Joseph Jordania (2014). In: *Tigers, Lions and Humans: History of Rivalry, Conflict, Reverence and Love*. Logos Publishing. ISBN 978-9941-437-60-1.

Short History of the idea of Aposematism

Every idea has its history, consisting of a birth, early growth and a coming of age. The death of ideas can also happen. Sometimes an idea is stillborn, but an image of successful life is given by caretakers. In other cases a healthy idea is considered stillborn, until someone later manages to revive it and gives it new life. Apart from a biological parent (or parents if it is collaboration), ideas may also have godparents, individuals who will adopt an early idea and raise it into something more widespread. Sometimes the identity of the parent or godparent of an idea is lost in the mists of history, or in the depths of scholarly intrigue. The idea of the warning display, later coined as aposematism, has the most glorious biological parents that the history of evolutionary study can provide: the famed co-discoverers of the theory of natural selection: Charles Darwin and Alfred Wallace. The idea of a warning display, or "warning flags" was born in February 1867, during the communication of these two great scholars. Despite these glorious parents the idea of warning display for some reason never really received its "coming of age", the attention it deserved.

1867 was the year when Darwin was busy writing his second big book, "The Descent of Man." The full title of this book reads as "The Descent of Man, and Selection in Relation to Sex." You can already anticipate from the title of the book that Darwin will attribute sexual selection as having crucial importance in human evolution. The book indeed argues that sexual selection was the driving force in the evolution of humans as well as many other species. Because of this, Darwin's book was criticized both by his contemporaries and following generations of scholars. More precisely, Darwin was criticized for two reasons, (1) that his book was more about sexual selection than about human origins and evolution, and more importantly, (2) that Darwin overrated the importance of sexual selection in human evolution (and in evolution in general).

Scholars still remain divided about the importance of sexual selection in evolution, and in particular in human evolution.

It is true that Darwin was attributing the large diversity of animal species to the forces of sexual selection. Virtually everything that could not be explained by the forces of natural selection through the ubiquitous "struggle for survival", Darwin attributed to the forces of sexual selection. All the exaggerated morphological features of animal bodies such as the bright colours of insects to the tail of the peacock (known as its "train"), plus all the strange behaviours ("antics") and sounds of many animal species, were stated by Darwin to be the result of the work of sexual selection.

By its potential, the model of sexual selection was about as potent and the model of Creation. The main difference between them is that instead of God's will

and desire as the creative power behind all changes, sexual selection puts in the centre of the evolution the will and desire of our female counterparts. Male behaviour and morphology, according to the proponents of sexual selection, totally depended on females' arbitrary choices. This idea is clearly expressed in the following phrase from an American scholar from the University of New Mexico, Geoffrey Miller, one of the most ardent contemporary proponents of sexual selection: "for the most part adult male hominids must have been rather peripheral characters in human evolution, except as bearers of traits sexually selected by females for their amusement value or utility" (Miler, 1998: 109-110).

All was going well for Darwin, as he could find plenty of difference in the shapes, sizes, colours, sounds and behaviours between the different sexes of a vast array of animals. But suddenly he hit a brick wall. It was when he was trying to explain the brilliant colours of several species of caterpillars. You may be thinking that he would not have hesitated to attribute their brilliant colour schemes to the power of sexual selection, but there was one huge problem - caterpillars were not yet sexually active, so sexual selection was theoretically and ultimately ruled out, at least for caterpillars. So what then was the reason for their beauty? As a staunch evolutionist, Darwin was sure that such brilliant colours could not have been developed without a practical reason to do so. He would not accept the dominating theological explanation at the time, suggesting that the existence of beauty was proof of the existence of an almighty and conscious Creator. According to the creationist view, the beauty has no utility other than to give aesthetic pleasure, and that humans (God's 'highest' creatures) are the only creatures who can truly appreciate such beauty.

Finding himself in a troubling situation and unable to use his favourite model of sexual selection to explain this discovery, Darwin wrote to Wallace on February 23, explaining his predicament and asking if his friend had a solution to this problem.

Wallace's answer, written the next day on February 24th, to Darwin is one of the most important letters written in the history of biology. Wallace had noticed that the animal species which had good secondary defences (for example stingers, poison, or an unpalatable/noxious body texture), were also the ones with visible colours, seemingly a warning to predators that it was advisable to refrain from attacking them. Wallace wrote:

> "*The animals in question are possessors of some deadly weapons, as stings of poison fangs, or they are uneatable, and are thus so disagreeable to the usual enemies of their kind that they are never attacked when their peculiar powers or properties are known. It is therefore, important that they should not be mistaken for defenseless or eatable species of the same class or order since they might suffer injury, or even death, before their enemies discovered the danger or uselessness of their attack. They require some signal or danger flag which shall serve as a warning to would-be enemies not to attack them, and they have usually obtained this in the form of conspicuous or brilliant colouration, very distinct from the protective tints of the defenseless animals allied to them*" (Wallace, 1889:232).

Continuing this idea, Wallace also suggested that birds and other predators would reject the conspicuously looking prey, and would rather chose the more cryptic (built for concealment), non-conspicuous looking prey or food items. After learning about Wallace's ideas, John Weir from the Entomological Society of London conducted experiments with caterpillars and birds in his aviary, and after a few years in 1869, he reported the first experimental evidence of the effectiveness of warning colouration in animals.

Wallace's letter to Darwin contained two brilliant ideas, (1) the idea of a "warning display," later developed by Sir Edward Poulton into the idea of aposematism (Poulton also coined the term "aposematism"), and (2) the suggestion that predators would reject colourful and unknown preys, developed later into the idea of neophobia among predators (avoidance of new and unusually flamboyant-looking animals).

Darwin's reaction to Wallace's letter was overtly positive. He was very pleased that the dilemma of the conspicuous-looking caterpillars was settled, and he wrote in reply to Wallace's letter: "I have never heard anything more ingenious than your suggestion, and I hope that you may be able to prove it true." Receiving Darwin's letter must have been one of the happiest moments of Wallace's scholarly life.

Here we are closing in on a crucial idea, so far mostly neglected in scholarly literature: animal species can develop distinctive colours, hard-to-explain morphological structures and strange behaviours in order to attract mates on one hand, but on the other hand, animal species can develop exactly the same kind of distinctive colours, sounds, morphological structure and strange behaviours in order to ward off predators and competitors, thereby avoiding unnecessary and violent confrontations. This idea was implicit in Wallace's letter to Darwin, but was unfortunately dismissed by Darwin, as Charles was at the moment still overwhelmed at finding such an abundance of "evidence" of the importance of sexual selection. For Darwin, Wallace's idea was only there to explain the cases of bright colours that did not already fit the model of sexual selection.

Quite amazingly, Wallace himself did not grasp the implicit importance of his suggestion regarding the animal kingdom. Just a couple of years later Wallace and Darwin had a discussion about the peacock's amazingly beautiful train. Darwin was sure that the power of sexual selection was at work here. Wallace had another idea, but instead of suggesting that the peacock train could have had a function of scaring away competitors and predators (we will discuss this idea later), Wallace instead came up with a very implausible suggestion that the bright colours and long tails of the peacock were not adaptive in any way. According to him, bright colouration could have been the result from non-adaptive physiological mechanisms. For example, he argued, the internal organs of animals that are impossible to see are often still brightly coloured.

Therefore, we have a very sensitive situation for scholars interested in the mechanisms of both sexual selection and aposematism. Sexual selection and the warning display (aposematism) work using the exact same elements: bright colours, sounds, smells and behaviours, but with totally different driving mechanisms: sexual

selection is driven through the female choice (which can be arbitrary) leading to mating success, but aposematism is driven by the mechanisms of natural selection through the warning display, leading to survival from predators and avoidance of unnecessary violent conflicts. *Attracting* in one case, and *intimidating* in other case.

Of course, there is no good reason why these two forces, aposematism and sexual selection, could not work together. Essentially, females may find attraction the same traits that help their male counterparts avoid violence and survive, particularly as these traits are more colourful, noisier, and generally more attention-grabbing. But here comes the crucial question: Which of these two forces is the primary and which of them is secondary? Proponents of sexual selection of course would suggest that sexual selection is the primary reason, to the extent that certain traits are not only unnecessary for survival, but actually detrimental to it. The idea of this "handicap principle," suggested by the celebrated Israeli evolutionary biologist Amotz Zahavi, proposes that the true ("honest") signal for the mate's choice must in theory be detrimental to survival. A peacock's amazingly beautiful train is the best proof available for this line of thinking and was featured on the cover of Zahavi's book. We will discuss the possible reasons for the beauty of a peacock's train later in the book, but I would like to propose that, in the case of the shared responsibilities of sexual selection and aposematism which are carried by bright colours, loud sounds and exaggerated shapes, the aposematic warning display is most likely the primary force, thereby making sexual selection a secondary objective of these traits. As we are going to discuss this issue in detail a bit later, let us go back to Darwin-Wallace communication about the idea of a warning display.

Unfortunately, whilst reading Wallace's letter, Darwin was too engrossed in the power of sexual selection to be able to appreciate the wider explanatory potential of Wallace's new and brilliant idea. For him the idea of a "warning display" was a good enough explanation for the sexually-immature caterpillar's brilliant colour schemes, and after solving this troubling problem Darwin never looked back to Wallace's idea of warning displays. This is why Darwin did not go any further in considering the importance of warning displays in the evolution of the morphology and behaviour of a large array of conspicuously looking animal species. It was through this process that the big chance for early appreciation of the principle of warning displays was lost.

Here is more evidence that Darwin did not even consider the possibility that brilliant colours, exaggerated morphology and different behavioural displays of males could serve as anything else but as a means for successful sexual selection through a possibly arbitrary female choice. Arguing for the importance of sexual selection, Darwin famously wrote: 'To suppose that the females do not appreciate the beauty of the males, is to admit that their splendid decorations, all their pomp and display, are useless; and this is incredible' (Darwin, 2004:557). We can all certainly agree with the great scholar that all the 'splendid decorations' and 'all their pomp and display' were definitely created by the forces of evolution for a good reason. This reason was definitely to impress, but to impress who? Were they created to impress females for better mating opportunities, or to impress predators and rivals for better survival chances through avoiding unnecessary violence? Darwin did not even

mention the survival benefits of bright colours and unusual behaviours, which means that he never looked at the alternative explanation of brilliant colours. If he did, possibly his book on human origins might have had a different title and quite different content.

It was Poulton who proved Wallace's idea to be true in 1887. And still, even after 130 years, the idea of the warning display remains in the shadow of the bigger idea of sexual selection. The unique position and extremely high authority that Darwin commanded must have been one of the central catalysts to the popularity of the idea of sexual selection on one hand, and also to the neglect of aposematism on the other hand.

Certain progress was definitely made in the subsequent decades, but the idea and notion of aposematism is still very much on the periphery of contemporary biological science. According to my observation, some scholars do not even know what the term "aposematism" means (I have also discovered through my writing that Microsoft Word also does not recognise this term). For a long time even the origin of aposematism itself was considered a puzzle as, according to R. A. Fisher (Fisher, 1930), aposematic individuals have more issues with survival from predators than cryptic ones. It was only by the beginning of the 21st century that scholars came to the more realistic conclusion that aposematic prey individuals might have good chances of survival because of the natural aversion shown by many predators when introduced to new and unusual food. This phenomenon is known as "neophobia."

"There is evidence that predators are particularly cautious in dealing with potential prey having bright colour patterns" suggests the 2008 edition of an Australian Biology textbook (Campbell, 2008: 1223). Furthermore, even in this grandiose book, aposematism is mentioned only once in connection to colours, without mentioning sounds, smells, or behaviours as other important elements of an aposematic display.

Also, it was only in the 21st century that scholars started appreciating the idea of aposematism among plants (see: Lev-Yadun, 2009). Scholars started finding more and more aposematic species not only among insects and reptiles, but among plenty of mammalian species as well. For a long time only the skunk and zorilla (striped polecat) were considered as rare examples of aposematic mammalian species, later studies suggested that the list of the aposematic mammalian species can be indeed rather large (see, for example, Caro, 2009). When discussing the reasons for contrasting colouration, under the categories "aposematism likely" and "aposematism very likely" Tim Caro lists the following animal groups: echidnas, tenrecs, hedgehogs, possums, wolves, foxes, raccoons, enotes, skunks, civets, moonrats, porcupines, weasels, and mongooses. If we remember that in his article Caro is discussing **only** black-and-white coloured species (hence "contrasting colouration"), we can start to get an idea of how large the list of species using aposematic colouration can really be.

Joseph Jordania (2014). In: *Tigers, Lions and Humans: History of Rivalry, Conflict, Reverence and Love*. Logos Publishing. ISBN 978-9941-437-60-1.

A Few Facts and Ideas about Aposematism

As I have already mentioned, aposematism is gradually gaining scholarly recognition despite still being very far from its dues. From personal experience, I can testify that the term "aposematism" is rarely mentioned even by scholars of evolution. The term "warning colouration" is routinely used instead of aposematism. Alternatively, "warning signals" or "warning display" would both be better substitutes for aposematism than "warning colouration", as aposematism definitely involves more elements than colouration. The Wikipedia article on aposematism, for example, starts the article with the words "Aposematism (from *apo-* away, and *sematic* sign/meaning), perhaps most commonly known in the context of warning colouration...". Another Wikipedia article, this time on the skunk, a classically obvious aposematic animal, still did not even contain the word "aposematic" when I last checked in June 2012. Even the title of the most recent book on animal defence strategies, in which you can learn plenty of things about aposematism, reads like this: "Avoiding attack: The evolutionary ecology of crypsis, warning signals, and mimicry". If the term "aposematism" was better known, I guess the book would be titled a more fluent "Avoiding attack: The evolutionary ecology of crypsis, aposematism, and mimicry."

By now we already know that aposematism is not only colouration. We know that when aposematic animals try to get attention, they mostly do this by using warning flags in several modalities simultaneously. Apart from colouration, aposematic animals try to look tall and wide, they make various sounds, and they also often emit a body odour. Together with these morphological signals, they also use behavioural signals such as moving slowly and awkwardly, as if signaling to the predator their confidence in that they have no need to run for their lives.

Here is for example a description of the behaviour of a threatened skunk from Wikipedia: "black and white warning colour aside, threatened skunks will go through an elaborate routine of hisses, foot stamping, and tail-high threat postures before resorting to the spray."

As we can see, there is definitely "more than meets the eye".

The aim of this chapter is to give the reader more information about this fascinating and still not-so-well-known evolutionary strategy.

So let us first of all try to classify aposematic warning signals. As the first attempt of this kind, my suggested classification cannot be exhaustive; however I do hope it will encourage scholars to put some energy and time into creating a more refined classification scheme for aposematic signals.

So, aposematic signals can be:

(1) Visual
(2) Audio
(3) Olfactory (smell)
(4) Behavioural

Each of these modalities can be divided further on several sub-types:

(1) Visual signals can be based on use of

(1.1) Bright colours, where the message is "I do not need to hide from anyone!"

(1.2) Contrasting colours (with the same message "I do not need to hide from anyone").

(1.3) Display of size ("Do not assume I am easy to kill! See how big I can get?").

(1.4) Display of weapons – spikes, fangs, etc. ("See what I got? If you attack, I **will** use them!").

(1.5) Display of eyespots (differences in pigmentation that try to simulate the look of open eyes), being preferably bigger ones ("I am always alert!").

A display of special morphological additions adds several advantages: it can be effective for the increase of the size of animal (see 1.3), it often makes animal more colourful (see 1.1), and also sometimes eyespots are also displayed on these extensive morphological additions to further their overall believability in the eyes of a predator (see 1.5).

(2) Audio signals can also be based on several different components, namely:

(2.1) Making as loud as possible sounds ("I am as strong as I am loud, and I am not giving up!").

(2.2) Making as low/deep as possible sounds ("I am bigger and stronger than you think!").

(2.3) Making hissing sounds ("I have venom!" – mimicry of the warning sound of a venomous snake).

(2.4) Making sound in groups ("If you attack, we will all fight together!");

(2.5) Group sounds made deliberately at different pitches, particularly on dissonant intervals, giving any listener the impression of a bigger group, the so called Beau Geste effect ("We are more than you think!").

(2.6) A wide range of sounds, for example, foot stomping, drumming on external subjects, chest beating, can be made without one's voice. The

most popular threatening sound across the wide range of animal species, hissing, also does not need a voice.

(3) Olfactory signals are often quite linear in their range and use and do not seem to be as varied as visual or audio signals are, but can still send a strong aposematic message:

(3.1) A Strong smell is designed to signal the non-palatability of an animal. The smells often get stronger in danger or excitement ("you could and would not eat me, so why waste your time and energy killing me?").

(3.2) A not so strong smell is designed simply to advertise the presence of the creator and trigger the predator's memory of an unsuccessful prior meeting. ("Remember me?").

(4) Behavioural signals can take on arguably the widest variety of different forms:

(4.1) Slow walking pace, even when confronted by predator, or even stopping ("You don't represent much of a challenge to me, so why would I avoid you?!").

(4.2) A demonstratively sluggish style of walking ("I can just take my time, I have no need for running away from you at all!").

(4.3) Displays of overtly aggressive behaviour ("I am ready and willing to fight you, so you'd better be absolutely sure!").

(4.4) Congregating in a big groups ("We will fight together against you if you decide to attack!").

(4.5) Mobbing ("you don't have a chance when we are united against you!") .

(4.6) Strange movements, designed to confuse and dazzle the opponent ("You have no knowledge of my fighting techniques! But you will know them first-hand if you come closer!").

Although we've already distinguished several types and sub-types of aposematic signals, I must say that virtually every sub-type of the above mentioned list of aposematic signals can be divided further into categories, for example, according to the **factor of time**. Some display signals are constant (such as colouration or eyespots) and some are temporary (appear briefly only when needed, such as a skunk's smell). Caro mentions them as "permanent" and "facultative" signals (Caro, 2004: 261). We will now have a quick look at these categories, as their differences are of great importance.

Joseph Jordania (2014). In: *Tigers, Lions and Humans: History of Rivalry, Conflict, Reverence and Love*. Logos Publishing. ISBN 978-9941-437-60-1.

Constant and Temporary Aposematic Signals

Visual signals

Visual signals are so numerous and abundant that, for a long time, the overall warning display was mostly known as "warning colouration." Visual signals form the following groups and sub-groups:

(1.1) Bright colours – this signal may at first seem to be constant, but there are still some animals that change their colours according to the situations they find themselves in. Apart from well-known examples such as the chameleon or the squid, plenty of animals can intensify the colours on their body or face when they are excited or angry (the colourful face of a mandrill is a good example, as it becomes brighter when it is excited or in danger). Here we should also note that human faces can also change colours when we are excited, afraid, or angry (a common example is blushing, another one being turning pale when extremely afraid).

(1.2) Contrasting colours – possibly the most constant factor in the appearance of many creatures, however there are very few that are able to achieve a sudden transformation into contrasting colours (sailfish is one such rare species, and can change its colours to become light blue with yellowish stripes).

(1.3) Display of size – Although size may also seem as a constant, there are a number of tricks to make your appearance much more impressive in a critical moment. The presence of a large number of morphological and behavioural tricks of quick size change strongly suggests that in the evolutionary game for survival, size truly matters. Animal species can drastically increase their visual representation with the help of a number of special display patterns. Here are several means with which to reach this the sudden size increase:

(1.3.1) Stand on your hind legs – This behaviour allows the most drastic increase of an animal's size. Plenty of animals stand on their hind legs when they are confronted by competitors or predators. This posture is appropriately labelled as "threat display." A few animals, like bears or some primates, can even move on their hind legs for periods of time without losing balance. It seems that height is arguably the most important measurement of size when an animal wants to impress or intimidate a competitor with its body size. The drastic increase that the visual effect has on the animal's size can be seen clearly in some animal shows. For example, although we know that lions and tigers are heavier and bigger than humans, we only truly appreciate their size and power when they stand on their hind legs and put their paws on the shoulders of their suddenly dwarfed human trainers or friends.

Joseph Jordania (2014). In: *Tigers, Lions and Humans: History of Rivalry, Conflict, Reverence and Love*. Logos Publishing. ISBN 978-9941-437-60-1.

(1.3.2) Raise any mobile part of your body above your head – This behaviour is not as potent and popular as standing on the hind legs, but is still used by a large number of species. A common example to observe is cats and dogs walking with their tails up in the air when they feel confident and want to be seen. On the contrary, if they are frightened (for example, after sighting a bigger and potentially dangerous animal) they often drop their tails under their legs in an attempt to become as invisible as possible.

(1.3.3) Erect the hair on your body and head – This is possibly one of the most widespread means in the increase of body size in a moment of threat or confrontation. Some animals achieve a noticeably bigger effect with their hair erect. A classic example is the male lion, who erects his long mane when threatened (as if the view of his canines and loud roaring were not already enough for intimidation). Even the fine hairs on a human body instinctively rise in moment of fear or other strong emotions, although the visual effect this has is quite negligible considering the amount of hair on a human body relative to creatures with fur coating.

(1.3.4) Stand sideways – strike a pose in order to look bigger. This is a well-known trick known widely among fish, mammals, reptiles and insects. Many fish will readjust in order appear sideways to their opponents, and many species of birds partly open their wings to increase the size of their body. You may have also noticed how conflicting cats approach each other: also sideways. As the frontal view of many animals does not show their true size, walking at a sideways angle is often the preferred way to approach an opponent.

(1.3.5) Erect, open, raise or display any available morphological structure of your body in order to seem higher and bigger – Even elephants open their huge ears as if their size was not already a sufficient deterrent. Many animal species (for example, many bird species) have seemingly random additional morphological structures that may seem totally useless at first or even a hindrance in the everyday survival game. Darwin explained the presence of such morphological additions as the result of the power of sexual selection. We should not forget though, that such "useless" visual artifacts might play an important role in intimidating competitors with a bigger body size and colours, *particularly* when suddenly displayed in a moment of confrontation, as if to suggest to their opponent that the feature is, or relates to, a defence mechanism rather than simply being a 'bluff'. So for example, if you are suddenly confronted by a potentially dangerous and aggressively behaving animal, and by chance you happen to have an umbrella with you, I suggest that instead of using it as a club, just open it and raise it above your head. You will be surprised with the outcome.

(1.4) Display of weapons – Showing the opponent your available weapons such as spikes, fangs, or antlers can also be saved for the moment of confrontation (both for defence or offense). Some weapons, like antlers, are carried around permanently in the same "display mood", but other weapons are only consciously displayed in a moment of need. Baring the teeth is possibly the most popular and easily understood gesture of threat across a wide range of species. Showing your canines is a strong warning message, particularly if the canines are of good proportions like in most carnivores, and also in ground-dwelling primates such as baboons or mandrills. Showing the teeth in a smile or laughter among humans and some primates as a sign of *good* intentions is a very interesting phenomenon, and must be used with caution in order to not to be misunderstood by some animals as a sign of threat (van Hooff, 1972; see also Gregory, 1924; Black, 1984; Harris, 1999). Display of spikes is also very popular among those who are lucky to be endowed with them (e.g. hedgehogs, porcupines). Spikes are usually raised, often shaken and often coloured in easy to see patterns, and can also accompanied with sounds.

(1.5) Display of eyespots – It is not easy to be sure about the precise function of eyespots, but one of possible functions is definitely the intimidation of competitors and predators. Some eyespots are carried around constantly, like eyespots on the backs of the ears of many big cats, however eyespots of many other species of animals are displayed only in a moment of danger or confrontation. A classic example is several species of butterflies who do not always display eyespots on their wings as their eyespots are placed on the second pair of the wings, which are covered by the first pair of wings. What is the point of having eyespots if you do not display them? Eyespots are hidden when a butterfly is sitting undisturbed. But when disturbed, butterflies suddenly open their top layer of wings (without flying away!), clearly displaying the big eyespots to their attacker (mostly to birds who prey on them). Therefore, a butterfly with such a function can instantly go from a cryptic mode of defence into an aposematic mode of defence (a double primary defence!).

(1.6) Display of morphological additions – Some morphological additions are carried around constantly, like the huge antlers of some species of deer; however, the majority of morphological additions among animals are only displayed in a moment of threat. Insects, reptiles and birds will open (or raise) the usually-hidden morphological additions of their bodies when they face predators or competitors.

(1.7) I propose one more aposematic category which, unlike any other signal, is displaced in time and territory. I am referring to markings that animals leave on different objects, which are on display constantly without requiring the actual presence of the displaying animal. Examples of such aposematic signals are the marks of clawing that big cats leave on the trees, or faeces and urine markings left in strategically important places. I call them "displaced aposematic signals." These signals are addressed to other animals (and usually to the same species) and are

aimed to notify them that the territory is occupied. Displaced aposematic signals are an important part of an animal's claim on territory. This kind of displaced aposematic signals can exist only in visual and olfactory modalities, but not in audio and behavioural modalities.

Audio signals

(2) Now we move to audio signals, and see if they too can be categorised as constant or temporary. Because of its nature, audio signals are as a rule used only in a moment of confrontation. Snakes do not hiss, rattlesnakes do not make rattling sounds and lions do not growl in a peaceful, undisturbed moment. At the same time we should remember that producing constant sound (if somehow kept at a low level) can also be a big part of animal behaviour. For example, porcupines are constantly making "booming" sounds when they are on the move. Other species also have a specific 'careless' moving pattern which creates plenty of accompanying sounds. Such careless locomotion creates a noisy aposematic message to everyone that they are formidable and, as a result, have no need to conceal themselves.

(2.1) Making as loud as possible sounds – Making loud sounds requires strong effort and energy, and this is why loud sounds in most animals are reserved for very specific occasions only. Apart from the use of loud vocalization in a moment of confrontation, a number of animal species also use occasional loud calls to make sure that competitors are aware of their presence and to keep them clear from their territory. It must be said that making loud sounds is a double-edge sword: on the one hand it warns competitors, but on the other hand the noise can work as an invitation for possible predators. Stags making loud calls during a mating season (to simultaneously find mates and scare away competitors) can make them vulnerable, as their call may also invite hungry tigers to the location of the romantically attuned male. As we have established, loud vocalization among animals that live on the ground always carries an inherent risk factor. Birds on the other hand can advertise their territory and their presence largely without fear of predators, and this is why bird sounds are the most constant of calls heard throughout nature.

(2.2) Making as low (or deep) as possible sounds – also connected to specific critical situations. Bigger animals, as a rule, produce deeper sounds, and emitting such a sound can give the impression that the threatened animal creating the sound is not as small as it may seem. Elephant herds are known to produce low frequency sounds, and apart from keeping in touch with each other, these sounds are used to communicate their presence to everyone, particularly when they cannot be seen in some of their thick forest habitats. Humans (particularly males) produce very low sounds for their relative body size, and we will discuss the possible function of this later in the book.

(2.3) Making hissing sounds – We already mentioned that hissing is used by a wide range of animals, even those whose image does not seem to fit this relatively soft sound (such as big cats). Hissing is a technique employed only when the necessity to scare away competitors and enemies arises. As vocal chords and "true voice" is a relatively late evolutionary product, for many tens or even hundreds of millions years hissing, which does not need vocal chords, must have been the most popular component of an audio warning display. This must be reason that such a wide range of animal species such as geese, tigers and even some cockroaches all hiss when disturbed.

(2.4) Making sounds together in groups – So far we have been discussing sound production by individuals, but it is obvious that making threatening sounds in groups would also be a very effective way to warn (or intimidate) your enemies or competitors. When a lion pride roars together, they give a powerful message to all the roaming lions in the vicinity that the territory is occupied. Wolves are doing the same with their coordinated howling. The Gibbon family often sings together, very likely to signal that the territory is occupied and also that the resident family has a high level of coherence and unity. In this case the quality of singing communicates the quality of coalition (see on this topic the enlightening paper by Hagen & Bryant, 2003). Making sounds together can be organised for a special occasion, or as a response to a challenge (for example, when a lion pride hears other lions roaring). Kortlandt wrote that chimpanzees sometimes organize a loud evening "concert," most likely to scare away any potential predators from the vicinity (Kortlandt, 1973). On the other hand, bees and many related insects produce constant a group sound around their dwelling place, which gives a strong message of their famous cooperative defence to all prospective aggressors.

(2.5) Group sounds made deliberately in different pitches – This is a very interesting audio phenomenon, and particularly interesting for musicians. If you have a group of several animals, singing together in unison, on the same pitch, and another group of the same animals, singing at different pitches, you will hear the difference. The overall sound in the latter, multi-pitch case will be much more impressive. This phenomenon is known as the "Beau Geste" effect. Hearing the sounds of a wolf pack is a good example, as sometimes two or three wolves can create the audio effect of a larger pack of wolves. Hearing the vocal cacophony of a frog choir is yet another example of such group vocalizing. Such sounds can be made in a critical moment of confrontation, or as a warning to a yet-unseen opponent.

(2.6) A wide range of sounds can be made without the voice. Do not forget that voice is a relatively late evolutionary product, and definitely much younger than hearing. The earliest warning audio signals (like hissing) were definitely made before the emergence of voice. Foot stomping, drumming on external subjects, or chest

beating are other examples of such non-vocal sounds. Most of these sounds are produced when animals are confronted by competitors or predators, but these sounds can also be produced to give a preliminary warning message to everyone in the vicinity (such as the aforementioned chimpanzee evening gala).

Olfactory signals

(3) We need to discuss olfactory signals as well. As we have already established, these signals are not as diverse as visual and audio signals. The question is whether they are produced constantly or in the moment of confrontation.

(3.1) Strong body odour – Strong body odour gives two warning signals, (1) that the animal is not hiding away, and (2) that the animal body might not be an ideal food source for the predator. As we remember, some animals' body odour can give a predator the impression that the body has been dead for a long time and that it is actually already gone off. Importantly for the temporary factor we are discussing, in several animals a pre-existing smell intensifies in a moment of critical confrontation. Huge and strong Gorillas also produce strong body door in moments when they are facing the possibility of a physical challenge. This behaviour is known, among others, in two related species: gorillas and humans. Human sweating, as we know all too well, also intensifies in moments of danger. In some animal species (including gorillas and humans) sudden and strong life threatening stress can also induce instant defecation, which is possibly another innate function to increase the strength of smell.

(3.2) The presence of a not-so-strong smell is possibly designed to trigger memories within the mind of a predator, and this feature is most likely a more constant one. Of course we should remember that not all animals react similarly to the same odours, and that the same odour might be disgusting to some predators but quite acceptable (and even considered a delicacy) to others. Some predators have a bad sense of smell, and this is very bad news for the animals that rely on their faulty odour for protection. Even the legendary skunk is commonly attacked, killed and eaten by the Great Horned Owl which, as scholars have suggested, hardly has any sense of smell at all. This suggestion must be correct, as skunks are avoided by most of other predators exactly because of their powerful odour, and that the Great Horned Owl is possibly the only predator that a skunk will desperately try to flee from.

(3.3) Olfactory modality also offers the relatively rare possibility to create "displaced aposematic signals", where the signal is displayed permanently without requiring the displaying animal to be present. This type of displaced warning signal is widely used by territorial animals in order to notify others that the territory

belongs to them. Cats, dogs, lemurs and wildebeest all mark their territories by either spraying or leaving faeces in prominent locations, or by rubbing their body parts which contain scent glands against prominent objects (mostly tree branches and leaves). As we may remember, displaced warning signals can be used only in visual and olfactory modalities but not in audio or behavioural modalities. In some cases an olfactory channel can be more effective than any other channel. For example, hyena pups which have never seen lions do not react fearfully upon seeing them, but react fearfully upon detecting their scent.

Behavioural Signals

(4) Now we will discuss behavioural warning signals. They can also be divided into the temporary and constant categories. Certain behaviours appear only in a moment of need, but others are present at all times, or at least most of the time. Behavioural warning signals can compete in popularity and variety with visual and audio signals.

(4.1) Slow walking pace – Possibly the most characteristic feature of many animal species that have strong secondary defences. Most venomous snakes and spiders move very slowly. Most of us who have seen hedgehogs and turtles would know that most quill and armour-covered animals also walk very slowly. Even when confronted by a predator, they do not attempt to move any faster. This feature (slow walking speed), as a rule, is mainly found in more physically-threatening creatures, largely as these slow-moving animals are actually unable to move as fast as other animals whose survival depends on fast legs and more defence-minded mechanisms rather than having their strengths lie in the course of an actual physical confrontation. Slow walking animals have another drastic means of warning signal: stopping. When confronted by predators, many slow walking animals stop moving altogether. In this tense moment they usually face their opponent and express their disgust with aggressive sounds, visual gestures, and any other aposematic features at their disposal. Many predators prefer their prey to run away – this is because the instinct of freezing is the initial defensive reflex in the more fearsome predators, therefore they can actually become confused if their prey does not initially run away, forcing them to contemplate the chance that what initially seemed as prey may be stronger than initially thought due to its "predator-esque" reaction to them.

(4.2) Sluggish style of walking – In the same vein as slow walking and the freezing instinct, a demonstratively sluggish style of walking is another potent signal to other creatures that the animal has strong secondary defences. This feature also seems to be fairly constant rather than being employed only in confrontations. At the same time, at least in theory, there is the possibility that an animal would be able to walk normally and quite fast, then only adopt the awkward sluggish to in a display of strength when confronted by a predator.

(4.3) Overtly aggressive behaviour – As many politicians and teenagers know, pretending to be aggressive and adopting threatening behaviour is sometimes (only sometimes!) a potent means to avoid further aggression from others. Most such aggressively-behaving animals are gentle and cooperative and friendly with their family group and kin, but can also suddenly become overtly aggressive towards predators and competitors. This overtly aggressive behaviour is more a temporary feature of aposematic display than a constant one.

(4.4) Being in groups – The advantages of having strength in numbers are well known both to animals and in particular humans, but is this feature constant or temporary? This may initially seem like more of a constant feature, as social animals such as lions and many primate species do spend 'relaxed' time together and do not really come together from different parts of the jungle or savannah for a single moment of need. On the other hand, many social animals (especially humans) demonstrate an increase in group density and coherence as the necessity arises. Humans demonstrate a strong tendency of bunching together in moments of perceived strong danger (natural disasters, wars and even protests).

(4.5) Mobbing – Aposematic animals do not only passively aggregate in large groups. Often when there is a danger from a predator, they actively attack the predator simultaneously to drive it away. Mobbing can only work if none of the animals attempt to escape the predator, but instead behave fearlessly and together harass and try to injure the mortal enemy. Of course, mobbing is solely a temporary function which occurs only in critical moments of survival where there is a need to defend young offspring or the group in general.

(4.6) Strange, obscure movements – Unusual behaviours in a moment of confrontation are designed to confuse and dazzle an opponent. Darwin extensively wrote about such behaviours in his "Descent of man" (he called them "antics"). Unfortunately, Darwin was explaining such behaviours as merely the means to attract the attention of the opposite sex. Today we know very well that strange movements can also be a potent weapon in a confrontation. These movements are integral to ritualized fights, and can be designed in to avoid a scenario of all-out violence.

Conclusions

I hope I did not bore the readers of this book too much with the differing descriptions of a vast array of visual, audio, olfactory and behavioural warning signals. I myself find them extremely fascinating. When animals of the same species

are scaring each other with their looks, sounds, and other ritualized behaviours, or when prey animals try to impress their predator using the same means, the central function of all these strategies is the same: to get the required result without the costly all-out fight and associated physical harm.

Aposematism seems to be an integral factor of natural selection for many different classes of animal species for several, sometimes varying reasons:

(1) For predators aposematism is convenient as it allows them to distinguish well defended prey animals from the undefended ones (undefended animals most likely will try to run away, as running away is a popular means of avoiding predation);

(2) For the prey species aposematism is good as it allows them to demonstrate (or merely remind) to predators that they should not be wasting their time hunting them. For example, if a tiger is approaching a venomous snake, the possibility of both of them getting killed in a lethal confrontation can be avoided once famous audio signal "sssss" is sounded (most likely from *both* snake and tiger). As a result, they have avoided a dangerous violent confrontation, quite possibly lethal for both.

(3) For conflicting animals of the same species aposematism allows them to avoid an all-out fight and possible death, and instead substitutes real fights with a ritualized means of aposematic display. These displays are known as "ritualized fights" (or as agonistic behaviour, see Scott & Fredericson 1951). This "ritualized fight" is the primary deterrent and reason why many animals do not use their other, possibly lethal means of offense when they are fighting their fellow creatures (even when males are fighting for the attention of females). Most animals use aposematism when dealing with their counterparts and prefer to settle disputes without costly fighting and the associated injuries.

(4) The same is true for some conflicting animals of different species: a ritualized display, in most cases, is enough for the participants to clearly state their interests to each other, and also for them to assess each-other based on the aposematic signals they perceive (this exact process is also prevalent in human street fights and confrontations). As a result the competing animals can usually settle the dispute without having to resort to a physical fight. Therefore, contrary to popular perception, animal life is not only one where the tooth, claw and fang rules. In the animal kingdom body size, colours, shapes, sounds, smells and behaviours also play a fundamental role in the survival of many creatures.

The Importance of Being Earnest

Animal determination and the readiness to fight is a crucial factor of any confrontation. When two animals are displaying their body size and exchanging warning signals, it is not always the bigger and louder one who wins the confrontation. By some subtle, harder-to-notice elements of behaviour, conflicting

animals can feel which of them is more determined to fight. As a result, the less determined animal usually backs down, avoiding the confrontation from descending into physical violence. This does not always mean that the lenient animal is weaker; this only means that in this situation the animal was less ready or less willing to fight than the more determined competitor. A classic situation to illustrate this point is when a huge male backs down when up against the aggressive behaviour of a smaller mother animal that is ready to die defending her young.

And here comes the question: what are the factors that make animals more determined?

These are possibly the two most important factors: hunger and parental instinct.

Hunger is possibly the most widespread factor. This factor is particularly clear in such ubiquitous situations such as confrontations over a recently killed prey animal. For example, when lions (or a single lion) come across feeding hyenas, the outcome can depend immensely on how long the hyenas have been feeding and how hungry the lions are. Sometimes a single lion can be enough to chase away a large group of hyenas, but on the other hand a small pack of hyenas can chase away not only a single lion, but several of them. Most interestingly, those animals that are pushed away by competing animals do not usually go away completely. Instead they wait nearby, allowing time for their stronger (or hungrier) competitors to feast on the kill. After a period of waiting, the waiting animals make a comeback. By this point the second side, who has now been feeding for a while, is not as hungry as before. Therefore, they are now not as ready to fight for a food as they were before, and as a result the side that was originally defeated comes back and reclaims the kill.

When predators are not hungry, they may avoid confrontations with aggressively behaving animals that they could otherwise easily kill. There have been cases of pumas being chased up a tree by a single barking dog. No dog can survive a confrontation against a puma or even a lynx, but when pumas aren't in need of food they will usually try to avoid any confrontation, even if this means running from an attacking (yet weaker) competitor. On the other end of this spectrum, if predators are desperate for food then there is almost nothing that can stop them. Skunks are sometimes killed and eaten (despite their famously smelly defence glands), not only by Great Horned Owls (who do not have a sense of smell), but also by very hungry dogs and coyotes as well, who would normally be disgusted by the skunk's odour. In much the same way, porcupines are also occasionally hunted despite their long and sharp quills. In such cases no display can divert a predator's will, and they attack determined to either kill or to be killed. Hungry lions have even been known to tackle adult African elephants. This is why the only fully guaranteed defence from a predator is to kill the predator (Ruxton et al., 2004). We can now agree that relative hunger and desperation are both crucial factors in the precarious equation that is a confrontation between two animals.

Defending the young - Another important element that strongly affects animal warning displays and confrontations is parental instinct. Animals (usually mothers with most species) that are defending their young form can go into an all-out-battle

without reservations and with total neglect to any warning displays used by the opposing side. The silver lining to this kind of attack (if you are attacked) is that the attack usually remains solely as a defence mechanism aimed at protecting their young, so if you have a chance to retreat you will be safe. The inherent negative factor to add is that even if you are not endangering their young and you came close only by mistake, you may not have enough time to demonstrate your good will to the enraged parent. Out of these two factors (hunger and defending the young) the latter seems to me a more potent reason for animals to enter into unprovoked fights without reservations and without any care for their own health.

Apart from hunger and parenting instinct, there are other factors also affecting the determination of conflicting animals. Fighting for mates is one obvious factor, and fighting for territory is another such important factor. Therefore, when there are two animals in a confrontation (for food, territory, defending their young, or for mates) their size, strength and variety of display patterns are not the only signs to observe. Other psychological and physiological factors (offspring located in the vicinity, animal in heat, starving animal) must be taken into consideration if one is to have a true idea of the challenge they are likely to face. Similar to many of the world's human political landscapes, determination and confidence play an undoubtedly integral role in all success.

A true fight to the death is actually a very rare occurrence in animal everyday life (this of course does not include regular hunting undertaken by prey, in which there is no real "stand-off" as such), and a wise strategy of aposematism is a central factor in avoiding unnecessary and damaging confrontations. Huxley was wrong – the battle for survival is **not** the continuous combat of every single animal all other animals of both other and its own species. On the contrary, the battle for survival in the animal kingdom seems to be more about utilising psychology and morphology in avoiding such combat and fruitless violence.

Conclusion: Aposematism, Cold War and Peace

We come to a somehow surprising conclusion: Aposematism (warning display) is in fact a strategy for peace. A possibly better way to say this is that it allows conflicting animals to avoid physical confrontations and all-out fights, replacing them with ritualized displays of size and power. An aposematic confrontation might seem like a serious fight brewing, with lots of intimidating gestures being thrown around, but in reality none or little serious physical violence actually eventuates.

This strategy from the animal kingdom is somehow close to the international political strategies employed in the notorious "Cold War" between the USSR and the USA, where conflicting parties were often engaged in different (usually bluffing for the most part) displays of their weapons and readiness to engage in combat, yet at

the same time both sides would desperately attempt to avoid any real all-out physical engagement in the event that such a confrontation seemed imminent. It is no coincidence that, after the creation of the most devastating weapon, the nuclear bomb, there has been no large-scale all-out wars between any major world powers. The successful detonation of the nuclear bombs above Hiroshima and Nagasaki instantly became the most powerful aposematic tool ever employed by humans. The idea that the emergence of nuclear-powered weapons helped to establish a peace between major world powers (although at the same time increased the danger of catastrophic terrorist attacks) is coined under the term "nuclear peace" and is almost as old as the weapons themselves.

Throughout history we have been shown that if we have to have a conflict with other parties, it is much better to have a ritualized display of strength rather than an all-out fight to a point of mutual destruction. Politicians only realized this during the last half-century. The forces of natural selection realized this many hundreds of millions of years ago.

Can a Predator Be an Aposematic Species?

Predators come in different sizes, shapes and exhibit many different behaviours. If you ask a person in a street to name five species of predators from the top of their heads, most people would probably name the big predators, such as lions, tigers, bears, wolves, sharks and crocodiles among others. Very few would recall that there are in fact many more different forms of predators, with a vast array of sizes, behaviours and types of prey. For example, not many would recall that virtually all birds (not only eagles and falcons) are also predators, which prey upon insects in prodigious quantities.

Predators differ from each other largely by the prey they hunt (from flies to giraffes and baby blue whales), by their method of getting to their prey (some run or fly after them over large distances, some use stalking, some lure them, some just wait), and also by their method of killing (some use a killer bite in the nap, others suffocate their prey, some tear the prey apart, and some swallow their prey alive). I have only mentioned the most well-known methods of predator behaviour, but in specialized books you can find many more means used for obtaining prey. We are not going into the subtleties details of different methods of predation. We need to discuss another, more important and relevant question – can predators in general actually be classified as aposematic species?

The reason I am asking this question is that aposematic species, as we remember, do not try to hide and instead try to demonstrate their presence at all times. It is not too difficult to notice that that the basic strategy of aposematism is in direct contrast with what many predators are trying to do: conceal themselves from the prey animals in order to hunt them with a greater success rate. A lion or a tiger who advertises their presence by walking openly and roaring will starve to death as all their potential prey will be aware of their presence. On the other hand, virtually

any animal can use an aposematic display in certain situations, mostly to avoid unwanted violent confrontation. Tigers and lions are no exception, and express their desire to be left alone with growling, as do bears by standing on hind legs and cats by raising their back and hissing and raising their body hair, however these behaviours alone do not necessarily mean that these animals are aposematic species. Aposematic species are those who use a whole system of aposematic signals virtually all the time, seemingly in an orchestral and organised nature. As a rule these are the generally weaker species that have their bodies covered in bright, often contrasting colours, make loud sounds, often emit smells and move slowly and awkwardly. By this definition it is evident that neither lions nor tigers are aposematic species.

The most famous predators of all, the family of big cats, and their domestic descendants are a perfect illustration of the demands survival has put on predator species. They often have camouflaging body colours, they are masters of natural disguise and can stay unnoticed, they can move without making a sound and do not have body odour (herein lies the evolutionary source of domestic cats' legendary cleanliness).

But not all predators have all these heavy demands. Wolves, for example, and the big group of their relatives, known as "canidae," hunt their prey using a different strategy. The hunting method of a canine tribe does not depend on silent stalking and a surprise attack. Instead it is a test of endurance and speed. They run after their prey over long distances, wearing them down, and attack the now-tired prey as a group, leaving virtually no chance for survival. As a result, dogs do not care too much if they are seen by their prey before the chase begins, or if they emit body odour. This is why at least some of their domestic counterparts are coloured in contrastive colours, and also why they do not pay as much attention to their personal hygiene as domestic cats do. Therefore it would be more common for dogs to have more constant aposematic features, such as clearly seen colours or a strong body odour. We must remember that canine predators cannot afford to use certain aposematic features such as a slow and awkward movement style.

There are many other predators that can maintain aposematic features while remaining skilled in hunting. Many birds, for example, hunt insects and therefore qualify as predators, however they do not care if they are seen by their prey. Another important point to include at this time is that many animal species can be both predators and prey at the same time.

So we come to the conclusion that some aposematic display features are unacceptable for the lifestyles of certain predators, but are acceptable for others. For example, features such as contrastive body colouring or body odour are acceptable for 'cursorial' predators such as wolves, but not for stalking predators.

I do not want to delve too deep in discussing the presence of aposematic features in a wider range of animals, but I would like to remind the reader that most animals have at least some arsenal of temporary warning display and they use them primarily in order to avoid violent confrontation. We must remember that temporary

displays are those which are not permanently present in the apparent morphology or behaviour of an animal. Temporary warning signals can also be used by cryptic species as well, who initiate their aposematic display only after they have been spotted by a predator (for example, certain cryptic butterflies open their first layer of wings to display the second layer of wings with eyespots to attacking predators).

It would be a grand mistake to attribute the use of aposematism to prey species only. Aposematism has a much larger role in natural selection. It had the crucial evolutionary function of avoiding rampant and endemic physical violence. It was the neglect of the importance of warning displays in natural selection that brought some earlier evolutionists to the erroneous picture of the struggle for existence as a constant physical ("gladiatorial") battle.

A Few Words on Sexual Selection from the Point of View of Natural Selection

Before we continue our discussion on aposematism, I would like to briefly mention several elements of sexual selection which seem to me very important to include.

Firstly let us recall that sexual selection operates via two very different mechanisms: (1) male competition, or *intrasexual competition*, and (2) female choice, or *intersexual competition*.

Secondly, male combat itself also contains two different forms of competition (1) intimidation, which is based on a wide set of elements of ritualized display, and (2) physical combat aiming to defeat (or even kill) an opponent.

The differences between these two forms of male combat are too important to view them as simply two elements of the same mechanism. The intimidation tactics of rival males involve the display of aposematic elements and a ritualized showcase of size, colours, smells, behaviours. This display is identical to the other main use of aposematism, which is to avoid predation. The primary aim of the ritualized display in both cases is to avoid violence, and to substitute violence with the ritualized displays. While on the topic of physical combat between males, we need to remember that physical combat in most species as a general rule is very short, and violence very rarely escalates into a real all-out fight. Relatively minor elements of a violent clash in male competition must be understood as a part of intimidation strategy. During a ritualized display of size, colours, sounds, smells and behaviours the bigger and louder animal gradually pushes the smaller opponent towards conceding defeat, and as soon as any actual physical confrontation starts to develop, the smaller male as a rule will retreat backwards. As a result of this, both males will have avoided unnecessary violence and injuries.

I therefore suggest that *intrasexual selection* (competition between males) and aposematism are often directly intertwined. They have the same morphological and

behavioural elements, and the same internal forces. Without an aposematic ritualized display, any encounter between confrontational males would lead to the injuries and deaths of participating animals, and this kind of constant in-fighting between the conflicting males would be disastrous for the species, even more so in today's world where human expansion has pushed wildlife into more confined and condensed areas.

On the other hand, there is a considerable difference between aposematism and *intersexual selection*. This is when males try to impress females via the mechanism of female choice, as opposed to merely competing with each-other via the *intrasexual* model. These two mechanisms, natural selection via aposematism and sexual selection via female choice have confusingly similar morphological and behavioural features, but they are driven by two very different internal forces: beauty (or display of healthy genes) on one hand, and the intimidation of an opponent on the other.

Which of these two forces is the primary evolutionary agent for the development of these characteristics? This is a tricky question, and to have a chance at answering it we will need to find cases where natural selection through aposematism and sexual selection through female choice have had conflicting interests. We will now look at two possible scenarios:

(1) In the first scenario it should be possible to demonstrate that a clear and unique visible (or audible) characteristic is very effective for attracting mates, but at the same time the very same feature is harmful for the displaying animal's chances of survival against predation;

(2) In the second scenario it should be possible to demonstrate that an exclusively aposematic feature does not attract females and does not therefore contribute to more offspring.

The first scenario above was proposed by Charles Darwin. As a matter of fact, his entire theory of sexual selection was almost entirely based on the idea of unnecessary (and even harmful) beauty that is favoured by females and leads to more offspring. This intriguing idea was later developed into the well-known notions of the "honest signal" and "handicap principle" (see Zahavi, 1975; Zahavi & Zahavi, 1997). According to this principle, in order to be "honest" the signal has to be costly for the survival of the bearer. The famed peacock's tail is the best known example of this and a true symbol of this evolutionary principle.

The second scenario can be called true aposematism, or the warning display without any indications of any involvement of female choice. The best examples of this scenario were provided also by Charles Darwin, when he found cases of brilliant colours used by sexually inactive larvae. Darwin himself could not explain this phenomenon, but an effective and elegant explanation was suggested by Wallace.

As the author of this book is clearly fascinated by the power and many faces of aposematism, the readers can guess that I believe that, in the complex interaction between the principles of sexual selection via female choice and the aposematism, the latter must be a much more potent evolutionary force than the former. It seems to me

logical to propose that females who happen to develop a passion for mates who exhibit traits and behaviours harmful to their survival would be themselves doomed by the forces of natural selection. My suggestion is in direct contradiction with the idea of the "handicap principle" and I want to assure readers that I will soon discuss the "handicap principle" on the example of the best known and the most iconic example of the power of sexual selection via female choice – the famed peacock train.

At the same time, I have to admit that even if we accept the primary power of natural selection as the formation of aposematic signals, we should not exclude the possibility that sexual selection might also be a factor in forming (and particularly intensifying) certain aposematic signals. For example, there is an interesting case study on the strawberry poison frog, and the authors of the study suggest that the power of sexual selection is behind the existing colour differences of local varieties of this frog (Maan & Cummings, 2009). Although it is difficult to be sure whether the existing local sexual preferences are the primary driving force behind these colour differences, the possibility that sexual selection can provide the pressure to form or to intensify aposematic features should not be ignored. As a precautionary tale I would remind the readers the similar interpretation provided by Charles Darwin on the differences in skin colour of different human populations. Very much like the researchers on the study of strawberry poison frog, Darwin was also sure that the differences in skin colour of different human populations were a result of female choice, not of natural selection via adaptation to the differences in solar intensity. Today the idea of sexual selection determining human skin colour has lost most of its supporters (although see Frost, 2009).

Here I would like to suggest a few concrete suggestions in order to distinguish which of the two central primary forces are behind traits in animals as bright colours, sounds, smells, and behaviours: (1) sexual selection via female choice, or (2) natural selection via aposematism. Here are the suggestions:

(1) As sexual selection is mostly arbitrary, a single trait (for example, bright colours) can be present in isolation, and it does not have to be intertwined with the other signals (sound, smell and behaviour); Natural selection, on the contrary, is not arbitrary, and if the trait was designed by the forces of natural selection as a warning signal, these signals will very likely involve other accompaniments as well, as a wide-ranging aposematic display in several modalities is much more potent than a linear one. Therefore, if the presence of bright colours is the single distinguishable feature of an animal, this is most likely a case of sexual selection, but if bright colours are accompanied by other forms of display: loud sounds, strong (and particularly unpleasant) smells and unusual behaviours, then the primary function of this multi-modal signalling is most likely to be aposematism.

(2) If males of the same species are engaged in direct male-to-male competition for the females, the stronger males win females via this competition and there can be little to no real female choice of the males involved. In such cases a female is more like a "trophy for the winner", than a picky beauty queen with the right of the last decisive word. The factor of female choice in sexual selection in such species must be considered close to nil;

(3) If males and females of the same species both have the same traits such as colours, sounds, smells or behaviours, and particularly if these signals are presented simultaneously, then aposematism must be the preferred logical explanation;

In the next section we will discuss the possibility of measuring the amount of aposematism in particular animal species.

How to Distinguish Aposematic Species: Aposematic Index

In order to introduce a methodology to measure the presence of aposematism in an animal species, and to see if there is an objective way to qualify different animal species as "aposematic species" I would like to introduce the **"aposematism index."** What is an aposematic index? Aposematic Index (AI) is a numerical expression of the relative importance of aposematic warning signals used by any given animal (both constantly and in specific situations). This functions on a percentage medium, thereby making the maximum AI 100%.

As there are four basic modalities (visual, audio, olfactory, behavioural) I propose to give each of these modalities an equal maximum 'impact' share of 25% to reach a maximum total 100%. If an aposematic element is present only in specific situations and only briefly (like a dog's growl for the defence of a bone, or a cat arching its back to avoid a conflict), this temporary signal will have the value of 5% in any given modality. On the other hand, if an aposematic signal is constantly displayed (like the contrastive colours of a skunk or the spikes of a hedgehog) this will be equivalent to the value of 20%. The presence of both constant and temporary signals in a given modality will result in the maximum of 25%. 100% AI means that a given species is constantly displaying aposematic signals in all four modalities, and that in critical situations it also displays stronger additional signals in all four modalities.

In order to qualify a given species as an "aposematic species", without any doubt the AI should be 100%. This high requirement for qualification derives from the strict demands of natural selection: if a species follows the aposematic lifestyle as a survival strategy for thousands of generations, it will naturally and gradually develop the means to advertise warning signals through all four modalities. Therefore it is very likely that any true aposematic species will be advertising aposematic signals constantly in all modalities, and they will also have ability to increase the intensity and possibly variety of warning signals in critical situations.

Let me present some examples of this AI system with brief comments:

For example, when using **visual** signals, an aposematic animal should have a constantly visible body (ideally a large, colourful one). Additionally, in the time of

need, an animal should be able to increase its body size more drastically (by changing its body posture, erecting hair, or extending various parts of the body to seem taller or wider). The constant feature on its own gives the animal 20% AI in this modality ("visual"), and the temporary feature gives 5%. The presence of both constant and temporarily features together will give the total 25% in a given modality. According to my observation, animal species that have constant aposematic signals as a general rule will have means to further increase their size (and even colour) in a moment of need. Therefore when a constant visual signal is present it is most likely that a temporary signal is also available. On the other hand there are many species that have temporary visual signals, but do not possess constant warning signals (for example, cats raising their back and fluffing their hair). Aposematic animals as a rule have highly visible bodies, often coloured in bright or contrasting colours and sometimes sporting unique patterns or features over prominent areas such as the head or the body.

When using the **audio** modality an aposematic animal is expected to be making some kind of constant noise to advertise its presence. Much in the same way as visual signals, an animal will be able to increase the sound level and make additional, stronger sounds when in a critical moment. There are many animals that remain mostly silent and only make noise when disturbed (for example many different cat species that can walk with incredible silence but can make various sounds when irritated) will only score a 5% in this modality, while animals that exert noise constantly in addition to doing so in critical situations will score the full 25%. Porcupines, for example, most of the times produce a specific booming sound, and if disturbed, add the rattle of quills and other sounds from the rich repertoire of their sounds, ranging from high-pitched whistles to whines, grunts and snuffles. As a rule, aposematic species are more vocal and noisy than non-aposematic species.

When talking about the **olfactory** modality in an aposematic species, we are looking for a constant body odour that the animal's body produces. As the absence of odour is important for hiding from a wide array of predators, the mere presence of a clearly detectable body odour will itself indicate the aposematic nature of that odour. Unlike visual and audio signals that can produce a strong intimidating impression, body odour is a more subtle signal. Porcupine and skunk body odours (without the deadly skunk gland) can illustrate this state. While maintaining a constant body odour, aposematic species often increase their odour production in moments of need, commonly resulting from increased sweat production through excitement. It is theoretically more difficult to produce a strong temporary odour for an animal which does not already have a constant odour in place. We can essentially conclude that body odour can be present either constantly, or both constantly and temporarily (with the stronger smell produced in critical situations).

While discussing the principles of aposematic display and aposematic index (AI), I would like to make a short list - effectively a summary of the most widely used designing features used by the cryptic and aposematic strategies. This list of features is based on binary opposition; with one set belonging to the cryptic strategy

of staying unnoticed, and the other belong to the aposematic display of advertising one's presence with all possible means[1]:

Cryptic	**Aposematic**
Dull colours, matching environment;	Bright, contrastive colours
Staying close to the ground;	Rising on hind legs;
Lowered tail;	Raised tail;
Being silent;	Being noisy;
Absence of body odour;	Presence of body odour;
Swift movements;	Slow movements;
Running away from danger;	Aggressive response to danger;

We are now approaching the most interesting part of our discussion, as we are going to analyse several examples of evaluating AI in different species. We will start from very well-known species whose aposematic nature by this point has been established, and then we will move on to more unexpected cases.

Skunk – Classic Case of Aposematism

The aposematic nature of a skunk's defence is quite well known, albeit the full arsenal of skunk aposematic possibilities is often understated, meaning that only the black & white colour scheme and the notorious odour are widely known. In reality, the skunk uses array of aposematic signals via each four of the above-mentioned modalities, and what is particularly important is that skunks advertise their warning signals constantly. These signals may also be intensified in critical moments, as per the general rule of aposematism.

Visual signals - Skunk body colours consist of a highly visual and contrastive black-and-white pattern. The skunk also raises its tail when walking (a) to be better seen (b) to look bigger and (c) to look confident (skunks do not lower their tail even when confronted by a predator). In critical moments they cycle through the whole repertoire of visual signals including bipedal posture, raising their tail and stomping their feet. Interestingly, a skunk's bipedal posture is very different from ours in that stand on their front feet (like some humans who can stand on their hands). Skunks do this in order to gain more impressive height by extending their tail upwards rather than having it sweep at the ground. If they were standing on their hind legs,

[1]Darwin was probably the first who wrote about the principle of antithesis of intentions on the example of play signalling in dogs (Darwin, 1873).

most of their tail length and potential would be not in clear view and essentially wasted.

Audio signals of the skunk consist of the sounds they make to accompany themselves while walking. Apart from this constant sound, skunks can also hiss (the oldest and the most universal aggressive sound), growl and tap their feet – all these audio signals are employed before the skunk's last resort, when turns its back and raises its tail in preparation to use its deadliest weapon.

Olfactory signals - Do we really need to discuss this factor? Apart from the famous spray used in critical situations, skunks also produce a constant musky smell. A skunk's deadly spray is actually a combination of its primary and secondary defences.

Behavioural signals consist of demonstratively slow walking with a raised tail and not running away from predators. Instead of running away, skunks gain an arrogant and aggressive confidence in response to many predator advances. The only behavioural feature that does not fit the typical aposematic framework is that skunks do not aggregate in large groups. Why don't they aggregate? I propose their defence is so relatively potent that they need not rely on "safety in numbers".

Therefore, the morphology and behaviour of skunk clearly defines their constant dependence on the strategy of aposematism. When measured on the Aposematic Index, the skunk scores a full 100%, therefore skunk can be clearly classified as an "aposematic species". Airborne predators (and particularly the Great Horned Owl), catastrophically for the skunk, have zero or minimal sense of smell and are therefore only predators that are largely invulnerable to the skunk's defences. When sighting an avian predator a skunk quickly forgets about all of its aposematic talents and tries to run away as quick as it can with its not-so-swift feet.

Porcupine – Another Classic Case

Porcupine is another species with an obviously very high Aposematic Index (AI). Let us have a quick look at all four modalities.

Visual signals - consist of long and usually contrastive coloured spikes, which the porcupine can raise and rattle for a better visual and audio effect in a time of critical need. Rising quilts also makes the porcupine seem bigger to opponents.

Audio signals - while moving, porcupines and their close relatives often make a constant "booming" sound and are basically quite noisy while going about their day-to-day business. The stomping of feet, chattering of teeth and particularly the rattling of the quills of porcupine family members in critical moments are other audio reminders of the deadly power of their quills, which can even seriously injure animals as ferocious as tigers.

Olfactory signal - Porcupines constantly emit a smell which is reminiscent of the odour of sweaty human armpits. Apart from this, when disturbed they also

produce a strong noxious odour (used in conjunction with the raising of their quills and chattering of their teeth as warning signs).

Behavioural signals are also clearly present: all members of this family walk slowly and awkwardly, clearly advertising that they do not need to run for their lives. Also, when seeing a predator they usually stop moving altogether. By raising their spikes they also warn predators of their weapon, as well as the raised spikes making their body seem bigger. In a critical situation they will often move threateningly towards the predator, displaying an aggressive character. Very much like skunks, porcupines also do not aggregate in groups, and the same explanation of the potency of their defences can be used as the explanation of this fact.

The conclusion is clear: porcupine AI also reaches the maximum 100% mark, clearly identifying the porcupine as a member of the group of truly aposematic species.

Let us now discuss a relatively unknown case.

Norwegian Lemming – Unknown Classic

This species is definitely not as universally well known as the skunk or the porcupine, but it shows a remarkably high AI. Malte Anderson published a special article in 1976 on the possible aposematic character of the colouration and behaviour of this species (Anderson, 1976).

Unlike all other rodents from the Scandinavian region, who are cryptically coloured and try to conceal themselves from their predators, Lemmings on the contrary are conspicuously coloured with contrasting bright yellow, reddish brown, white and jet black hues. They are also very noisy, making different sounds which include loud calls. Their behaviour is very aggressive towards their usual predator bird of prey, the long-tailed Jaeger. Lemmings are aggressive even towards approaching human observers, first by turning towards the approaching humans and sounding a call. If approached further their call will grow louder, they will rise on their hind legs, leap and try to bite the intruder. Anderson observed lemmings and another local rodent, the vole (which is not aposematic), and specially studied their survival strategies in their encounters with their mutual natural predators, Long-tailed Jaegers, in the wild. The cryptic vole was killed and eaten in 10 cases out of 12 encounters while the aggressively behaving Lemming was killed only once out of 6 cases. The Jaeger never hesitated to attack a vole, but was always wary of approaching the aggressively behaving lemming. Other important characteristics are that, compared to voles, lemmings are also slower in running, and also that lemmings constantly produce a strong body odour (which resembles sour milk) from a special dorsal skin gland.

The Norwegian Lemming has all the attributes of an aposematic species: its body is colourful and highly visible; it makes loud noises and calls, has a strong body

odour, runs slower than its relatives, and behaves explicitly aggressively towards possible predators and enemies. Conclusion: Norwegian Lemming has a 100% AI.

After the examination of two well-known species whose aposematic qualities are quite widely known (skunk and porcupine), and one of a relatively unknown species who apparently is also a clear example of aposematic morphology and behaviour, I am going now to surprise readers and discuss a couple of animal species whose morphology and behaviour has never been discussed in relation to aposematism.

Is There an Elephant In the Room?

Is it possible that the elephant is an aposematic species that has never had all of its characteristics and features fully identified? I have never heard of anyone proposing that elephants use an aposematic strategy, and if you do a Google search for "elephant" and "aposematism", you will most likely find only references for an aposematically coloured frog which has so much poison that it could kill an elephant. Well, we need to remember that aposematism is still a "rare guest" in biological and ethological thinking and publications, so there are potentially thousands of aposematic animals have not been yet been identified as such in scholarly literature. A closer look at elephant morphology and behaviour reveals a very interesting picture.

Visual signals - An elephant body does not have any conspicuous colours, but there is hardly a need for this, as the elephant body is one of the most visually recognizable symbols in the natural world as it is simply the largest land animal on earth. Apart from their extraordinary body size, in critical moments elephants can also open their ears and raise their trunks, making their size even more impressive, particularly when accompanied by their trumpet-like loud calls while running towards an opponent.

Audio signals - Although elephants can walk silently, when moving around they usually make plenty of noises and are easy to locate. They hardly need to hide their presence as it is, and of course they are able to produce loud and piercing sounds on command when required.

Olfactory signals - Elephants have a quite a strong constant body odour, clearly recognizable even by such smell-deprived species as humans. In a specific season (known as "musth"), when male elephants become highly aggressive and dangerous, they activate a smell-producing gland so that the strong smell emitted clearly notifies everyone to stay away from them.

Joseph Jordania (2014). In: *Tigers, Lions and Humans: History of Rivalry, Conflict, Reverence and Love*. Logos Publishing. ISBN 978-9941-437-60-1.

Behavioural signals - An elephant's behavioural strategy also fits very well within the aposematic model of defence. They are slow moving animals and they rarely run away from any other animals. On the contrary, they often charge aggressively towards lions and other possible enemies in order to scare them away with their impressive presence and loud sounds.

Therefore we can make a conclusion that elephants actively and constantly use aposematic warning signals, and as a result, they should be categorised as aposematic species with an AI of 100%. As aposematic characteristics work according to a principle of "the more the better", the growth of the body size alone could become a factor of permanent selective pressure (unless the size itself becomes problematic for survival). The massive size of an elephant, apart from securing them from predator attacks, is a decisive factor in intimidating bouts between rival males, which as a rule consists of bluffing display of size and sounds and rarely leads to physical injuries.

In regards to aposematism, we can say that there are a few more elephants in the room.

Gorilla – The Scary Gentle Giant

Gorilla, the biggest and strongest of the primates, also exhibits a number of aposematic characteristics. Since these characteristics are not enough to reach the 100% AI level (as it was in the case of elephants), I would not include the gorilla in a definitive list of aposematic species. Let us examine:

Visual signals - Gorillas are not as visible as elephants, of course, but their size (and particularly the size of a silverback adult gorilla) can definitely be intimidating for predators and competitors alike. Apart from their constant big size, in a moment of confrontation gorillas will rise on their feet, making themselves seem taller. They also shake their arms, beat their chest, and break branches around in what is essentially a display of strength, determination and physical aptitude.

Audio signals - Gorillas are usually silent, so we cannot say that they are advertising their presence constantly, however in critical moments male gorillas do make plenty of sounds which include roaring, beating their chest and breaking tree branches and foliage in their vicinity. Together with the fierce looks and body size, this display is extremely impressive, generating unfounded legends of gorillas' incredible fierceness and lethality. Being strict vegetarians, gorillas are basically gentle giants, and are much more peaceful than the more 'approachable' chimpanzees, who have been known to exhibit quite violent behaviour, including hunting and killing (not for food) other chimpanzees. I must add that the notion of a "gentle giant" is very aposematic by nature, as animals (and also humans) with large and intimidating bodies often do not need to be fierce in order to be respected, and are left mostly undisturbed.

Olfactory signals - Gorillas do have a specific body odour, however they do instantly produce a very strong and pungent smell in sudden moments of confrontation.

Behavioural signals - Gorillas walk slowly and awkwardly. In moments of confrontation with predators and rivals they do not run away from danger, instead standing their ground to face the threat. Their behaviour in such moments seems very aggressive, albeit their aggression largely consists sound and sight, rarely reaching the stage of physical violence.

We can conclude that gorillas do exhibit a number of strong aposematic signals, but at least one of these signals (audio) are of a temporary use only. Another important characteristic when taking into consideration the AI among gorillas is that males are definitely more aposematic than females. This kind of sexual dimorphism in the use of aposematic features is quite common among a wide range of animal species in which males and females differ in size, colours and behaviours. For example, in comparison to males, female gorillas do not engage in audio-visual-olfactory intimidating display, do not beat their chest, do not break branches, and do not produce a strong smell in critical situations. Despite of this it must be remembered that female gorillas are still incredibly strong and can do plenty of damage to any predator if need be. In a gorilla clan it is the male's duty to provide security for the family, and although a male gorilla may sometimes fall prey to a leopard (usually while sleeping) or a lion, they perform their task admirably. They are able to do so without usually having to resort to violence due to their fierce size, look and their array of effective aposematic signals.

Peacock – The Rise and Fall of a Symbol?

For many readers who strongly believe in the evolutionary power of sexual selection, the discussion of a peacock's aposematic features will be of crucial importance as the peacock train has been an enduring symbol of sexual selection.

Readers should note from the beginning that the term "peacock" refers only to a male. Females of the same species are known by the name "peahen", and the overall species name is "peafowl". Therefore a peacock is a male peafowl, and in this section we will be predominantly discussing the evolutionary importance of the peacock's tail (correct terminology for their tail is "train").

Through the works of Charles Darwin, the amazing size and dazzling colours of the peacock train became the most prominent symbol of the power of sexual selection. The peacock's visual features were considered so unnecessary for survival, even harmful, that it was believed that the only reason for the peacock sporting the huge train was to entice the female peahens with their beauty. According to this model, a more impressive train ensures the better chances of its bearer in having many offspring. Amotz Zahavi famously dedicated a book to the "handicap

principle", where he argued that for a signal of sexual selection to be "honest", it must actually be a hindrance to the bearer. Zahavi placed a picture of a peacock on the cover of the book as the best and undisputed example of a beautiful but harmful morphological addition to a male body.

Before we discuss the possible aposematic nature of some of the peacock's features, we must recall that the morphological and behavioural elements that are routinely discussed as the designing features of sexual selection via female choice (colourful and big sized body, exaggerated morphological additions, various sounds, smells, strange behaviours), are absolutely identical to the designing features used by the aposematic warning display. Therefore **any scholar dealing with animal species with colourful bodies, ostensibly unnecessary morphological additions or strange behaviours and smells should always take into account that both sexual selection and aposematic strategy use the same visual, audio, olfactory and behavioural signals**.

Unfortunately, as aposematism and warning display have never been properly acknowledged in biological science, plenty of aposematic signals from a vast array of species have never been properly studied. As a result, the model of sexual selection via female choice is virtually reigning unchallenged in discussions on the evolution of the colours, sounds, smells and behaviours of thousands of species, ranging from insects to humans.

This disregard toward the aposematic strategy of natural selection flowered from Charles Darwin. When writing about the amazingly beautiful display of colours and additional morphological features on many animal species, Charles famously wrote: 'To suppose that the females do not appreciate the beauty of the males, is to admit that their splendid decorations, all their pomp and display, are useless; and this is incredible' (Darwin, 2004:557). It is clear from these words that the great scholar did not even consider the possibility that the "beauty and splendid decorations" could all be potent tools to scare away predators and competing rival males.

Because of his one-sided approach, Darwin was sometimes puzzled by the strange features of sexual selection in some species. For example – why, in some species, are females just as distinctly coloured as their male counterparts? Or – why, in species where a male can win a female's affection by physically defeating a competing male, do males still retain these beautiful colours and unusual features that hinder their fighting abilities? The answers to these questions start to become clearer if we take into account that the appearance of colours, morphological additions and strange behaviours may instead be to intimidate rivals and predators. For example, the presence of distinct colouring on both sexes most likely means that their colours are primarily to scare away predators and competitors, avoiding unnecessary physical violence and injuries. The initial notion of natural selection as a total and all out struggle of each living organism against all other living organisms, of different and the same species, is hopelessly out-dated. We need to acknowledge that **avoiding physical conflict is a crucially important strategy in the survival of most animal species**. A complex system of ritual fights with elaborate and

intimidating displays serves this strategy in an integral manner. This was the crucial point neglected in the writings of Darwin, and the same point is still absent in the writings of most of his contemporary proponents on the sexual selection model.

Now let us return to the discussion of peacocks and their unique look, asking ourselves the crucial question: Was it developed to garner female attention or to scare away rivals and predators? Or was it possibly formed to serve both purposes?

Before proceeding further, let us first assess the peacock's AI (Aposematic Index).

Visual signals - A peacock (the male peafowl) with an opened tail is one of the most spectacular sights of the natural world. First of all it is huge, reaching a height of 1.5 meters and three meters in width, making peacock one of the largest birds of our planet. The colours of the peacock's body and tail are also possibly one of the most visually impressive sights of our world. Even with a closed tail, a peacock's colourful body and crowned head are amazingly impressive. As if this were not enough, a peacock's opened tail has plenty of eyespots. Eyespots, as we remember, are often used for intimidating predators and competitors. Visually, peacocks are one of the most potent aposematic species on the planet.

Audio signals – When peacock's beauty is discussed, it is often overlooked that apart from their visually-screaming attire peacocks also make a huge, literally 'screaming' call as well. The volume and persona of a peacock's call are very far from the beauty of its tail, reminding one more of the screaming of some alien species from a horror movie. This call is often described as a negative side to having a peacock as a pet, as the call is much stronger than a rooster's call and can easily disturb the peace of a whole neighbourhood. Their most common calls are a loud *pia-ow* or *may-awe*. The frequency of calling increases before the Monsoon season and may be delivered in alarm or when disturbed by loud noises. In forests, their calls often indicate the presence of predators such as the tiger (Whistler, 1949:401-410; Ali & Ripley, 1980:123-126). Apart from these loud calls, peacocks also make rattling sounds when displaying their train.

Olfactory signals – I have not found any information indicating that peacocks have any constant body odour, but when grabbed by humans (and we could assume, by predators as well) they defecate on them, and according to people lucky enough to have of these beautiful birds the smell of peacock droppings is quite strong. I have never had the pleasure of having this magnificent bird as a pet, but we can read the testimony of a person who has some first-hand experience. When he took the peacock for the first time in his hands, the peacock defecated on his clothes, and according to him: "…the smell of peacock shit is the worst of all the shits I've ever smelled, cats included. It's true! Peacock poo is bad to match the sound..." Such a strong smell from a mostly non-predatory bird, together with the habit of defecation when constrained against its will, suggests that peacocks also use an olfactory aposematic signal.

Behavioural signals – Aposematic species usually walk slowly, and do not run upon seeing a predator. They instead often behave aggressively, even moving

towards an antagonist that is bigger and stronger. Peacocks also walk slowly and are not easily frightened to run away or fly away. They often come close to humans and are sometimes known to follow them, which can actually be intimidating considering their size. Peacocks in the wild are not even frightened by the sight of tigers. George Schaller wrote: "The peafowl at Kanha [National Park in India] were not greatly alarmed by the proximity of a tiger. One cock walked past a tigress at a distance of thirty-five feet; on another occasion, when a tigress suddenly stood up in the grass thirty feet from a cock, the bird merely looked up, then continued to forage" (Schaller, 1984:279). These are typical aposematic behavioural signals. Females (peahens) also actively use their (albeit much smaller) tail to scare away competitors or predators.

Darwin noticed how peacocks open their tails when pigs entered the yard but made, in my opinion, the wrong conclusion: "evidently [peacock] wishes for a spectator of some kind, and, as I have often seen, will show off his finery before poultry, or even pigs' (Darwin, 2004:444). Well, if I was to choose out of these two reasons as to why peacocks open their tail when a pig enters the same yard, (1) to show off the beauty of their colourful tail to a pig, or (2) to defend his territory from the intruder - I would choose the latter option.

So, contrary to the opinion (or even the belief) of the long list of distinguished scholars from Darwin to Zahavi, who were/are sure that the peacock's legendarily impressive tail was designed by the forces of sexual selection, I am coming to the conclusion that the **primary force behind the beauty and size of the peacock was natural selection trough the mechanism of warning display (aposematism)**.

Of course, as I have already mentioned several times, these two forces of evolutionary change are not necessarily mutually exclusive. On the contrary, the same signals that can scare away predators and rivals can also attract mates. However, when choosing the primary force behind these signals I opt for natural selection – scaring away rival males and predators and replacing violent fights with ritualized display must essentially be the primary reason behind the dazzling beauty of a peacock.

Unfortunately we cannot ask the peacocks and peahens about the main reason behind their beauty, but there are other ways to check the relative importance of these two evolutionary forces. Why do scholars need to be guessing whether the peacock train is for sexual selection of for some other reason? Scholars should merely observe peafowl behaviour and see if the males with more beautiful trains have more success with the females!

Sexual selection in peafowl: studies – Amazingly, scholars were so sure about the sexual nature of the attractiveness of a peacock's dazzling display that they did not even consider it necessary to test this tacitly agreed idea with an objective and solid field study. It was only in the beginning of the 1990s that Marion Petrie, Tim Halliday and Carolyn Sanders published the results of their study on peacocks' mating behaviour. According to their results, as it was expected, females were

choosing males with bigger trains and with the biggest number of eyespots. Unfortunately the study was not large enough (researchers studied only one Lek of 10 males for very limited time. A Lek is a congregation of males).

In the second half of the 1990s, a seven year-long study was conducted in Japan to verify the Petrie/Halliday/Sanders finding with a larger sample and ground the sexual nature of the peacock's attributes into popular thinking with solid field results. During seven mating seasons, observed from 1995 to 2001, researchers from the Graduate School of Arts and Sciences at the University of Tokyo, under the leadership of Mariko Takahashi, studied a free-ranging population of Indian peafowl at Izu Cactus Park in Shizuoka, Japan. They naturally expected to find confirmation of the power of sexual selection in a peacock's morphology.

Amazingly for the Japanese researchers as well as a big section of scholars, researchers came to the sensational conclusion that the female peahens were indifferent to the peacocks' tail size, and that brilliant colouring and tail condition did not correlate with the reproductive success of their bearers.

The publication of the results of this study, as expected, stirred heated debate. According to an article in Discovery News, "The feather train on male peacocks is among the most striking and beautiful physical attributes in nature, but it fails to excite, much less interest, females, according to new research. The determination throws a wrench in the long-held belief that male peacock feathers evolved in response to female mate choice. It could also indicate that certain other elaborate features in galliformes, a group that includes turkeys, chickens, grouse, quails and pheasants, as well as peacocks, are not necessarily linked to fitness and mating success" (Viegas, 2008).

Creationists also benefited from this unexpected result, suggesting that if sexual selection was not behind the peacock's tail, then what else could be the reason for this 'unnecessary beauty' if not the will and aesthetic sense of the Creator? Petrie and her French colleagues actually wrote a rebuttal of the revealing Takahashi et al. study (Loyau et al., 2008). They suggested that, first of all, more observations were needed to come to final conclusions, and secondly they proposed that a phenomenon known as 'plasticity of female choice' can be involved. When translated into plain English, this term means that peahens possibly change their taste in choosing males much like humans do, and that contemporary peahens are not as interested in the size and beauty of the classic peacock train as their grandmothers were.

I agree with Marion Petrie and her French colleagues in that more observations are needed to come to final conclusions, but in regards to the "plasticity of female choice" I do have some doubts. It seems quite difficult to believe that, after tens and hundreds of thousands (possibly even millions) of years of female excitement for their male counterparts' trains that suddenly, before the close of the 20th century during a 4-5 year period in the 1990s (between the studies of Marion Petrie and Mariko Takahashi), that they suddenly lost interest towards the peacock's dazzling display.

Joseph Jordania (2014). In: *Tigers, Lions and Humans: History of Rivalry, Conflict, Reverence and Love*. Logos Publishing. ISBN 978-9941-437-60-1.

I strongly suggest to those who will be studying the reasons behind the beauty of peacock tail not to discount the possibility that a peacock's tail's amazing size and beauty, with an immense number of large eyespots (over 150), together with their loud calls, smelly droppings, and fearless behaviour can be a set of warning and intimidating signals to their rivals and predators.

Academics are notoriously difficult and reluctant in accepting new ideas and even new facts. The groundbreaking Japanese study of Takahashi sometimes gets simply neglected (see, for example, a recent article by Patricia Brennan from the Department of Ecology and Evolutionary Biology, Yale University, Brennan, 2012). Proponents of sexual selection in peacocks also try to draw on a number of previous short-term studies as well: "The authors seem to ignore the fact that three previous independent studies have found relationships between mating success and train morphology. Rather than consider what is unusual about their study, they conclude that peahens in general do not prefer males with elaborate trains" declared Marion Petrie (Barras, 2008).

Well, as I can understand, the biggest difference between the previous studies that Petrie mentions and the Japanese study is evidently clear: Japanese scholars spent a much longer amount of time in observing the behaviour (seven years as opposed to one). Furthermore, unlike the previous studies, Japanese scholars did not change the peacocks' appearance by erasing their eyespots. We should be grateful that the Japanese team of scholars, despite the fact that they were confused by their findings (they expected their results to merely confirm previous studies), still published their alarming results. It is, unfortunately, a quite common and sad practice among academics that studies with negative/undesirable results are almost never brought to a wider audience.

It would be natural to expect that a bigger study of the peacock train and its importance for sexual selection is currently under way, in an eager bid to prove the Japanese results wrong. Losing this iconic argument will take a heavy toll on the proponents of sexual selection, but will we ever hear of the outcome of such studies if the new results confirm the conclusions of the Japanese study?

Conclusion: if we take into account that to look bigger (and more colourful) is one of natural selection's favourite strategies to scare away predators and competitors and avoid unnecessary physical confrontations, the idea that the peacock train was primarily designed by the forces of natural selection in order to scare away rivals and predators seems very plausible.

Another suggestion: scholars who are interested in researching the power of sexual selection should first acquire a solid knowledge of aposematic signals and strategies, as both aposematism and sexual selection thrive on virtually the same set of morphological and behavioural features. Therefore, completely ignoring one of the two great evolutionary strategies designed by the evolutionary forces is an unwise and detrimental research strategy.

Joseph Jordania (2014). In: *Tigers, Lions and Humans: History of Rivalry, Conflict, Reverence and Love*. Logos Publishing. ISBN 978-9941-437-60-1.

The problem is far from being resolved, as only one long-term study is not enough to settle such an important question. We can say that the old axiom is currently viewed with a healthy dose of scepticism, and for a good reason. The tail of a peacock, arguably the greatest symbol of the power of sexual selection, might in turn become the symbol of the decline of the importance of the theory of sexual selection.