Antipredator deception in terrestrial vertebrates

Tim CARO*

Department of Wildlife, Fish and Conservation Biology, and Center of Population Biology, University of California, Davis, CA 95616, USA

Abstract  Deceptive antipredator defense mechanisms fall into three categories: depriving predators of knowledge of prey’s presence, providing cues that deceive predators about prey handling, and dishonest signaling. Deceptive defenses in terrestrial vertebrates include aspects of crypsis such as background matching and countershading, visual and acoustic Batesian mimicry, active defenses that make animals seem more difficult to handle such as increase in apparent size and threats, feigning injury and death, distractive behaviours, and aspects of flight. After reviewing these defenses, I attempt a preliminary evaluation of which aspects of antipredator deception are most widespread in amphibians, reptiles, mammals and birds [Current Zoology 60 (1): 16–25, 2014].

Keywords  Amphibians, Birds, Defenses, Dishonesty, Mammals, Prey, Reptiles

1 Introduction

In this paper I review forms of deceptive antipredator defenses in terrestrial vertebrates, a topic that has been largely ignored for 25 years (Pough, 1988). I limit my scope to terrestrial organisms because lighting conditions in water are different from those in the air and antipredator strategies often differ in the two environments. I define antipredator deception as a behavioural or morphological trait that reduces the profitability of a predatory attempt through dishonesty by obscuring the presence of an animal, increasing its apparent handling time, or lowering the apparent benefits of consumption.

Antipredator deception can occur by means of (i) depriving the predator of information, (ii) by providing cues and (iii) through signals and all are seen in vertebrates. Most examples of crypsis, be they principally morphological as in background matching, behavioural as in remaining still, or both are selected so as to prevent the predator detecting the presence of prey in the environment. Cues (which are generated inadvertently for purposes other than communication [Bradbury and Vehrencamp, 2011]) may be honest markers of unprofitability or dishonest markers in that they increase apparent handling time of an otherwise profitable prey item. For example, body inflation in anurans may make gripping prey more difficult or it may fool the predator into assessing the prey is too large to handle (Toledo et al., 2011). Similarly, a rapid change in flight path in homeotherms may increase the distance between prey and the pursuing predator or dupe the predator about the flight path trajectory, or both (FitzGibbon, 1990).

Last, an antipredator defense may be a dishonest signal. Bradbury and Vehrencamp (2011) state that “true deception occurs when a sender produces a signal whose reception will benefit it at the expense of the receiver regardless of the condition with which the signal is supposed to be correlated” (see also Maynard Smith and Harper, 2004). Examples of Batesian mimicry or death feigning fall into this category. These have been selected to make the predator respond in a way that benefits the signaler but not the receiver.

Unfortunately, it is often problematic to demonstrate dishonesty because the trait may be honest but imperfect or incomplete (Endler, 1978). For instance, a bluff charge might be deceitful or simply a charge that failed to be carried through raising the issue of intent which is difficult to investigate operationally. In addition, a signal may be honest to a small predator but dishonest to a large one. Empirical data and sensory and economic analyses are required to tease apart these possibilities yet none exist for vertebrates. Therefore many of the putative cases of antipredator deception listed below, broadly in predatory sequence, are difficult to attribute unequivocally as dishonest because convincing data on their beneficial consequences for prey, and the mechanisms by which they are achieved, are lacking even in these well known taxa.

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* Corresponding author. E-mail: tmcaro@ucdavis.edu

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2 Crypsis: Depriving the Predator of Information

2.1 Background matching

Crypsis is a range of strategies that prevents detection (Stevens and Merilaita, 2009) and is therefore a type of deception in that the colour, morphology and behaviour of an individual make it difficult to distinguish from the background (Diamond and Bond, 2013). I concur with Ruxton (2011) that a cryptic organism has an impact on the sensory system of the receiver such that if the organism was removed, the flow of information would change. This distinguishes crypsis from hiding. Crypsis occurs by means of several mechanisms only some of which are found in terrestrial vertebrates (Edmunds, 1974; Ruxton et al., 2004). The principal one is background matching, where the appearance of the animal generally matches the colour, lightness and pattern of one (specialist) or several (compromise) background types (Stevens and Merilaita, 2011). The most famous example of background matching is of industrial melanism in the peppered moth Biston betularia (Kettlewell, 1973). In mammals, comparative studies reveal that patterns of colouration in species of artiodactyls (Stoner et al. 2003a), carnivores (Ortolani and Caro, 1996; Allen et al., 2011), lagomorphs (Stoner et al., 2003b), cetaceans (Caro et al., 2011) and pinnipeds (Caro et al., 2012) often resemble the general colour features of their habitat suggesting that predators (generally) are being deceived about the presence of prey in the environment. Within species, experiments with different coloured plasticine Peromyscus mice show that there is strong selection by predators for prey to match the background closely (Vignieri et al., 2010).

In birds, females are often drab compared to males, and it has long been thought that female ground nesting species need to be brown or speckled to avoid being detected while incubating their eggs (Wallace, 1868; Sober and Moreno, 2012). In addition, speckled egg colouration is thought to be an adaptation to avoid detection by predators (Kilner, 2006) especially in open nesting passerines (Westmoreland and Kiltie 1996; but see Cherry and Gosler, 2010). In quail Coturnix japonica, eggs of different hue may be laid on the types of substrate that make them optimally camouflaged (Lovell et al., 2013).

Remarkable resemblances are found between lizards and snakes and their backgrounds (Cooper, 2012; Farallo and Forstner, 2012; Isaac and Gregory, 2013). Across snakes, blotched patterns are seen in large, slow ambush-hunting species, spots are found on species residing near cover, and small speckled patterns are found on habitat generalists (Allen et al., 2013). Testudines and crocodilians have dark and mottled shells and skins that appear to match their aquatic environment (Norris and Lowe, 1964; Greene, 1988). Anuran and salamander species appear to match leaf litter, pond and river vegetation using uniform or mottled colouration to avoid detection by predators (e.g., Hoffman and Blouin, 2000; Cooper et al., 2008; Eastman et al., 2009). For example, lighter Ambystoma barbouri salamander larvae have higher survival than darker larvae in fish filled streams (Storfer et al., 1999). As an aside, glass frogs (Centrolenidae) have transparent ventra which might possibly help to blend in with the background and avoid detection (Rudh and Qvarnstrom, 2013).

In general, mammals do not change colour during their lifetimes but some species have particularly coloured natal coats. For example, pinniped species that have white natal coats live in the arctic and are subject to terrestrial predation whereas species that give birth on islands or in caves where predation risk is low have black natal coats (Caro et al., 2012). Artiodactyl species that hide their young after birth have spotted neonates (Stoner et al., 2003a). Some arctic and tundra artiodactyls and carnivores show seasonal colour change taking on lighter coats in winter (Ortolani and Caro, 1996; Stoner et al., 2003a). Similarly, in birds, some arctic species have white winter plumage (Ward et al., 2007). Other gaudy birds change colour only when they reach sexual maturity, or revert to drab plumage out of the breeding season (Berggren et al., 2004). All these are strongly suggestive of colour change being linked to predator avoidance.

Colour change is more prevalent and can be more rapid in poikilotherms where it is used for both social signaling and crypsis (Waring, 1963). Regarding the latter, some morphs of Pacific tree frogs Hyla regilla change from green to brown in a matter of weeks (Wente and Phillips, 2003). Ambystoma barbouri salamander larvae change their colour to resemble their background whereas A. texanum move to backgrounds that match their colour (Garcia and Sih, 2003). Moorish geckos Tarentola mauritanica change colour to match their background (Vroonen et al., 2012) and dwarf chameleons Bradypodion taeniabronchum change colour in response to both background and type of predator (Stuart-Fox et al., 2006).

Crypsis can also be behaviourally mediated with an animal choosing a microhabitat to increase similarity to
a background, or aligning its orientation to increase localized similarity, or choosing a background with greater scene complexity where searching is difficult (Webster et al., 2011). Many vertebrates select habitats in which they are cryptic such as spotted felids resting and hunting in trees (Allen et al., 2011), align themselves to match background patterns such as great bit terns Botaurus stellaris pointing their bill upwards and turning to expose their vertically striped breasts when standing in reeds (Cott, 1940); and rest in leaf litter such as mottled copperhead Agkistrodon contortix (Bechtel, 1978).

Usually morphological crypsis is closely associated with behavioural crypsis as predators often detect prey through movement (Roosevelt, 1910). For instance, species that show morphological crypsis often move slowly or rest quietly for considerable portions of the day, or freeze when threatened by predators. For example, artiodactyls with spotted young lie hidden when their mothers leave to forage (Stoner et al., 2003a); willow grouse Lagopus lagopus become motionless when approached by a predator (Gabrielsen et al., 1985); and lizard sit-and-wait predators show cryptic freezing behaviour when threatened whereas widely foraging species flee from predators (Vitt and Congdon, 1978). Blotched and ringed snakes rely on immobility and threat whereas striped and unicoloured snakes flee when disturbed (Jackson et al., 1976). Similarly, immobility may reduce the severity of predatory attack in salamanders (Brodie, 1977).

2.2 Countershading

Dorsal pigmentary darkening takes the form of a light ventral surface and darker dorsum (Poulton, 1888; Thayer, 1896; Kiltie, 1988). Many invertebrates and vertebrates show this pattern of colouration (De Ruiter, 1956; Gomez and Thery, 2007). Dorsal pigmentary darkening may help to make an animal cryptic through self-shadow concealment where directional light that would lead to the creation of shadows cast by the animal’s own body is reduced or cancelled out by countershading (Stevens and Merilaita, 2011). Alternatively, it could reduce conspicuous brightness contrast when viewed from above or below, especially in birds in the air and amphibians in water; or it could reduce three-dimensional cues making it difficult to be recognized as a prey item; or it could blur the outline of an animal when viewed from above (Rowland, 2011). Allen and coworkers showed experimentally that countershading in ruminants is well matched to that expected for minimizing self-shadow, and that countershading in artiodactyls is associated with desert habitats, small body size and living near the equator where lighting and predation risk are intense (Stoner et al., 2003a; Allen et al., 2012). Dorsal pigmentary darkening is so widespread in vertebrates that it might not only be involved in countershading but could also serve in protecting the animal from UV light, in thermoregulation or in protection from abrasion (Rowland, 2011).

2.3 Masquerade

Another means of depriving a predator of information is through masquerade where prey recognition is prevented by prey resembling an uninteresting object, such as a leaf or stick (Stevens and Merilaita, 2011). It differs from crypsis because it foils recognition rather than detection but I have included it here for convenience. Masquerade is found in some caterpillars (Skelhorn et al., 2010a) where it has been shown to foil recognition by bird predators (Skelhorn et al., 2010b) but it has never been formally investigated in terrestrial vertebrates and there are only a few anecdotal examples. These include resting frogmouths Podargus strigoides resembling the ends of broken branches (Kortner and Geiser, 1999); tree-living colubrids with long thin bodies that look similar to vines (some Oxybelis species move in an irregular swaying motion akin to a vine trembling in the wind [Gower et al., 2012]); and toads in the Rhinella typhonius group resembling a fallen leaf (Duellman and Trueb, 1994).

2.4 Using the environment to change appearance

Some species anoint themselves with soil to change colour. Male ptarmigan Lagopus mutus are white in winter but they dirty their plumage at the arrival of snowmelt in spring and as opportunities for attracting mates dwindle (Montgomerie et al., 2001). California ground squirrels Spermophilus beecheyi and Siberian chipmunks Eutomias sibiricus anoint themselves with snake scent by chewing on shed skin and then licking themselves probably deceiving snake predators as to their identity (Kobayashi and Watanabi, 1981; Clucas et al., 2008). European hedgehogs Erinaceus europaeus perform similar behaviour possibly to disguise their smell from predators (Herter, 1965).

3 Batesian Mimicry: Dishonest Signals

3.1 Visual

In Batesian mimicry, a harmless mimic resembles an aposematic animal, the model, so that the predator confuses the two and avoids the mimic (Mallet and Joron, 1999). Batesian mimicry is common in invertebrates (McIver and Stonedahl, 1993; Mallet and Gilbert, 1995;
Oxford and Gillespie, 1998). In contrast to insects (Guilford, 1990), however, aposematism is comparatively rare in homeotherms (Dumbacher and Fleischer, 2001; Caro, 2013), and anecdotes about mammals resembling dangerous heterospecifics seem unfounded (Caro, 2005). In venomous snakes, however, aposematism is more common and many instances of Batesian mimicry have been reported, in particular in harmless or mildly venomous colubrid and aniliid snakes mimicking highly venomous elapid coral snakes in the Americas (Greene and McDiarmond, 1981; Savage and Slowinski, 1992; Brodie, 1995). Other non-venomous snakes mimic the highly characteristic dorsal patterns of venomous vipers (Gans, 1961; Brodie and Brodie, 2004). Some of these mimics are imperfect (Sherratt, 2002) either because the strong toxicity of the model makes predators generalize across a variety of snake colour patterns (Pough, 1988) or because of limited predator cognitive abilities (Kikuchi and Pfennig, 2010). A behavioural example of snake mimicry is when colubrids flatten their heads to resemble European vipers so as to reduce attacks by raptors (Valkonen et al., 2011). Batesian mimicry has been reported in salamanders too: experimental studies show hesitancy of bird predators attacking putative mimics of toxic model species (Howard and Brodie, 2004). The extent of mimetic resemblance depends on model toxicity with more precise mimicry of less toxic models that are less immune to predatory attack (Darst and Cummings, 2006).

Less well-worked cases of mimicry include juvenile Kalahari desert lacertids *Eremias lugubris* using a jerky motion that resembles movements of noxious beetles (Huey and Pianka, 1977). Also, pygopodids are limbless lizards that show false strikes that might mimic the behaviour of elapid snakes (Bustard, 1968). Some frogs produce odours that resemble those of smashed plants perhaps misleading the predator that a larger danger is present (Smith et al., 2004).

### 3.2 Acoustic

When disturbed in their burrows, burrowing owls *Athena cunicularia* produce hisses that sound like an agitated rattlesnake *Crotalus viridis*. California ground squirrels with experience of rattlesnakes respond by becoming more cautious when entering these burrows, so it is possible that these sounds deter carnivores that might dig for fledglings or roosting adults (Rowe et al., 1986).

In Mullerian mimicry two toxic species resemble each other so as to share predator education. Mullerian mimics are each aposematic and advertise relatively honestly unless levels of toxicity are very unequal. Mullerian mimicry in vertebrates has been documented in *Pitohui* birds (Dumbacher and Fleischer, 2001), Asian pit vipers (Sanders et al., 2006) and poison dart frogs (Symula et al., 2001).

## 4 Bluff: Dishonest Cues and Signals

### 4.1 Apparent size

Some vertebrates increase their apparent size when threatened by predators. Piloerection in response to heterospecific and conspecific threat is well documented in mammals. For example, many carnivores erect their dorsal hair and appear larger when threatened (Ewer, 1968). Many avian species fluff up their feathers when standing their ground against predators. Cobras erect hoods and elapids and colubrids flatten their foreparts when in a defensive posture which enlarges the size of their heads (Greene, 1988); some crotaline vipers, elapid vipers depress and raise loops of their body off the ground (Gower et al., 2012). *Corytophanes cristatus*, a neotropical iguana, elevates a dorsal crest to increase its size when viewed laterally (Davis, 1953). Some lizards elevate frills around their throat when threatened. Ranids, hylids and especially bufonids inflate their bodies when in jeopardy (Marchisin and Anderson, 1978; Toledo et al., 2011). Markings and spots on enlarged parts of the body may draw attention to an increase in apparent size: some mammals have darker dorsal crests, for instance. These strategies may fool predators about true body size and are therefore dishonest signals, or make prey handling more difficult and are therefore honest cues, or both.

### 4.2 Charges

Large species with weaponry may initiate bluff charges at predators. For example, a charge by an African elephant *Loxodonta africana* deters most people approaching on foot. Other large mammals including Cape buffalo *Synercus caffer* and black rhinoceros *Diceros bicornis* bluff charge. Large birds such as ostrich *Struthio camelus* will see off predators in this way.

### 4.3 Exaggerated threat displays

Startle signals are common in Lepidoptera where bright patches of colour are displayed when the animal is disturbed at rest (Stevens, 2005). In vertebrates putative examples of dishonest threat include “eyespots” on the dorsolateral surface of the gecko *Sphaerodactylus*
semasiops that may frighten predators (Thomas, 1975). Physalaemus frogs have eyespot-like toxic glands on their lateral skin that they display when alarmed (Lenzi-Mattos et al., 2005) but it is not clear whether this is honest or dishonest signaling. More commonly, terrestrial vertebrates gape, hiss or spit at their persecutor showing intention movements to bite. For example, collared peccaries Pecari angulatus, duck-billed platypuses Ornithorhynchus anatinus, American coots Fulica americana and crested guans Penelope purpurascens growl, whereas young carnivores, parids and tetraroids hiss at predators (Caro, 2005). Some testudines, such as the common snapping turtle Chelydra serpentine, hiss and gape; and snakes, Boidae for instance, hiss vociferously when danger threatens. Other snakes, such as desert horned vipers Cerastes cerastes, rub body scales together creating a hissing sound (Greene, 1988); yet others such as the western hook-nosed snake Gyalopion canum make popping noises by expelling air through the cloaca (Gower et al., 2012). The Australian gecko Nephrurus asper lunges at predators (Bustard, 1967). Several anuran taxa open their mouths and gape at predators (Duellmann and Trueb, 1994), others additionally scream (Toledo and Haddad, 2009). Such threats may honestly draw attention to dangerous jaws or teeth but may carry dishonest information about the prey’s ability to defend itself.

Some birds utter distress calls when grasped by a predator which serves to attract other predators but can simultaneously startle the predator into releasing its grip (Conover, 1994; Moller et al., 2011).

5 Feignts: Dishonest Signals and Cues

5.1 Injury

Charadriiformes, galliformes, anseriformes, columbiiformes and passerines perform a wide variety of deceptive behaviours while nesting that include distraction displays (in which the parent runs off in a crouched position resembling a small rodent); feigning injury (erratic fluttering where the bird makes convulsive attempts to run, fly, and jump); or false brooding (in which the parent squats on the ground apparently incubating) (Gochfeld, 1984). These are instances of dishonest signaling. Many of these behaviours, such as pretending that the wing is broken or mimicking death throes, apparently make the parent easier to capture. Moreover, some involve entrapment whereby the parent returns to the intruder if it loses interest. Armstrong (1954) outlined six factors that predispose birds to show injury feigning: when the young are in open terrain because prey can see predators from a distance, (ii) when the nest is accessible to non-avian predators; (iii) when the nest is inconspicuous or insubstantial; (iv) among birds that nest alone; (v) when predation occurs in daylight and by mammalian or reptilian predators; and (vi) in northern latitudes with extended daylight. These ideas constitute an interesting and novel attempt to identify ecological drivers of deception in one group of vertebrates.

5.2 Death

Death feigning, tonic immobility or thanatosis is widespread in terrestrial vertebrate taxa (Dodd and Brodie, 1976; Caldwell et al., 1980; Greene, 1988; Caro, 2005) especially in birds. For example, tonic immobility in European avian species is strongly associated with extent of goshawk Accipter gentilis and cat Felis catus predation (Moller et al., 2011). In reptiles, death feigning has been reported in crocodilians, snakes, testudines, and is ubiquitous in gekkotan lizards (Greene, 1988). Dwarf boas autohemorrhage from the eyes and mouth; hognosed snakes bleed from the cloaca (Gower et al., 2012). Some anurans will flip onto their backs in a death-like pose (Toledo et al., 2011). Rigid postures in snakes and lizards and immobility in anurans are also known. Superficially thanatosis in homeotherms resembles sleep but differs from it in several ways. In common possums Didelphis marsupialis, for instance, the eyes and mouth are open in death feigning, the lateral but not dorsal aspect is uppermost, feet and toes are visible andflexed, the ears twitch at a sharp sound, and no responses are elicited by prodding (Franqc, 1969). Little work has been performed on thanatosis and it may be that, rather than providing dishonest cues that the animal is dead, lack of movement in some prey species confers selection benefits by depriving predators of the necessary movement stimulus to launch a final attack (Thompson et al., 1981).

6 Distraction: Dishonest Signals

An attack to the tail is less costly than to the head and some species have morphological or behavioural mechanisms for attracting attention to this part of the body. Powell (1982) showed that trained red-tailed hawks Buteo jamaicensis more often missed artificial long-tailed weasels Mustela freneta that had a spot on their tail than models with spots in other places. Iguanids and agamids sometimes elevate and wave their tails at approaching predators before they flee which may divert attack from the head. Snakes and amphibiaeans may divert attack in the same way. For instance, Asian...
sand boas *Eryx tataricus* wave their tails which are patterned to resemble their head. Many snakes hide their heads under coiled bodies removing this critical feature from attack (Greene, 1988).

Lepidosaurian lizards, some salamanders, and a few snakes and rodents autotomize their tails when attacked (Cooper, 1998). Tails are usually shed after the tail has been seized and may then act as a distraction especially if they thrash as occurs in some lizards (Arnold, 1988). Some skinks thrash their attached tail in the presence of a snake apparently to draw the snake’s strike, the tail is then autotomized (Cooper and Vitt, 1985). Whether autotomy is necessarily a means of deception or a means of providing predators with alternative food to the prey’s body is an open question. Autotomy also occurs in some rodents but is unlikely to be deceptive as tails are not thrashed or waved in anticipation of attack. Some snakes, such as atractaspine lamprophids, have pointed hardened tail tips that they poke into predators that have seized them which may dupe the latter into perceiving they have been bitten.

Some snakes regurgitate recent meals when disturbed which may distract predators from the live animal. Defecation after being contacted by a predator is widespread in vertebrate taxa and foul smelling cloacal discharge occurs in amphibians, and in snakes, especially large, slow ambush-hunters (Allen et al., 2013). These may distract the attention of the predator (deception) or provide alternative food to the body (provide resources). Most of these antipredator defenses seem to have been selected to signal to predators. Some appear to be honest in providing a meal or signaling noxiousness, others appear to dishonestly attract a predator to less critical parts of the body.

### 7 Flight: Dishonest Cues

Certain rodents such as kangaroo rats and artiodactyls such as Thomson’s gazelles *Gazella thomsonii* flee from predators by running in zigzags; California ground squirrels jump sideways; and great tits *Parus major* roll and loop in flight. Rapid changes in flight direction or bursts of speed could be possible forms of deception in that they fool the predator about the path or speed of flight. Zig-zagging, looping, twisting or sudden bouncing (termed protein behaviour, Humphries and Driver, 1967) may confuse the predator making it difficult to select individual targets, in aiming at quarry, in pursuing it, in concentrating attention on it, or in filtering complex information from several individuals showing different coloured surfaces or colour patches displayed in or out of synchrony (Milinski, 1977; Ohguchi, 1981; FitzGibbon, 1990); it is difficult to know whether to interpret these as deceptive.

Motion camouflage is movement in a fashion that decreases the probability of movement detection (Stevens and Merilaite, 2011). There are no known examples in homeotherms but it is believed to occur in some snakes (Lindell and Forsman, 1996). Longitudinally striped snakes and unicoloured speckled snakes can flee quickly and it is difficult for humans to ascertain that the animal is moving forward without individually recognizable markings such as dorsal blotches that provide reference points. In addition, if movement is detected the apparent velocity is lower in uniformly coloured than blotched species (Jackson et al., 1976). A separate point is that contrasting patterns in some snakes may make speed and trajectory difficult to estimate (Brodie, 1992; Stevens et al., 2008).

Some species display prominent patches of colour during flight including lagomorphs such as European rabbits *Oryctolagus cuniculus* and artiodactyls such as bushbuck *Tragelaphus scriptus*. Towards the end of flight these conspicuous patches are suddenly hidden causing prey to apparently vanish.

### 8 Conclusions

While antipredator deception can occur at any point during the predatory sequence from where the predator is searching for prey to where it is about to consume it, our present knowledge of antipredator defenses suggests that instances of deception other than crypsis are not widespread in terrestrial vertebrates (see Table 1). Thus antipredator deception in vertebrates principally relies on depriving predators of information. Deception is

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<td>Background matching</td>
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+++ denotes common, ++ sometimes observed, + rare; unfilled cells denote not recorded.
maintained in evolutionary terms if the costs to the receiver are low or if the costs of detecting cheats are very high. Generally, most terrestrial vertebrate prey-predator systems likely fall into the first type as predators can always find other prey items if they are duped into failing to detect, recognize or pursue prey. Only in snake or salamander mimicry systems are there likely to be very high costs of trying to ascertain cheats. Snake models can be highly venomous, potentially making mistakes in prey classification lethal. Unlike invertebrates, absence of toxicity in most terrestrial vertebrate taxa makes instances of Batesian mimicry unusual and this path to deceptive trait evolution relatively rare.

How can we explain the distribution of different forms of deception across vertebrate taxa? In every terrestrial vertebrate class evolution has favoured crypticity through background matching (Cott, 1940). This means of avoiding detection by predators perhaps confers greatest benefits in avoiding predatory attack although it carries potential costs of restricting organisms to certain habitats or to foraging at certain times of day (Ruxton et al., 2004). Crypticity through self-shadow concealment by means of dorsal pigmented darkening may be common in mammals although countershading may be driven by other factors such as background matching from above and below during flight in birds. Reptiles and amphibians have less need to reduce self shadow as they have short legs and move nearer to the ground. Batesian mimicry is restricted to some groups of snakes and salamanders. Bluff attacks and exaggerated threat displays are seen in all classes and constitute a defense of last resort where similar-sized or smaller predators may be intimidated. Feigning injury is principally found in birds: likely these are geared towards duping mammalian predators but the reasons that these are not seen in mammalian prey are unclear. Death feigning is seen in all taxa and it deserves more study because the extent to which this behaviour helps avoid attack and the mechanisms by which it affects predatory behaviour are poorly understood. Distraction behaviours are found in only a few groups; furthermore it is not clear whether such traits are strictly deceptive. Protean behaviour and motion camouflage during flight is similarly difficult to attribute unequivocally to deception (Table 1).

In summary, all classes of terrestrial vertebrates exhibit deceptive antipredator defenses but the extent to which they are deployed by a given prey species must depend on the background on which it lives, prey morphology and defenses, the visual capabilities and behaviour of the predator, its relative size compared to its predators, and even defenses of sympatric prey species. This eclectic mix of evolutionary drivers makes it difficult to predict where antipredator deception occurs in nature and whether the paucity of deceptive antipredator defenses recorded thus far in terrestrial vertebrates is representative or simply reflects a lack of scientific attention to this topic.

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