

Ethology of fear: Responses, actions, universes

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Original source:

Revista Catalana de Psicoanàlisi, 28(2): 1-18 (2011)

(<http://www.sep-psicoanalisi.org/ca/publicaciones/revista-catalana-de-psicoanalisi/>)

Translated from Catalan by Mary Black

Abstract

In this paper we describe the motivational-behavioural system of fear from an ethological point of view. Fear behaviour is primarily considered reactive, that is, dependent upon past events, so its manifestations should be classified as responses rather than actions. The behavioural outcomes of fear which are closer to actions are those involved in defensive aggression and in deceit targeted at predators or rivals. We also analyse the perceptual worlds around fear and relate them to two important polarities of animal adaptation, namely fear-security and fear-aggression. Both animal expressive patterns and intentional actions often reflect the conflict between these opposites, and decisions in the face of danger are based on a balance between the cost and benefit and the adaptive value of behaviour in its ecological context.

Key words: ethology of fear, fear behaviour, defensive aggression, fear and security, animal deceit, perception of danger, fear adaptive value

"... fear, the only measuring device that consciousness has; the lack of another thing is what makes it something..."
Juan Benet, *Volverás a región*

1. Fear on the flow of animal behaviour

We use "fear" to denote a state of motivation which, like others, is activated by specific stimuli and is manifested via observable physiological and behavioural changes. The stimuli inform the animal or its family group about dangerous or risky situations. For this reason, the most common behaviours that express or manage fear are avoidance or defence, as we shall outline below. Yet it is difficult to examine the experience of fear in animals firsthand, although when emotions are involved we feel it more directly. This holds true in mammals –

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especially primates – and perhaps in some birds. The use of the term “fear” applied to a crocodile, a frog or a shark is not as convincing, and it is even less so when applied to a fly or a worm. These animals are very different to us. But if instead of inferring an animal’s experience of fear based on our own experience we do it based on how they respond to situations that entail danger and risk to their survival, then it is a reasonable hypothesis to conjecture that practically any metazoan with a brain can experience fear, regardless of how it is represented or experienced, since fear and its behaviours are, as we shall see, fully adaptive. Survival would be unlikely without fear, just like without pain, because beings would lack a system of control over the threats around them. Yet there is no doubt that phylogenetic proximity helps us to infer how both fear and pain are experienced, so we can intuit the fear of a dog or a chimpanzee better than that of a fish. In any event, a comparison of the brain centres responsible for fear in different species and in different zoological groups reveals similarities and furnishes indices whose psychological contents may correspond to states of fear in the perspective of each animal (Rodgers et al, 1997).

Following a core tradition in ethology, this article shall focus on the behaviours of fear, even though logically they will lead us to the stimuli and environmental circumstances that activate it, as well as the purposes they serve. We shall strive to situate fear within the framework of animal-environment relations, and within a temporal context as well, specifically the past-future axis in which each response or action falls. We hold that fear is a motivational-behavioural system that looks more toward the past than the future in different time scales, a negative or reactive system, though unquestionably an adaptive one as well in that even though we can say that any behaviour depends on the past, either near or distant, we can add that in fear this dependence is more complete.

In order to set up the frame over which to weave our arguments, we shall use a metatheoretical schema which comes from pragmatics and which we have used on other occasions (Riba, 1992; 2000). First of all, on a semiotic note, any representation or sign for an observer refers first to an object, deed or referent and next to a rule of interpretation or interpreter. If we project this triangular relationship onto the interaction sequences between organism and environment, and therefore onto chronological time, we make this schema dovetail with another which is clearly nestled at the heart of biological and psychological (and thus, ethological) thinking: Any behaviour *C* (a sign for the observer) can be interpreted in two ways, as a *reaction* or *response R* to a preceding event or an object *O*, in a phase that looks toward the *past* and reflects *causal* relationships; or as action *A* aimed at targets, effects or consequences on the environment projected toward the *future*, in a phase that corresponds to *functional* relationships (what is the behaviour for?) or, if you will, teleological relationships. In this latter case, ethology, aided by philosophy, dares to introduce the idea of intentionality, even though it defines it as operationally as possible and distinguishes degrees of intentionality according to the complexity of each animal’s central nervous system (Dennett, 1983). This second facet is also the one that allows the observer to reach interpretation *I* by connecting an environmental state that affects the organism with the behaviour that it actively adopts to achieve a goal. Therefore,

$$O \leftarrow R / A \rightarrow I$$

in which $O \leftarrow R$ is the reactive or passive phase and $A \rightarrow I$ the active phase or the one targeted at the goal. Here, the arrows represent the direction of the interpretation, which is retrospective on the left half and prospective on the right half, although this direction is more psychological than temporal. In the first of these phases, the signs (a smell, a footprint, the snap of broken branches) dominate, whereas in the second half symbols dominate as signs oriented toward the future (a threatening gesture; see Thom, 1980).

In order to situate fear in the context of past-future interpretation, we shall apply this prototypical situation of danger to the predator-prey dynamic. Fear is essentially fear of the predator within interspecies competition, even though it can also arise with a rival from the same species when vying for resources (food, water, males, females, refuges, etc.) or when faced with large-scale phenomena in the physical environment, such as thunder, flooding or fire. Therefore, let us assume that a leopard detects a possible prey and stands still lying in wait. He stalks the prey, leaps and captures it, and then devours it. In this sequence, a reaction-action sequence would look like this:

Prey (detected) \leftarrow Wait / Approach \rightarrow Capture, ingestion

The perception of the prey leads to immobility and waiting; after that, the sequence progresses actively towards the satisfaction of hunger and the return to homeostasis. Once it has located the prey, the predator stalks it, approaches it and appropriates it. It displays appetitive behaviours that seek to fill a void. Naturally, *the opposite is not true*. The prey does not seek the predator – at least in animals! – not even to flee from it. This obvious asymmetry reveals important aspects in the adaptive function of fear and in the selective pressure that it must have exerted throughout evolution. At first glance, the majority of fear behaviours are totally reactive or aversive, such as the vocalisation of terror, fur standing on end or quick flight. If these behaviours seek anything it is precisely distance and avoidance, and only as a last resort do they morph into an attack, but always a *counterattack*. The signs and behaviours of fear are preferably located in that phase of environment-organism relationship in which the latter is fundamentally passive, always at the mercy of the events around it.

2. The alarm systems of birds and the reactive nature of fear

We shall try to perform a more in-depth analysis of the asymmetry we have just noticed and to further define it. To do this, we shall superimpose this interpretative schema used in the previous section over alarm systems which socially regulate responses adapted to fear. We shall use several examples that are familiar to ethological readers, especially the two calls that many palearctic forest birds (blackbirds, robin redbreasts, chaffinches, tits, etc.) use to warn about the presence of predators (Thorpe, 1972). *The long call* displays a very narrow-band frequency and a relatively long duration. It follows detection of small “celestial” aerial predators, that is, ones outlined against the sky, perhaps

birds of prey like the falcon. The consequence of a long call on the social environment, and even on bird species other than the caller's own, is immobilisation, silence and concealment. *The short call* shows a very wide-band frequency and responds to the presence of an aerial predator inside the forest, perhaps an eagle owl or a common owl. The effect of this call is collective agitated behaviour, a disorderly, wavering (forward and backward) flight around the predator which ethologists have called "mobbing". Therefore, we have:

Falcon ← Long call → Immobilisation, concealment
Owl ← Short call → Mobbing

We could believe that each of these calls can be interpreted as alarm behaviour in either the reactive or active phase, as in the example of the leopard. However, the fact that evolution has conducted these responses towards the purpose of alerting fellow birds does not necessarily mean that the calls have a social function but that *the potential recipients must be capable of processing them correctly*. There is an old controversy regarding whether this kind of behaviour is simply an expressive response (which reveals the animal's internal state) or whether it also has a communicative value because the emitter's goal is to somehow modify the behaviour of the potential recipients. Simply put, it is clear that these alarm vocalisations are functional in that they trigger adapted responses, but it is not clear whether they are proactive, "intentional" and more than simply an individual manifestation of fear. In short, there is doubt as to whether they are selfish or altruistic behaviours. We shall return to this point later.

Now, apart from this somewhat byzantine controversy (with resolutions linked to the cognitive competence of each species studied), we should focus our attention on the kind of behaviours activated by the alarm calls. In the case of the falcon, immobilisation, silence and concealment are behaviours with "zero" value or a negative valence, since they consist of erasing the individual from the scene where it lives; these behaviours reveal a strict function of erasure and show no indication of consummation of action. Nor do they imply attainment or appropriation of a goal by the emitter of the call. We could extend this argumentation beyond the example of the alarm call towards other "zero" defensive or avoidance behaviours, such as the chameleon's or octopus' camouflage, which also makes the animal disappear from its setting.

We could claim that mobbing does entail a positive social action transferred to the phase of social consequences. However, ethologists have doubts regarding this behaviour similar to the doubts explained above (Berlyne, 1960: 122 – 123; see below). In terms of its effects, does mobbing grant fear a positive vector of intentionality in that it implies an attack on the predator, or is it a simple ceremony aimed at triggering bewilderment and confusion? Its function is most likely not so much to attack the predator but to prevent it from taking decisions on capturing individual prey in the midst of the whirl of birds.

One fact that poses serious doubts regarding the intentionality of the altruism of the alarm calls is that many birds make identical or similar calls

when suffering, an instant before being trapped by the predator or once they have already been captured by it. We would have to assume, for example, that the thrush about to perish in the claws of a falcon whistles to warn its fellow thrushes. Even though these agony calls are clearly functional and do alert other birds (to such an extent that these recorded calls are played on farms to fend off unwanted eating of the crops), we have already said that producing them does not require a prior representation of social goals. Instead, they are responses to pain, stress and fear, and consequently they do not even warrant the label “selfish”. However, some hypotheses suggest that these calls can be selfish in the sense of promoting the interference of another predator and generating a conflict that is beneficial to the prey, which could be freed, or in the sense of gaining and enlisting the aid of nearby members of the victim’s own species (Högsted, 1983; Møller & Nielsen, 2010). This latter possibility, which is difficult to prove in birds, would be more acceptable in social mammals, especially when the captured prey is young.

3. Alarm systems of vervet monkeys and the possibilities of fear

The question of whether the social transmission of fear can be understood in the context of selfishness or altruism often appears in another light when we consider species with a more complex social organisation and higher cognitive competences. A species of African *Cercopithecidae*, the vervet monkey (*Cercopithecus aethiops*), has become the star of ethological research in the past 30 years thanks to a series of studies which have revealed that it has a sophisticated alarm system which implies a fine-tuned analysis of its ecological niche and enables referential communication (Seyfarth, 1982; Seyfarth and Cheney, 1982; Seyfarth, Cheney and Marler, 1980). For vervet monkeys, the three categories of predators are the leopard (as the main representative of terrestrial predators), the eagle (as a representative of aerial predators) and the African viper (as a representative of venomous, lethal snakes). Detection of each of these predators arouses a spectrographically different vocalisation, which in turn triggers an equally different and clearly functional social response. Thus, after the “leopard” vocalisation, we can note a rapid ascent into the *highest* branches of the trees in the quest for a safe haven; after the “eagle” vocalisation we see the opposite response, a quick descent from the trees to land on the ground; and after the “viper” vocalisation the actions triggered include looking at the ground and jumping backward. Obviously, these behaviours, just like the ones mentioned in the previous section, entail avoidance or flight, but if we examine the social use of the corresponding vocalisations we capture variations that merit further examination. For example, the “leopard” alarm is mainly issued by adult males, who, however, rarely issue the other two calls, which are largely attributed to the females and young individuals. Therefore, the males have a higher response threshold in the perception of risk, given that a leopard implies a more dire risk, or one that is more difficult to avoid, than an eagle or a snake. What is more, females with young become “alarmed” more easily than the females without young in their care. All of this perhaps enables us to deduce a kind of altruistic social intentionality in these calls in that they serve the group and are not merely the emotional expression of the individual issuing them.

4. Flight and the search for refuge

Let us now abandon alarm systems, which for the end recipients of the message are nothing more than indirect contact with the danger, and instead let us focus on those behaviours that involve the actor's proximity to the material threat (such as behaviours when faced with a predator or a belligerent rival). Now, after exhibiting its expressive response of panic, instead of hiding or disappearing, the animal may simply decide to flee. And flight is a negative conduct in the same way that immobility or concealment were and is, in fact, a variation on the latter.

However, we must recognise that escaping does not always mean throwing oneself into the void; it does not always or only entail increasing the distance from the danger. Flight is often not towards nothing but instead towards the refuge of the nest or den, towards the progenitors, the family group, the shoal or school of fish, the flock of birds, the herd. The fish that becomes separated from the school flees back to its fellow fish at the first sign of danger; when they spot a falcon, starlings group together to present a solid front of indistinct bodies; the tiny baboon that has been alerted to some ominous presence returns frightened to the congress from which it had been separated. The threatened animal which fearfully merges with its group not only feels more protected but also substantially lowers the uncertainty of expectations and decision-making: from this moment on, wrapped in the motivational or emotional tone of the group, the behavioural routes are simplified and decisions do not have to be taken individually (Delgado and Aylett, 2007). It must not be by chance that a brain centre responsible for evaluating uncertainty is the amygdala, the same one that is profoundly involved in activating and processing fear (Rosen and Donley, 2006).

In mammals and birds like *Psittacidae* (parrots, lorikeets, parakeets), this kind of phenomenon has suggested deep-seated ties between fear and security through attachment, in an avenue of research that has had enormous influence on evolutionary and clinical psychology through figures like Bowlby and Ainsworth (Ainsworth & Bowlby, 1991; Bretherton, 1992). These ties, which in mammals also depend upon nursing, are clearly crucial to the development of the individual and in particular to the fine-tuning of their adaptation. And one decisive argument in favour of the mutual dependence of fear and security lies in the fact that some of the behaviours involved in both fear and security are shared (Stevenson and Hinde, 1991). Furthermore, it is not difficult to find examples of the adaptive fine-tuning of both systems. One example would be the vocalisations and calls for help that many bird and mammal young use when they perceive a significant decline in their security, when they become separated from their parents or isolated: in the fear-security continuum, the fact that these vocalisations are codified with remarkable precision (in that their duration rises and the initial high frequencies vanish as the fear intensifies) clearly reflects their high adaptive value (Salzen, 1979).

Therefore, the quest for refuge and security could be judged as appetitive behaviour given that it is consummated at the moment the animal rejoins the protective social environment and gains contact with the mother, the parents or the group. Here we can see a certain appropriation of the body or bodies to which they flock, similar to trophic or sexual behaviour. Still, once again it is true that in these circumstances, the animal which returns to the reference

group does so spurred by a situation imposed by the environs, not by their own decision, not by spontaneously setting their own goals.

5. Aggression against the predator or social rival

Harlow said that fear is avoidance and flight, while aggression is approximation and attack (1980). We would venture to shade this statement by claiming that fear is avoidance and flight until it enters its agonistic phase once a certain level of intensity has been reached and with certain parameters. At that point, fear and aggression are articulated (Chance, 1980), just as frustration and aggression are articulated, following the homologous model familiar to psychologists (Gray, 1987: 201 forward). The animal in danger prolongs the behavioural chain towards agonistic albeit defensive goals, such that its first responses to fear transform into true opposition actions or attack on the predator. It is true that sometimes these actions are more reactions driven by the autonomic nervous system, such as the skunk's reaction in situations of stress in which it vacates its anal glands and spreads a foul smell (Pruitt and Burghardt, 1977). However, defensive attack actions usually place the frightened animal at the lower limit of their passivity, at the boundary in which fleeing or disappearing is no longer enough or possible and they must do something else instead to survive.

A significant amount of animal aggression is defensive, without necessarily being submissive (Ursin, 1985). Consequently, this kind of aggression is also reactive, the outcome of panic or stress (Archer, 1988, chapters 3 and 4). However, it is well known that the prey's or the cornered animal's defensive reaction to the predator, though more intense than its rival precisely because it is more desperate (if the predator fails, it does not eat; if the prey fails, it dies), only occurs in extreme situations and when there is no other way out; the majority of times it tends to be the threatened animal's last resort. In both the predator-prey dynamic and in a confrontation with a social rival (in the ritual combats between males during reproductive season, and in disputes over food or shelter), aggression tends to be counterbalanced, and often cancelled out, by fear. This balance has an expressive chain which has been amply studied in the faces of mammals, in the muscle configurations which are appropriate for translating this articulation of fear and aggression. In Lorenz's oft-cited classification of the facial expressions of canids (1971, p. 114), the distinctive features can be found in: 1) the ears, with a variation of 90 degrees from horizontal to totally erect; and b) the mouth, open with the fangs bared or totally closed. Combinations of intermediate values in this range of variation yield a total of nine expressions with different meanings regarding the animal's degree of motivation, and therefore regarding the likelihood of attack or flight and surrender. There are other similar systematisations of the expressions of other mammals (Hinde, 1970: 383 - 384).

With regard to the possibility of surrender, we should bear in mind that it only makes adaptive sense in struggles between animals of the same species. The sheep cannot surrender to the wolf, but a wolf can surrender to another wolf. In this context, once they have given up aggression, the majority of vertebrates have useful appeasement behaviours which do indeed imply submission and which, incidentally, are an alternative way of handling fear. Another extremely important alternative in intraspecies competition is the communicative behaviours which ethologists label "displacement", assigning

them a very different meaning than this term has in psychoanalysis. In ethology, displacements are ritual movements that replace or reorient the action, through which the animal conveys to its opponent its doubts as to whether it should flee or attack, whether it should remain in the fray or abandon it. For example, in many passeriform birds, as well as in roosters, it can be observed that in scenarios of social conflict the animals display actions that are apparently out of context, that is, that involve neither attack nor defence or flight. One example would be fluffing their feathers or pecking at the ground (even though there is not a grain of feed). At that time, the individual is neither dominant nor submissive; rather it is expressing a balance between behavioural tendencies of approximation and distance in motivational coordinates somewhere between fear, or frustration, and aggression (see Hinde, *op. cit.*: 406).

Still, if the animal in danger of being devoured or injured cannot flee, hide or surrender, nor can it be compliant with the adversary, it may show threatening signs, and if they have no effect, it may attack – or counterattack – as a last-ditch option. However, logically, not all animals will do this but only those with motivational-behavioural systems which enable them to do it in congruence with their adaptation pattern: a rat or a dog would do it, but a rabbit or an antelope would not. In short, the animal that counterattacks shows a more oriented behaviour than the one that is resigned to fleeing or vanishing, and in consequence we can attribute an added intentionality to their action, even if it is totally selfish and aimed at individual survival. Once again, this intentionality is essentially understood in the operational realm: the action is targeted at a goal and ceases when this goal has been attained, in the event of success – such as when the predator quits the battlefield.

6. Deceit of predators or rivals

The defensive strategy is quite different when the goal set by the threatened animal is not to aggressively stop the predator or rival but to deceive it. One anatomic resource for achieving this objective is the well-known mechanism of preventing or deflecting the attack by protections in the guise of spikes, shells, carapaces and stinging appendages. The animal (hedgehog, porcupine, tortoise, etc.) only has to adopt the best posture to activate these defences, a posture that often coincides with foetal position or a ball, meaning that this behaviour nothing more than a totally passive adaptation to the threat. We can see a further degree of intentionality in bluffing, behaviours when faced with a rival aimed at simulating bulk or extreme aggressiveness far beyond the possibilities of the animal simulating them. Bluffing tends to prompt an apparent increase in the animal's size, or it attempts to intimidate the other by raising the hair on end, ruffling the feathers, producing strident calls, inflating the dewlaps, erecting the crest or appendages, etc. Despite the fact that these behaviours are visibly oriented at threatening the rival, they are controlled by the autonomic nervous system and have a major automatic or reactive component that is highly visible in reptiles and birds.

However, if the deceit is active or the action is clearly targeted at deflecting or suspending the predator's attention, the proactive orientation of the behaviour does become clear at some point, even though it may once again suggest a purely selfish functionality. This is the case of animals that simulate death when faced with a predator, like some weevils, like the oyster toadfish

(*Opsanus*), which when faced with a predator issues a kind of cry, pales and seems to suffocate, and like the opossum which becomes totally immobile, retracts the lips and emits a foul-smelling liquid as if it were already in a state of putrefaction (Franco, 1969). Sometimes, however, the simulation of death ends as the predator is about to touch the animal feigning death, when the latter leaps up at the last second (such as mice with snakes, or some lizards).

In contrast, the deceit used to save the young is difficult to interpret in any terms other than family altruism. This kind of deceit is also executed based on complex actions developed on the ground. Surely the best-known example is the simulation of an injured wing (Heinroth, 1979), which can be seen in quails, feral chickens and river birds, and, if analysed carefully, the American piping plover (*Charadrius melodus*; Ristau, 1991). When they realise the proximity of a predator, both the male and female piping plover abandon the nest with eggs or chicks and walk dragging their wing, attracting the predator behind them and deflecting attention away from their chicks. In this case, we can easily recognise a vector of directionality or functional intentionality in the planning and execution of this action, an intense enough vector to separate the parents from the young and to risk the former's life far from the nest. The component of altruism in the sense of preserving the family genes is quite obvious in this case.

Examples of altruism like this one would unquestionably signal the upper limits of the proactive capacity of fear, the boundaries of its projection into the future in the planning of behaviour. However, in these examples, as well as in the examples of defensive aggression, we can sense that the action comes in the wake of contingent and often unpredictable events. Basically, fear motivates the animal from the past to the future, from the past of the species, from the ontogenetic past of the individual, from the most immediate past that materialises in responses and actions. Even when it is used to prevent and avoid future dangers, fear sets its negative goals, the presences it wants to save, based not on the experience in the here and now but on memory; it seeks not to appropriate anything but instead to avoid and reject something.

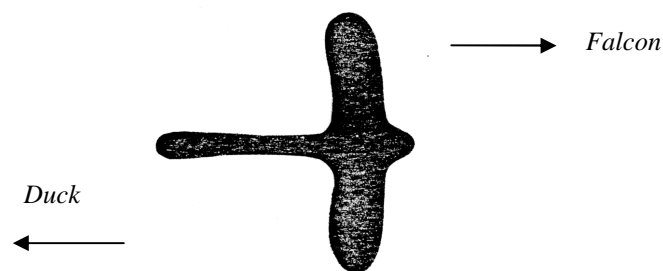
7. The perceptive universe of fear

Each animal lives in the perceptive universe unique to its species, a world that includes both potential environmental perceptions (according to the peripheral and central nervous systems) and the kinaesthetic information that its actions send it through its proprioception. We call this universe its *Umwelt* following the historic contribution of Jakob von Uexküll (1934/1965). Thus far we have grounded our analysis on animals' observable behaviour, and we have been cautious when referring to the cognitive facet of a given behaviour. However, even though we cannot access the animal's mind or experience, we can relate the patterns of environmental events, at the beginning or end of the chain of behaviours, with the responses or actions which the animal executes; we psychologists and ethologists have always done this. Consequently, we have several options when characterising the forms and environmental patterns that promote or incite certain behaviours. We cannot experience the world as the animal does, but we can create models of their representation of this world.

There is no doubt that fear is under genetic control and that the core responses that express and regulate it are innate (Gray, op. cit.). The objects of

fear, the environmental stimuli and patterns that trigger it, are maximally laden when they correspond to innate schema or stimuli-sign (according to the ethological nomenclature); they are powerful attractors which evolution has selected and which absorb the animal's attention and responses from its very birth or after a longer or shorter maturation period. The conditioned responses to these contingent stimuli which have been associated with innate stimuli are a subset of the set of responses that the latter activate. René Thom has formalised this logically and topologically (1980). In vervet monkeys, the indicators that anticipate the presence of a snake – the alarm signal which must be partly learned (Seyfarth and Cheney, 1982), the friction on the dry leaves that warns as to its presence, the leap backward of a fellow monkey that has seen the snake first – induce responses that will be part of the repertoire with which the monkey will handle the direct, close-up view of the snake. The learning of the behaviour of fear lies totally in the animal's innate programming. It should be borne in mind that the ability to detect and respond to dangerous situations is crucial to the survival of the individual and its genus, so it cannot be dependent upon early learning since this would not guarantee adaptation to the danger quickly and widely enough (Ackerl, Atzmueller and Grammer, 2002). Naturally, learning ends up fine-tuning the fear system to fit the particular circumstances that arise in the individual's environment and spreads the avoidance function to those gaps in space and time that the animal's innate programming does not reach.

The innate schemas are primitive visual, acoustic and olfactory forms which inoculate fear automatically and tend to show a very simple structure. One classic example of these forms is the visual channel of the “duck-falcon” pattern, which is illustrated below. If the silhouette moves from left to right over a group of *Gallinacea* or *Anatidae*, the animals scatter in bewilderment upon perceiving the outline of a falcon or a small bird of prey gliding over them; however, if the movement is in the opposite direction they are calm because they perceive the image of a flying swan or duck.



Based on phenomena like this, the ethologist has to reconstruct the structure perceived by the animal and come up with a model, which will always be a construct which needs to be validated. Fortunately for the animals, these mechanisms triggered are automatic, quick and relatively safe, and they prepare it properly for the risk. In jest, the animal in danger and permeated by fear does not wonder whether it is facing a noumena or phenomena. Here, a convinced referentialism, a metaphysical realism situated and justified within each animal species' *Umwelt*, is apt. When frightened, the animal is frightened by

something: there always has to be a referent. Therefore, the meaning of fear cannot be resolved in a logical or structural approach to the events or situations that trigger it (Thom, 1980: 1985: 157 - 161). Beyond culture and language, at the core of natural law it is not valid to speak about the flight of meanings and infinite webs of reference. To the contrary, the meanings of fear are profoundly rooted in specific places in the phylogenetic and ontogenetic memory, and in the behaviours linked to this fear. A leopard is a leopard, something that could devour us, and it has a spatiotemporal location in the here and now. Neither the perception of the leopard nor the behaviours that strive to avoid it are too far from this primitive affirmation.

8. Fear as adaptation

Fear, its experience and the behaviours that control it, has become embedded in organisms over the course of evolution because it is useful and yields more benefits than costs: it is adaptive. In the majority of circumstances, a lack of fear is not adaptive because it exposes the animal to excessive risk without rewards, except in the cases we have examined above in which the animal defends itself in desperation or protects its young without evaluating the risks. Incidentally, fear of imaginary dangers is not adaptive either in that the demand for energy expended is not compensated (Marks and Nesse, 1994; Kennair, 2007).

Having said this, not all responses to fear and not all actions derived from this response have the same adaptive value. For example, there are debates as to whether mobbing has much adaptive value in that it rarely leads the predator to fly away and instead places the birds involved in the mobbing at risk; ultimately, based on the typical vacillating flight pattern, it could be understood as a result of the conflict between approach and avoidance (Berlyne, *ibid.*). Feigning an injured wing entails its own uncertainties, but it seems to be adaptive because it is the least harmful solution. To the contrary, in other cases the behaviour reveals an extreme level of adaptation. The long and short calls of birds which we examined in the beginning of this article show precise adaptation of their acoustic structure to the circumstances in which they are emitted. While the alert to falcons selfishly requires that the emitters' location not be found in congruence with the immobilisation response it arouses, what follows the detection of an eagle owl or a common owl does not entail this requirement, since the response it triggers is the bold manifestation of the prey in the eyes of the predator. In line with this contrast, the long calls show a narrow-band frequency which makes it difficult to pinpoint the source by preventing the comparison of phases from one ear to the other, while the short calls show a very wide-band frequency, since preventing the predator from locating the emitter no longer brings an adaptive advantage (Thorpe, *op. cit.*).

The adaptation value of fear is not only revealed in each particular behaviour but especially in the web of relations among the different motivation and behaviour systems. Many years ago, Churchman and Ackoff (1950) sketched the general framework of an organism's adaptation via a simple yet understandable classification. Theoretically, adaptation functions can be defined based on the problems with which the environment challenges each animal of each species; problems such as how and what to eat, where to drink, where to take refuge, where to keep their offspring safe and how to safeguard their own survival.

- 1) On the first level, the most precarious or primitive one, the animal has one or few solutions for all the problems the environment can pose.
- 2) On the second level, the animal has a solution for each problem it must deal with in biunivocal correspondence.
- 3) On the third level, the most highly evolved, the animal has more than one solution for each problem it may face and chooses the best one according to the characteristics of the problem.

Since we have listed many useful behaviours for managing fear and its circumstances, we might believe that the majority of examples we have cited are situated at the third level. However, it is clear that not all the behaviours mentioned are available to every species. It is absurd to imagine that a mouse can use the recourse of defensive aggression against a cat, although a rat could. A gazelle will not resort to immobilisation to flee from a lion, nor will it try to defend itself against the feline. In any event, the number of behavioural resources available is proportional to the complexity of the species' nervous system and to the plasticity of its fit within its environment. In known mammal repertoires, this number is surprisingly high (see, for example, a rat's defensive resources in Rodgers et al, 1997).

Within its sphere of activity, the animal has a variable perception of risk arising from its experience. Fear prevents it from going certain places where it knows that predators are more likely to be, and, in compensation, confidence leads it to circulate along routes which it knows to be relatively safe. We could talk about a veritable landscape of fear according to the gradient of risk that each individual senses in its environment (Laundré, Hernández and Ripple, 2010). However, generally speaking, if it comes upon a predator or rival, or vice-versa, if they come upon it, the animal will take on the risk of attacking it when it sees itself as a potential victim and its situation becomes desperate: when cornered, when protecting the den or young, when flight is not an option. Bees fight furiously against wasps invading their hive. Soldier ants precisely exist to protect the anthill from outside attacks. Male bison and other bovids face down virtual predators by circling their females and children, and if needed they will attack a predator that comes too close. The canonical sequence of the decisions taken by metazoans in a dangerous situation would be: concealment or immobility → flight or the quest for refuge → defensive aggression. The animal moves from one stage to the next according to the cost-benefit values and the corresponding estimate of the likelihood of success in each stage depending on the parameters of the situation (distance from and size of the predator, escape routes, proximity of a safe haven, etc.).

In this range of possibilities, we can once again note the tension between fear and aggression revealed in the sphere of mammals' facial expressions. And we have already indicated as well that the dynamic balance between these two poles is clear not only in the realm of predator-prey confrontation but also in intraspecies or social conflicts. However, the framework from which to consider situations of conflict entailing approximation-avoidance is obviously broader than what is delimited by the fear-aggression polarity and indeed has been outlined in detail by both ethology and behaviouralism. In this broader context,

fear must be understood as the engine driving the animal away from a stimulus, situation or another animals, and the novelty or lack of familiarity with these stimuli, situations or animals is often what regulates the distancing function. For this reason, the fearful, fleeing animal is not only balanced with aggression but with the approach of whatever repelled or stopped it through exploratory, trophic, sexual or other appetitive behaviours. The contribution of the modern field of the behaviour ecology lies precisely in devising decision-making models on the aforementioned basis of calculating the cost or benefit, that is, what the animal wins or loses by letting itself fall into the well of fear or emerging from it to face uncertainty or death.

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