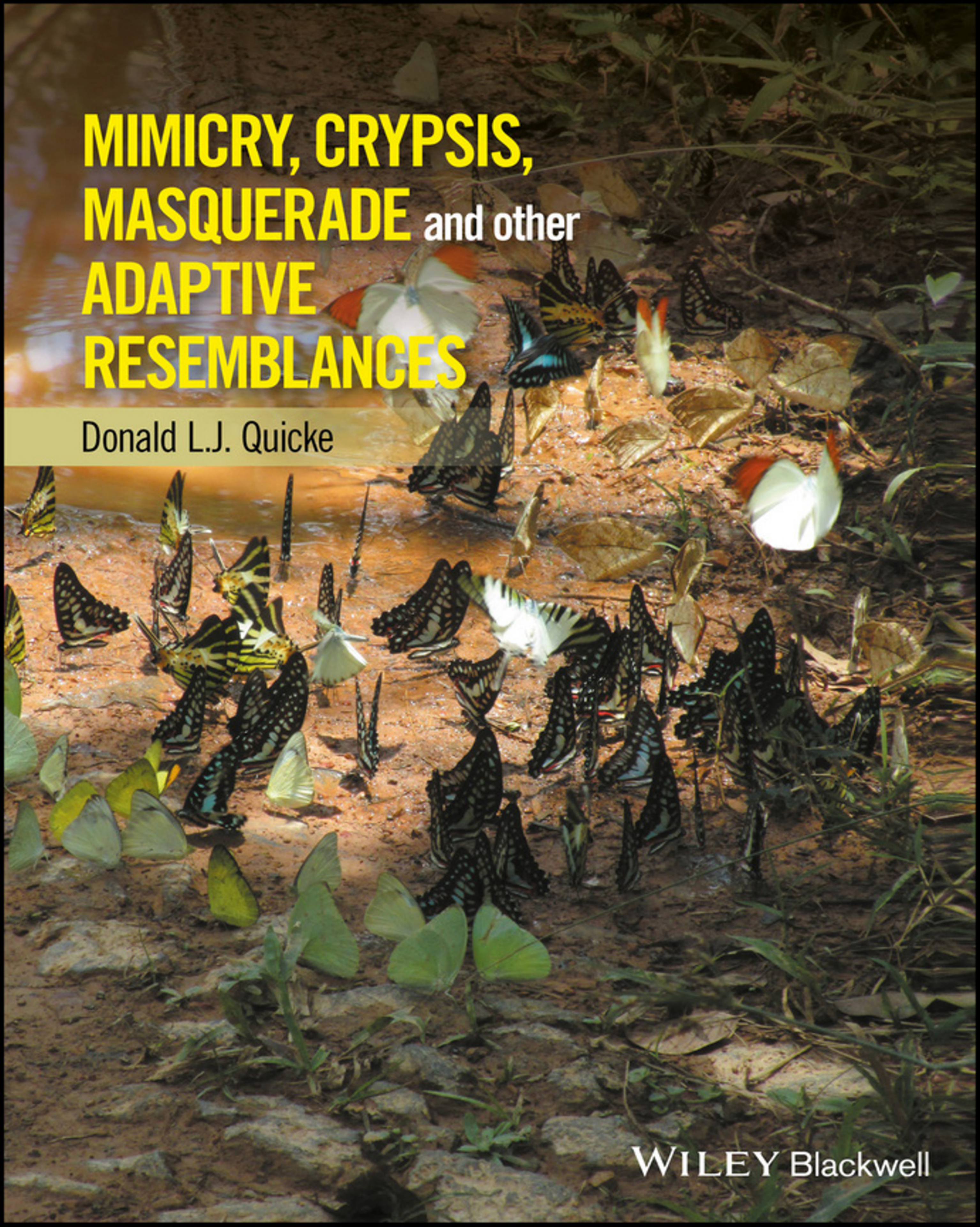

# MIMICRY, CRYPSIS, MASQUERADE and other ADAPTIVE RESEMBLANCES

Donald L.J. Quicke

WILEY Blackwell

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*For all the dogs who live on streets everywhere with no-one to love them,*
*and to those wonderful organisations such as Soi Dog Foundation in Thailand,*
*that work hard to care for them.*

*This is wonderful Puii. She lives at Saphan Taksin Pier.*

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# PREFACE

*The ever expanding field of mimicry requires a clear, but very elastic, definition which avoids hair splitting but allows for the constant stream of new examples and concepts.*

Miriam Rothschild 1981

This book started almost 40 years ago with discussions with my old friend and fellow undergraduate Peter Kirby at Oxford University and subsequently in Derby and Nottingham, to whom I am greatly indebted for many a valuable discussion and pint of beer. Since then it has expanded due to discussions with many people. As things do, plans got shelved and occasionally revisited, and shelved again. This whole period has seen a remarkable increase in interest in various forms of mimicry and adaptive resemblance with a huge body of more experimental work in addition to theory supplementing the already vast number of casual and sometimes insightful descriptions of mimicry systems around the world.

Ever since Henry Bates (1825–92), an English naturalist working in tropical South America from 1848[1] to 1859, realised that some butterflies were not what they might at first appear to be, and interpreted this as being due to palatable species looking like unpalatable models (Bates 1862, 1864), mimetic phenomena have fascinated professional and amateur biologists alike, including Charles Darwin, whose theory of evolution had been part of Bates' inspiration (Moon 1976, Stearn 1981). As time passed the literature on the topic grew as more and more examples were described and as Holling (1963) said, "A small mountain of information about mimicry has been collected since Bates".

Unfortunately though, after a while this fascination became been tinged with rather negative views among some academic biologists who for some while tended to dismiss it as a quaint set of observations that are easily explained and not worth dwelling over in any great detail – though it was still used for its 'wow factor' in undergraduate lectures. Vane-Wright (1981) also lists some of the negative or simply dismissive views that were put forward, especially soon after Bates' publication, including that the resemblances described were just coincidental and therefore pointless to investigate. However, some researchers continued to investigate mimicry both theoretically and experimentally and, with clearer thought emerging about the detailed processes involved, mimicry (and camouflage) have had a resurgence of scientific interest with the result that many new examples have come to light in recent years and many new insights are continuing to emerge. Large-scale studies are becoming increasingly common; molecular techniques are allowing the evolution of mimicries and other adaptive resemblances to be viewed from a phylogenetic perspective; and increasingly sophisticated use of computer games allows testing of theories that are relatively new to the scene. Lichter-Marck et al.'s (2014) 4-year study of caterpillar predation in a temperate project is a nice example that combines all of these aspects and enabled comparison of the effectiveness of warning and camouflage strategies.

This book sets out to survey mimicry and camouflage (and the related topic of how aposematism evolved in the first place) and to place these in the context of results of the growing numbers of experimental tests that have been conducted. It further seeks to explain key and relevant models and experimental set-ups in a way intelligible to everyone and not just scientists. All of this draws on a wide range of examples from animals, plants, fungi and even protists, covering different modalities such as behaviour, colouration, bioluminescence, structure, chemistry and sound. Most examples are of the whole organism type but mimicry is also relevant to the success of various disease agents, so bacteria are also included. It also covers adaptive resemblances which have evolved for protection from predation or herbivory, to obtain prey (aggressive mimicries), to obtain

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[1] Initially he was accompanied by his friend Alfred Russel Wallace, but Wallace returned to England in 1852 and sadly his collection was lost at sea.

matings or, more precisely, fertilisations (sexual mimicry), to disperse seeds or spores, to avoid aggression from conspecifics and to protect from host immune systems, some of which lead to unfortunate autoimmunity consequences.

I have tried to combine as much interesting biology related to the topic as reasonable, and also to explain how mathematical models of various degrees of sophistication give new insights into how mimicry systems work and why warning signals and mimicry evolve under some circumstances and not others. I also touch on aspects such as the genetics underlying wing pattern polymorphisms in various insects, notably in the genus *Heliconius* and the sex-limited cases among swallowtails, which should at least give an inroad into the relevant booming genomics literature. Where enough data exist I have tried to separate out the more mathematical parts from descriptions of the mimetic systems themselves and also to some extent I have separated out some of the basic experimental tests of mimetic advantage when there are enough of them to make a separate coherent section. It is one thing to think that a harmless dronefly has evolved to resemble and mimic a stinging honey bee because of the potential protection that would afford it, but quite another to actually demonstrate that this is what has happened. Indeed, one could ask, why haven't honey bees evolved to look like wasps, or vice versa? Well, in some ways they do resemble one another, and as nearly all entomologists can vouch, a large number of non-biologists do confuse them. Indeed, in many languages there is no separate word for them – maybe they are just some sort of stinging insect or, maybe, Hymenoptera-like insect. And yet honey bees, despite many an illustration in children's books, are not normally boldly banded black and yellow; they may have orangey bands, but they are hardly highly conspicuous (see Fig. 7.24a). Not surprisingly, humans are also quite bad at distinguishing harmless hoverfly mimics from potentially stinging bees and wasps (Golding et al. 2005a). The fact that humans often do not distinguish wasps from bees does not mean that many insectivores do not, and indeed, the amazing similarities between some models and their mimics is testament to the amazing discriminatory powers of predators that have shaped and coloured them over evolutionary time. Wickler (1968), with rather fewer examples and far less experimental evidence, gives some lovely descriptions of many cases discussed here. His book was also beautifully and inspiringly illustrated so, although I have tried to obtain photographs to illustrate most systems, his work provides lots of informative pictures that I have cited where I could not find better.

For the vast majority of supposed cases of mimicry there have been no experimental tests, and for quite a few there is very little by way of field observations, perhaps just assumptions based upon museum specimens. Thus, I rather think that Vane-Wright's (1971) note with regard to his discussion of mimicry: "In this discussion such words as 'possibly', 'perhaps', 'presumably' are frequently omitted for convenience, where strictly they ought to be employed" could be applied to many examples herein. Certainly some suggested instances of mimicry could be considered as verging on the fanciful and some have been subsequently disproven. However, there is probably truth in the vast majority of cases. Applications of more modern techniques, such as visual modelling of potential predators, sometimes reveal things that human eyes miss, and may provide clearer explanation. As Grim (2013) points out, actually demonstrating that some feature has evolved due to mimicry is extremely difficult and proof positive can only be achieved by manipulatory experiments. Sometimes what human observers perceive as close resemblance may simply reflect our own limitations in discriminatory ability, and not necessarily those of the organisms involved. Nevertheless, although some suspected instances have turned out not to involve mimicry, I feel that the vast majority of described cases will be verified in due course. Further, as numbers of system types are subjected to experimental studies we might be justified in allowing some degree of inclusivity in terms of individual examples studied – after all, it is unrealistic to test experimentally, say, all cases of, for example, snakes using tails to lure prey – if it is found proven in a few species it seems likely that it will be true also of at least the majority of other species.

Where possible, I have included photographs to illustrate the main types of resemblances and adaptations that are discussed, though sadly space does not permit everything. In discussing individual examples, it also soon becomes clear that many adaptive resemblances serve dual functions (e.g. Gomez & Thery 2007). A bright yellow and black wasp once in the hand, so to speak, is clearly aposematic, but from a distance against a dry, yellow African savanna it may be hard to spot; similarly, bright red wasps against red lateritised tropical soils. The similarity of a flower mantis to a flower or cluster of flowers is both a device that helps it to avoid being detected by, and probably also positively attracts, the butterflies and bees upon which it feeds, but it also conceals it from avian or other predators; thus it is both a protective and an aggressive mimicry and it seems impossible to know which came first. Particularly convoluted is the case of 'cuckoos' and their hosts. Their eggs are typically very similar to those of the host bird, and that mimetic resemblance is determined by the mother cuckoo's genes, but once the cuckoo chick has hatched the young bird's gape, mimicking that of the host-bird's chick, is controlled by the chick's genes, as are the calls made by the cuckoo chick. But it doesn't stop there because in some species the adult birds may mimic their hosts' calls to distract them away from their nests or mimic prey with the same result and as an even more complicated twist in the case of some widow-birds, which also behave like cuckoos, the females will only mate if their male partner mimics the call of their brood host species. Given such complexity, I largely gave up in the case of cuckoos and discuss their various mimetic adaptations all together, despite their mimicries having multiple functions and involving different individuals, models and genes.

## A comment on statistics

This book is meant to be of interest to both academic readers and lay people with an interest in natural history, mimicry, evolution, etc. Thus where I have presented equations I have tried to explain them, and I have also tried to explain the numerous graphs so that they are as comprehensible and interesting as possible. However, it must be understood that in the real world there is variation and 'noise' in the data that scientists collect in order to test hypotheses. Researchers therefore need to appraise their results against some 'yardstick' – a measure of whether their particular findings are probably important or whether some observed trend might most likely just be due to chance. To make such assessments, researchers use a wide range of statistical tests which are essentially aimed at asking one (theoretically) simple question – how likely is it that the trend that has been observed is due to chance alone?

Just because, say, a bird in a study eats more red seeds than green ones when presented with equal numbers of each, it does not necessarily mean that this is a real effect. To assess whether the result reflects a true feature of that bird's behaviour rather than just being due to chance, scientists estimate, as accurately as possible, what the probability of obtaining that particular result purely by chance would have been. Then, completely arbitrarily but almost universally accepted in biology, a result is deemed statistically significant if the chance of it having been found due just to noise in the system is less than one in 20. In other words, a result is deemed significant if it was likely to occur in less than 5% of observations/tests if there was no actual effect or interaction between the variables. In that case, the probability is expressed as a '*p*-value' and it is written as '$p < 0.05$', i.e. less than 5%.

If the effect is strong, one might distinguish a *p*-value of <0.01 (one in a hundred) or <0.001 (one in a thousand). Of course, it does not necessarily mean that there is a real effect, perhaps a real causal relationship between observed measures, because if you do 20 experiments where you know that there cannot be any effect, on average one in 20 will generate results that have a *p*-value of about one in 20. Finding the same effect in multiple *independent* experiments adds to the experimenter's confidence that they are dealing with a real phenomenon.

Many different tests are used by researchers depending upon the nature of the data, and the maths behind them can be quite complicated. One hopes that scientists have used appropriate tests and that referees during the peer-review process will have spotted any potential errors and had them corrected.

Let us go back to the bird and its choice of a particular number of red or green seeds. Even if the result seems extreme, say the bird eats nine green and only one red seed, when the null expectation given even numbers of each type were presented to start with, would be five red and five green, we want to know whether the 9:1 result can be considered a significant departure from random. If that result would be very unlikely to occur by chance alone, it might indicate a significant food colour bias by the bird. The appropriate statistical test in such a case would be the chi-square ($\chi^2$) test and in this case it is significant: $\chi^2 = 6.4$, d.f. = 1, $p = 0.01141$, i.e. the chance of the bird picking nine out of ten of all the same colour purely by chance if it had no particular bias is one in 1/0.01141 or one in 87.6. A result of eight of one type and just two of the other is not significant (N.S.) at the 0.05 level ($\chi^2 = 3.6$, d.f. = 1, $p = 0.05778$). You can get a feel for this by thinking about tossing coins. If you toss ten coins, how likely is it that you will have nine or more out of ten heads, or nine or more out of ten tails? This sample size is small, but if you were gambling and there was a highly significant departure from 50:50 in the coin tosses, one might start to think that there was some skulduggery going on. Larger sample sizes provide better tests of the data.

The other thing that you will see in most of the results of statistical tests is something called 'degrees of freedom' or d.f. for short. This value is the number of values that went into the calculation of the statistic that are free to vary without *necessarily* changing the final statistic, and this is generally the number of classes or observations minus one, but for some tests there can be more than one degree of freedom. For example, if there are ten numerical observations recorded then you can vary nine of them, and still obtain the same value of the test statistic by adjusting the 10th value, hence nine degrees of freedom.

The final important aspect to understand some of the experiments and results presented is independent. If the experimenter had got the N.S. 8:2 result the first time and then the next day ran the test again ran and got, say, 7:3 in the same direction, well then the total (15:5) is now significantly different from an even expectation ($p = 0.00254$), and may indeed reflect a true bias against eating red seeds. However, if the same individual bird were used, all it tells you is that one bird probably has a preference for green over red seeds. It does not necessarily mean that all members of its species have such a preference, nor that all birds do.

While mammalian and human physiologists have their laboratory rats (preferred, easy to work with, experimental animals, often rats but sometimes mice, cats, dogs, monkeys, etc., whatever is appropriate for a particular study) so too have experimenters on mimicry, and birds in particular. American blue jays, European blue tits and great tits have been the source of a very large proportion of the results referred to here. The hope, of course, is that the decisions they make are representative of those that many insectivorous birds would make, and while that might be true, there are bound to be exceptions.

For those wishing to get to grips with statistical analysis of data or making nice graphical outputs, I highly recommend Mick Crawley's 'R book' (Crawley 2007).

## A comment on scientific names

Every formally named species is given a unique scientific name that comprises two parts, a species name and a genus name. A genus is a group of one or more species that taxonomists recognise as probably being a monophyletic unit, i.e. they have a single common ancestor and all the known descendants are included in the same genus. Genus and species names are distinguished from the rest of a text by being set differently, usually in italics. Genus names always start with a capital letter; specific names never do. No two different groups of animals are allowed to share the same generic name, and the same applies to plants, although the same species name may be used for different species so long as they are in different genera.

The taxonomic level of animal names between subtribe and superfamily is indicated by the suffix. Thus in increasing hierarchical order: -ina = subtribe, -ini = tribe, -inae = subfamily, -idae = family and -oidea = superfamily. For plants and fungi, family names end in -aceae. Animal names up to superfamily level are typified by a type genus, but above superfamily, such as order, class and phylum, the names are not standardised. In plants algae and fungi, all levels are typified, and phyla are traditionally called divisions. Fungal phylum names bear the suffix -mycota, and plant and algal phyla names have the suffix -phyta.

When higher group names are used as nouns they start with a capital letter, but when they are used as adjectives they do not (unless at the beginning of a sentence).

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All graphs were produced using the statistical computing language R (R Development Core Team 2009). Image manipulations were carried out using GIMP (© 2001–2015 The GIMP Team).

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## Chapter 1

# INTRODUCTION AND CLASSIFICATION OF MIMICRY SYSTEMS

*It is hardly an exaggeration to say, that whilst reading and reflecting on the various facts given in this Memoir, we feel to be as near witnesses, as we can ever hope to be, of the creation of a new species on this earth.*

Charles Darwin (1863) referring to Henry Bates' 1862
account of mimicry in Brazil

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## A BRIEF HISTORY

The first clear definition of biological mimicry was that of Henry Walter Bates (1825–92), a British naturalist who spent some 11 years collecting and researching in the Amazonas region of Brazil (Bates 1862, 1864, 1981, G. Woodcock 1969). However, as pointed out by Stearn (1981), Bates' concept of the evolution of mimicry would quite possibly have gone unnoticed were it not for Darwin's review of his book in *The Natural History Review* of 1863. Bates' observations of remarkable similarity between butterflies belonging to different families led him to ponder what might be the reason for this. He concluded that there must be some advantage, for example, for a 'white butterfly', *Dismorphia theucharila* (Pieridae), to depart from the typical form and colouration of the family, and instead to resemble unpalatable *Heliconius* species.[1] He also noticed that in all the bright and conspicuous butterfly colour pattern complexes there was at least one species that was distasteful to predators of butterflies (Sheppard 1959). Bates was also ahead of his time in his estimation of the huge and largely undescribed diversity of the Neotropical insect fauna. During his time in Amazonia he estimated that he had collected some 14,712 species, of which approximately 8000 were new, a number that seemed utterly implausible to most entomologists working in the UK at that time (Stearn 1981).

Some groups of insects seem to have an enormous propensity for evolving mimicry, and within apparently closely related groups can have evolved to resemble models of a wide range of colour patterns, shapes and sizes, such as, for example, the day-flying, chalcosiine zygaenid moths, which are no doubt mostly or entirely Müllerian mimics (Yen et al. 2005), or the day-flying Epicipeiidae moths which, with only 20 or so species, collectively mimic various papillionid, pierid, geometrid, zygaenid and lymantriid butterfly and moth models. No wonder this astonishing potential for variation has fascinated entomologists for years.

A lot of early research involved the collection and publication of field observations and relatively simple experiments, such as feeding various insects to predators and observing reactions (fine examples include G.A.K. Marshall & Poulton 1902, Swynnerton 1915b, R.T. Young 1916, Carpenter 1942). A rather lovely, if quaint, example is that of G.D.H. Carpenter (1921), a medical doctor by profession who was based in Uganda for some time before becoming Hope Professor of Zoology (Entomology) at Oxford University. He describes the results of extensive experiments in which insects were presented to a captive monkey and its responses observed. The article is over 100 pages long and in the foreword he notes that a lot of the observations are tabulated rather than given *seriatim* because of the "great increase in the cost of printing". Nevertheless, such observations are essential first steps in understanding whether species are models or mimics or have unsuspected defences.

Around the middle of the nineteenth century, another Englishman, Alfred Russel Wallace (1823–1913), an intrepid traveller, natural historian and thinker, was coming up with important notions concerned with mimicry and aposematism (Wallace 1867). He had earlier travelled to Brazil and collected with Henry Bates and later went on to explore South-East Asia. Indeed, he came up with the idea of evolution by natural selection more or less contemporaneously with Charles Darwin, though unlike Darwin he had little formal education (H.W. Greene & McDiarmid 2005). His early appreciation of the nature of aposematism and thoughts on poisonous snake mimicry are particularly pertinent here.

Mimicry and adaptive colouration have long been popular topics that have grabbed the imagination of both the public and academic biologists due to the incredible detail in many resemblances. Good early treatments include those of Poulton (1890), G.D.H. Carpenter & Ford (1933) and Cott (1940), all of which document numerous natural history observations and interesting ideas. Wolfgang Wickler's (1968) popular book on mimicry in plants and animals with many fine illustrations by H. Kacher no doubt fired many people (including myself) with enthusiasm for the topic. Komárek (2003) provides an excellent and more biographic description of the arguments, ideas and personalities that shaped our understanding of crypsis and mimicry up until 1955 (with some comments on subsequent works up to 1990). Other good general books include Pasteur (1972), D.F. Owen (1980), Forbes (2011) and J. Diamond & Bond (2013), as well as more academic works such as Ruxton et al. (2004a), Stevens & Merilaita (2011) and Stevens (2016). The book by Ruxton et al. provides a critical review of many experiments, models and arguments to do with anti-predator adaptations in general, not just mimicry and camouflage, but there is a great deal of overlap.

Many arguments, often heated, were also involved in the early discussions of mimicry. Some of the examples show such perfect matching of detail that many scientists found it hard to believe that they could have resulted from natural selection for progressively more similar forms from disparate starting points. Some thought that only major mutations could be involved rather than Darwinian gradual accumulation of small changes. This led to hearty debate about how natural selection and genetics work, for example

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[1] Butterfly systematics has progressed since Bates' time and many of the species he collected and referred to as Heliconiidae are now placed in the tribe Ithomiini in the nymphalid subfamily Danainae, while his Heliconini are now classified as a tribe of Nymphalidae.

Punnett (1915) and R.B. Goldschmidt (1945) on the side of major mutational leaps versus R.A. Fisher (1927, 1930), L.P. Brower et al. (1971) and, more or less, de Ruiter (1958) leaning towards gradualism. The current consensus is a combination, with an initial mutation that causes a large phenotypic shift followed by subsequent evolutionary refinement, called the 'two-step hypothesis', most probably being the major route, though gradualism might be sufficient in some circumstances (see Chapters 4 and 5). As J.R.G. Turner (1983) notes, in the complicated *Heliconius* system some quite large jumps in phenotype can occur as a result of simple genetic changes.

When it comes to camouflage, much credit should be given not to a scientist, but instead to the American portrait, animal and landscape artist Abbott Handerson Thayer (1849–1921), who discovered the principle of concealment by countershading, discussed disruptive colouration, and dazzle markings and distractive features, and even tried to help the military in disguising troops and ships (J. Diamond & Bond 2013). Interestingly, many of his suggestions came under attack from many naturalists and even hunters. While not all of his suggestions might have been correct, and indeed he probably went over the top in trying to explain all animal colouration as having some concealing function, the argumentation employed on both sides is of interest. People such as United States president Theodore Roosevelt, who was an enthusiastic hunter,[2] dismissed Thayer's claim that a zebra's stripes acts to help conceal it (Roosevelt 1911). Thayer's counter-argument was that just because someone saw something, it did not mean that they saw everything, because they do not know what they failed to notice. In an amusing section, Thayer wrote:

> Forty years of daily meeting the poacher at the post office does not strengthen his credit. And forty years of Roosevelt's seeing zebras not hidden by their costume, and failing to guess what the animal's stripes are for, are just as little to the point.

Kingsland (1978) wrote a very nice discussion of Thayer's work and how it was received, and two of Thayer's oil paintings illustrating camouflage are reproduced in J. Diamond & Bond (2013, pp. 44 and 45); Ruxton et al. (2004b) reproduce Thayer's photographs of a dead grouse positioned as 'in nature' and with its underside dyed darker, illustrating the effectiveness of countershading (see Chapter 2).

The past 30 or so years have seen an enormous resurgence in research on adaptive colouration and mimicry (Guilford 1990b, Komárek 2003), both experimental and theoretical, as can be seen by a quick scan of the dates of the articles cited here. Computer-generated graphics, usually but not always in conjunction with human subjects, have played an increasingly large role in investigations. Nevertheless, much is still being achieved with low-tech solutions, such as pastry model caterpillars exposed to predation by garden birds, or baited triangular shapes that roughly resemble moths resting on tree trunks exposed to woodland birds. Increasing awareness of the visual capabilities of predators, or in some cases of potential mates, is leading to quite a lot of more carefully controlled work, but there is still room for greater awareness. It is all too easy to think that because a model looks life-like to the experimenter, it will also appear life-like to a bird. Some birds can see well into the UV part of the spectrum, and if the signal receiver is an insect, it is important to understand that although insects can see UV light, most cannot see much at the red end of the spectrum.

Sometimes biologists get it wrong. For example, for a long while the North American viceroy butterfly, *Limenitis archippus* (Nymphalidae), was thought to be a Batesian mimic of the monarch butterfly, *Danaus plexippus* (e.g. J.V.Z. Brower 1958a). Now it is known to be actually unpalatable itself (Ritland & Brower 1991) (see Chapter 4, section *Plant-derived toxins*), and more recently it has been shown most probably to be a Müllerian mimic (S.B. Malcolm 1990, Guilford 1991, Ritland 1991, Ritland & Brower 1991, Rothschild 1991) and to contain phenolic glucosides (salicortin and tremuloidin) (Prudic et al. 2007b) sequestered from its *Salix* food plant, though these are rather different from those of the monarch and have different physiological effects.

Another often neglected aspect is the need for correct identification. D.F. Owen et al. (1994), for example, discovered that anomalous findings in an African butterfly mimicry system were resolved once it was realised that one of the mimic species was actually a pair of different but closely similar (cryptic) species.

## ON DEFINITIONS OF 'MIMICRY' AND ADAPTIVE RESEMBLANCE

Mimicry can be defined in many ways but in most of these there exists the concept that some subject forms a model for the resemblance of another, the mimic. In biological examples, this resemblance also carries with it the notion that it serves to deceive another organism, though this is not as clear cut as it may seem and certainly deception is not

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[2] The large game and some 11,000 other specimens that Roosevelt and other expedition members shot or collected on the 1909 Smithsonian–Roosevelt African Expedition became a major part of the collections of both the Smithsonian Institution (Washington D.C.) and the American Museum of Natural History (New York). Some of the diaramas in the latter are real masterpieces of natural history display.

**Table 1.1** Some selected definitions of mimicry and adaptive resemblance. (Adapted from Endler 1981 with permission from John Wiley & Sons.)

| Publication | Definition |
|---|---|
| Cott 1940 | 'In the former [protective resemblance or crypsis] an animal resembles some object which is of no interest to its enemy, and in so doing is concealed; in the latter [protective mimicry] an animal resembles an object which is well known and avoided by its enemy, and in so doing becomes conspicuous.' |
| Wickler 1968 | 'If a signal of interest to the signal receiver is imitated, then this is a case of mimicry, whereas if the general uninteresting background or substrate is imitated, then camouflage (or mimesis) is involved.' |
| Wiens 1978 | '… the process whereby the sensory systems of one animal (operator) are unable to discriminate consistently a second organism or parts thereof (mimic) from either another organism or the physical environment (the models), thereby increasing the fitness of the mimic.' |
| Vane-Wright 1980 | 'Mimicry involves an organism (the mimic) which simulates signal properties of a second living organism (the model) which are perceived as signals of interest by a third living organism (the operator) such that the mimic gains in fitness as a result of the operator identifying it as an example of the model.' |
| M.H. Robinson 1981 | 'Mimicry involves an organism (the mimic) which simulates signal properties of another organism (the model) so that the two are confused by a third living organism and the mimic gains protection, food, a mating advantage (or whatever else we can think of that is testable) as a consequence of the confusion.' |
| Maran 2005 | 'Proceeding from semiotics the essence of mimicry is the presence of two living beings (object) who have different applicability (interpretant) to the receiver (interpreter) and who because of the similarity of their messages or cues (representamen) are at least partly undistinctable for the receiver.' |
| Grim 2013 | 'Mimicry refers to functional 'model–mimic–selecting agent' trinity (with varying number of species involved) when the selecting agent (i.e. signal receiver) responds similarly to mimic and model to the advantage of the mimic.' |
| Speed 2014 | 'In its most general form mimicry refers to phenotypes of an organism that are adaptively modified to resemble living or nonliving components of its environment." |
| Dalziell et al. 2015 | '…a [signal] is mimetic if the behaviour of the receiver changes after perceiving the … resemblance between the mimic and the model, and the behavioural change confers a selective advantage on the mimic.' |

necessary for a large set of adaptive resemblances. A number of influential definitions of mimicry were cited by Endler (1981) and his Table 1 is reproduced here with a few additions (Table 1.1). Von Beeren et al. (2012) provided a summary of how various authors have applied terms related to camouflage and mimicry in relation to how the operator (dupe, signal receiver) perceives them and I have extended it with further examples in Table 1.2. Pasteur (1982, Fig. 1) presents a neat timeline showing where various authors drew the distinction between mimicry (homotypy in his terminology) and crypsis. The range is considerable – some workers restricted use of the term mimicry to anti-predator resemblances with defined models (essentially the Batesian–Müllerian spectrum with unpalatable models), while at the other extreme (e.g. Bates 1862, Turner 1970) all forms of camouflage were included under the definition as well. A number of people drew the line between crypsis due to background matching, countershading, etc. and cases where the model was definable. In present parlance, that includes masquerade (i.e. resemblance of an organism to a definite object of no interest to a predator or herbivore) (Endler 1981), along with all classical protective, reproductive, dispersal and social mimicry cases. In a lot of older literature, masquerade is called mimesis.

That arguments have raged for years over the precise meaning of the term mimicry indicates that there are categories of relationships between organisms, or between organisms and inanimate subjects, which some people see as hard and fast examples of mimicry while others do not. Such grey areas serve to highlight what for more than a hundred years has been a fermenting, and sometimes acrimonious, debate. Probably the main reasons why there has been such a long history of debate on this issue is precisely because of some people's notions that 'mimicry' must involve deceit and that it must involve a definite model. Thus Müllerian mimicry, which is the convergence in

**Table 1.2** Relationships proposed between various terms used in anti-predator mimicry and camouflage in relation to the predator's response to the prey, as employed by various authors. (Adapted from von Beeren et al. 2012 under the terms of the Creative Commons Attribution Licence CC BY 3.0.)

| **Predator's reaction to potential prey** | | | |
|---|---|---|---|
| **Not detected as a discrete entity (causing no reaction)** | **Detected as an uninteresting entity (causing no reaction)** | **Detected as an interesting entity (causing a reaction beneficial to the mimic)** | **Reference(s)** |
| Crypsis | Masquerade | Mimicry | Endler 1981, 1988 |
| Eucrypsis | Mimesis | Homotypy | Pasteur 1982 |
| Eucrypsis | Plant-part mimicry | Mimicry | M.H. Robinson 1981 |
| Crypsis | Masquerade | Mimicry | Ruxton et al. 2004a |
| Cryptic resemblance | Cryptic resemblance | Sematic resemblance | Starrett 1993 |
| Crypsis | Masquerade | — | Stevens & Merilaita 2009b |
| Crypsis | Crypsis | Mimicry | Vane-Wright 1976, 1980 |
| Camouflage or mimesis | Camouflage or mimesis | Mimicry | Wickler 1968 |
| Crypsis | Masquerade | Mimicry | Endler 1981, 1988 |
| Eucrypsis | Mimesis | Homotypy | Pasteur 1982 |
| Eucrypsis | Plant-part mimicry | Mimicry | M.H. Robinson 1981 |
| Crypsis | Masquerade | Mimicry | Ruxton et al. 2004a, Ruxton 2009 |
| Cryptic resemblance | Cryptic resemblance | Sematic resemblance | Starrett 1993 |
| Crypsis | Masquerade | — | Stevens & Merilaita 2009b |

appearance between members of a guild of unpalatable species to mutual benefit, has often been excluded because the signal displayed by members of the guild does not deceive a predator.

Similarly, the form of camouflage called 'crypsis', in which organisms show a general resemblance to background properties such as colour, luminance and texture but not to any definite model, fails to satisfy the definitions of mimicry provided by many authors (Wickler 1968, Wiens 1978), whereas a camouflaging resemblance of an organism to a defined model, maybe a caterpillar to a twig, does. Examples of camouflage with a definite (definable) model are now usually referred to as 'masquerade' (see Chapter 3) but there is an inevitable grey area – after all, masquerading animals have almost always evolved from cryptic ones by gradual increases in similarity to a more precisely defined model. At some stage it becomes apparent that something is masquerading, but there are many intermediate cases. The differences may also depend on the perceptions of a given observer.

Many people have tried to make a clear distinction between mimicry and camouflage, for example Pasteur (1982), but this is not always an easy matter and may in fact be impossible in some cases. A particularly widespread problem when considering mimicry systems, alluded to by M. Edmunds (1974a), is our frequent lack of detailed understanding of the systems of interest. Edmunds considers various sea-slugs (nudibranch molluscs) that closely resemble, both in colouration and in texture, the sponges and hydroids upon which they feed (see Fig. 2.2). Whether such cases are mimetic or cryptic depends crucially on whether a potential predator, say a fish, ignores the sponges or hydroids because they are not suitable food, or actively avoids them because they pose a threat. Both situations are quite possible and may be expected to occur. Thus in these and perhaps many more instances, an adaptive resemblance can be both mimetic and cryptic, depending on which particular type of predator one is considering. Edmunds (1991) concluded that although some nudibranch molluscs are very brightly coloured (see Fig. 4.32), evidence that they are warningly coloured is rather scant (see also Guilford & Cuthill 1991 and Chapter 4, section *Evidence for individual selection*). Nevertheless, it would appear that some nudibranchs may act as Müllerian models for young fish (Randall & Emery 1971).

Early discussions of mimicry were almost entirely centred on examples at the extreme end of the spectrum of what are now considered to be mimetic resemblances (Rothschild 1981). This had the effect of emphasising differences, whereas in nature there is often a continuum; indeed there must be because of the way organisms evolve. That narrow view also tended to draw attention away from how the species got there in the first place, and, as Rothschild points out, "mimicry may be fluid, and the category we assign a species to may be different according to time and place".

Vane-Wright (1980) created a flurry of interest, debate and even dissent as a result of various aspects of his attempt to define mimicry (Table 1.1) in which he distinguished between models that are of no interest to the predator, such as twigs, dead leaves, etc., and those that are. Mimics of the former would then be regarded as cryptic by his definition. More than half of an issue of *Biological Journal of the Linnean Society* (volume 16, part 1) was devoted to criticism and useful commentary on Vane-Wright's definition (Cloudsley-Thompson 1981, M. Edmunds 1981, Endler 1981, M.H. Robinson 1981, Rothschild 1981) and, of course, Vane-Wright's (1981) reply. The issue also includes a shortened version of Henry Bates' famous 1862 paper which set out the basis of his thought on the mimicry that now bears his name.

Cloudsley-Thompson (1981) felt that the term mimicry should be restricted to resemblances of one animal by another and the word 'disguise' used for when an animal is "like a stick, lichen, bark, faeces, a stone or some other inanimate object unattractive to potential predators", though he notes that he might have been unduly influenced in this respect by his supervisor Hugh Cott, who considered that all animal resemblances to plants should be referred to as crypsis. Cloudsley-Thompson quotes from a written response to him from Dick Vane-Wright concerning the nature of mimicry and it is worth repeating here:

> I'm afraid I stick to my contention that it is the 'reference frame' of the operator that determines whether or not crypsis or mimicry should be employed. Tiger stripes 'are' aggressive crypsis, leaf-insects are defensively cryptic. But mantids which look like flowers (e.g. *Idolomantis diabolicum*) are aggressive mimics, as their victims are (presumably) actively seeking out flowers and we imagine that most flowers have evolved their 'flashy' signals to attract pollinators. I don't see how you could define such a general word as disguise in an operational way different to mimicry and crypsis as I have defined them, or as others have tried to do so. It might be useful as a word for lumping both phenomena together.

M. Edmunds (1981) argued that Vane-Wright's definition of mimicry could be seen as too broad, and presented a number of examples emphasising the fine borderline between a 'mimic' being of no interest to a receiver and being of potential interest. For example, in reference to the blue jay/stick caterpillar experiments of de Ruiter (1952), Edmunds notes that:

> [the] jays could not distinguish stick-like caterpillars from twigs until they accidentally trod on one. The question then is, was the signal of the caterpillar of no interest at all (crypsis), or was it of possible interest as an object to grip with the claw, in which case it becomes mimicry.

This seems rather nit-picking to me though I agree that some borderlines are hard to define. Vane-Wright (1981) published a rejoinder to Edmunds and noted, among other things, that his "original attempt at a general definition was introduced in the context of trying to define 40 theoretically different types of mimicry and to separate them from all possible types of crypsis."

M. Edmunds (1974a) defined the occurrence of Batesian mimicry as being when "a predaceous animal, which avoids eating one animal producing a particular signal, is deceived into avoiding a second animal which produces a similar but counterfeit signal". He went on to conclude that animals that precisely mimic other types of inedible objects, such as leaves, twigs, thorns, etc. in order to avoid predation, are Batesian mimics. I do not think that such broad definitions are useful because there are distinctly different effects on the models; if models are living then the more palatable Batesian mimics there are, the more the model species suffers, but it is hard for twigs or pebbles to suffer in the same sense.

Similarly, Endler (1981) also found difficulty with Vane-Wright's system when it comes to determining whether some resemblances are mimetic or cryptic because of the animate/inanimate distinction. For example, resemblances involving sticks or twigs (i.e. parts of a plant) involve a potentially animate model, whereas resemblances to a stone or some dung do not. Neither of these types of model is of interest to the predator, but Vane-Wright used the term mimicry for when the model "is an organism or part of one", which therefore excludes cases with stones or dung as models.

M.H. Robinson (1981) criticised Vane-Wright's definition primarily because it requires interpretation of the phrase "of interest" and as a remedy he couched his definition only in terms of confusion. While Robinson's definition (Table 1.1) overcomes some difficulties, as with Vane-Wright's (1980) definition, it precludes resemblances to non-living entities such as pebbles, bubbles, etc. Vane-Wright (1981) points out that Robinson's definition also ignores both evolution by natural selection and the receiver's perception, as well as being in itself a gross over-simplification of Bates' original notion. M.H. Robinson (1969), on the other hand, made an important contribution to classifying different types of crypsis, and particularly distinguishing eucrypsis (homochromy, countershading and disruptive colouration) from 'plant part mimicry' (*contra* Vane-Wright 1980) (i.e. Cott's (1940) 'special protective resemblance' and Turner's (1961) 'disguise').

Crypsis and hiding from predators are probably the basic (plesiomorphic) defensive strategies in most major groups (M. Edmunds 1990), and masquerade, mimicry and aposematism may evolve when circumstances are right

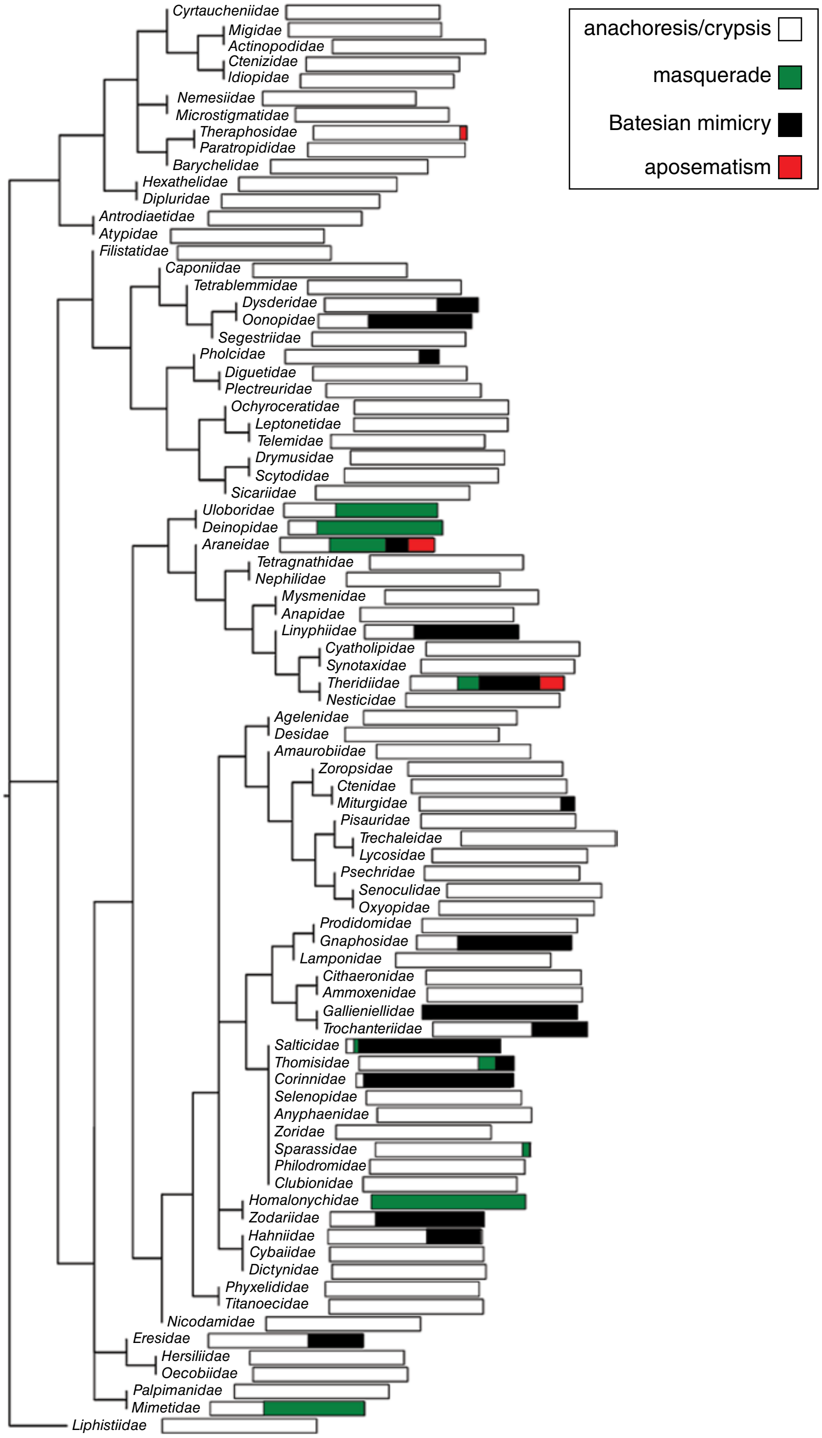

**Fig. 1.1** Modes of passive defence mapped onto independent phylogeny of families of spiders (pruned to show only those families for which hypotheses about modes of anti-predator defence could be assessed). (Source: Adapted from Pekár 2014. Reproduced with permission from John Wiley & Sons.)

(i.e. probably when the background is not uniform but complex and contains many discrete or nearly discrete prey-sized items). Pekár (2014) has examined defensive strategies across the whole of the Arachnida (spiders) and shown that masquerade and mimicry have evolved in a restricted number of families in a very non-random way (i.e. the strategies are phylogenetically clustered) (Fig. 1.1). The most basal extant spiders, the liphistiids[3] and mygalomorphs, are generally large bodied, ground dwelling and nocturnal or spend most of their time concealed in silk-lined holes (anachoresis), so it is not really surprising that they have not evolved bright colours (with rare exceptions in the Theraphosidae, such as the red-headed mouse spider, *Missulena occatoria*) or mimetic resemblances to particular objects – the evolutionary advantage was not there. Orb-web weaving spiders such as aranaeids, tetragnathids and nephilids, however, are often fully visible in their webs in the daytime, and among these bright patterns are much more prevalent, and may, in fact, be attractive to certain prey (see Chapter 10, section *Alluring mimicries*). A similar phylogenetic pattern of ancestral crypsis has recently been shown for North American darkling beetles (Tenebrionidae: Asidini) by A.D. Smith et al. (2015), some of which are Batesian mimics of species of the related and well-protected genus *Eleodes* (see Chaper 6, section *Experimental tests of mimetic advantage*).

Schaefer & Ruxton (2009) coined the term 'exploitation of perceptual biases' (EPB) to differentiate what they regarded as true mimicry from simple exploitation of the sensory biases and loopholes of another organism. In their definition, the term mimicry only applies to cases where a receiver really misidentifies the mimic as a specific model.

Here I have decided first to discuss camouflage (crypsis and masquerade), as despite differences of opinion about what constitutes mimicry and what does not, these evolutionary strategies differ from what is generally nowadays called mimicry, in that the mistakes made by operator (dupe, receiver) have no effect on the model (Vane-Wright 1980, 1981, Endler 1981). Thereafter, I have largely followed a functional classification similar to that of S.B. Malcolm (1990) (Table 1.3), though with variations on the terminology and a greater number of divisions. Because of the many biological roles that mimicry affects there has long been a need to pigeon-hole examples to make it easier to compare and gain better understanding of different systems.

## The concept of 'adaptive resemblance'

The term 'adaptive resemblance' (AR) was introduced by Starrett (1993) as a "broad inclusive term" for a wide range of mimetic and cryptic phenomena and was defined as: "any resemblance that has evolved or is maintained **as a result of selection for the resemblance**." It specifically excludes "incidental resemblance or convergence, which is due to common adaptive responses to functional requirements."

AR incorporates everything normally regarded as mimicry as well as most things that are only occasionally regarded as mimicry. Starrett uses the term selective agent (SA) for what others have variously called the detectee, dupe, receiver, signal receiver or operator. AR includes both crypsis and masquerade (both crypsis in Starrett's definition) and makes no distinction about whether the model is alive, dead or inanimate. It [AR] encompasses Müllerian mimicry even though some authors have strongly objected on the grounds that no deception is involved, but it is clearly an adaptive resemblance. It also includes various topics rejected by Pasteur (1982), such as vocal mimicry (some bird song or alarm call mimicry) or behavioural mimicry by primates. Pasteur's reasoning was that vocal mimicry was a 'conscious imitation' and not something that had been a direct result of natural selection, though of course the cognitive ability or propensity to do so was selected. It is far from clear which instances of such mimicries are consciously done. When a female baboon goes off with a subordinate male for sex and they hide from the dominant male to avoid his aggression – that is probably conscious, but when a bird imitates alarm calls of conspecifics to deter a competing male, is that consciously thought out or a behavioural pattern that has been directly selected to be part of the species' repertoire? Starrett includes most if not all such cases under AR but also asks whether along the gradient of increasingly complex behavioural complexity (cognitive ability) there is a line "beyond which release from unconscious stereotyped behaviour allows discretionary situational and consciously deceptive imitation that might not be subject to natural selection". Surely there is, but beyond that we enter the realm of psychology and that goes largely beyond the scope of this book and AR. Nevertheless, I will discuss various human behaviours to highlight the similarities between what evolution has done and how people deceive, sometimes unconsciously.

This useful definition also makes for clearer thinking. Starrett pays particular attention to various other "troublesome" cases. For example, the widespread occurrence of bold black and white colouration in marine carnivores such as penguins, killer whales and various dolphins (see Fig. 10.3a–d) is clearly not due to the different species evolving to resemble one another. At least in *Spheniscus* penguins the colouration may be selected for because its

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[3] These South-East Asian spiders, which retain a partially segmented abdomen and lack venom glands, are the sister group to all other living spiders.

**Table 1.3** Simple classification of mimicry based on kind of interaction, trophic level and selective agent as summarised by S.B. Malcolm. (Adapted from Malcolm 1990 with permission from Elsevier.)

| Mimicry category | Interaction | Selective agent (operator) | Examples |
|---|---|---|---|
| **Interspecific interactions** | | | |
| Defensive | Prey–predator | Predator | Müllerian, Batesian, 'masquerade', 'predator mimicry' |
| Foraging mimicry | Prey–predator | Prey | Aggressive and 'masquerade' (lampyrid beetles, bolas spiders, cleaner wrasse) |
| | Flower–pollinator | Pollinator | Flower mimicry (orchid mimicry of bees) |
| Parasitic mimicry | Host–parasite | Host or vector | Parasites, dispersion and mating (cuckoos, trematodes, fruit dispersal, orchid mimicry of bees) |
| **Intraspecific non-trophic interactions** | | | |
| Sexual mimicry | Male–female | Same, or opposite, sex | Mating lures ('sneaky' mating, egg or prey dummies) |
| Social mimicry | Any sex, juveniles | Same, or opposite, sex | Signals of hierarchy, deceptive alarm calls |

conspicuousness causes schools of prey fish to 'depolarise', making some prey individuals easier to see and capture (R.P. Wilson et al. 1987). Why exactly these conspicuous markings might have this effect is unclear; maybe they 'mimic' signals from other potential predators that might best be thwarted by a confused response. After all, over millions of years of evolutionary time, if the bold black and white pattern of piscivores leads to greater overall mortality one might have expected schooling fish not to respond to it any longer.

## THE CLASSIFICATION OF MIMICRY SYSTEMS

While the concept of mimicry is generally understood by everyone, mimetic relationships have evolved in relation to a wide range of biological processes, which has made attempts to classify the different types complicated. Different workers have also highlighted different factors as being important, and there is considerable overlap. While some authors are clearly willing to accept the idea that some resemblances have elements of more than one type of mimicry, for example many cases of crypsis, and sometimes masquerade, serve to hide the aggressor simultaneously from potential predators and from potential prey (see Figs 2.29 and 10.7d,e). There may be other 'grey areas'. Perhaps some authors have concentrated heavily on pigeon-holing particular hard-to-place examples. While this can serve as a test of classificatory systems, it is hard to imagine that any one simple system can accommodate all the results of evolution.

In terms of creating frameworks for classifying different types of mimicry, three people in particularly have made great advances – Wolfgang Wickler, Richard [Dick] Vane-Wright and Georges Pasteur. I will discuss their contributions in some detail below.

### Wickler's system

Wickler (1965) proposed a formal notation for mimicry as a communication network in which three players interact and on which the costs or benefits of the signals to the participants could be represented. Two of the parties he termed signal senders (S, called S1 and S2) and one the signal receiver (R), which responds to the signals emitted by the senders. By convention, the model is represented by S1 and the mimic by S2. Endler (1981) preferred to use the notation P, S and R, referring to primary and secondary signal generators and a receiver, but here I use Wickler's system. Wickler then provided the following formal definition of mimicry as a system:

1. comprising two signal senders (S1 + S2) which have one or more receiver(s) in common,
2. in which the receiver(s) respond similarly to the signals of the two senders,
3. in which it is advantageous for the receiver to respond to one signal sender in a given way but disadvantageous for it to respond to the other signal sender in the same way.

In terms of Wickler's notation this is

$$\mathrm{S1} + \mathrm{R} - \mathrm{S2}$$

from which the mimic in the system can be defined as the signal sender that elicits a response in the receiver that would be disadvantageous (negative) for the receiver, while the other sender is the model (S1). In other words, the mimic is the party that emits counterfeit signals that elicit maladapted responses in the receiver. As noted by Wickler, the mimic always has a selective advantage. This can be represented in terms of his notation as

$$\mathrm{S1} + \mathrm{R} - + \mathrm{S2}$$

Note that the mimic (S2) must always benefit because otherwise the mimicry would not have been selected for in the first place. The receiver's response, of course, does not have to be negative to the other sender and in the broader context of adaptive resemblance it is possible for all the interactions to be positive, as for example in classical 'Müllerian mimicry', which would be represented as

$$\mathrm{S1} + \ + \mathrm{R} + \ + \mathrm{S2}$$

## Vane-Wright's system

Vane-Wright (1976) provided a broader basis for the classification of mimetic relationships, extending Wickler's analysis of interactions between the three components of the system, S1, S2 and R. Vane-Wright's (1976, 1981) definition differs from that of Wickler (1968) in that it does away with the need for deception – thus it comfortably incorporates Müllerian mimicry in which the receiver is not deceived, and single or mixed schools of fish in which one individual gains protection because of predator's difficulty in visually separating it from all the other school members (arithmetic mimicry).

The first part of Vane-Wright's analysis considered whether signals from the mimic (S2) are advantageous or disadvantageous to the receiver (R), and whether signals from the mimic (S2) are disadvantageous to the model (S1). Systems in which the mimic's signal are not harmful to the model are referred to as 'synergic' and in the opposite case, 'antergic'. He depicted the full range of possibilities as shown in Fig. 1.2.

The second part of Vane-Wright's system considered the actual embodiment(s) of these three components (i.e. the species they belong to). While for many familiar cases of mimicry, the model, mimic and receiver are each different species, termed 'disjunct' systems, there are cases in which all three are members of the same species (conjunct systems), or any two may belong to one species (bipolar systems).

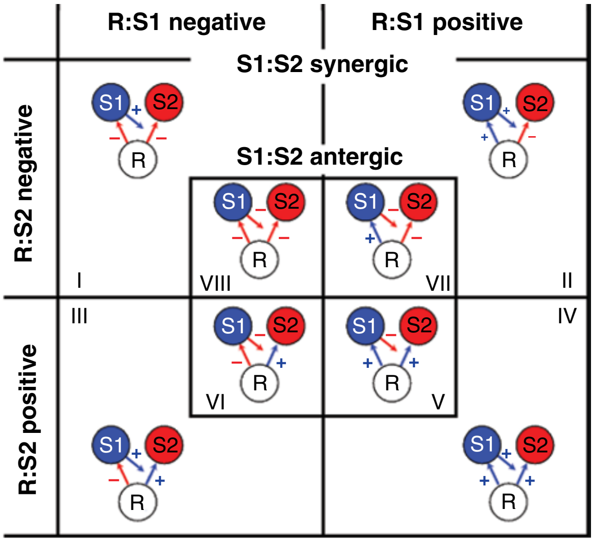

**Fig. 1.2** The eight interactions that can occur in mimetic relationships with the signal receiver (R or dupe) and two signal transmitters (S1 and S2) showing how the signals and responses of each member of the triad are either beneficial (positive) or harmful (negative) to the others. The outer relationships are synergic, meaning that the existence of the mimic (S2) is beneficial to the model (S1), whereas in the inner set of four the mimic has a detrimental effect on the model. (Source: Adapted from Vane-Wright 1976 with permission from John Wiley & Sons.)

The three possible polar systems can be represented by S1 + R/S2, S2 + R/S1 and S1 + S2/R, as illustrated in Fig. 1.3.

Vane-Wright's classification was not intended to be a complete treatment of adaptive resemblances as it only deals with cases in which the model is definable and animate; his choice of criteria in fact prevents the inclusion in his classification of crypsis and masquerade. Nor does it embrace ill-defined features such as deflective markings and dazzle, as these cannot be classified as being either synergic or antergic and do not have a clearly defined model.

Out of the 40 conceivable types of mimetic relationship allowed for in his classification (Table 1.4), Vane-Wright was able to find non-human examples for 21 with some certainty, a couple rather more speculatively, and human examples (e.g. military decoys and spies) for a further three. Vane-Wright notes that the bipolar S1/S2 + R system, in which the mimic and dupe belong to one species while the model belongs to another, seemed to be completely empty, though he did suggest that some courtship activities of spiders and empidid flies which incorporate simulation of prey organisms could belong to this category. To these possibilities might be added the food lures used by certain male fish that resemble invertebrates and