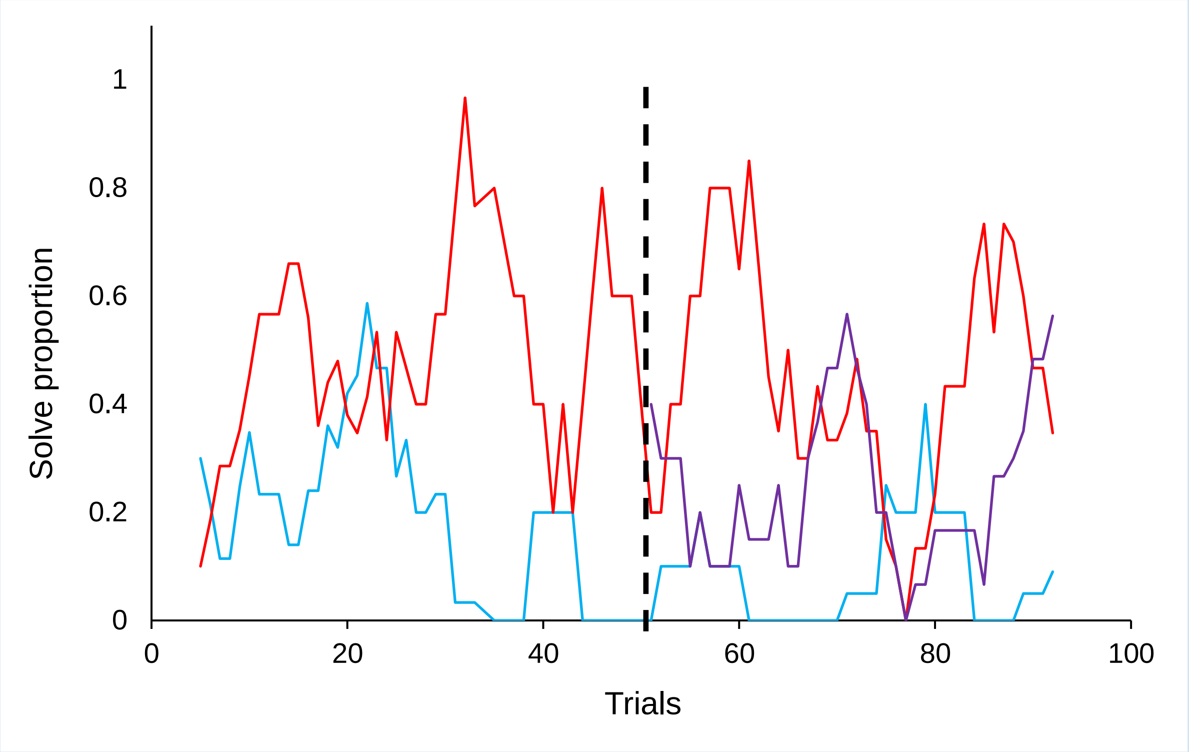


Figure 18. Trends in the proportion of solves relating to different stimuli (red=control, blue=model, purple=mimic) over the training phase (trials 1:46) and testing phase (trials 47-92. Lines are moving averages with a window of 5 trials. Vertical dotted black line shows the change from training to testing.

Across the population of zebra finches housed at Harewood 27 out 53 (51%) individuals solved the mimetic pots throughout the testing phase. Amongst the 27 individuals, 15 (56%) solved the mimic pots at least once during the testing phase. Across the testing phase specific individuals solved the mimic pots more often than others. Birds 30 and 51 solved the mimic task almost 2.5x more frequently than their counterparts. When compared to the social network outputs (Rowlands, 2019) the degree of connectedness for each individual varied (Table 3). When mimic solves were compared to the fight network, the node corresponding to bird 30 had 0 connections, where-as bird 51 had 18, indicating a high degree of connectedness across the population. Conversely, across the small proportion that solved the mimic trials 87% had a value of 4 or below for degree of connectedness.

Table 3. Bird ID's and degree of connectedness for individuals who solved the mimic trials. The values correspond to the dominance in the observed fight matrix.

Bird ID	**Degree**
NtkdbL	0
NgR	0
PplR	0
FblR	0
CblL	0
PdgR	1
WwL	1
FplL	1
NctoL	2
FpkRL	2
FwR	3
WrL	4
CoL	4
WrR	5
CrL	18

Overall network topology seemingly influenced the mimicry trial solving across the population of finches. Social network structure based on foraging associations was associated with the order in which individuals exploited mimics during the testing phase. Various models were tested using networks to assess whether social transmission had any influence on the solving of the trials. The combination association matrix offered the greatest improvement over the asocial model and was the only social network that showed a significant improvement (Table 2). Additionally, the actual vs expected matrix (also based on association) fitted performed better than the asocial model (ΔAICc = 1.34) but the improvement was not statistically significant (p = 0.056; Table 4).

Table 4. Statistical analysis of the different models for social transmission.

Matrix	**Asocial AICc**	**Social AICc**	**Δ AICc**	**p-value**	**S**	**SE**
Combined Association Matrix	114.7	109.2	5.5	0.005	31247829557	1.49E+14
Actual vs Expected Matrix	114.7	113.4	1.3	0.056	18656936	88116960338
Observed Fights Matrix	114.7	117.0	-2.3	>0.999	0	0.5764521
Sum Time Dominance Matrix	114.7	117.0	-2.3	>0.999	0	NaN
Average Time Dominance Matrix	114.7	116.7	-2.0	0.577	0.003412	0.007343339
Fight Score Matrix	114.7	116.7	-2.0	0.574	0.005850379	0.01248739
Net Rate Matrix	114.7	116.7	-2.0	0.551	0.005696547	0.0116486

4.5 Discussion

I have shown, for the first time, that social information transfer may influence the fitness consequences of mimicry. My results show that social networks based on associations among zebra finches predicted the order in which finches exploited novel mimics after having been trained on unrewarding models and control prey. This finding suggests that social learning can reduce the benefits of mimicry by increasing the rate at which groups of co-foraging predators learn to differentiate them from their models. From this finding, we can infer that social learning also increases the protection afforded by aposematism by reducing predator naivety when sampling the model-mimic community. Additionally, we can deduce 1) social transmission is used by predators as a cue for the exploitation of harmless mimetic prey within prey communities 2) if predators are doing better at exploiting mimics, the mimics are losing out and 3) if the mimics are being spotted more easily then the models might be protected more effectively (fewer incorrect sampling attempts by the predators). Several previous studies state zebra finches employ a social learning strategy linked to status (David et al., 2011; Boogert et al., 2014; Guillette and Healy, 2017; Boogert et al., 2018), however no current literature on zebra finches provides direct evidence to support the idea social transmission is facilitated through association. Zebra finches are known to travel and forage in colonies of 30 or more individuals, with breeding pairs operating as submodules within the wider network (McCowan et al., 2015). This form of natural foraging lends itself to a situation in which social information is both available and useful. This often relates to the monogamous behaviour of zebra finches and their ability to form pair bonds (Zann, 1996). The study went on to add despite the colony perhaps housing upwards of 30 individuals, the pairs of individuals formed a sub social structure which led males to direct their corresponding female around. With the captive population of 53 birds being housed in a reasonably spacious aviary the population had room for reasonable movement mimicking natural conditions seen in wild zebra finches. This subsequently allowed individuals to replicate wild behaviours such as foraging. If previous observed work has noted small groups when individual finches forage, this may provide reasonable support for association as a method of social transmission.

With the social model for association being a significantly better fit than the asocial model, it is suggested that social information transfer can help predators to exploit novel prey. The costs associated with novel prey can be high for many predators (Pasteels et al., 1983; Zalucki et al., 2001; Kikuchi and Sherratt, 2015). Some species of prey if consumed or handled incorrectly by predators can result in mortality or a severe reduction in fitness (Kikuchi and Pfennig, 2010). However, the results presented by this study demonstrate the costs associated with novel prey can be negated by social learning.

In all predator-prey systems, a wide range of factors can affect the foraging decisions made by the predator. When faced with novel prey many predators' cognitive processes rely on their decision to either attack or avoid the prey. The result of such choice successively leads to the cognitive associations being formed and thus learning. In some environments, innate avoidance for certain novel prey can be seen (Smith, 1975). This behaviour thus can temporarily influence the composition of specific prey in communities. Throughout the study the training phase illustrated the captive finches did not have any innate tendencies to avoid the colour of the model pots (yellow), as first thought, with various literature evidencing zebra finches like bright colours. A prime example of this is, is when the influence of leg band colour was evaluated amongst female and male zebra finch (Burley et al., 1982). With both genders finding different colours more attractive (males preferred females with darker coloured bands, and females preferred males with red). On top of the fitness cost mortality, many predators have to balance additional factors when foraging. These can include the likes of toxic burden, nutritional value, energetic state and time (Skelhorn et al., 2016). However, with correct socially acquired information some shortcuts can be utilised mitigating some of these burdens. Interestingly, once particular novel prey have been consumed, predators are able to associate specific prey traits with the prey toxicity, nutritional value and their profitability (Barnett et al., 2007; Skelhorn and Rowe, 2010). Prey size can also play a major role in a predator's decision to attack, as the larger the prey the more nutritionally enriched the prey will be (Smith et al., 2014).

Based on the empirical evidence of our study, the level of protection afforded to mimics via mimicry can be dependent on the social characteristics of the predator population. Our results suggest the level of protection attributed to models is enhanced through social learning and the protection afforded mimics is reduced. Based on the graph (Figure 17) containing the proportion of solves for the control, model and mimic, we can see a change in solves for each pot. The models can be seen to have a distinct reduction in their proportion of solves rate moving from the training phase to testing phase. With mimicry being a product of natural selection the fitness benefits in varying environments are often high, however this can depend on the model and mimic – as well as the costs associated with each species The phenotypes presented on the model and mimic pots in our study represented imperfect mimicry from a Hymenoptera/Syrphidae mimetic system. Theoretically the fact imperfect mimics exist is credited to a large number of theories. The most prominent include the relaxed selection hypothesis which states there is a trait that results in lower predation rates and, hence, less selection pressure to evolve. For example, smaller hoverflies are attacked less because they are less profitable. (Penney et al., 2012). Moreover, the information limitation hypothesis which describes predators as taking a general rule of thumb when foraging (Sherratt and Peet-Paré, 2017), for example avoiding all yellow and black striped insects, allows imperfect mimics that meet that general rule to persist in the environment.

Throughout the testing phase, the pattern of results concurred with multiple literature when looking at explore, exploitation models (Sherratt, 2011). From a theoretical perspective, our results suggest the ‘trial and error learning’ phase in the multi arm bandit model (exploration) is reduced through the process of social information transmission (Figure 16). Therefore, individuals were able to distinctly identify the model phenotype (black stripe) when compared to yellow mimic. Thus, we were able to observe a sudden drop in model mortality in comparison to the introduced mimic, alongside an overall drop in model mortality from training to testing phase. A reduction in the exploration phase leads to an increase in the exploitation phase of prey information collation, allowing individuals to extend foraging and prey handling times whilst also continually gaining information on their environment. Within the Hymenoptera/Syrphidae mimicry system, it can be extremely difficult for predators to distinguish between models and mimics because hoverflies have evolved behavioural and visual methods to fool their common predator (Golding and Edmunds, 2000; Howarth and Edmunds, 2000; Penney et al., 2014). The acquisition of social information may to a degree allow educated predators to make accurate foraging decisions. Our results shed light on the impact of social transmission and mimicry, with much prior work focussing on aposematic prey and the effect of social learning (Landová et al., 2017). A recent study looking at the impact of social transmission on prey avoidance supported the view that social learning has the power to influence prey populations and dynamics (Thorogood et al., 2018). With predators continually having to adjust their foraging strategies (Abrams, 1992; Halpin et al., 2014; Skelhorn et al., 2016), some mimetic prey can be susceptible to predation. Empirical evidence from our study highlights the influence of social transmission on acquiring novel behaviours. Not only did the social model of association significantly outperform asocial learning, it also demonstrated its role in enhancing predator mimetic avoidance. The results concur with the idea that the benefits of exploitation were present for co-foragers.

One theory discussed selective association whereby a select few would follow a more dominant conspecific around which subsequently can lead to a greater attainment in social information. However, the author did state this can also be a result of gregariousness, which is plausible (Van Schaik, 2010). Gregariousness is a common method in the animal kingdom where many species gain an increased fitness benefit through aggregation (Van Horn et al., 2004; Mcfarland et al., 2015). Additionally, an experiment involving bees learning how to pull string to access a reward observed the spread of the behaviour among colony foragers through the observation of a knowledgeable individual (Alem et al., 2016). One point to note regarding bees spreading novel behaviours via association is the population structure of the species (Coussi-Korbel and Fragaszy, 1995). With the majority of bees being eusocial, all worker bees are equal in social status across the colony. In the case of this study *Bombus terrestris* was the test species in question. Compared to other species such as chimpanzees (*Pan trogodytes*), wild vervet monkeys (*Chlorocebus pygerythrus*) and even the dog (*Canis familiaris*) the structure to their populations differ by having an increased level of sociality. Additonally across species a dominance hierarchy has been known to influence social learning (Pongrácz et al., 2008; Van De Waal et al., 2010; Kendal et al., 2015). Previous studies involving zebra finches have found different empirical evidence on how social information is used within foraging contexts. One recent study identified that female zebra finch only adopt social information when they scarcely forage across the environment and therefore would be more inclined to copy (Rosa et al., 2012). Additionally, another study focussed on coloured rings on demonstrators (red and green) and how these influenced feeding preferences in zebra finches. The results identified males and females were more inclined to feed from the same hopper as the male demonstrator wearing a red band. Furthermore, females had a greater preference for male over female demonstrators. Where-as males showed no preference. Finally, males opted to feed from the same hopper as familiar conspecifics as opposed to strangers (Benskin et al., 2002). Overall the study considered the idea attention was key to feeding preferences in zebra finches. The more attention attracted by the individual who was employed as the demonstrator, the greater the influence being exerted on the observer. Our results perhaps could be explained by a similar hypothesis. With foraging associates being the greatest source of social information, it could be the attention attracted by the forager which allowed for the increased rate of information transmission amongst conspecifics. This again could very much link the idea that individuals are found in pair bonds. In theory, if naïve individuals are in the presence of others who are acquiring new information and are successfully being rewarded or punished (appropriately) they are going to acquire this information a lot quicker than if they were left to discover it themselves (Heyes, 1994). Additionally, the idea presented above, links back to the original social – asocial trade off. Is it better to extend the time in acquiring the correct behaviour and relying on its validity, or acquiring the behaviour through social means but not knowing its reliability (Rendell et al., 2011).

Our results can be assessed through the degree of connectedness for individuals in the network. Using the observed fights matrix, we were able to obtain a set of degree values for birds within the social network that solved the mimic pots. Following on from the zebra finch work by Benskin et al (2002) looking at feeding hoppers amongst individuals, we observed that 47% of individuals had a degree of connectedness value of 2 or above. This indicated that these individuals within the social network interacted with 2 or more individuals. Out of those birds with a higher degree of connectedness 57% possessed a form of red banding on one of their legs. This is plausible evidence that red individuals may have attracted more attention within the population and thus attained a greater level of interaction when foraging, which subsequently may have influenced the social model of association for social information transmission within my study.

As this task focussed on the foraging behaviours of zebra finch (predator), it may be worth considering the implications of association when individuals are foraging. Gregariousness provides many advantages from both a predator and prey perspective. Many mimetic predators themselves have multiple predators and benefit from group living to identify any threats when foraging (Treisman, 1975). This tendency can be observed in zebra finches and was witnessed throughout the study with pairs of birds and sometimes more landing in the task area. This associative behaviour can link to the results of the study. If placed with others especially when foraging, their effect could evidently influence their acquisition of novel traits. With time a significant limiting factor with many mid-trophic predators, social acquisition through association eliminates the need for individuals to risk additional time foraging and can increase the speed of information acquisition.

Across the study the population collectively exhibited waves of interest towards the trials. Due to the trials being carried out approximately at the same time every day the birds seemed to generate interest across the first few trials at the start of the morning but then would evidently become less interested as time passed. The time of year (April – June) may have played a significant part in this behaviour as many individuals began to continue foraging in the aviary looking for nesting materials – which can occur at any time in the year (Vriends, 1997). Frequently different individuals were observed with branches, leaves and twigs. Alongside this behaviour, many conflicts seemingly occurred around the task area, with displays of dominance being showed by certain birds. This temporarily removed select conspecifics from the area.

Through the use of NBDA we have been able to unlock a new avenue for research in the evolution of mimicry. With different mimetic systems incorporating different species, social learning in a natural environment can allow us to understand the implications of predator-prey dynamics and the possible evolutionary consequences. With much recent research looking at predator cognition with aposematic prey (Gittleman and Harvey, 1980; Skelhorn and Rowe, 2007; Exnerová et al., 2010) unveiling social learning strategies when applied to mimicry may pave the way for future work to build upon the framework created by my results. Social networks of the different populations within a community have the potential to be placed alongside each other to gain a greater understanding of ecosystems, thus creating a meta network with sub modules. Networks don’t only have the power to uncover foraging strategies, but can provide key information on species interactions (Proulx et al., 2005). Therefore, through continuous refinement and work looking at alternate predators in an open foraging environment and through social learning, we can begin to uncover aspects of the evolution of mimicry which may have not been considered before.

4.6 Conclusion

The results from this study are one of the first of its kind, demonstrating that individuals within a population can successfully acquire social information from co foragers which can influence foraging behaviours. From a mimetic perspective, the implications of group predators successfully using social learning to enhance the rate at which they learn to differentiate models and mimics can be detrimental to fitness. Not only do these results open the door to social learning within mimicry but also highlights the benefits predators can obtain through social information. However, with social learning potentially benefitting predators, it can come at a high cost for prey if the information to recipient is accurate. Using an open aviary with a fixed population of avian predators freely interacting solving a mimetic task, has pathed the way for additional studies to follow similar methods when trying to replicate an open world environment across mimetic studies.

Chapter 5 - General Discussion

Overall our results provide a glimpse into the different avenues Batesian mimicry can be studied. These avenues offer alternate insights into the dynamics of Batesian mimicry, ranging from bipartite networks to social networks. These approaches allowed us to supplement previous work on Batesian mimicry, adding methods for the study of its evolution. Following on from previous work identifying predators as strong evolutionary drivers for Batesian mimicry (Ruxton et al., 2004; Skelhorn et al., 2016) and Hymenopteran Syrphidae co-occurrence investigations (Waldbauer, 1988; Howarth and Edmunds, 2000), our results have enhanced the field of mimicry and paved the way for future studies to build upon the findings presented in this thesis.

Our primary study focussed on model-mimic relationships and found that these relationships can be inferred from human visual assessments in citizen science, and that those relationships mirror what we'd expect to observe based on natural history observations. Additionally through the use of a large ecological dataset, we show that there is no statistical evidence to support the co-occurrence of high fidelity models and mimics compared to other mimetic pairings. Supporting our findings, we look at the use of bipartite motifs in understanding the structure of model-mimic networks, something that has not been done before.

My secondary study discovered for the first time that social information transfer may impact the fitness consequences of mimicry. My results demonstrate that social networks based on associations amongst zebra finches predicted the order in which finches exploited novel mimics. This key finding highlights social learning can reduce the benefits of mimicry by increasing the rate at which groups co-foraging predators learn to differentiate them from their models. Inferring from this study, we are able to deduce social learning increases the overall protection afforded by aposematism by creating a reduction in predator naivety when sampling the model-mimic community.

Through the use of citizen science experiments and a large ecological dataset we were able to analyse the co-occurrence of models and mimics. Despite our results not supporting the idea, high fidelity models and mimics are more likely to co-occur than by chance, we were able to analyse the bipartite motif network of model-mimic pairings. Interestingly, our results did not consider the idea of environmental gradients, which have the potential to play a significant part in model-mimic co-occurrence as well as network structures. This has been found to influence species' abundance, for example the common bumble bee (*Bombus pascuorum*) is known to decrease in abundance the more North you go (Else, 2002) . Therefore, additional work is required to be carried out on these environmental gradients in order to gain a greater understating of mimetic relationships and co-occurrence across different ecological environments. This again, can also be applied to mimetic networks, which may give a greater insight to species morphology across environmental gradients.

Both social and ecological networks have been evidenced in this thesis as successful methods of obtaining information on Batesian mimicry systems. This technique has shown how a) we can obtain key information on species specific relationships across a network, which can be Batesian mimicry specific and b) we can test the influence of social networks on mimetic systems. The application of networks, such as bipartite networks, can assist in uncovering evolutionary drivers of mimicry, such as model-mimic interactions across different ecological environments. This method, moving forward could be used through comparing several model-mimic networks across multiple regions in the U.K, which when coupled with our data could allow us to identify environmental variation between regions in terms of models and mimics. Region variability between species can be a key measure telling us how the dynamics between models and mimics change across different areas. Network motifs and clusters can be derived from within a network. These are strong empirical tools to analyse a specific network on a meso-scale level. Applying motifs and clusters can help us understand common network patterns, which then can be used to compare other networks of the same type.

Contrasting the use of bipartite networks, we can apply social networks to mimicry which analyses the transmission of information across a network of predators. In our study this looked at the model-mimic phenotype of artificial prey (coloured pots), when placed in an artificial foraging environment. Similar studies have been produced when looking at aposematism (Thorogood et al., 2018) indicating avoidance behaviour of aposematic prey is enhanced through social learning. However, our study is the first of its kind from a Batesian mimicry perspective, whilst also using an open environment with the predators free to roam. Our results indicate that the benefits of mimicry can be reduced through the co-foraging of predators where individuals increase the rate at which they can differentiate mimics from their models. With predators exerting a strong selection pressure on Batesian mimicry systems, this found influence of social learning can assist the field in understanding the significance of predators on both the models and mimics, in more detail. With our results, moving forward additional studies should evaluate the effect of social learning on those avian species that prey upon Hymenopteran and Syrphidae. Ultimately across regions where predators co-forage the benefits of mimicry can be deemed to reduce. This process reduces the trial and error phase of foraging, avoiding any costs that may associated with this phase of foraging. Interestingly, species that forage in isolation across Batesian mimicry systems, such as the red tailed hawk, its model eastern coral snake and the mimic scarlet kingsnake, may obtain aposematic avoidance through innate tendencies as opposed to distinct learning.

The maintenance of mimics possessing mimetic traits can be attributed to a combination of factors, which all contribute to the explosion of diversity seen today within Batesian mimicry systems. Across different environments, there are multiple factors that influence these mimetic relationships, all to a different proportion. In sum, these key factors can be listed as (not exhausted to):

1. **The predator**. The predator (signal receiver) plays a key role in the maintenance and evolution of Batesian mimicry, exerting selection pressures on both the model and mimic. The predator can be influenced by its current cognitive state, whether it is naïve (Waldbauer, 1988) or even other foragers providing a social influence. Additionally, across different mimetic systems predators can be both asocial and social. Again this could have added implications on the mimic and model. Supplementing these factors, the availability of additional prey; the predators energetic state and toxic burden (Skelhorn et al., 2016); the predators range and innate tendencies can affect the mimetic prey.
2. **The environment**. The environment plays an important role in the evolution and maintenance of Batesian mimicry. Both biotic and abiotic factors influence models and mimics, exerting selective pressures. The combination of these factors not only play a part in the success of these species but also contribute to their distribution.
3. **Species abundance**. The ratio of models to mimics has been found to be key to the benefits accrued by mimics. If models are more abundant throughout the time naive fledglings begin to forage the models educate and the mimics

avoid the costs associated with this. Following abundance, co-occurrence is another factor that plays a significant role in Batesian mimicry's maintenance and evolution. Although studies, such as the coral snake in the USA, have identified models and mimics do not need to co-occur for its maintenance (Harper and Pfennig, 2007; Pfennig and Mullen, 2010) certain species require their model within the same range for success.

4. **Model palatability**. Across Batesian mimetic networks, the model can be deemed unpalatable. Those that are highly unpalatable will educate the predator to a larger degree, thus the stimulus of the model's phenotype will carry a strong negative association. Therefore, mimics are able to avoid predation through their resemblance to the model, exerting a positive selection for mimetic fidelity.

The understanding of Batesian mimicry evolution has advanced drastically over the last 30 years, with developments in the field ranging from model-mimic co-occurrence to predator response and signal salience (Howarth et al., 2004; Kazemi et al., 2014; Landová et al., 2017). Current studies around the field of Batesian mimicry have focussed on predator cognition, featuring distinct aspects that effect predation of aposematic prey. For example, the salience of the signal, the toxic burden of the predator or even the previous encounter have all be known to influence the foraging decision of the predator. Future studies should consider native mimicry systems and by using a similar method to my first study, evaluate the relationships and distribution of mimetic species across their native ranges.

Previous work has looked into the decoupling of mimetic relationships through the process of urbanisation, with work already identifying an increase in mimic abundance in urban towns (Azmeh et al., 1998). If this abundance change is down to the building of anthropogenic settlements, this relaxed selection may subsequently result in a signal divergence between the model and mimic. This over time will evidently lead to the decoupling of mimetic relationships. Additionally climate change has been evidenced to have negatively impacted species on a global scale (Pacifici et al., 2017). Batesian mimicry has been looked at in little detail in regards climate change (Hassall et al., 2018), however looking forward at the potential effects this may have on species relationships, mimetic relationships may become decoupled over time. This will also be heavily influenced by the expansion of species' ranges

(Pecl et al., 2017), where models or mimics may enter regions which have not been occupied before.

Chapter 6 – Conclusion

I have shown in this thesis, for the first time, that social learning can play a large part in the dynamics of a Batesian mimicry system, resulting in different implications for the model, predator or mimic. Additionally, it has been evidenced that human visual assessments can assist us in deriving model-mimic relationships. Through the application of networks we have been able to unveil meso-scale network structures as well as specific species relationships, further supporting the use of networks as an applicable toolkit. Ultimately the evolution of Batesian mimicry is fluid and dynamic and has been driven by a continuous trade off between both predator and prey whilst also being refined over time. Going forward Batesian mimicry faces many challenges with a continually changing world, including both the increased risk of climate change and urbanisation threatening to decouple mimetic relationships. With various advancements in our understanding of Batesian mimicry's evolution, we are well equipped to build upon the current field of study. This coupled with studies focussing on predator cognition pave the way for future research into the evolution of mimicry.

List of References

Abrams, P.A. 1992. Adaptive foraging by predators as a cause of predator-prey cycles. *Evolutionary Ecology*. **6**(1), pp.56–72.

Akcali, C.K., Kikuchi, D.W. and Pfennig, D.W. 2018. Coevolutionary arms races in Batesian mimicry? A test of the chase-away hypothesis. *Biological Journal of the Linnean Society*. **124**(4), pp.686–676.

Akcali, C.K. and Pfennig, D.W. 2017. Geographic variation in mimetic precision among different species of coral snake mimics. *Journal of Evolutionary Biology*.

Akcali, C.K. and Pfennig, D.W. 2014. Rapid evolution of mimicry following local model extinction. *Biology Letters*. **10**(6).

Alem, S., Perry, C.J., Zhu, X., Loukola, O.J., Ingraham, T., Søvik, E. and Chittka, L. 2016. Associative Mechanisms Allow for Social Learning and Cultural Transmission of String Pulling in an Insect. *PLoS Biology*. **14**(10).

Allen, J., Weinrich, M., Hoppitt, W. and Rendell, L. 2013. Network-based diffusion analysis reveals cultural transmission of lobtail feeding in humpback whales. *Science*. **340**(6131), pp.485–488.

Aplin, L.M., Farine, D.R., Morand-Ferron, J., Cockburn, A., Thornton, A. and Sheldon, B.C. 2015. Experimentally induced innovations lead to persistent culture via conformity in wild birds. *Nature*. **518**, pp.538–541.

Arenas, L.M. and Stevens, M. 2017. Diversity in warning coloration is easily recognized by avian predators. *Journal of Evolutionary Biology*. **30**(7), pp.1288–1302.

Arenas, L.M., Troscianko, J. and Stevens, M. 2014. Color contrast and stability as key elements for effective warning signals. *Frontiers in Ecology and Evolution*. **2**, p.25.

Aronsson, M. and Gamberale-Stille, G. 2008. Domestic chicks primarily attend to colour, not pattern, when learning an aposematic coloration. *Animal Behaviour*. **75**(2), pp.417–423.

Aronsson, M. and Gamberale-Stille, G. 2013. Evidence of signaling benefits to contrasting internal color boundaries in warning coloration. *Behavioral Ecology*. **24**(2), pp.349–354.

Attard, M.R.G., Medina, I., Langmore, N.E. and Sherratt, E. 2017. Egg shape mimicry in parasitic cuckoos. *Journal of Evolutionary Biology*.

Azmeh, S., Owen, J., Sorensen, K., Grewcock, D. and Gilbert, F. 1998. Mimicry profiles are affected by human-induced habitat changes. *Proceedings of the Royal Society B: Biological Sciences*. **265**(1412), pp.2285–2290.

Bacheler, N.M., Paramore, L.M., Buckel, J.A. and Hightower, J.E. 2009. Abiotic and biotic factors influence the habitat use of an estuarine fish. *Marine Ecology Progress Series*. **377**, pp.263–277.

Baker, N.J., Kaartinen, R., Roslin, T. and Stouffer, D.B. 2015. Species’ roles in food webs show fidelity across a highly variable oak forest. *Ecography*. **38**(2), pp.130–139.

Ballantyne, G., Baldock, K.C.R., Rendell, L. and Willmer, P.G. 2017. Pollinator importance networks illustrate the crucial value of bees in a highly speciose plant community. *Scientific Reports*. **7**, pp.1–13.

Ballantyne, G., Baldock, K.C.R. and Willmer, P.G. 2015. Constructing more informative plantpollinator networks: Visitation and pollen deposition networks in a heathland plant community. *Proceedings of the Royal Society B: Biological Sciences*. **282**(1814).

Barnett, C.A., Bateson, M. and Rowe, C. 2007. State-dependent decision making: Educated predators strategically trade off the costs and benefits of consuming aposematic prey. *Behavioral Ecology*. **18**(4), pp.645–651.

Barnett, C.A., Skelhorn, J., Bateson, M. and Rowe, C. 2012. Educated predators make strategic decisions to eat defended prey according to their toxin content. *Behavioral Ecology*. **23**(2), pp.418–424.

Bates, H. 1862. Contributions to an Insect Fauna of the Amazon Valley. *Transactions of the Linnean Society*. **23**, p.495.

Beckett, S.J. 2016. Improved community detection in weighted bipartite networks. *Royal Society Open Science*. **3**(1), p.140536.

Bell, W.. 1990. *Searching behaviour: The Behavioural Ecology of Finding Resources*. Springer Science & Business Media, Berlin, Germany.

Benskin, C.M.H., Mann, N.I., Lachlan, R.F. and Slater, P.J.B. 2002. Social learning directs feeding preferences in the zebra finch, Taeniopygia guttata. *Animal Behaviour*. **64**, pp.823–828.

Benson, W.W. 1972. Natural selection for Müllerian mimicry in heliconius erato in Costa Rica. *Science*.

Berger-Tal, O., Nathan, J., Meron, E. and Saltz, D. 2014. The exploration-exploitation dilemma: A multidisciplinary framework. *PLoS ONE*. **9**(4), p.e95693.

Bergman, C.M., Fryxell, J.M., Gates, C.C. and Fortin, D. 2001. Ungulate foraging strategies: Energy maximizing or time minimizing? *Journal of Animal Ecology*. **70**(2), pp.289–300.

Bocakova, M., Bocak, L., Gimmel, M.L., Motyka, M. and Vogler, A.P. 2016. Aposematism and mimicry in soft-bodied beetles of the superfamily Cleroidea (Insecta). *Zoologica Scripta*. **45**(1), pp.9–21.

Boogert, N.J., Farine, D.R. and Spencer, K.A. 2014. Developmental stress predicts social network position. *Biology Letters*. **10**(10).

Boogert, N.J., Lachlan, R.F., Spencer, K.A., Templeton, C.N. and Farine, D.R. 2018. Stress hormones, social associations and song learning in zebra finches. *Philosophical Transactions of the Royal Society B: Biological Sciences*. **373**.

Boppré, M., Vane-Wright, R.I. and Wickler, W. 2017. A hypothesis to explain accuracy of wasp resemblances. *Ecology and Evolution*. **7**(1), pp.73–81.

Boyd, R. and Richerson, P. 1985. *Culture and the Evolutionary Process* First edit. Chicago: The University of Chicago Press.

Brady, S.G., Sipes, S., Pearson, A. and Danforth, B.N. 2006. Recent and simultaneous origins of eusociality in halictid bees. *Proceedings of the Royal Society B: Biological Sciences*. **273**(1594), pp.1643–1649.

Brodie, E.D. 1993. Differential avoidance of coral snake banded patterns by free-ranging avian predators in Costa Rica. *Evolution*. **47**, pp.227–235.

Brodie, E.D. 1981. Phenological Relationships of Model and Mimic Salamanders. *Evolution*. **35**(5), pp.988–994.

Brodie III, E.D. and Brodie Jr, E.D. 1999. Costs of exploiting poisonous prey:

evolutionary trade-offs in a predator-prey arms race. *Evolution*. **53**(2), pp.626–631.

Brodie III, E.D. and Janzen, F.J. 1995. Experimental Studies of Coral Snake Mimicry: Generalized Avoidance of Ringed Snake Patterns by Free-Ranging Avian Predators. *Functional Ecology*. **9**, pp.186–190.

Brown, J.S. 1999. Vigilance, patch use and habitat selection: Foraging under predation risk. *Evolutionary Ecology Research*. **1**, pp.49–71.

Burley, N., Krantzberg, G. and Radman, P. 1982. Influence of colour-banding on the conspecific preferences of zebra finches. *Animal Behaviour*. **30**(2), pp.444–455.

Carle, T. and Rowe, C. 2014. Avian predators change their foraging strategy on defended prey when undefended prey are hard to find. *Animal Behaviour*. **93**, pp.97–103.

Cazelles, K., Araújo, M.B., Mouquet, N. and Gravel, D. 2016. A theory for species co-occurrence in interaction networks. *Theoretical Ecology*. **9**(1), pp.39–48.

Chandler, M., See, L., Copas, K., Bonde, A.M.Z., López, B.C., Danielsen, F., Legind, J.K., Masinde, S., Miller-Rushing, A.J., Newman, G., Rosemartin, A. and Turak, E. 2017. Contribution of citizen science towards international biodiversity monitoring. *Biological Conservation*. **213**, pp.280–294.

Chantal, V., Gibelli, J. and Dubois, F. 2016. Male foraging efficiency, but not male problem-solving performance, influences female mating preferences in zebra finches. *PeerJ*.

Cheney, K.L. 2010. Multiple selective pressures apply to a coral reef fish mimic: A case of Batesianaggressive mimicry. *Proceedings of the Royal Society B: Biological Sciences*. **277**(1689), pp.1849–1855.

Cooke, I.R., Whitelaw, B., Norman, M., Caruana, N. and Strugnell, J.M. 2015. Toxicity in cephalopods *In*: *Evolution of Venomous Animals and Their Toxins*., pp.1–15.

Corso, G., De Araujo, A.I.L. and De Almeida, A.M. 2011. Connectivity and nestedness in bipartite networks from community ecology *In*: *Journal of Physics: Conference Series*., pp.1–6.

Cott, H.B. 1940. Adaptive Coloration in Animals. *Methuen, London*.

Coussi-Korbel, S. and Fragaszy, D.M. 1995. On the relation between social dynamics and social learning. *Animal Behaviour*. **50**, pp.1441–1453.

Coyte, K.Z., Schluter, J. and Foster, K.R. 2015. The ecology of the microbiome: Networks, competition, and stability. *Science*. **350**(6261), pp.663–666.

Cuthill, I.C., Allen, W.L., Arbuckle, K., Caspers, B., Chaplin, G., Hauber, M.E., Hill, G.E., Jablonski, N.G., Jiggins, C.D., Kelber, A., Mappes, J., Marshall, J., Merrill, R., Osorio, D., Prum, R., Roberts, N.W., Roulin, A., Rowland, H.M., Sherratt, T.N., Skelhorn, J., Speed, M.P., Stevens, M., Stoddard, M.C., Stuart-Fox, D., Talas, L., Tibbetts, E. and Caro, T. 2017. The biology of color. *Science*. **357**(6350).

D’Amen, M., Mod, H.K., Gotelli, N.J. and Guisan, A. 2018. Disentangling biotic interactions, environmental filters, and dispersal limitation as drivers of species co-occurrence. *Ecography*. **41**, pp.1233–1244.

Dafni, A. 1984. Mimicry and Deception in Pollination. *Annual Review of Ecology and Systematics*. **15**, pp.259–278.

Dall, S.R.X., Giraldeau, L.A., Olsson, O., McNamara, J.M. and Stephens, D.W.

2005. Information and its use by animals in evolutionary ecology. *Trends in Ecology and Evolution*. **20**, pp.187–193.

Dalziell, A.H. and Welbergen, J.A. 2016. Mimicry for all modalities. *Ecology Letters*. **19**(6), pp.609–619.

Darst, C.R. and Cummings, M.E. 2006. Predator learning favours mimicry of a less-toxic model in poison frogs. *Nature*. **440**, pp.208–211.

David, M., Auclair, Y. and Cézilly, F. 2011. Personality predicts social dominance in female zebra finches, Taeniopygia guttata, in a feeding context. *Animal Behaviour*. **81**(1), pp.219–224.

Davies, J., Meiri, S., Barraclough, T.G. and Gittleman, J.L. 2007. Species co-existence and character divergence across carnivores. *Ecology Letters*. **10**(2).

Diamond, J.M. 1975. The island dilemma: Lessons of modern biogeographic studies for the design of natural reserves. *Biological Conservation*. **7**, pp.129–146.

Dickinson, A. 1980. *Contemporary Animal Learning Theory*. Cambridge University Press, Cambridge.

Dieckmann, U., Marrow, P. and Law, R. 1995. Evolutionary cycling in predator-prey interactions: Population dynamics and the red queen. *Journal of Theoretical Biology*.

Dittrich, W., Gilbert, F., Green, P., Mcgregor, P. and Grewcock, D. 1993. Imperfect mimicry: A pigeon’s perspective. *Proceedings of the Royal Society B: Biological Sciences*. **251**, pp.195–200.

Dormann, C.F. 2011. How to be a specialist? Quantifying specialisation in pollination networks. *Network Biology*. **1**, pp.1–20.

Dreher, C.E., Cummings, M.E. and Pröhl, H. 2015. An analysis of predator selection to affect aposematic coloration in a poison frog species. *PLoS ONE*. **10**.

Dunson, W.A. and Travis, J. 2002. The Role of Abiotic Factors in Community Organization. *The American Naturalist*. **138**(5).

Easley, J.L. and Hassall, C. 2014. Field estimates of survival do not reflect ratings of mimetic similarity in wasp-mimicking hover flies. *Evolutionary Ecology*. **28**(2), pp.387–396.

Edmunds, M. 2000. Why are there good and poor mimics? *Biological Journal of the Linnean Society*. **70**, pp.459–466.

Else, G. 2002. Invited comment on Bombus terrestris (L.) in mid-winter. *The Entomologist’s Record and Journal of Variation*. **114**, p.54.

Endler, J.A. 1991. Interactions between predators and prey *In*: *Beheavioural Ecology: An Evolutionary Approach*. Blackwell, Oxford, pp.169–196.

Endler, J.A. 1986. *Natural Selection in the Wild*. Princeton University Press.

Endler, J.A. and Mappes, J. 2004. Predator Mixes and the Conspicuousness of Aposematic Signals. *The American Naturalist*. **163**(4), pp.532–547.

Exnerová, A., Ježová, D., Štys, P., Doktorovová, L., Rojas, B. and Mappes, J. 2015. Different reactions to aposematic prey in 2 geographically distant populations of great tits. *Behavioral Ecology*. **26**(5), pp.1361–1370.

Exnerová, A., Svádová, K.H., Fučíková, E., Drent, P. and Štys, P. 2010. Personality matters: Individual variation in reactions of naive bird predators to aposematic prey. *Proceedings of the Royal Society B: Biological Sciences*. **277**(1682), pp.723–728.

Farine, D.R. and Whitehead, H. 2015. Constructing, conducting and interpreting animal social network analysis. *Journal of Animal Ecology*. **84**(5), pp.1144–1163.

Fisher, J. and Hinde, R. 1949. The opening of milkbottles by birds. *Br.Birds*. **42**, pp.347–357.

Flanagan, N.S., Tobler, A., Davison, A., Pybus, O.G., Kapan, D.D., Planas, S., Linares, M., Heckel, D. and McMillan, W.O. 2004. Historical demography of Mullerian mimicry in the neotropical Heliconius butterflies. *PNAS*.

Fortunato, S. and Barthélemy, M. 2007. Resolution limit in community detection. *Proceedings of the National Academy of Sciences of the United States of America*. **104**(1), pp.36–41.

Franz, M. and Nunn, C.L. 2009. Network-based diffusion analysis: A new method for detecting social learning. *Proceedings of the Royal Society B: Biological Sciences*. **276**(1663), pp.1829–1836.

Freilich, M.A., Wieters, E., Broitman, B.R., Marquet, P.A. and Navarrete, S.A. 2018. Species co-occurrence networks: Can they reveal trophic and non-trophic interactions in ecological communities? *Ecology*. **99**(3), pp.690–699.

Galef, B.G. and Laland, K.N. 2006. Social Learning in Animals: Empirical Studies and Theoretical Models. *BioScience*. **55**(6), pp.489–499.

Garren, S.T. 2019. jmuOutlier: Permutation Tests for Nonparametric Statistics.

Gittleman, J.L. and Harvey, P.H. 1980. Why are distasteful prey not cryptic? *Nature*. **286**, pp.149–150.

Golding, Y.C. and Edmunds, M. 2000. Behavioural mimicry of honeybees (Apis mellifera) by droneflies (Diptera: Syrphidae: Eristalis spp.). *Proceedings of the Royal Society B: Biological Sciences*. **267**(1446), pp.903–909.

Golding, Y.C., Ennos, A.R.R. and Edmunds, M. 2001. Similarity in flight behaviour between the honeybee *Apis mellifera* (Hymenoptera: Apidae) and its presumed mimic, the dronefly *Eristalis tenax* (Diptera: Syrphidae). *The Journal of experimental biology*.

Gosak, M., Markovič, R., Dolenšek, J., Slak Rupnik, M., Marhl, M., Stožer, A. and Perc, M. 2018. Network science of biological systems at different scales: A review. *Physics of Life Reviews*. **24**, pp.118–135.

Gotelli, N.J. 2000. Null model analysis of species co-occurrence patterns. *Ecology*. **81**(9), pp.2606–2621.

Gotelli, N.J. and Graves, G.R. 1996. *Null models in Ecology*.

Griffin, A.S. 2004. Social learning about predators: a review and prospectus. *Learning & behavior*. **32**(1), pp.131–140.

Griffith, D.M., Veech, J.A. and Marsh, C.J. 2016. Cooccur: Probabilistic species co-occurrence analysis in R. *Journal of Statistical Software*. **69**(2), pp.1–17.

Guilford, T. and Dawkins, M.S. 1991. Receiver psychology and the evolution of animal signals. *Animal Behaviour*.

Guillette, L.M. and Healy, S.D. 2017. The roles of vocal and visual interactions in social learning zebra finches: A video playback experiment. *Behavioural Processes*. **139**, pp.43–49.

Halpin, C.G., Skelhorn, J. and Rowe, C. 2008. Being conspicuous and defended: Selective benefits for the individual. *Behavioral Ecology*. **19**(5), pp.1012–1017.

Halpin, C.G., Skelhorn, J. and Rowe, C. 2014. Increased predation of nutrient-enriched aposematic prey. *Proceedings of the Royal Society B: Biological Sciences*. **281**(1781).

Ham, A.D., Ihalainen, E., Lindström, L. and Mappes, J. 2006. Does colour matter? The importance of colour in avoidance learning, memorability and generalisation. *Behavioral Ecology and Sociobiology*. **60**(4), pp.482–491.

Harper, G.R. and Pfennig, D.W. 2007. Mimicry on the edge: Why do mimics vary in resemblance to their model in different parts of their geographical range? *Proceedings of the Royal Society B: Biological Sciences*. **274**(1621), pp.1955–1961.

Harpole, W.S. 2010. Neutral Theory of Species Diversity. *Nature Education Knowledge*. **1**(8), p.31.

Hassall, C., Billington, J. and Sherratt, T.N. 2018. Climate-induced phenological shifts in a Batesian mimicry complex. *PNAS*. **116**(3), pp.929–933.

Hauglund, K., Hagen, S.B. and Lampe, H.M. 2006. Responses of domestic chicks (Gallus gallus domesticus) to multimodal aposematic signals. *Behavioral Ecology*. **17**(3), pp.392–398.

Hazen, E.L., Friedlaender, A.S. and Goldbogen, J.A. 2015. Blue whales (Balaenoptera musculus) optimize foraging efficiency by balancing oxygen use and energy gain as a function of prey density. *Science Advances*. **1**(9).

Herberstein, M.E. 2011. *Spider behaviour: Flexibility and versatility*.

Heyes, C.M. 1994. SOCIAL LEARNING IN ANIMALS: CATEGORIES AND MECHANISMS. *Biological Reviews*. **69**(2), pp.207–231.

Heyes, C.M. and Galef Jr., B.G. 1996. *Social Learning in Animals: The Roots of Culture*.

Hilgard, E. and Bower, G. 1966. *Theories of learning* 3rd Editio. Appleton-Century-Crofts.

Hoiss, B., Krauss, J., Potts, S.G., Roberts, S. and Steffan-Dewenter, I. 2012. Altitude acts as an environmental filter on phylogenetic composition, traits and diversity in bee communities. *Proceedings of the Royal Society B: Biological Sciences*. **279**(1746), pp.4447–4456.

Holloway, G., Gilbert, F. and Brandt, A. 2002. The relationship between mimetic imperfection and phenotypic variation in insect colour patterns. *Proceedings of the Royal Society B: Biological Sciences*. **269**.

Hoppitt, W. 2019. A Package For Implementing Network-Based Diffusion Analysis (NBDA).

Hoppitt, W. and Laland, K.N. 2013. Social Learning: An Introduction to Mechanisms, Methods, and Models. *The Quarterly Review of Biology*. **89**(4), pp.392–393.

Van Horn, R.C., Engh, A.L., Scribner, K.T., Funk, S.M. and Holekamp, K.E. 2004. Behavioural structuring of relatedness in the spotted hyena (Crocuta crocuta) suggests direct fitness benefits of clan-level cooperation. *Molecular Ecology*. **13**(2), pp.449–458.

Horner-Devine, C., Silver, J.M., Leibold, M.A., Bohannan, B.J.M., Colwell, R.K., Fuhrman, J.A., Green, J.L., Kuske, C.R., Martiny, J.B.H., Muyzer, G., Øvreås, L., Reysenbach, A.L. and Smith, V.H. 2007. A comparison of taxon co-occurrence patterns for macro- and microorganisms. *Ecology*. **88**(6), pp.1345–1353.

Howarth, B. and Edmunds, M. 2000. The phenology of Syrphidae (Diptera): Are they Batesian mimics of Hymenoptera? *Biological Journal of the Linnean Society*.

Howarth, B., Edmunds, M. and Gilbert, F. 2004. Does the abundance of hoverfly (Syrphidae) mimics depend on the numbers of their hymenopteran models? *Evolution*. **58**(2), pp.367–375.

Hubbell, S. 2001. *The unified neutral theory of biodiversity and biogeography (MPB-32)*. Princeton University Press.

Huheey, J.E. 1988. Mathematical Models of Mimicry. *The American Naturalist*. **131**, pp.22–41.

Ihalainen, E., Lindström, L. and Mappes, J. 2007. Investigating Müllerian mimicry: Predator learning and variation in prey defences. *Journal of Evolutionary Biology*. **20**(2), pp.780–791.

Iserbyt, A., Bots, J., van Dongen, S., Ting, J.J., van Gossum, H. and Sherratt, T.N. 2011. Frequency-dependent variation in mimetic fidelity in an intraspecific mimicry system. *Proceedings of the Royal Society B: Biological Sciences*. **278**(1721), pp.3116–3122.

Jackson, R.R. and Wilcox, R.S. 1993. Spider flexibily chooses aggressive mimicry signals for different prey by trial and error. *Behaviour*. **127**(1), pp.21–36.

Jacoby, D.M.P. and Freeman, R. 2016. Emerging Network-Based Tools in Movement Ecology. *Trends in Ecology and Evolution*. **31**(4), pp.301–314.

Jamie, G.A. 2017. Signals, cues and the nature of mimicry. *Proceedings of the Royal Society B: Biological Sciences*. **284**(1849).

Johnstone, R.A. 1995. Honest advertisement of multiple qualities using multiple signals. *Journal of Theoretical Biology*.

Kashtan, N. and Alon, U. 2005. Spontaneous evolution of modularity and network motifs. *Proceedings of the National Academy of Sciences of the United States of America*. **102**(39), pp.13773–13778.

Katz, M. and Lachlan, R.F. 2003. Social learning of food types in zebra finches (Taenopygia guttata) is directed by demonstrator sex and feeding activity. *Animal Cognition*. **6**(1), pp.11–16.

Kazemi, B., Gamberale-Stille, G. and Leimar, O. 2015. Multi-trait mimicry and the relative salience of individual traits. *Proceedings of the Royal Society B: Biological Sciences*. **282**(1818).

Kazemi, B., Gamberale-Stille, G., Tullberg, B.S. and Leimar, O. 2014. Stimulus salience as an explanation for imperfect mimicry. *Current Biology*. **24**(9), pp.965–969.

Kazemi, B., Gamberale-Stille, G., Wåtz, T., Wiklund, C. and Leimar, O. 2018. Learning of salient prey traits explains Batesian mimicry evolution. *Evolution*. **72**(3), pp.531–539.

Kendal, R., Hopper, L.M., Whiten, A., Brosnan, S.F., Lambeth, S.P., Schapiro, S.J. and Hoppitt, W. 2015. Chimpanzees copy dominant and knowledgeable individuals: Implications for cultural diversity. *Evolution and Human Behavior*. **36**(1), pp.65–72.

Kendal, R.L., Coolen, I., van Bergen, Y. and Laland, K.N. 2005. Trade-Offs in the Adaptive Use of Social and Asocial Learning. *Advances in the Study of Behavior*. **35**, pp.333–379.

Kerr, J.T., Pindar, A., Galpern, P., Packer, L., Potts, S.G., Roberts, S.M., Rasmont, P., Schweiger, O., Colla, S.R., Richardson, L.L., Wagner, D.L., Gall, L.F., Sikes, D.S. and Pantoja, A. 2015. Climate change impacts on bumblebees converge across continents. *Science*. **349**, pp.177–180.

Kikuchi, D.W., Malick, G., Webster, R.J., Whissell, E. and Sherratt, T.N. 2015. An empirical test of 2-dimensional signal detection theory applied to Batesian mimicry. *Behavioral Ecology*. **26**(4), pp.1226–1235.

Kikuchi, D.W. and Pfennig, D.W. 2013. Imperfect Mimicry and the Limits of Natural Selection. *The Quarterly Review of Biology*. **88**(4), pp.297–315.

Kikuchi, D.W. and Pfennig, D.W. 2010. Predator cognition permits imperfect coral snake mimicry. *American Naturalist*. **176**(6), pp.830–834.

Kikuchi, D.W. and Sherratt, T.N. 2015. Costs of Learning and the Evolution of Mimetic Signals. *The American Naturalist*. **186**(3), pp.321–332.

Kilner, R.M. and Langmore, N.E. 2011. Cuckoos versus hosts in insects and birds: Adaptations, counter-adaptations and outcomes. *Biological Reviews*. **86**(4), pp.836–852.

Kraemer, A.C. and Adams, D.C. 2014. Predator perception of batesian mimicry and conspicuousness in a salamander. *Evolution*. **68**(4), pp.1197–1206.

Kristiansen, E.B., Finkbeiner, S.D., Hill, R.I., Prusa, L. and Mullen, S.P. 2018. Testing the adaptive hypothesis of Batesian mimicry among hybridizing North American admiral butterflies. *Evolution*. **72**(7), pp.1436–1448.

Kuhlmann, M., Else, G.R., Dawson, A. and Quicke, D.L.J. 2007. Molecular, biogeographical and phenological evidence for the existence of three western European sibling species in the Colletes succinctus group (Hymenoptera: Apidae). *Organisms Diversity and Evolution*. **7**(2), pp.155–165.

Landová, E., Hotová Svádová, K., Fuchs, R., Štys, P. and Exnerová, A. 2017. The effect of social learning on avoidance of aposematic prey in juvenile great tits (Parus major). *Animal Cognition*. **20**, pp.855–866.

Lee, S.Y. 1999. Tropical mangrove ecology: Physical and biotic factors influencing ecosystem structure and function. *Austral Ecology*. **24**(4), pp.355–366.

Lehmann, J. and Boesch, C. 2009. Sociality of the dispersing sex: the nature of social bonds in West African female chimpanzees, Pan troglodytes. *Animal Behaviour*. **77**(2), pp.377–387.

Leimar, O., Enquist, M. and Sillen-Tullberg, B. 1986. Evolutionary Stability of Aposematic Coloration and Prey Unprofitability: A Theoretical Analysis. *The American Naturalist*. **128**(4), pp.469–490.

Lev-yadun, S. 2009. Aposematic (Warning) coloration in plants *In*: *Plant-Environment Interactions, Signaling and communication in plants*.

Lindstrom, L., Alatalo, R. V., Lyytinen, A. and Mappes, J. 2001. Strong antiapostatic selection against novel rare aposematic prey. *Proceedings of the National Academy of Sciences*. **98**, pp.9181–9184.

Lindstrom, L., Alatalo, R. V. and Mappes, J. 1997. Imperfect Batesian mimicry - The effects of the frequency and the distastefulness of the model. *Proceedings of the Royal Society B: Biological Sciences*.

Louthan, A.M., Doak, D.F. and Angert, A.L. 2015. Where and When do Species Interactions Set Range Limits? *Trends in Ecology and Evolution*. **30**(12), pp.780–792.

Maan, M.E. and Cummings, M.E. 2008. Female preferences for aposematic signal components in a polymorphic poison frog. *Evolution*. **62**(9), pp.2334–2345.

Maan, M.E. and Cummings, M.E. 2012. Poison Frog Colors Are Honest Signals of Toxicity, Particularly for Bird Predators. *The American Naturalist*. **179**, pp.E1–E14.

Mackenzie, D.I., Bailey, L.L. and Nichols, J.D. 2004. Investigating species co-occurrence patterns when species are detected imperfectly. *Journal of Animal Ecology*. **73**, pp.546–555.

Mackintosh, N.J. 1976. Overshadowing and stimulus intensity. *Animal Learning & Behavior*. **4**, pp.186–192.

Mallet, J. and Joron, M. 1999. Evolution of Diversity in Warning Color and Mimicry: Polymorphisms, Shifting Balance, and Speciation. *Annual Review of Ecology and Systematics*.

Mappes, J. and Alatalo, R. V. 1997. Batesian Mimicry and Signal Accuracy. *Evolution*. **51**(6), pp.2050–2053.

Mappes, J., Marples, N. and Endler, J.A. 2005. The complex business of survival by aposematism. *Trends in Ecology and Evolution*.

Marchini, M., Sommaggio, D. and Minelli, A. 2017. Playing with Black and Yellow: The Evolvability of a Batesian Mimicry. *Evolutionary Biology*.

Marples, N.M., Kelly, D.J. and Thomas, R.J. 2005. Perspective: The evolution of warning coloration is not paradoxical. *Evolution*. **59**, pp.933–940.

Maynard-Smith, J. and Harper, D. 2003. *Animal Signals*. Oxford Univ. Press, Oxford.

McCowan, L.S.C., Mariette, M.M. and Griffith, S.C. 2015. The size and composition of social groups in the wild zebra finch. *Emu*. **115**(3), pp.191–198.

Mcfarland, R., Fuller, A., Hetem, R.S., Mitchell, D., Maloney, S.K., Henzi, S.P. and Barrett, L. 2015. Social integration confers thermal benefits in a gregarious primate. *Journal of Animal Ecology*. **84**(3), pp.871–878.

McNamara, J.M. and Houston, A.I. 1985. Optimal foraging and learning. *Journal of Theoretical Biology*. **117**, pp.231–249.

Miller-Rushing, A.J., Gallinat, A.S. and Primack, R.B. 2019. Creative citizen science illuminates complex ecological responses to climate change. *Proceedings of the National Academy of Sciences*. **116**, pp.720–722.

Milo, R., Shen-Orr, S., Itzkovitz, S., Kashtan, N., Chklovskii, D. and Alon, U. 2002. Network motifs: Simple building blocks of complex networks. *Science*. **298**(5584), pp.824–827.

Mitchell, R.M., Bakker, J.D., Vincent, J.B. and Davies, G.M. 2017. Relative importance of abiotic, biotic, and disturbance drivers of plant community structure in the sagebrush steppe. *Ecological Applications*. **27**(3), pp.756–768.

Morimoto, J. 2019. Foraging decisions as multi-armed bandit problems: Applying reinforcement learning algorithms to foraging data. *Journal of Theoretical Biology*. **467**, pp.48–56.

Mostler, G. 1935. Beobachtungen zur Frage der Wespen- mimikry. *Z. Morphol. Oekol. Tiere*. **29**, pp.381–454.

Mullen, S.P., Dopman, E.B. and Harrison, R.G. 2008. Hybrid zone origins, species boundaries, and the evolution of wing-pattern diversity in a polytypic species complex of North American admiral butterflies (Nymphalidae: Limenitis). *Evolution*. **62**(6), pp.1400–1417.

Müller, F. 1879. Ituna and Thyridia: a remarkable case of mimicry in butterflies.

Transactions of the Entomological Society of London.

Newman, M.E.J. and Girvan, M. 2004. Finding and evaluating community structure in networks. *Physical Review E - Statistical, Nonlinear, and Soft Matter Physics*. **69**(2).

Oksanen, J., Blanchet, F.G., Kindt, R., Legendre, P., Minchin, P.R., O'Hara, R.B., Simpson, G.L., Solymos, P., Stevens, M.H.H. and Wagner, H. 2018. Vegan: community ecology package.

Pacifici, M., Visconti, P., Butchart, S.H.M., Watson, J.E.M., Cassola, F.M. and Rondinini, C. 2017. Species' traits influenced their response to recent climate change. *Nature Climate Change*. **7**, pp.205–208.

Page, R.A. and Ryan, M.J. 2006. Social Transmission of Novel Foraging Behavior in Bats: Frog Calls and Their Referents. *Current Biology*. **16**(12), pp.1201–1205.

Pannell, J.R. and Farmer, E.E. 2016. Mimicry in plants. *Current Biology*., pp.784–785.

Parmesan, C. and Yohe, G. 2003. A globally coherent fingerprint of climate change impacts across natural systems. *Nature*. **421**, pp.37–42.

Pasteels, J.M., Grégoire, J.C. and Rowell-Rahier, M. 1983. The Chemical Ecology of Defense in Arthropods. *Annual Review of Entomology*. **28**, pp.263–289.

Pecl, G.T., Araújo, M.B., Bell, J.D., Blanchard, J., Bonebrake, T.C., Chen, I.C., Clark, T.D., Colwell, R.K., Danielsen, F., Evengård, B., Falconi, L., Ferrier, S., Frusher, S., Garcia, R.A., Griffis, R.B., Hobday, A.J., Janion-Scheepers, C., Jarzyna, M.A., Jennings, S., Lenoir, J., Linnetved, H.I., Martin, V.Y., McCormack, P.C., McDonald, J., Mitchell, N.J., Mustonen, T., Pandolfi, J.M., Pettorelli, N., Popova, E., Robinson, S.A., Scheffers, B.R., Shaw, J.D., Sorte, C.J.B., Strugnell, J.M., Sunday, J.M., Tuanmu, M.N., Vergés, A., Villanueva, C., Wernberg, T., Wapstra, E. and Williams, S.E. 2017. Biodiversity redistribution under climate change: Impacts on ecosystems and human well-being. *Science*. **355**(6332).

Penney, H.D., Hassall, C., Skevington, J.H., Abbott, K.R. and Sherratt, T.N. 2012. A comparative analysis of the evolution of imperfect mimicry. *Nature*. **483**, pp.461–464.

Penney, H.D., Hassall, C., Skevington, J.H., Lamborn, B. and Sherratt, T.N. 2014. The Relationship between Morphological and Behavioral Mimicry in Hover Flies (Diptera: Syrphidae). *The American Naturalist*. **183**(2), pp.281–289.

Pfennig, D.W., Akcali, C.K. and Kikuchi, D.W. 2015. Batesian mimicry promotes pre- and postmating isolation in a snake mimicry complex. *Evolution*.

Pfennig, D.W. and Mullen, S.P. 2010. Mimics without models: Causes and consequences of allopatry in Batesian mimicry complexes. *Proceedings of the Royal Society B: Biological Sciences*. **277**(1694), pp.2577–2585.

Pongrácz, P., Vida, V., Bánhegyi, P. and Miklósi, Á. 2008. How does dominance rank status affect individual and social learning performance in the dog (Canis familiaris)? *Animal Cognition*. **11**(1), pp.75–82.

Poulin, R. 2010. Network analysis shining light on parasite ecology and diversity. *Trends in Parasitology*. **26**(10), pp.492–498.

Poulton, E. 1909. Mimicry in the Butterflies of North America. *Annals of the Entomological Society of America*. **2**(4), pp.203–242.

Premnath, S., Sinha, A. and Gadagkar, R. 1996. Dominance relationship in the establishment of reproductive division of labour in a primitively eusocial wasp (Ropalidia marginata). *Behavioral Ecology and Sociobiology*. **39**(2), pp.125–132.

Proulx, S.R., Promislow, D.E.L. and Phillips, P.C. 2005. Network thinking in ecology and evolution. *Trends in Ecology and Evolution*. **20**(6), pp.345–353.

Prudic, K.L., Skemp, A.K. and Papaj, D.R. 2007. Aposematic coloration, luminance contrast, and the benefits of conspicuousness. *Behavioral Ecology*. **18**, pp.41–46.

Pulver, J.R., Liu, H. and Scott-Denton, E. 2016. Modelling community structure and species co-occurrence using fishery observer data. *ICES Journal of Marine Science*. **73**(7), pp.1750–1763.

Pyke, G.H. 2019. Optimal Foraging Theory: An Introduction *In*: *Encyclopedia of Animal Behavior*., pp.111–117.

R Core Team 2018. R: A language and environment for statistical computing. Available from: https://www.r-project.org/.

Rashotte, M.., O'Connell, J.. and Djuric, V.. 2013. Mechanisms of signal-controlled foraging behavior. *In*: M. Commons, A. Kacelnik and S. Shettleworth, eds. *Foraging: Quantitative Analyses of Behavior*. Lawrence Erlbaum Associates, p.153.

Raubenheimer, D. and Simpson, S.J. 2018. Nutritional ecology and foraging theory. *Current Opinion in Insect Science*. **27**, pp.38–45.

Rendell, L., Fogarty, L., Hoppitt, W.J.E., Morgan, T.J.H., Webster, M.M. and Laland, K.N. 2011. Cognitive culture: Theoretical and empirical insights into social learning strategies. *Trends in Cognitive Sciences*. **15**(2), pp.58–76.

Ries, L. and Mullen, S.P. 2008. A rare model limits the distribution of its more common mimic: A twist on frequency-dependent batesian mimicry. *Evolution*. **62**, pp.1798–1803.

Rodríguez-Rodríguez, M.C., Jordano, P. and Valido, A. 2017. Functional consequences of plant-animal interactions along the mutualism-antagonism gradient. *Ecology*. **98**(5), pp.1266–1276.

Rojas, B., Valkonen, J. and Nokelainen, O. 2015. Aposematism. *Current Biology*. **25**(9), pp.350–351.

Roper, T.J. 1993. Effects of novelty on taste-avoidance learning in chicks. *Behaviour*. **125**(3–4), pp.265–281.

Rosa, P., Nguyen, V. and Dubois, F. 2012. Individual differences in sampling behaviour predict social information use in zebra finches. *Behavioral Ecology and Sociobiology*. **66**(9), pp.1259–1265.

Rothschild, M. 1961. Defensive Odours and Mullerian Mimcry Among Insects. *Transactions of the Royal Entomological Society of London*. **113**(5), pp.102–123.

Rowe, C. 1999. Receiver psychology and the evolution of multicomponent signals. *Animal Behaviour*.

Rowland, H.M., Fulford, A.J.T. and Ruxton, G.D. 2017. Predator learning differences affect the survival of chemically defended prey. *Animal Behaviour*. **124**, pp.65–74.

Rowland, H.M., Hoogesteger, T., Ruxton, G.D., Speed, M.P. and Mappes, J. 2010. A tale of 2 signals: Signal mimicry between aposematic species enhances predator avoidance learning. *Behavioral Ecology*. **21**(4), pp.851–860.

Rowland, H.M., Mappes, J., Ruxton, G.D. and Speed, M.P. 2010. Mimicry between unequally defended prey can be parasitic: Evidence for quasi-Batesian mimicry. *Ecology Letters*. **13**(12), pp.1494–1502.

Rowlands, A. 2019. Network-based diffusion analysis reveals directed social learning in Zebra Finches, Taeniopygia guttata. *Unpublished*.

Ruxton, G.., Sherratt, T.. and Speed, M.. 2018. *Avoiding attack: the evolutionary ecology of crypsis, warning signals and mimicry* Second Edi. Oxford:Oxford University Press.

Ruxton, G.D., Sherratt, T.N. and Speed, M.P. 2004. *Avoiding Attack: The Evolutionary Ecology of Crypsis, Warning Signals and Mimicry*.

Sbordoni, V., Bullini, L., Scarpelli, G., Forestiero, S. and Rampini, M. 1979. Mimicry in the burnet moth Zygaena ephialtes: population studies and evidence of a Batesian—Müllerian situation. *Ecological Entomology*. **4**, pp.83–93.

Van Schaik, C.P. 2010. *Social learning and culture in animals*.

Schoener, T.W. 1971. Theory of Feeding Strategies. *Annual Review of Ecology and Systematics*. **2**, pp.369–404.

Schowalter, T.D. 2006. *Insect Ecology: An Ecosystem Approach: Fourth Edition*.

Seddon, N., Tobias, J., Eaton, M. and Odeen, A. 2010. Human Vision can Provide a Valid Proxy for Avian Perception of Sexual Dichromatism. *The Auk: Ornithological Advances*. **127**, pp.283–292.

Sherratt, T.N. 2002. The evolution of imperfect mimicry. *Behavioral Ecology*. **13**(6), pp.821–826.

Sherratt, T.N. 2008. The evolution of Müllerian mimicry. *Naturwissenschaften*.

Sherratt, T.N. 2011. The optimal sampling strategy for unfamiliar prey. *Evolution*. **65**(7), pp.2014–2025.

Sherratt, T.N. and Peet-Paré, C.A. 2017. The perfection of mimicry: An information approach. *Philosophical Transactions of the Royal Society B: Biological Sciences*. **372**(1724).

Shettleworth, S.J. 1998. *Cognition, evolution and behaviour* First Edit. Oxford Univ. Press, Oxford.

Sih, A. 1984. The Behavioral Response Race Between Predator and Prey. *The American Naturalist*. **123**(1), pp.143–150.

Sillén-Tullberg, B. 1985. Higher survival of an aposematic than of a cryptic form of a distasteful bug. *Oecologia*. **67**(3), pp.411–415.

Simmons, B.I., Sweering, M.J.M., Schillinger, M., Dicks, L. V., Sutherland, W.J. and Di Clemente, R. 2018. bmotif: A package for motif analyses of bipartite networks. *Methods in Ecology and Evolution*.

Sirois-Delisle, C. and Kerr, J.T. 2018. Climate change-driven range losses among bumblebee species are poised to accelerate. *Scientific Reports*. **8**.

Skelhorn, J., Halpin, C.G. and Rowe, C. 2016. Learning about aposematic prey. *Behavioral Ecology*. **27**(4), pp.955–964.

Skelhorn, J. and Rowe, C. 2010. Birds learn to use distastefulness as a signal of toxicity. *Proceedings of the Royal Society B: Biological Sciences*. **277**(1688), pp.1729–1734.

Skelhorn, J. and Rowe, C. 2007. Predators’ Toxin Burdens Influence Their Strategic Decisions to Eat Toxic Prey. *Current Biology*. **17**, pp.1479–1483.

Skelhorn, J. and Rowe, C. 2006. Prey palatability influences predator learning and memory. *Animal Behaviour*. **71**(5), pp.1111–1118.

Smelser, N. and Baltes, P. 2001. *International Encyclopedia of the Social & Behavioral Sciences* 2001st ed. New York: Elsevier.

Smith, K.E., Halpin, C.G. and Rowe, C. 2014. Body size matters for aposematic prey during predator aversion learning. *Behavioural Processes*. **109**, pp.173–179.

Smith, S.M. 1977. Coral-snake pattern recognition and stimulus generalisation by naive great kiskadees (Aves: Tyrannidae). *Nature*. **265**, pp.535–536.

Smith, S.M. 1975. Innate recognition of coral snake pattern by a possible avian predator. *Science (New York, N.Y.)*. **187**, pp.759–760.

Speed, M.. and Ruxton, G.. 2005. Aposematism: what should our starting point be? *Proceedings of the Royal Society B: Biological Sciences*. **272**(1561), pp.431–438.

Speed, M.P. 1993. Muellerian mimicry and the psychology of predation. *Animal Behaviour*. **45**(3), pp.571–580.

Speed, M.P. 2000. Warning signals, receiver psychology and predator memory. *Animal Behaviour*.

Speed, M.P. and Ruxton, G.D. 2007. How bright and how nasty: Explaining diversity in warning signal strength. *Evolution*. **61**(3), pp.623–635.

Stander, P.E. 1992. Cooperative hunting in lions: the role of the individual. *Behavioral Ecology and Sociobiology*. **29**(6), pp.445–454.

Stevens, M. 2007. Predator perception and the interrelation between different forms of protective coloration. *Proceedings of the Royal Society B: Biological Sciences*. **274**(1617), pp.1457–1464.

Stevens, M. and Ruxton, G.D. 2012. Linking the evolution and form of warning coloration in nature. *Proceedings of the Royal Society B: Biological Sciences*. **279**(1728), pp.417–426.

Stoddard, M.C. and Stevens, M. 2010. Pattern mimicry of host eggs by the common cuckoo, as seen through a bird’s eye. *Proceedings of the Royal Society B: Biological Sciences*.

Stuckert, A.M.M., Venegas, P.J. and Summers, K. 2014. Experimental evidence for predator learning and Müllerian mimicry in Peruvian poison frogs (Ranitomeya, Dendrobatidae). *Evolutionary Ecology*. **28**(3), pp.413–426.

Symula, R., Schulte, R. and Summers, K. 2001. Molecular phylogenetic evidence for a mimetic radiation in Peruvian poison frogs supports a Müllerian mimicry hypothesis. *Proceedings of the Royal Society B: Biological Sciences*. **268**, pp.2415–2421.

Taylor, C.H., Gilbert, F. and Reader, T. 2013. Distance transform: A tool for the study of animal colour patterns. *Methods in Ecology and Evolution*. **4**, pp.771–781.

Thomas, J.A. and Settele, J. 2004. Butterfly mimics of ants. *Nature*.

Thorogood, R., Kokko, H. and Mappes, J. 2018. Social transmission of avoidance among predators facilitates the spread of novel prey. *Nature Ecology and Evolution*. **2**, pp.254–261.

Treisman, M. 1975. Predation and the evolution of gregariousness. I. Models for concealment and evasion. *Animal Behaviour*. **23**, pp.779–800.

Troscianko, J. and Stevens, M. 2015. Image calibration and analysis toolbox - a free software suite for objectively measuring reflectance, colour and pattern. *Methods in Ecology and Evolution*. **6**(11), pp.1320–1331.

Udino, E., Perez, M., Carere, C. and D'Ettorre, P. 2017. Active explorers show low learning performance in a social insect. *Current Zoology*. **63**(5), pp.555–560.

Ulrich, W. and Gotelli, N.J. 2013. Pattern detection in null model analysis. *Oikos*. **122**(1), pp.2–18.

Valkonen, J.K., Mäkelä, A., Mappes, J. and López-Sepulcre, A. 2018. Evaluating the potential for evolutionary mismatch in Batesian mimics: A case study in the endangered smooth snake (Coronella austriaca). *Evolutionary Applications*. **11**(9), pp.1512–1517.

Valkonen, J.K., Nokelainen, O., Niskanen, M., Kilpimaa, J., Björklund, M. and Mappes, J. 2012. Variation in predator species abundance can cause variable selection pressure on warning signaling prey. *Ecology and Evolution*. **2**(8), pp.1971–1976.

Vane-Wright, R.I. 1980. On the definition of mimicry. *Biological Journal of the Linnean Society*. **13**(1), pp.1–6.

Vriends, M. 1997. *The Zebra Finch*. New York: Howell Book House.

Vršanský, P., Bechly, G., Zhang, Qingqing, Jarzembowski, E.A., Mlynský, T., Šmídová, L., Barna, P., Kúdela, M., Aristov, D., Bigalk, S., Krogmann, L., Li, L., Zhang, Qi, Zhang, H., Ellenberger, S., Müller, P., Gröhn, C., Xia, F., Ueda, K., Vďačný, P., Valaška, D., Vršanská, L. and Wang, B. 2018. Batesian insect-insect mimicry-related explosive radiation of ancient alienopterid cockroaches. *Biologia*. **73**(10), pp.987–1006.

Van De Waal, E., Renevey, N., Favre, C.M. and Bshary, R. 2010. Selective attention to philopatric models causes directed social learning in wild vervet monkeys. *Proceedings of the Royal Society B: Biological Sciences*. **277**, pp.2105–2111.

Waldbauer, G. 1988. Asynchrony between Batesian mimics and their models. *American Naturalist*.

Wallace, A.R. 1882. Dr. Fritz Müller on some difficult cases of mimicry. *Nature*.

Whiten, A., Horner, V. and De Waal, F.B.M. 2005. Conformity to cultural norms of tool use in chimpanzees. *Nature*. **437**, pp.737–740.

Wickler, W. 1968. Mimicry in Plants and Animals. *Translated from the German by R. D. Martin. McGraw-Hill, N. Y.*

Wickler, W. 2013. Understanding Mimicry - with Special Reference to Vocal Mimicry. *Ethology*. **119**(4), pp.259–269.

Wilson, E.O. 1987. Causes of Ecological Success: The Case of the Ants. *The Journal of Animal Ecology*. **56**, pp.1–9.

Wüster, W., Allum, C.S.E., Bjargardóttir, I.B., Bailey, K.L., Dawson, K.J., Guenioui, J., Lewis, J., McGurk, J., Moore, A.G., Niskanen, M. and Pollard, C.P. 2004. Do aposematism and Batesian mimicry require bright colours? A test, using European viper markings. *Proceedings of the Royal Society B: Biological Sciences*. **271**(1556), pp.2495–2499.

Yamaguchi, N., Cooper, A., Werdelin, L. and Macdonald, D.W. 2004. Evolution of the mane and group-living in the lion (Panthera leo): A review. *Journal of Zoology*. **263**, pp.329–342.

Zalucki, M.P., Malcolm, S.B., Pauste, T.D., Hanlon, C.C., Brower, L.P. and Clarke, A.R. 2001. It’s the first bites that count: Survival of first-instar monarchs on milkweeds. *Austral Ecology*. **26**, pp.547–555.

Zanin, M., Sousa, P.A. and Menasalvas, E. 2014. Information content: Assessing meso-scale structures in complex networks. *EPL*. **106**(3), p.30001.

Zann, R. 1996. *Zebra Finch: A Synthesis of Field and Laboratory Studies*.

List of Abbreviations

BWARS = Bees, wasps and ants recoding scheme

HRS = Hoverfly recording scheme

HWARS = Hoverfly and wasp recording scheme

NBDA = Network based diffusion analysis

OADA = Order of acquisition diffusion analysis

Glossary

Allopatry - The occurrence of a particular species who are geographically isolate from the main population of the same species.

Aposematism - A term coined to describe a species with a specific warning signal, telling a predator it is toxic, unpalatable or dangerous. The warning signal is associated with the individuals unprofitability

Batesian mimicry - When a palatable species imitates the warning signal of a noxious or unpalatable species in order to avoid predation.

Imperfect mimicry - When mimics dot not closely resemble their model but still gain the benefits of mimicry.

Information transmission - Process by which information is passed along to another individual/individuals within a network.

Mimetic fidelity - How accurate a mimics signal is to the models.

Müllerian mimicry - Two or more species possess a similar warning signal and equally share the costs associated with educating the predator.

Salience - Being prominent of distinctly noticeable.

Sympatry - The occurrence of two related species (models and mimics) within the same geographical range.

Toxic burden - Amount of toxin within a living organism that is yet to be excreted or metabolized.

Appendix A

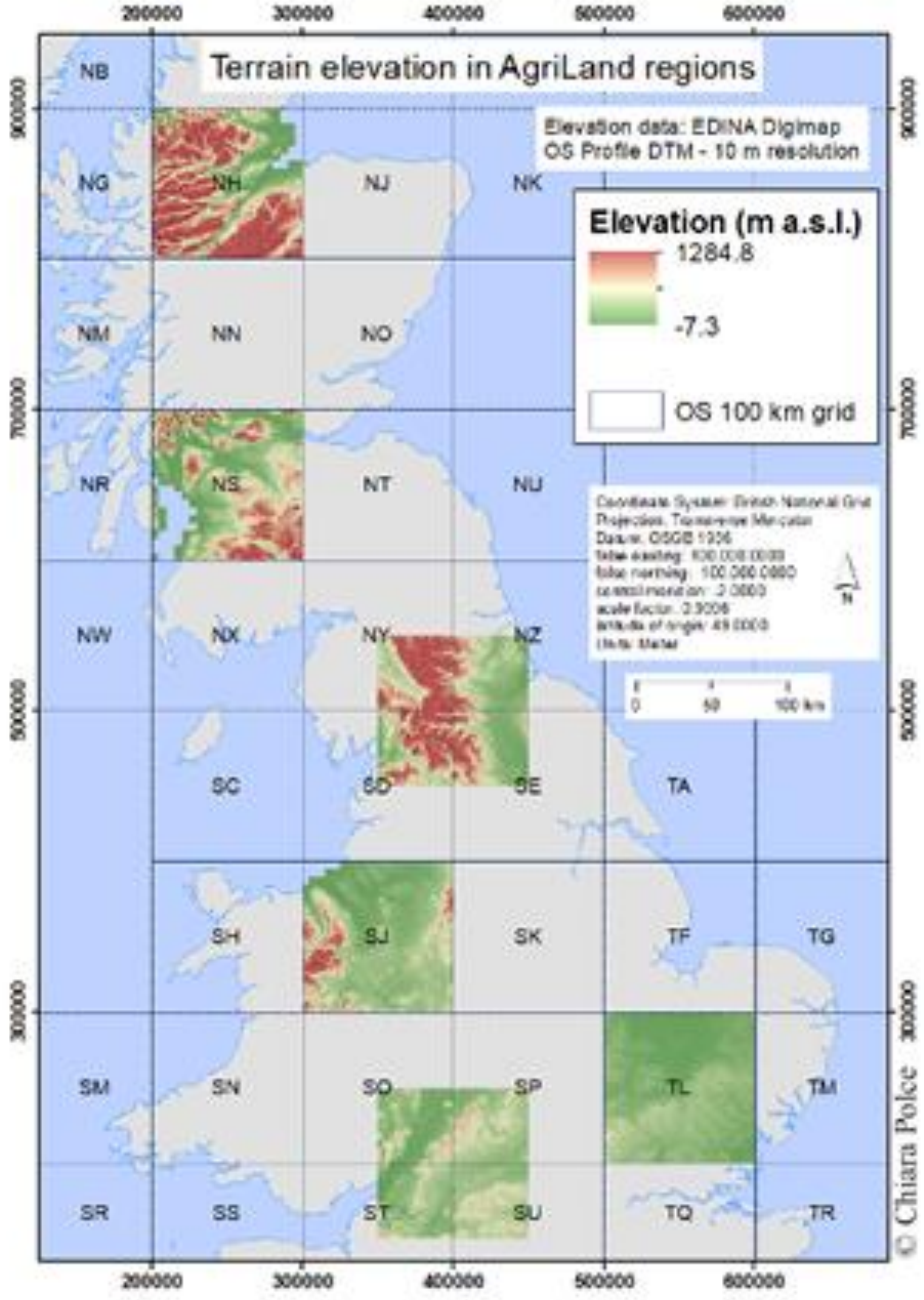


Figure A.1 Agriland map showing all regions used across the UK.

Table A.1 Abbreviations for species illustrated in network figures. Syrphidae (n=56) and Hymenoptera (n=42).

Hymenoptera		**Syrphidae**	
Epeolus cruciger	Ecr	*Epistrophe grossulariae*	Egr
Epeolus variegatus	Eva	*Sericomyia silentis*	Ssi
Vespula vulgaris	Vvu	*Portevinia maculata*	Pma
Vespula rufa	Vru	*Chrysotoxum cautum*	Cca
Colletes succinctus	Csu	*Anasimyia lineata*	Ali
Lasioglossum malachurum	Lma	*Ferdinandea cuprea*	Fcu
Dolichovespula sylvestris	Dsy	*Cheilosia illustrata*	Cil
Apis mellifera	Ame	*Dasysyrphus albostriatus*	Dal
Dolichovespula media	Dme	*Orthonevra nobilis*	Ono
Vespula germanica	Vge	*Chrysotoxum festivum*	Cfe
Andrena chrysosceles	Ach	*Lejogaster metallina*	Lme
Colletes daviesanus	Cda	*Melangyna lasiophthalma*	Mla
Vespa crabro	Vcr	*Chrysotoxum bicinctum*	Cbi
Nomada goodeniana	Ngo	*Volucella zonaria*	Vzo
Osmia spinulosa	Osp	*Eristalinus aeneus*	Eae
Megachile centuncularis	Mce	*Paragus haemorrhous*	Pha
Halictus rubicundus	Hru	*Eupeodes luniger*	Elu
Lasioglossum zonulum	Lzo	*Xanthogramma pedissequum*	Xpe
Lasioglossum leucozonium	Lle	*Scaeva pyrastri*	Spy
Andrena nitida	Ani	*Myathropa florea*	Mfl
Nomada flava	Nfl	*Eumerus funeralis*	Efu
Hylaeus hyalinatus	Hhy	*Chalcosyrphus nemorum*	Cne
Lasioglossum calceatum	Lca	*Pipiza austriaca*	Pau
Lasioglossum albipes	Lal	*Syrphus ribesii*	Sri
Osmia bicornis	Obi	*Parhelophilus versicolor*	Pve
Hylaeus communis	Hco	*Eristalis intricarius*	Ein

Anthophora bimaculata	Abi
Halictus tumulorum	Htu
Tachysphex pompiliformis	Tpo
Myrmosa atra	Mat
Lasioglossum morio	Lmo
Anthophora plumipes	Apl
Sphecodes gibbus	Sgi
Nomada fabriciana	Nfa
Bombus terrestris	Bte
Bombus hortorum	Bho
Bombus pascuorum	Bpa
Bombus pratorum	Bpr
Bombus lucorum	Blu
Astata boops	Abo
Bombus ruderarius	Bru
Bombus lapidarius	Bla

Volucella inanis	Vin
Leucozona lucorum	Llu
Cheilosia impressa	Cim
Parasyrphus punctulatus	Ppu
Rhingia campestris	Rca
Eristalis tenax	Ete
Meliscaeva auricollis	Mau
Riponnensia splendens	Rsp
Criorhina ranunculi	Cra
Eristalis pertinax	Epe
Arctophila superbiens	Asu
Helophilus pendulus	Hpe
Platycheirus rosarum	Pro
Dasysyrphus tricinctus	Dtr
Tropidia scita	Tsc
Volucella bombylans plumata	Vbp
Criorhina berberina	Cbe
Episyrphus balteatus	Eba
Platycheirus clypeatus	Pcl
Melanogaster hirtella	Mhi
Xylota sylvarum	Xsy
Platycheirus granditarsus	Pgr
Volucella pellucens	Vpe
Neoascia podagrica	Npo
Melanostoma mellinum	Mme
Syritta pipiens	Spi
Xylota segnis	Xse
Sphegina clunipes	Scl
Sphaerophoria scripta	Ssc

	Baccha elongata	Bel

Table A.2 Table illustrating model and mimic pairings based on the Agriland dataset. The type of model is listed alongside the corresponding mimic.

Type of model	**Hymenopteran model species**	**Syrphid mimic species**
Bumble bee model	*Bombus lapidarius*	*Criorhina ranunculi*
Bumble bee model	*Bombus lapidarius*	*Volucella bombylans*
Bumble bee model	*Bombus lucorum*	*Criorhina ranunculi*
Bumble bee model	*Bombus lucorum*	*Volucella bombylans*
Bumble bee model	*Bombus muscorum*	*Arctophila superbiens*
Bumble bee model	*Bombus muscorum*	*Criorhina floccosa*
Bumble bee model	*Bombus pascuorum*	*Arctophila superbiens*
Bumble bee model	*Bombus pascuorum*	*Criorhina berberina*
Bumble bee model	*Bombus pascuorum*	*Criorhina floccosa*
Bumble bee model	*Bombus pascuorum*	*Volucella bombylans*
Bumble bee model	*Bombus pratorum*	*Cheilosia illustrata*
Bumble bee model	*Bombus pratorum*	*Criorhina berberina*
Bumble bee model	*Bombus pratorum*	*Eristalis intricarius*
Bumble bee model	*Bombus ruderarius*	*Criorhina ranunculi*
Bumble bee model	*Bombus ruderarius*	*Volucella bombylans*
Bumble bee model	*Bombus terrestris*	*Criorhina berberina*
Bumble bee model	*Bombus terrestris*	*Criorhina ranunculi*
Bumble bee model	*Bombus terrestris*	*Eristalis intricarius*
Bumble bee model	*Bombus terrestris*	*Volucella bombylans*
Honeybee model	*Apis mellifera*	*Brachypalpus laphriformis*
Honeybee model	*Apis mellifera*	*Criorhina asilica*
Honeybee model	*Apis mellifera*	*Eristalis arbustorum*
Honeybee model	*Apis mellifera*	*Eristalis pertinax*

Honeybee model	*Apis mellifera*	*Eristalis rupium*
Honeybee model	*Apis mellifera*	*Eristalis tenax*
Social wasp model	*Crabro cribarius*	*Xanthogramma pedissequum*
Social wasp model	*Crossocerus quadrimaculatus*	*Melanostoma dubium*
Social wasp model	*Crossocerus quadrimaculatus*	*Melanostoma mellinum*
Social wasp model	*Crossocerus quadrimaculatus*	*Melanostoma scalare*
Social wasp model	*Crossocerus quadrimaculatus*	*Platycheirus albimanus*
Social wasp model	*Crossocerus quadrimaculatus*	*Platycheirus ambiguus*
Social wasp model	*Crossocerus quadrimaculatus*	*Platycheirus amplus*
Social wasp model	*Crossocerus quadrimaculatus*	*Platycheirus angustatus*
Social wasp model	*Crossocerus quadrimaculatus*	*Platycheirus aurolateralis*
Social wasp model	*Crossocerus quadrimaculatus*	*Platycheirus clypeatus*
Social wasp model	*Crossocerus quadrimaculatus*	*Platycheirus discimanus*
Social wasp model	*Crossocerus quadrimaculatus*	*Platycheirus europaeus*
Social wasp model	*Crossocerus quadrimaculatus*	*Platycheirus fulviventris*
Social wasp model	*Crossocerus quadrimaculatus*	*Platycheirus granditarsus*
Social wasp model	*Crossocerus quadrimaculatus*	*Platycheirus immarginatus*
Social wasp model	*Crossocerus quadrimaculatus*	*Platycheirus manicatus*
Social wasp model	*Crossocerus quadrimaculatus*	*Platycheirus melanopsis*
Social wasp model	*Crossocerus quadrimaculatus*	*Platycheirus nielseni*
Social wasp model	*Crossocerus quadrimaculatus*	*Platycheirus occultus*
Social wasp model	*Crossocerus quadrimaculatus*	*Platycheirus peltatus*
Social wasp model	*Crossocerus quadrimaculatus*	*Platycheirus perpallidus*
Social wasp model	*Crossocerus quadrimaculatus*	*Platycheirus podagratus*
Social wasp model	*Crossocerus quadrimaculatus*	*Platycheirus ramsarensis*
Social wasp model	*Crossocerus quadrimaculatus*	*Platycheirus rosarum*
Social wasp model	*Crossocerus quadrimaculatus*	*Platycheirus scambus*
Social wasp model	*Crossocerus quadrimaculatus*	*Platycheirus scutatus*
Social wasp model	*Crossocerus quadrimaculatus*	*Platycheirus splendidus*

Social wasp model	*Crossocerus quadrimaculatus*	*Platycheirus sticticus*
Social wasp model	*Crossocerus quadrimaculatus*	*Platycheirus tarsalis*
Social wasp model	*Dolichovespula media*	*Chrysotoxum arcuatum*
Social wasp model	*Dolichovespula media*	*Chrysotoxum cautum*
Social wasp model	*Dolichovespula media*	*Chrysotoxum elegans*
Social wasp model	*Dolichovespula media*	*Chrysotoxum octomaculatum*
Social wasp model	*Dolichovespula media*	*Chrysotoxum verralli*
Social wasp model	*Dolichovespula media*	*Helophilus groenlandicus*
Social wasp model	*Dolichovespula media*	*Helophilus hybridus*
Social wasp model	*Dolichovespula media*	*Helophilus pendulus*
Social wasp model	*Dolichovespula media*	*Helophilus trivittatus*
Social wasp model	*Dolichovespula media*	*Sericomyia silentis*
Social wasp model	*Dolichovespula media*	*Syrphus ribesii*
Social wasp model	*Dolichovespula media*	*Syrphus torvus*
Social wasp model	*Dolichovespula media*	*Syrphus vitripennis*
Social wasp model	*Dolichovespula norwegica*	*Chrysotoxum arcuatum*
Social wasp model	*Dolichovespula norwegica*	*Chrysotoxum cautum*
Social wasp model	*Dolichovespula norwegica*	*Chrysotoxum elegans*
Social wasp model	*Dolichovespula norwegica*	*Chrysotoxum octomaculatum*
Social wasp model	*Dolichovespula norwegica*	*Chrysotoxum verralli*
Social wasp model	*Dolichovespula norwegica*	*Helophilus groenlandicus*
Social wasp model	*Dolichovespula norwegica*	*Helophilus hybridus*
Social wasp model	*Dolichovespula norwegica*	*Helophilus pendulus*
Social wasp model	*Dolichovespula norwegica*	*Helophilus trivittatus*
Social wasp model	*Dolichovespula norwegica*	*Sericomyia silentis*
Social wasp model	*Dolichovespula norwegica*	*Syrphus ribesii*
Social wasp model	*Dolichovespula norwegica*	*Syrphus torvus*
Social wasp model	*Dolichovespula norwegica*	*Syrphus vitripennis*
Social wasp model	*Dolichovespula saxonica*	*Chrysotoxum arcuatum*

Social wasp model	*Dolichovespula saxonica*	*Chrysotoxum cautum*
Social wasp model	*Dolichovespula saxonica*	*Chrysotoxum elegans*
Social wasp model	*Dolichovespula saxonica*	*Chrysotoxum octomaculatum*
Social wasp model	*Dolichovespula saxonica*	*Chrysotoxum verralli*
Social wasp model	*Dolichovespula saxonica*	*Helophilus groenlandicus*
Social wasp model	*Dolichovespula saxonica*	*Helophilus hybridus*
Social wasp model	*Dolichovespula saxonica*	*Helophilus pendulus*
Social wasp model	*Dolichovespula saxonica*	*Helophilus trivittatus*
Social wasp model	*Dolichovespula saxonica*	*Sericomyia silentis*
Social wasp model	*Dolichovespula saxonica*	*Syrphus ribesii*
Social wasp model	*Dolichovespula saxonica*	*Syrphus torvus*
Social wasp model	*Dolichovespula saxonica*	*Syrphus vitripennis*
Social wasp model	*Dolichovespula sylvestris*	*Chrysotoxum arcuatum*
Social wasp model	*Dolichovespula sylvestris*	*Chrysotoxum cautum*
Social wasp model	*Dolichovespula sylvestris*	*Chrysotoxum elegans*
Social wasp model	*Dolichovespula sylvestris*	*Chrysotoxum octomaculatum*
Social wasp model	*Dolichovespula sylvestris*	*Chrysotoxum verralli*
Social wasp model	*Dolichovespula sylvestris*	*Helophilus groenlandicus*
Social wasp model	*Dolichovespula sylvestris*	*Helophilus hybridus*
Social wasp model	*Dolichovespula sylvestris*	*Helophilus pendulus*
Social wasp model	*Dolichovespula sylvestris*	*Helophilus trivittatus*
Social wasp model	*Dolichovespula sylvestris*	*Sericomyia silentis*
Social wasp model	*Dolichovespula sylvestris*	*Syrphus ribesii*
Social wasp model	*Dolichovespula sylvestris*	*Syrphus torvus*
Social wasp model	*Dolichovespula sylvestris*	*Syrphus vitripennis*
Social wasp model	*Ectemnius borealis*	*Xanthogramma citrofasciatum*
Social wasp model	*Ectemnius borealis*	*Xanthogramma pedissequum*

Social wasp model	*Ectemnius cavifrons*	*Xanthogramma citrofasciatum*
Social wasp model	*Ectemnius cavifrons*	*Xanthogramma pedissequum*
Social wasp model	*Ectemnius cephalotes*	*Xanthogramma citrofasciatum*
Social wasp model	*Ectemnius cephalotes*	*Xanthogramma pedissequum*
Social wasp model	*Ectemnius continuus*	*Xanthogramma citrofasciatum*
Social wasp model	*Ectemnius continuus*	*Xanthogramma pedissequum*
Social wasp model	*Ectemnius dives*	*Xanthogramma citrofasciatum*
Social wasp model	*Ectemnius dives*	*Xanthogramma pedissequum*
Social wasp model	*Ectemnius lapidarius*	*Xanthogramma citrofasciatum*
Social wasp model	*Ectemnius lapidarius*	*Xanthogramma pedissequum*
Social wasp model	*Ectemnius lituratus*	*Xanthogramma citrofasciatum*
Social wasp model	*Ectemnius lituratus*	*Xanthogramma pedissequum*
Social wasp model	*Ectemnius rubicola*	*Xanthogramma citrofasciatum*
Social wasp model	*Ectemnius rubicola*	*Xanthogramma pedissequum*
Social wasp model	*Ectemnius ruficornis*	*Xanthogramma citrofasciatum*
Social wasp model	*Ectemnius ruficornis*	*Xanthogramma pedissequum*
Social wasp model	*Ectemnius sexcinctus*	*Xanthogramma citrofasciatum*
Social wasp model	*Ectemnius sexcinctus*	*Xanthogramma pedissequum*
Social wasp model	*Trypoxylon attenuatum*	*Baccha elongata*
Social wasp model	*Trypoxylon attenuatum*	*Baccha obscuripennis*
Social wasp model	*Trypoxylon clavicerum*	*Baccha elongata*
Social wasp model	*Trypoxylon clavicerum*	*Baccha obscuripennis*

Social wasp model	*Vespula vulgaris*	*Chrysotoxum arcuatum*
Social wasp model	*Vespula vulgaris*	*Chrysotoxum cautum*
Social wasp model	*Vespula vulgaris*	*Epistrophe grossulariae*
Social wasp model	*Vespula vulgaris*	*Epistrophe nitidicollis*
Social wasp model	*Vespula vulgaris*	*Episyrphus balteatus*
Social wasp model	*Vespula vulgaris*	*Helophilus pendulus*
Social wasp model	*Vespula vulgaris*	*Parasyrphus annulatus*
Social wasp model	*Vespula vulgaris*	*Sericomyia silentis*
Social wasp model	*Vespula vulgaris*	*Syrphus ribesii*
Social wasp model	*Vespula vulgaris*	*Syrphus torvus*
Social wasp model	*Vespula vulgaris*	*Syrphus vitripennis*
Social wasp model	*Vespula austriaca*	*Chrysotoxum arcuatum*
Social wasp model	*Vespula austriaca*	*Chrysotoxum cautum*
Social wasp model	*Vespula austriaca*	*Chrysotoxum elegans*
Social wasp model	*Vespula austriaca*	*Chrysotoxum octomaculatum*
Social wasp model	*Vespula austriaca*	*Chrysotoxum verralli*
Social wasp model	*Vespula austriaca*	*Helophilus groenlandicus*
Social wasp model	*Vespula austriaca*	*Helophilus hybridus*
Social wasp model	*Vespula austriaca*	*Helophilus pendulus*
Social wasp model	*Vespula austriaca*	*Helophilus trivittatus*
Social wasp model	*Vespula austriaca*	*Sericomyia silentis*
Social wasp model	*Vespula austriaca*	*Syrphus ribesii*
Social wasp model	*Vespula austriaca*	*Syrphus torvus*
Social wasp model	*Vespula austriaca*	*Syrphus vitripennis*
Social wasp model	*Vespula germanica*	*Chrysotoxum arcuatum*
Social wasp model	*Vespula germanica*	*Chrysotoxum cautum*
Social wasp model	*Vespula germanica*	*Chrysotoxum elegans*
Social wasp model	*Vespula germanica*	*Chrysotoxum octomaculatum*
Social wasp model	*Vespula germanica*	*Chrysotoxum verralli*

Social wasp model	*Vespula germanica*	*Helophilus groenlandicus*
Social wasp model	*Vespula germanica*	*Helophilus hybridus*
Social wasp model	*Vespula germanica*	*Helophilus pendulus*
Social wasp model	*Vespula germanica*	*Helophilus trivittatus*
Social wasp model	*Vespula germanica*	*Sericomyia silentis*
Social wasp model	*Vespula germanica*	*Syrphus ribesii*
Social wasp model	*Vespula germanica*	*Syrphus torvus*
Social wasp model	*Vespula germanica*	*Syrphus vitripennis*
Social wasp model	*Vespula rufa*	*Chrysotoxum arcuatum*
Social wasp model	*Vespula rufa*	*Chrysotoxum cautum*
Social wasp model	*Vespula rufa*	*Chrysotoxum elegans*
Social wasp model	*Vespula rufa*	*Chrysotoxum octomaculatum*
Social wasp model	*Vespula rufa*	*Chrysotoxum verralli*
Social wasp model	*Vespula rufa*	*Helophilus groenlandicus*
Social wasp model	*Vespula rufa*	*Helophilus hybridus*
Social wasp model	*Vespula rufa*	*Helophilus pendulus*
Social wasp model	*Vespula rufa*	*Helophilus trivittatus*
Social wasp model	*Vespula rufa*	*Sericomyia silentis*
Social wasp model	*Vespula rufa*	*Syrphus ribesii*
Social wasp model	*Vespula rufa*	*Syrphus torvus*
Social wasp model	*Vespula rufa*	*Syrphus vitripennis*
Social wasp model	*Vespula vulgaris*	*Chrysotoxum elegans*
Social wasp model	*Vespula vulgaris*	*Chrysotoxum octomaculatum*
Social wasp model	*Vespula vulgaris*	*Chrysotoxum verralli*
Social wasp model	*Vespula vulgaris*	*Helophilus groenlandicus*
Social wasp model	*Vespula vulgaris*	*Helophilus hybridus*
Social wasp model	*Vespula vulgaris*	*Helophilus trivittatus*
Solitary bee model	*Andrena apicata*	*Cheilosia albipila*
Solitary bee model	*Andrena cineraria*	*Cheilosia illustrata*

Solitary bee model	*Andrena flavipes*	*Eristalis arbustorum*
Solitary bee model	*Anthidium manicatum*	*Chrysotoxum arcuatum*
Solitary bee model	*Anthidium manicatum*	*Chrysotoxum cautum*
Solitary bee model	*Anthidium manicatum*	*Chrysotoxum elegans*
Solitary bee model	*Anthidium manicatum*	*Chrysotoxum octomaculatum*
Solitary bee model	*Anthidium manicatum*	*Chrysotoxum verralli*
Solitary bee model	*Anthophora bimaculata*	*Callicera aenea*
Solitary bee model	*Anthophora bimaculata*	*Callicera rufa*
Solitary bee model	*Anthophora bimaculata*	*Callicera spinolae*
Solitary bee model	*Anthophora furcata*	*Callicera aenea*
Solitary bee model	*Anthophora furcata*	*Callicera rufa*
Solitary bee model	*Anthophora furcata*	*Callicera spinolae*
Solitary bee model	*Anthophora plumipes*	*Callicera aenea*
Solitary bee model	*Anthophora plumipes*	*Callicera rufa*
Solitary bee model	*Anthophora plumipes*	*Callicera spinolae*
Solitary bee model	*Anthophora quadrimaculata*	*Callicera aenea*
Solitary bee model	*Anthophora quadrimaculata*	*Callicera rufa*
Solitary bee model	*Anthophora quadrimaculata*	*Callicera spinolae*
Solitary bee model	*Anthophora retusa*	*Callicera aenea*
Solitary bee model	*Anthophora retusa*	*Callicera rufa*
Solitary bee model	*Anthophora retusa*	*Callicera spinolae*
Solitary bee model	*Colletes cunicularius*	*Brachypalpus laphriformis*
Solitary bee model	*Colletes daviesanus*	*Brachypalpus laphriformis*
Solitary bee model	*Colletes floralis*	*Brachypalpus laphriformis*
Solitary bee model	*Colletes fodiens*	*Brachypalpus laphriformis*
Solitary bee model	*Colletes halophilus*	*Brachypalpus laphriformis*
Solitary bee model	*Colletes hederae*	*Brachypalpus laphriformis*
Solitary bee model	*Colletes marginatus*	*Brachypalpus laphriformis*
Solitary bee model	*Colletes similis*	*Brachypalpus laphriformis*

Solitary bee model	*Colletes succinctus*	*Brachypalpus laphriformis*
Solitary bee model	*Eucera longicornis*	*Callicera aenea*
Solitary bee model	*Eucera longicornis*	*Callicera rufa*
Solitary bee model	*Eucera longicornis*	*Callicera spinolae*
Solitary bee model	*Lasioglossum albipes*	*Cheilosia fraterna*
Solitary bee model	*Lasioglossum albipes*	*Cheilosia impressa*
Solitary bee model	*Lasioglossum albipes*	*Cheilosia mutabilis*
Solitary bee model	*Lasioglossum albipes*	*Cheilosia nebulosa*
Solitary bee model	*Lasioglossum albipes*	*Cheilosia pagana*
Solitary bee model	*Lasioglossum albipes*	*Cheilosia scutella*
Solitary bee model	*Lasioglossum albipes*	*Cheilosia vernalis*
Solitary bee model	*Lasioglossum albipes*	*Orthonevra splendens*
Solitary bee model	*Lasioglossum fratellum*	*Cheilosia fraterna*
Solitary bee model	*Lasioglossum fratellum*	*Cheilosia impressa*
Solitary bee model	*Lasioglossum fratellum*	*Cheilosia mutabilis*
Solitary bee model	*Lasioglossum fratellum*	*Cheilosia nebulosa*
Solitary bee model	*Lasioglossum fratellum*	*Cheilosia pagana*
Solitary bee model	*Lasioglossum fratellum*	*Cheilosia scutella*
Solitary bee model	*Lasioglossum fratellum*	*Cheilosia vernalis*
Solitary bee model	*Lasioglossum fratellum*	*Orthonevra splendens*
Solitary bee model	*Nomada fulvicornis*	*Xanthogramma citrofasciatum*
Solitary bee model	*Nomada goodeniana*	*Xanthogramma citrofasciatum*
Solitary bee model	*Nomada marshamella*	*Xanthogramma citrofasciatum*
Solitary bee model	*Nomada argentata*	*Episyrphus balteatus*
Solitary bee model	*Nomada argentata*	*Xanthogramma pedissequum*
Solitary bee model	*Nomada armata*	*Episyrphus balteatus*

Solitary bee model	*Nomada armata*	*Xanthogramma pedissequum*
Solitary bee model	*Nomada baccata*	*Episyrphus balteatus*
Solitary bee model	*Nomada baccata*	*Xanthogramma pedissequum*
Solitary bee model	*Nomada conjungens*	*Episyrphus balteatus*
Solitary bee model	*Nomada conjungens*	*Xanthogramma pedissequum*
Solitary bee model	*Nomada errans*	*Episyrphus balteatus*
Solitary bee model	*Nomada errans*	*Xanthogramma pedissequum*
Solitary bee model	*Nomada fabriciana*	*Episyrphus balteatus*
Solitary bee model	*Nomada fabriciana*	*Xanthogramma pedissequum*
Solitary bee model	*Nomada ferruginata*	*Episyrphus balteatus*
Solitary bee model	*Nomada ferruginata*	*Xanthogramma pedissequum*
Solitary bee model	*Nomada flava*	*Episyrphus balteatus*
Solitary bee model	*Nomada flava*	*Xanthogramma pedissequum*
Solitary bee model	*Nomada flavoguttata*	*Episyrphus balteatus*
Solitary bee model	*Nomada flavoguttata*	*Xanthogramma pedissequum*
Solitary bee model	*Nomada flavopicta*	*Episyrphus balteatus*
Solitary bee model	*Nomada flavopicta*	*Xanthogramma pedissequum*
Solitary bee model	*Nomada fucata*	*Episyrphus balteatus*
Solitary bee model	*Nomada fucata*	*Xanthogramma pedissequum*
Solitary bee model	*Nomada fulvicornis*	*Episyrphus balteatus*
Solitary bee model	*Nomada fulvicornis*	*Xanthogramma pedissequum*
Solitary bee model	*Nomada goodeniana*	*Episyrphus balteatus*
Solitary bee model	*Nomada goodeniana*	*Xanthogramma pedissequum*
Solitary bee model	*Nomada guttulata*	*Episyrphus balteatus*
Solitary bee model	*Nomada guttulata*	*Xanthogramma pedissequum*
Solitary bee model	*Nomada hirtipes*	*Episyrphus balteatus*
Solitary bee model	*Nomada hirtipes*	*Xanthogramma pedissequum*
Solitary bee model	*Nomada integra*	*Episyrphus balteatus*
Solitary bee model	*Nomada integra*	*Xanthogramma pedissequum*

Solitary bee model	*Nomada lathburiana*	*Episyrphus balteatus*
Solitary bee model	*Nomada lathburiana*	*Xanthogramma pedissequum*
Solitary bee model	*Nomada leucophthalma*	*Episyrphus balteatus*
Solitary bee model	*Nomada leucophthalma*	*Xanthogramma pedissequum*
Solitary bee model	*Nomada marshamella*	*Episyrphus balteatus*
Solitary bee model	*Nomada marshamella*	*Xanthogramma pedissequum*
Solitary bee model	*Nomada obtusifrons*	*Episyrphus balteatus*
Solitary bee model	*Nomada obtusifrons*	*Xanthogramma pedissequum*
Solitary bee model	*Nomada panzeri*	*Episyrphus balteatus*
Solitary bee model	*Nomada panzeri*	*Xanthogramma pedissequum*
Solitary bee model	*Nomada roberjeotiana*	*Episyrphus balteatus*
Solitary bee model	*Nomada roberjeotiana*	*Xanthogramma pedissequum*
Solitary bee model	*Nomada ruficornis*	*Episyrphus balteatus*
Solitary bee model	*Nomada ruficornis*	*Xanthogramma pedissequum*
Solitary bee model	*Nomada rufipes*	*Episyrphus balteatus*
Solitary bee model	*Nomada rufipes*	*Xanthogramma pedissequum*
Solitary bee model	*Nomada sexfasciata*	*Episyrphus balteatus*
Solitary bee model	*Nomada sexfasciata*	*Xanthogramma pedissequum*
Solitary bee model	*Nomada sheppardana*	*Episyrphus balteatus*
Solitary bee model	*Nomada sheppardana*	*Xanthogramma pedissequum*
Solitary bee model	*Nomada signata*	*Episyrphus balteatus*
Solitary bee model	*Nomada signata*	*Xanthogramma pedissequum*
Solitary bee model	*Nomada striata*	*Episyrphus balteatus*
Solitary bee model	*Nomada striata*	*Xanthogramma pedissequum*
Solitary bee model	*Nomada succincta*	*Episyrphus balteatus*
Solitary bee model	*Nomada succincta*	*Xanthogramma pedissequum*
Solitary bee model	*Osmia aurulenta*	*Callicera aenea*
Solitary bee model	*Osmia aurulenta*	*Callicera rufa*
Solitary bee model	*Osmia aurulenta*	*Callicera spinolae*

Solitary bee model	*Osmia bicolor*	*Callicera aenea*
Solitary bee model	*Osmia bicolor*	*Callicera rufa*
Solitary bee model	*Osmia bicolor*	*Callicera spinolae*
Solitary bee model	*Osmia caerulescens*	*Callicera aenea*
Solitary bee model	*Osmia caerulescens*	*Callicera rufa*
Solitary bee model	*Osmia caerulescens*	*Callicera spinolae*
Solitary bee model	*Osmia inermis*	*Callicera aenea*
Solitary bee model	*Osmia inermis*	*Callicera rufa*
Solitary bee model	*Osmia inermis*	*Callicera spinolae*
Solitary bee model	*Osmia leaiana*	*Callicera aenea*
Solitary bee model	*Osmia leaiana*	*Callicera rufa*
Solitary bee model	*Osmia leaiana*	*Callicera spinolae*
Solitary bee model	*Osmia niveata*	*Callicera aenea*
Solitary bee model	*Osmia niveata*	*Callicera rufa*
Solitary bee model	*Osmia niveata*	*Callicera spinolae*
Solitary bee model	*Osmia parietina*	*Callicera aenea*
Solitary bee model	*Osmia parietina*	*Callicera rufa*
Solitary bee model	*Osmia parietina*	*Callicera spinolae*
Solitary bee model	*Osmia pilicornis*	*Callicera aenea*
Solitary bee model	*Osmia pilicornis*	*Callicera rufa*
Solitary bee model	*Osmia pilicornis*	*Callicera spinolae*
Solitary bee model	*Osmia rufa*	*Callicera aenea*
Solitary bee model	*Osmia rufa*	*Callicera rufa*
Solitary bee model	*Osmia rufa*	*Callicera spinolae*
Solitary bee model	*Osmia uncinata*	*Callicera aenea*
Solitary bee model	*Osmia uncinata*	*Callicera rufa*
Solitary bee model	*Osmia uncinata*	*Callicera spinolae*
Solitary bee model	*Osmia xanthomelana*	*Callicera aenea*
Solitary bee model	*Osmia xanthomelana*	*Callicera rufa*

Solitary bee model	*Osmia xanthomelana*	*Callicera spinolae*
Solitary bee model	*Stelis punctulatissima*	*Eristalis arbustorum*

Appendix B

Table B.1 Breakdown of the corresponding pots used in the mimicry experiment, highlighting the species and phenotypes they represented.

Species	Phenotype	Reward or no reward
Model	Opaque plastic pot with yellow colouration and black stripes.	Contained no millet seed representing non-rewarding model
Control	Standard plastic pot	Possessed millet seed to act as alternate prey
Mimic	Standard plastic pot with yellow colouration (intermediate phenotype)	Contained millet seed to act as a rewarding mimic

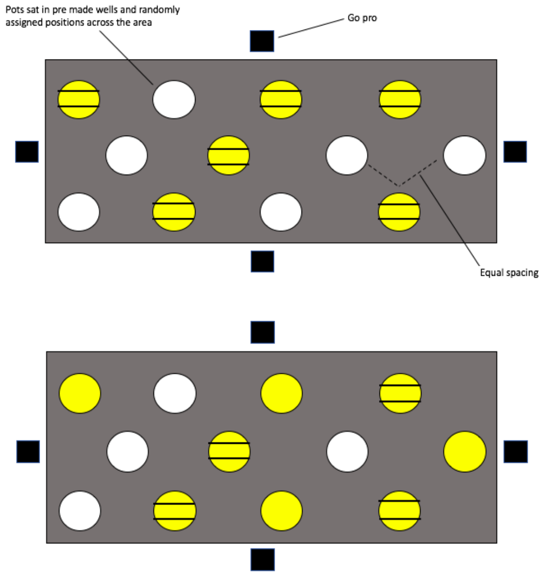


Figure B.1 A birds eye view of both stages of the mimicry task. The initial stage (top) and the latter stage (bottom). The pots were randomly distributed across the wells and exhibited multiple polymorphisms. The black squares represent the position of the go pros throughout the tasks.

Table B.2 Table illustrating mimic solves across the captive bird population. Bird ID corresponds to the individuals coloured ring, alongside the solve number which highlights the order in which each bird solved the trial.

Solve Number	**Bird Id**	**Matrix Number**	**Time (Seconds)**	**Order**
1	FblR	30	1500	1
4	WrL	24	17820	2
5	CrL	51	23520	3
6	PdgR	18	23580	4
7	NgR	11	24300	5
9	FwR	40	32160	6
10	CblL	46	36420	7
11	FpkRL	37	38940	8
12	CoL	48	40560	9
13	WrR	25	44280	10
16	FplL	38	50760	11
18	WwL	26	58620	12
21	NctoL	12	69480	13
22	PplR	19	71820	14
23	NtkdbL	8	70560	15