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Interspecific visual signalling in animals and plants: a functional classification

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Abstract

Organisms frequently gain advantages when they engage in signalling with individuals of other species. Here we provide a functionally structured framework of the great variety of interspecific visual signals seen in nature, then describe the different signalling mechanisms that have evolved in response to each of these functional requirements. We propose that interspecific visual signalling can be divided into six major functional categories: antipredator, food acquisition, antiparasite, host acquisition, reproductive, and agonistic signalling, with each function enabled by several distinct mechanisms. We support our classification by reviewing the ecological and behavioural drivers of interspecific signalling in animals and plants, principally focussing on comparative studies that address large-scale patterns of diversity. Collating diverse examples of interspecific signalling into an organised set of functional and mechanistic categories places anachronistic behavioural and morphological labels in fresh context, clarifies terminology, and redirects research effort towards understanding environmental influences driving interspecific signalling in nature.

INTRODUCTION

Organising and categorising visual signals is not a new endeavour. In “The Colours of Animals and Plants” Alfred Russel Wallace [1] presented a “functional classification” of biological colours into ‘protective’, ‘warning’, ‘sexual’, ‘typical’ and ‘attractive’ colours. Now, 140 years later, we can reflect that Wallace was visionary in recognising that ultimate function is the most useful level of organisation [2]. While his categories are still generally recognisable [3], increasing knowledge has necessitated some reformulation. For example, Wallace’s ‘Attractive’ colours included plants signalling to animal pollinators, but in terms of function there is overlap between them and most ‘sexual’ colours of animals, as both aim to directly improve reproductive success through securing appropriate mates. His rag-tag jumble of ‘typical’ colours, to which “we can assign no function or use” (p.654), can also been pruned, and entries can now be moved to well-defined functional categories, including new ones that have been identified since Wallace’s writing, such as antiparasite signals [58]. Yet such a functional reorganization has never been formally attempted and collating diverse and apparently unrelated examples of interspecific signalling together under one framework is our purpose here. We believe that a modern revision inspired by the intent behind Wallace’s original scheme can unify a variety of disparate concepts that are currently being investigated separately without broader appreciation of the way that they fit into a common communication charter. Additionally, juxtaposing different aspects of interspecific signalling can generate novel comparative functional analyses that examine the evolution of, say, different methods of defence against predators or parasites. Finally we aim to improve clarity in terminology that is frequently used in confusing and potentially misleading ways because it mixes descriptive, proximate and ultimate explanations.

Our primary objective, then, is to categorize the distribution of interspecific visual signals in nature. Our topical framework is organised on the basis of function, but with subtopics providing a non-exhaustive review of proximate high-level mechanisms through which function is achieved (see Figure 1). Specifically we address interspecific signals because intraspecific signals have been discussed at length in relation to cooperation [4], conflict [5] and mate acquisition [6] whereas interspecific signalling is a less explicitly discussed topic in communication.

Our secondary objective is to review what we have learnt about the evolutionary and ecological drivers of interspecific signal diversity using phylogenetic comparative approaches [7,8]. These measure colouration phenotypes in related species and use their phylogenetic relationships as well as information on ecological, social, life history, behavioural or geographical variables, to understand the evolutionary history of coloration traits, and how species have adapted to their circumstances compared to other species that have evolved in different situations.

We define an interspecific signal as a stimulus produced by a sender of one species that has evolved to modify the behaviour of a receiver of another species to the net benefit of the sender [4,9]. Signalling systems comprise sets of one or more inter and intraspecific signals (and potentially cues) used by individuals, that influence other signals in the system, both in terms of how they are interpreted by receivers, and their evolutionary consequences [5]. Signals in a signalling system typically share a message, for example the warning signals used by the individuals of all the species that make up a mimicry complex. Systems can also include cues; for example true eyes provide cues to receivers that support the evolution and stability of false eyespot signals. For signalling systems to persist, the signals within them must, on average, over evolutionary time, advantage receivers as well as senders (i.e., they are honest) [9–11], however any single signal used by an individual may be disadvantageous to the receiver (a dishonest signal). Aspects of camouflage such as background matching, transparency, disruptive coloration and countershading are excluded as signals because by preventing detection or recognition the receiver’s behaviour is not changed when the stimulus is effective compared with when the stimulus is absent. Conversely antipredator masquerade is a signal because it results in a misclassification of the stimulus as an inanimate object which modifies the receiver's behaviour causing it not to attack [12], benefitting the signaller, with the receiver benefitting on average from not expending effort attacking real leaves, pebbles or twigs. Cues are sources of information that have not evolved to influence receivers but which may still influence the behaviour of the receiver [9].

ANTI-PREDATOR

Potential prey often signal to predators in order to reduce the costs of attempting to escape, or the more significant costs of injury or death [13]. If information is honest, receiving it can benefit potential predators who avoid costs of making an unprofitable attack. We identify four distinct mechanisms through which interspecific signals function to reduce the costs of predation; aposematism, masquerade, pursuit deterrence and deflection, and a potential fifth mechanism, deimatism, that may be distinct from aposematic signalling.

Aposematism

Visual antipredator aposematism involves prey signalling a warning message, usually using conspicuous colouration, to predators that they are defended, and that attack is likely to have negative consequences for the predator. Examples include the black and yellow stripes of some bees and wasps and the orange and black wings of monarch butterflies. There is some comparative evidence showing the link predicted by aposematic theory between increasing conspicuousness and toxicity as for instance in opistobranchs [14] and dendrobatid frogs [15], and black and white pelage in carnivora being associated with toxic anal secretions [16]. In plants, bright spots and stripes on leaves are associated with thorns [17]. Nonetheless, there are also examples of negative associations between conspicuousness and toxicity in some poison dart frog species [18,19].

There has been a long-standing concern about how warning colouration might initially evolve, since a rare conspicuous morph will attract attention of predators and be poor at educating them. Fisher [20] suggested that aggregation could be an evolutionary precursor for conspicuous colouration in advertising defences, but there is only moderate comparative evidence for an association between these traits [21]. Another outstanding issue is the ecological correlates of aposematism in contemporary populations. Potential for sequestration of toxins through diet is a factor in some cases; for example in dentrobatid frogs aposematism is associated with feeding on ants, termites and mites that contain alkaloids [22,23]. Additionally aposematism tends to be associated with traits that allow easy detection, for example in dendrobatids again, increased body size is associated with conspicuous colouration [24], although the direction of the causal arrow is unclear since both might be promoted by visually mediated predation. In adult Lepidoptera, warning colouration has evolved far more often in diurnal clades where insects can be seen moving [25]. Finally, lacking options for alternative antipredator strategies appears important: conspicuous colouration in Carnivora is associated with stockiness that prevents fast flight, and living in exposed habitats where other forms of defence are limited [26].

There are many examples of species that benefit from predator aversion to the warning signals of other species by mimicking their appearance. These include examples of Müllerian co-mimicry, where species that invest approximately equally in the costs of defensive adaptations have common warning signal appearances in a mutualistic relationship that share the costs of predator learning [27–29] and Batesian mimicry. Here one species exploits the honest aposematic signal of another species to gain protection from predation while investing in little or no defence. The ecological circumstances in which Batesian and Müllerian mimicry evolve are poorly understood, though factors related to predator learning are likely to be key. Less toxic models are mimicked when multiple models coexist because predators generalize to other prey types more when educated on such models [30]. The abundance of models in an environment also determines the strength of selection for resemblance [29,31], with models predicting the evolution of Müllerian relationships when all co-mimics are numerous, and Batesian relationships evolving when the model is numerous but the mimic is not [13]. There is emerging comparative evidence supporting these predictions in hoverfly and coral snake mimicry complexes [32,33].

Masquerade

Masquerade is rarely presented explicitly as a signal because masquerading species are often quite cryptic (indeed crypsis and masquerade can operate simultaneously), yet their resemblance to an object that is not of interest to predators has evolved to send a deceptive identity message that results in misclassification of the organism as an object that is not attractive as food [12], with the signalling system maintained because it normally benefits the predator to ignore the masqueraded object. There is comparative evidence that evolutionary transitions to leaf masquerade in *Kallima* butterflies are gradual rather than sudden [34] but the ecological circumstances in which masquerade evolves have yet to be investigated. Skelhorn and colleagues [12] predict masquerade to be associated with specialised diet as this might associate species with specific backgrounds, but this hypothesis has not been tested.

Pursuit deterrence

Predators are less likely to attack when they judge success to be unlikely, such as when they have been detected, so prey send pursuit deterrence signals to predators in order to save them the costs of flight or capture, with predators also benefitting by avoiding the cost of mounting an attack that is unlikely to be successful [35,36]. Some pursuit deterrent signals are acoustic, as when skylarks *Alauda arvensis* signal to merlins *Falco columbarius*, but there are also visual examples. For example, across rails (Family

Rallidae), species with white undertail coverts tend to be found in open habitats [37]. Elimination of alternative hypotheses suggests that this colouration accentuates tail flick signals aimed at deterring predators [37]. In another example, some artiodactyls sport thick dark longitudinal stripes (side bands) on light brown pelage. Comparative analyses show that these are associated with stotting or leaping behaviour which acts as a quality advertisement signal dissuading predators from pursuit, suggesting that the side bands are signal amplifiers [38,39]. White tails in lagomorphs are found in grasslands which might also indicate they enhance the efficacy of pursuit deterrence movements [40]. A less worked example of pursuit deterrence are the bright blue wings of the Morpho butterflies signalling that they are difficult to catch [41].

Deflection

Adverse consequences of attack can be reduced for prey if the predator is directed towards a less-vital body area that might allow the prey to avoid mortal injury, with a classic example being brightly coloured tails in lizards that can be voluntarily shed [42]. The most well studied examples of deflection marks are so-called eyespots, concentric rings of contrasting colouration with an eye-like appearance. These are found in butterflies and moths, beetles, bugs, locusts and crickets, molluscs, frogs, birds and fish. Their use in deflection is suggested by their location on less vulnerable areas of the body, such as the edges of butterflies' wings [43,44]. There is emerging evidence that they are effective in deflecting attacks away from vital body regions [45], though the phenotype may also function as an antipredator signal via other mechanisms (see next section). There is debate over exactly how eyespots work: they may be a conspicuous signal that simply attracts the predator's attention to a less important part of the body [46], or they may be a dishonest signal that mimics the cue provided by a true eye, an organ that predators often preferentially target to disable prey [47]. In support of the latter, among butterflyfishes

(Chaetodontidae) spots and presence of eyespots are often found on species with an eyestripe that masks the true eye [48], and experiments show attacks are targeted at eyespots particularly when a stripe runs through the real eye [49,50].

Deimatism

Deimatic signalling is defined by Skelhorn and colleagues [51,52] as "as any defensive display that causes a predator to misclassify a prey as a potential threat to its immediate safety…. what defines deimatic displays is their ability to exploit classic fear responses in predators that have evolved, not to avoid prey, but to avoid imminent danger.". This distinguishes deimatic signals from aposematic signals that are based on signalling information about prey profitability. Deimatic displays often involve a dynamic component that startles the predator, provoking a reflexive response that leads to aborting attack [52]. For example, the European swallowtail *Papilio machaon* exposes a brightly coloured dorsal wing surface when attacked in a resting position and then exhibits intermittent jerky wing motions which can cause predators to flee [53].

'Eyespots' of many animals, including some cephalopods, fish, frogs, birds, and larval and adult Lepidoptera, have been proposed to work as deimatic signals by mimicking the eyes of an animal dangerous to the predator [47,54]. For instance, several moths display eyespots that bear an uncanny resemblance to owl eyes [55]. This phenotype seems to cause predators distress and display their own antipredator responses [56]; mimetic eyespots are as effective as the true eyes of owls in eliciting an aversive response in great tits *Parus major* [57]. Confusion of prey and predator may involve satiric mimicry whereby the ambiguity causes the predator to hesitate [58]. On lepidopteran larvae, eyespots are associated with large body size, and experiments show they are only effective predator deterrents on larger caterpillars [59]. Likely, eyespots give the caterpillar resemblance to a snake, natural enemies of caterpillar predators; domestic chicks are particularly wary of eyespots on experimental models that are placed anteriorly and are associated with thickened sections [60].

In summary, there are at least five mechanisms by which prey dissuade predatory attack using signals, some honest, some dishonest; some that elicit innate, others learnt responses in predators; and many of which constitute some of the most conspicuous and beautiful colours in nature.

FOOD-ACQUISITION

Food acquisition signalling is used by predators to increase hunting success. Compared to antipredator signalling, there are fewer examples of, and mechanisms via which, predators signal visually to potential prey.

Flushing

Some predators signal to potential prey to make them respond with escape initiation behaviours that actually make the prey easier to find and catch. For example, Neotropical redstarts (Parulidae) have brightly coloured tail feathers that they suddenly expose when hunting insect prey to flush them from hiding places to allow subsequent pursuit and capture. Obliterating the white colour of tail feathers reduces foraging success [61] and experimental model birds show that geographic variation in white tail feathers may maximize flush-pursuit foraging locally [62]. A slightly different mechanism is to signal to prey in a way that impairs escape behaviour. In cetaceans white flanks and white heads that may fluoresce under water are associated with feeding on fish and krill and these regions of the body may possibly be involved in prey confusion [63].

Luring

Prey luring is a strategy that many predators use to attract prey to them [64]. By exploiting aspects of prey behaviour or prey preferences for investigating particular stimuli (sensory traps), they give an inherently deceptive signal that they are an object that might be advantageous to approach. These may be as simple as bright lights or more complex signals that aggressively mimic the prey's own prey or a potential mate [64]. Many spider species are conspicuously coloured in this way [65,66]; experimental painting of orchid spiders shows that their colouration does indeed attract insect prey to the web [67].

Prey luring also occurs in vertebrates, for example toe-wiggling by predatory cane toads, *Chaunus marinus* [68] and by angler fish, *Lophiiformes* waving their esca, an organ atop a 'fishing rod' containing luminescent bacteria [69]. In some taxa, such as *Bothrops* (pit vipers), the evolutionary trajectory of caudal lures has been mapped out, although has yet to be linked to ecological variables [70]. In carnivores, conspicuous tail tips have been suggested to work as lures and are associated with hunting birds, ungulates and small mammals [71], but they may work more like a deflection mark, diverting the prey's attention from predator rather than attracting it to the tail.

Mimicry of innocuous species

As well as luring prey in, aggressive mimicry is also used by predators to escape the attention of their prey. For example, zone-tailed hawks *Buteo albonotatus*, predatory raptors, mimic innocuous turkey vultures *Cathartes aura* in both shape and colour [72].

REDUCING COSTS OF PARASITISM

Approximately 1% of bird species lay their eggs in the nests of other host species and thereby forgo the costs of parental care. Host species find themselves in arms races with their parasites, and the signals that they produce are a potential way of reducing the costs of parasitism to host individuals. Highly recognizable egg colour and patterning [73] and low intra-clutch variability [74], in addition to facilitating rejection by the host [2], may have evolved to signal to potential parasites that detection and rejection of the intruder's eggs is likely [75]. The conspicuous 'last-egg' in the clutches of hosts of avian brood parasites may also signal to potential parasites that the clutch is complete and no longer worth parasitizing, although this idea is controversial [74]. An interesting case of interspecific signalling that functions to both control parasites and in food acquisition occurs in cleaning symbiosis. Different species of cleaner fish have converged on a similar blue and yellow striped uniform that attracts clients and reduces client predation on them [76]. Again, antiparasite signalling systems are subject to cheating, for example fangblennys (*Plagiotremus rhinorhynchos*) change their colour to mimic the appearance of cleaner wrasse (*Labroides dimidiatus*) in order to approach and feed on would-be-clients' tissue [77].

INCREASING BENEFITS OF PARASITISM

The functional opposite to signals that reduce costs for host species are those that facilitate parasitism. In avian brood parasite systems, there is widespread use of colour to fool hosts into letting parasitic birds breed successfully. Specific mechanisms include the adult common cuckoo's *Cuculus canorus* breast colouration mimicking that of sparrowhawks *Accipiter nisus*, helping them to circumvent host nest defence [78]. Eggs of parasites are under strong selection to mimic the visual appearance of the host's eggs, with mimetic similarity across species pairs correlated with the host species' rejection rate [79]. In an extraordinary case of brood to host signalling, Horsfield's hawk cuckoo *Cuculus fugax* chicks shows a yellow wing patch believed to mimic the gape of a begging host chick [80].

INTERSPECIFIC SIGNALLING TO PROMOTE REPRODUCTION

For most sexual species, signals are a vital part of successful reproduction. Mating signals usually occur between conspecifics, but the process of finding a potential mate can involve interactions with heterospecifics too [81]. Animals make decisions about whether other individuals they encounter (both con and heterospecific) are suitable mates partly using what are commonly called species recognition signals (but see [82]). Sexually reproducing plants also signal visually to pollinators and seed dispersers to secure their services as intermediaries in successful reproduction.

Species recognition

Judging whether an animal is from the same species or not involves interpreting the signals and cues of both con and heterospecifics. The evolutionary consequence of species recognition signalling can be observed in patterns of reproductive character displacement, where related sympatric species often look more distinctive from each other than do allopatric congeners [81,83]. For example, in birds, colouration between sister species is more divergent at intermediate levels of sympatry (50-80% breeding range overlap) than in areas of allopatry [84]. Other good examples of likely reproductive character displacement at broad comparative scales are the increased visual distinctiveness of sympatric Cercopithecini primates' faces [85] and male wing colour in Agrodiatus butterflies [86].

It is often unknown whether visual signals that reduce the likelihood of interspecific matings have evolved primarily as a consequence of selection resulting from conspecific or heterospecific interactions [82,87]. In female pied flycatchers *Fidecula hypoleuca,* it appears to be the first possibility because females choose brown males in those populations where they are sympatric with black and white collared flycatchers *Fidecula albicollis* but are less choosy about male plumage in allopatric populations [88]. In a counter example of selection resulting from eschewing heterospecifics, aposematic male *Heliconius melpomene* males are very reticent about mating with *Heliconius cydno* females from sympatric populations, as hybrids are unlikely to be recognised as distasteful. Males from allopatric populations are not so choosy, however, suggesting assortative mating is driven by avoiding heterospecifics [89].

Pollinator attraction

A major subtype of interspecific visual mating signals are those found on the flowers of species that aim to attract visually oriented pollinators to act as vectors for pollen transfer [90]. Indeed the mutualistic relationship between plant and pollinator is a major driver of flower signal evolution and diversification [91]. There is a close relationship between red flower colour and targeting avian over apian pollinators since reds are more conspicuous to birds than non-targeted bees that may take rewards without pollinating the flower [92,93]. Similarly, insect pollinated flowers are more likely to be blue, tuning signals to the spectral sensitivities of hymenoptera, though it is unclear whether pollinator sensitivity preceded floral colouration or vice versa [94].

Signalling systems between flowers and pollinators are open to cheating. Approximately a third of species in Orchidaceae do not invest in production of nectar rewards, but mimic the signals of other species in order to attract pollinators [95]. In many examples this involves exploiting sensory biases in pollinators attracted by bright colours or mimicking the appearance of other nectar-containing flowers (Dodsonian mimicry), however more elaborate examples involve structures that mimic the appearance of female pollinators such as hymenoptera in order to attract males to the flower (Pouyannian mimicry) [96].

Seed dispersal

The fruits that plants produce to reward seed dispersers often feature attractive visual signals. Broadly, fruit colours fall into two syndromes: yellow, brown or green large smelly fruits with a protective husk that are dispersed by mammals, and red, black, blue or white small fruits lacking a husk and having no odour that are dispersed by birds [97,98]. These categories have been broadly confirmed both ecologically and in disperser colour space analyses [99,100]. Variation in fruit colour correlates with seed maturity and both antioxidant [101] and lipid content [102], valuable resources for dispersers, suggesting plants honestly signal reward to secure the services of dispersers at the right time. There is a long-standing idea that primate and bird colour vision evolved to better detect ripe fruit against a background of green leaves [103] but this is still a subject of active debate [104,105].

AGONISTIC SIGNALLING

Heterospecifics frequently compete over resources, whether food, resting places or breeding sites. Interspecific signalling is used to mediate these competitive interactions and reduce costs of fighting over resources; essentially signals de-escalate situations where both species could be harmed. In a pattern of agonistic rather than reproductive character displacement [106], the mating territory defence signals of different species of rubyspot damselflies have distinctive appearances, not to secure conspecific matings, but reduce heterospecific aggression resulting from misidentification of heterospecifics as conspecific competitors [107,108]. There are also several potential examples of interspecific social dominance mimicry, in which a subordinate species mimics the appearance of a dominant ecological competitor to avoid aggression by the dominant model species [109]. Although interspecific aggression is very widespread, it is understudied; to our knowledge there have been no other comparative studies of the role of agonistic interactions in interspecific signalling.

CONCLUSIONS AND ENCOURAGEMENT FOR COMPARATIVE STUDIES OF COLOURATION

We have presented a comprehensive functional framework for understanding interspecific signals in nature, a necessary addendum to understanding the overall diversity of colour displays of plants and animals that hitherto has focused disproportionately on intraspecific signalling. Indeed, broadly speaking, very large numbers of angiosperms use colour to signal to pollinators, a large minority of animals use warning colours to deter predators, whereas only a handful of species use visual signals to secure prey.

We suspect that visual signals used in interspecific signalling must be selected for maximum effectiveness in terms of optimizing conspicuousness tempered by competing drivers of appearance such as camouflage and thermoregulation, the signalling environment and receivers' vision, although this has been demonstrated in only a handful of cases. Additionally, selection is predicted to act on signals within each mechanistic category in consistent ways leading to common influences on appearance, for example species recognition signalling systems [85] should consistently select for appearances that improve memorability or distinctiveness from competing signals in order to facilitate discrimination. In contrast, in Müllerian mimicry rings selection instead is predicted to act to reduce the distinctiveness of signals across species to facilitate predator learning. In both examples there is predicted to be selection for reduced intraspecific variation in signals [110], but this pattern is not always observed: aposematic signals can be highly variable within species as a result of local differences in predation pressure (e.g., strawberry poison frog, *Oophaga pumilio* [111]) or access to toxins (e.g., seven-spot ladybirds, *Coccinella septempunctata* [112]). Whether these examples of deviations from simple predictions are exceptional cases or a reflection of the complexity of factors influencing signal design awaits further investigation, but the functional and mechanistic categories discussed here help make clear comparative predictions: category membership can generate data to answer questions such as "Why do some species evolve aposematic signals while others evolve deflective signals?".

What do comparative studies currently tell us about the ecology and evolution of interspecific visual signals? Certainly there is some evidence that conspicuous signals targeted at predators are associated with relatively large body size (caterpillars, dendrobatids), with specialist diets that allow toxin sequestration in aposemates (dendrobatids), and with certain habitat types (carnivores). But many tentative associations are not found consistently across taxa, for example aposematism being associated with gregariousness is not commonplace. It is even more difficult to make generalizations about conditions favouring the evolution of other mechanisms such as luring and flushing of prey. Indeed, although we now have a broad understanding of the functions of interspecific signals and the mechanisms involved, we are struggling to predict where different forms of antipredator defence occur in nature, in what circumstances, to what evolutionary effect, and why there are so many of them.

Furthermore, there are a great many unexplained conspicuous colouration patches on animals in nature that are likely to be interspecific signals but which are a challenge to assign a function. White rump patches on white-tailed deer, *Odocoileus virginianus*, are one such example [100]. Yet comparative studies led by clear *a priori* predictions can help in elucidating function, and can simultaneously uncover associations between external colouration and habitat, geographic, life history, and social variables. We advocate a renewed research drive to identify common ecological drivers of interspecific signals across taxa as we still have limited understanding of the diversity, distribution and evolution of animal interspecific signals. We expect that the framework proposed here is not comprehensive but its functional and mechanistic basis means that novel examples can be added in a straightforward manner.

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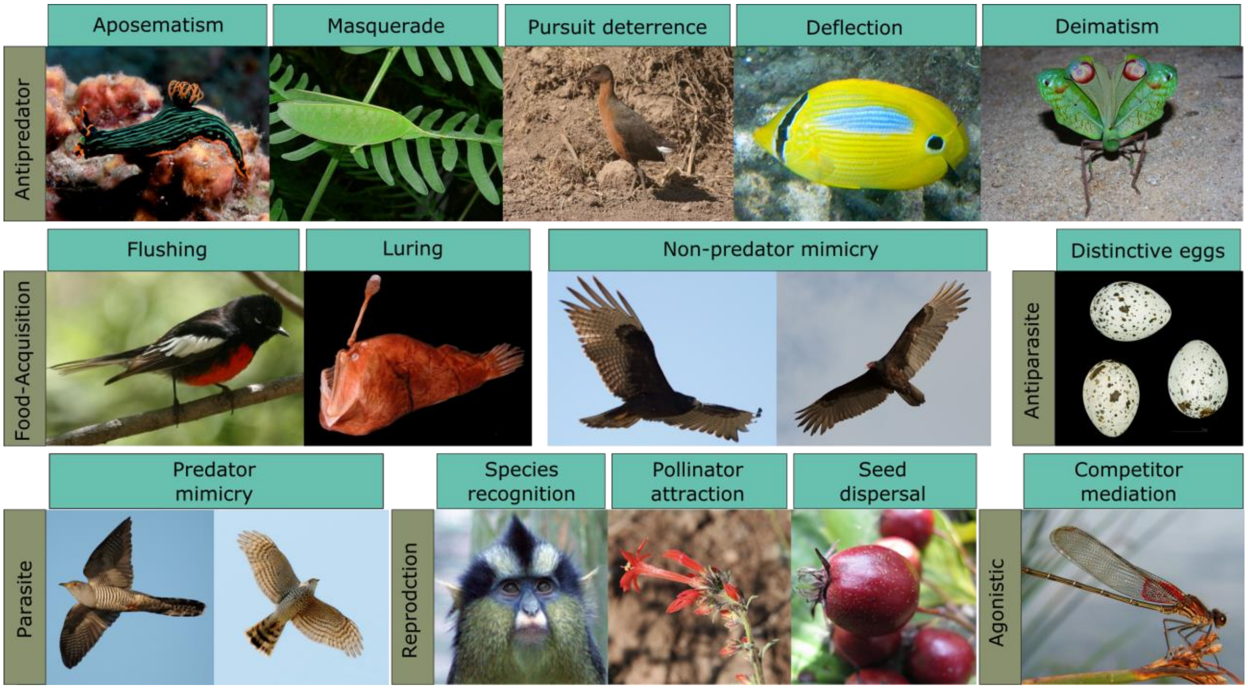

Figure 1.

Aposematism: *Nembrotha kubaryana*, Nick Hobgood; opistobranchs are highly toxic marine molluscs. Masquerade: *Pseudophyllus titan*, Bernard Dupont; this species resembles a pair of living leaves. Pursuit deterrence: *Rougetius_rougetii* Rouget's rail, Kris Maes; some rail species flash their tails upon detecting an approaching predator. Deflection: *Chaetodon plebeius* bluestreak butterflyfish, Paul Asman and Jill Lenoble; many fish have distinctive spots and additionally have distinctive bands of colour through their true eye. Deimatism: *Tanusia brullaei* André Almeida Alves; sudden exposure of brightly coloured parts of the body is thought to deter imminent attack. Flushing: *Myioborus pictus* painted redstart, Dominic Sherony; while foraging, certain insectivorous birds flash conspicuous parts of their body to flush prey. Non-predator mimicry: *Buteo albonotatus* mimicking *Cathartes aura*; predatory birds may gain benefits from resembling strict carrion feeders that pose no threat to live prey. Distinctive eggs: *Acrocephalus arundinaceus* great reed warbler eggs; highly recognizable colour patterns and low intraclutch variability are strategies to reduce parasitism in host species. Predator mimicry: *Cuculus_canorus* common cuckoo, Chris Romeiks, mimicking *Accipiter nisus* sparrowhawk, Christian Knoch; parasitic species that resemble predators species may be able to get closer to host nests without causing alarm. Species recognition: *Cercopithecus campbelli* Campbell's mona monkey William Allen; sympatric heterospecific monkeys look dissimilar to avoid costly hybridization. Pollinator attraction: *Ipomopsis aggregata* scarlet gilia Jane Shelby Richardson; floral coloration taps into spectral sensitivities of pollinators. Seed dispersal: *Crataegus punctata* fruit; fruit coloration can ensure secure dispersal when the seed is ripe by honestly signalling fruit nutrient content. Competitor mediation *Hetaerina americana* rubyspot damselfly Bruce Martin; colour signals may act to distinguish heterospecifics and thereby mollify aggressive interactions. All images are in the public domain or used under CC BY and BY-SA licenses. The figure is available on Figshare DOI:10.6084/m9.figshare.4299686.