Decorative patterns and the evolution of art

Animals often have patterns that they use as signals. A new and controversial theory attempts to understand these patterns as advertisements, and shows how one can progress from understanding advertisement to understanding art

Amotz Zahavi
is a professor at the Institute for Nature Conservation Research, Tel-Aviv

Decorative patterns are very common in the animal kingdom, where they often serve as signals between animals. Patterns may identify the species, and often also the age and sex of an individual. Certain patterns in young animals elicit particular behaviour from their parents, and patterns shown by parents may be important to their young. Parent thrushes feed the highly coloured gaping throat of their nestlings, for instance, and the young gull chick will peck at the red spot near the tip of the parent's bill to get it to regurgitate food. Patterns are also involved in sex. Males react to females' patterns, and females to males'. Patterns signal the presence of a sexual rival, as in the famous case of the male stickleback's red belly. It is clear that many patterns serve as signals, but so far as I am aware there have been no attempts to relate the use of *particular* patterns to signal *particular* messages. In this article I want to present a theory about the use of patterns, namely that animals use patterns to signal their own quality to others, and that specific decorative patterns are best for signalling specific qualities.

The best way to introduce my theory is to give a simplified example; for this purpose I will use the advertisement of a disc. Imagine that you have a set of discs, all of which are more or less circular but some of which are more circular than others. Imagine also that you are the judge in a competition to evaluate the quality of the discs. High quality discs are perfectly circular, with less circular ones being of lower quality. Now, because of the limitations of your senses you may experience great difficulty in deciding just how perfect one particular disc is. But a dot in the centre of the disc may well help you to assess the disc's circularity, and make it easier for you to separate a perfect disc from one that is only nearly perfect. (This effect is shown in Figure 1.)

If a dot in the centre helps the judges to assess the circularity of a disc, it will be to the advantage of a maker of perfect discs to put a dot in the centre of the discs. If the judges then decide to use the dot to discriminate in favour of perfect discs we have a coalition between the perfect discs (or their makers) and the judges as a result of which both benefit—the perfect discs because the judges will recognise their quality and the judges because their task is made easier. But then is there any point in putting a dot at the centre of an imperfect disc? After all, it will only draw attention to its imperfections. If the competition is not for first place alone the low quality discs will presumably have others that are even worse, so that with the exception of the very worst disc, all discs will be easier to rank if they contain a dot at the centre. Imperfect discs display their imperfections to reveal how much better they are than others of still lower quality.

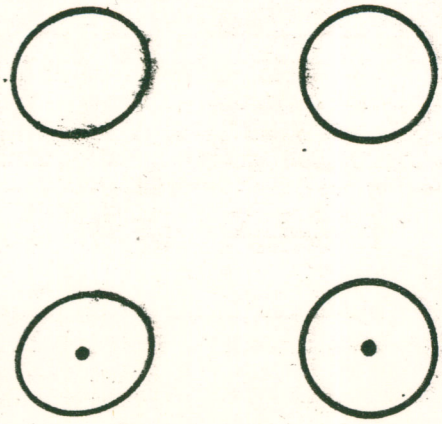


Figure 1 See how a dot helps you determine easily how perfect the circle is

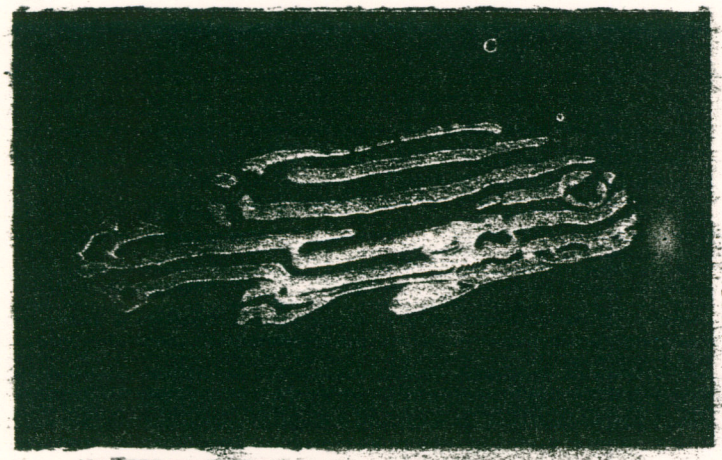
So, from a competition among discs, where the quality to be judged is circularity, we end up with all discs being easier to judge if they are decorated. Furthermore, there are some decorations, such as a dot in the centre or perhaps concentric rings, that are better than other for advertising circularity, and all discs will end up decorated with the optimal pattern. This is fine for a somewhat abstract competition betwen the makers of discs, but now I want to give a few examples where I believe certain patterns provide reliable advertisements of biologically important features.

Importance of size

It is often a good sign if an animal is bigger in some way than another. It may be able to feed better, or escape from predators, or produce more eggs. If, say, length were important an animal that displayed a clear line along its body axis would advertise its length much more clearly than one without a line. George Barlow, at Berkeley, surveyed the patterns of a host of different fishes, and found a strong correlation between the shape of the fish and direction of its stripes. Elongated fishes have lines that run along their body whereas high-bodied fishes have lines that run vertically. Barlow thought that the stripes were somehow important in camouflage, but I have watched some of these fishes over the coral reefs of the Red Sea, and they would be concealed much better if they simply matched the colour of their background and did not have prominent stripes. If, however, the fish were interested not in camouflaging but in advertising their body size, a stripe would be a great help. It draws attention to height or length and makes these dimensions easier to assess and it prevents cheating—you cannot display a stripe longer or higher than your physical body (Figure 2).

Lines can also be used to display the shape of a particular part of the body. Barlow found that fishes with a peculiar sloping head have lines that run parallel to the edge of the head, drawing attention to its shape. They seem to be advertising the slope of their head, advertising how close they are to a perfectly shaped sloping head.

Perhaps the archetypal striped animal is the zebra, and I believe that the stripes have evolved to display several features of the zebra's body. The lines on the neck display its breadth, while some of the body lines draw attention to body height. Those on the back and sides accentuate the form of the big muscles of the hind legs. Without stripes it would be much harder to see the individual differences between two zebras. Of course the width of the stripes is also important because this is the factor that determines the distance at which the stripes blend to a uniform grey. Most people believe that the main advantage of the stripes is that they hide the zebra, but if this is the case why are



Dr Pat Morris/ARDEA

Figure 2 Stripes exaggerate the body proportions: here an anemone fish looks long with its horizontal pattern

zebras not a uniform grey-brown like other wild asses?

Stripes, then, help advertise the dimensions of bodies. Smaller structures can be advertised, and their shape displayed, if they are coloured differently from the rest of the body. This seems to be a very common strategy, and we often see contrasting colours on claws (and nails), bill tips, combs, legs, fins, and spines. All draw attention to their own size and shape, and may also draw attention to the outline of the whole body.

Another aspect of the shape of bodily structures is their proportion with respect to the rest of the body. For example, the shape of a bird's wing determines its suitability for various types of flight; soaring birds have broad wings while agile flyers have narrower, longer wings. One difference between these two wing types is in the relative sizes of the thick leading edge of the wing and the thin trailing surface. The leading edge is the bird's arm and hand covered by the small wing covert feathers, while the trailing surface is made of the flight feathers. A bird whose flight feathers contrast with its wing coverts will be displaying the ratio between these two parts of the wing, and thereby advertising its suitability for one type of flight or another. Many birds do in fact have their wing coverts a different colour from their flight feathers, and it is on the border between the wing coverts and the flight feathers that we find many wing bars and other striking colour changes (Figure 3).

An animal can display a particular feature by drawing attention to it with bright or contrasting patterns, and in so doing may gain an advantage if it communicates more effectively. But there are disadvantages too, for bright colours may make the animal easier for a predator or rival to find. These costs of signalling are not simply an unfortunate by-product of wanting to signal effectively—they are an essential component of the signal because it is the costs that make a signal reliable. An animal may want to signal how brave it is. If it does so with a bright conspicuous signal we are much more likely to believe the signal than if it does so with a cryptic pattern, because cowards who bluff that they are brave might well get away with it if the signal for bravery is cryptic. But if the signal has a cost, if it attracts predators or rivals, only animals that can afford the cost, that actually are brave, can afford to give the signal. It is the cost that makes the signal reliable, and reliability is an essential component of any communication system.

The search for reliability, through cost, may lead to the paradox of an animal taking on a handicap better to signal its quality. For example, a long structure looks shorter with a transverse band around it.

An animal with a long neck may display the length of it by having a handicapping ring around the neck. Individuals with short necks will look even shorter-necked: "My neck is so long I can even afford to make it look short"; but short necked individuals cannot make this claim. The same may also be true of rings and fingers—our society favours long slender fingers but a short finger with a ring around it looks even shorter, so only those with truly long slender fingers can "afford" to wear rings.

Aside from signalling shapes and sizes, decorative patterns may also be used by an observer to detect certain kinds of movement. I would expect this to be important because movement is one of the major ways that animals differ, so if you can discover differences in movements you can find out about differences between animals. Eye movements in particular may disclose the intentions of an animal. For one animal to attack another successfully it should have an exact image of its opponent, and to get an exact image it should look directly at its opponent with a small pupil (to increase depth of field). It is clear that an animal with a ring around its eye or a light-coloured iris will disclose its eye movement more openly than one without an eye ring, where slight changes in direction of gaze and pupil size take place against a uniform background.

One corollary of attack needing a good image of the target is that a threat can be conveyed by a stare, and a stare will also be enhanced by an eye ring. Once again, costs ensure that the stare is a reliable signal, for only a dominant individual can afford to focus on another without worrying about being attacked from another quarter. A subordinate, on the other hand, has to keep an eye open (literally) not only for threats from elsewhere, but also for an escape route.

Lines as sights

Lines through the eye may also help an observer to pick up slight movements of the head. R. W. Ficken suggested that eyelines act as aims, helping the individual to sight prey before catching it. I agree that they are aims, but I think that they are used by the animal being looked at to gauge the direction its rival faces.

In this article I can only really discuss the "whys" of certain patterns, not the particular colours and shapes used in those patterns. The choice of one colour or another is dictated by the need to use a certain amount of contrast in the signal, because the degree of contrast determines the distance over which the message is visible. And coupled to this need for a contrast level that is suited to the distance for transmission is a need to match the signal to the receiver—to use colours that the receiving animal is sensitive to. An alternative to colour patches is provided by variegated patterns like dots or lines. At a distance these will fuse into an unpatterned surface. An animal that uses a variegated pattern like this is broadcasting its message over a short distance but staying quiet over a longer distance.

I have attempted to present and illustrate my ideas on a theory of optimal decorative patterns. The theory says that if animals differ in their possession of certain qualities they may benefit by advertising their qualities. And if they use decorative patterns to do their advertising the theory also suggests that there is one decorative pattern that is optimal for displaying a particular quality under given circumstances. Furthermore, it is reasonable to assume that in general animals advertise those adaptations that are most advantageous for them, so that if the theory is correct it follows that the patterns themselves may identify the important adaptations of the animal. It is competition between animals to advertise their superior qualities that leads to the evolution of a decorative pattern that is common to all the competing indviduals. The common pattern will often be restricted to members of one species, and once it is fixed for the purposes of advertisement can be used secondarily by individuals to identify members of the

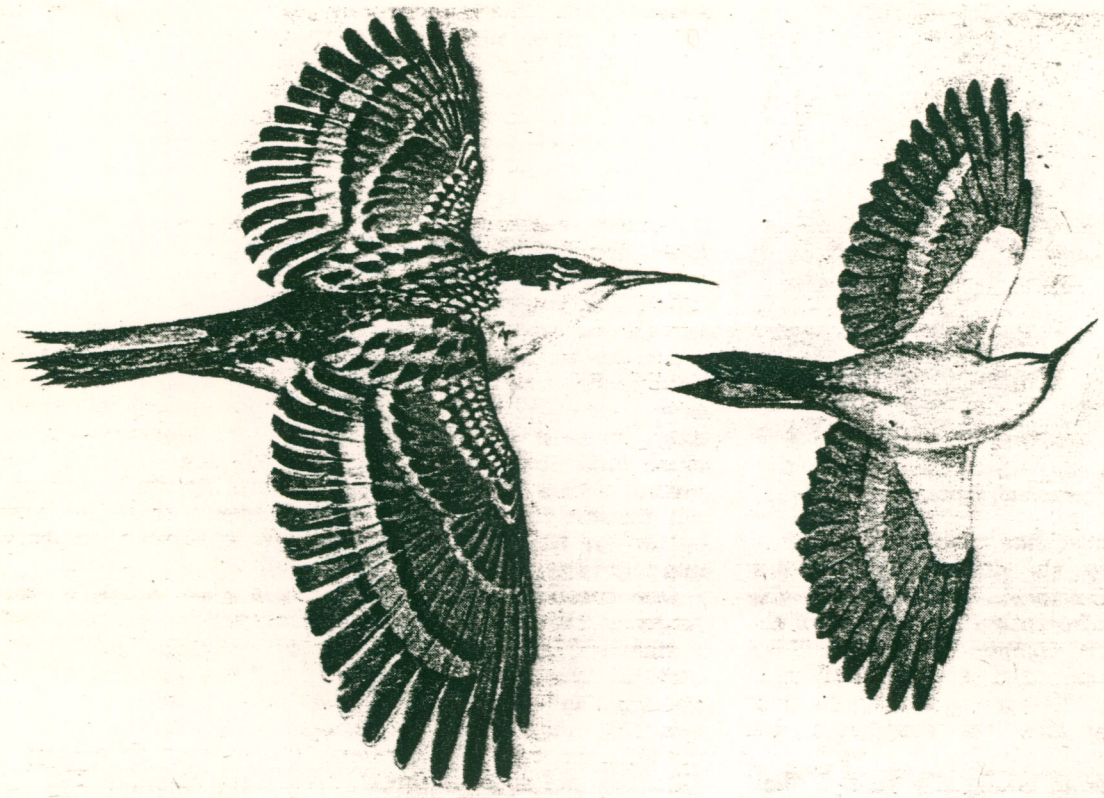


Figure 3 A male short-toed tree-creeper, showing striped patterns on its wing feathers. (Illustration from Bird Families of the World, *edited by C. J. O. Harrison, illustrated by Ad Cameron, published by Elsevier. Phaidon)*

species. In this regard. I am not at all surprised that different age groups, or sexes, of a single species have evolved different patterns because they usually possess, and advertise, different qualities.

My theory is not the first to attempt to understand the evolution of patterns. In 1963 Ernst Mayr put forward his ideas about the development of novel patterns. He suggested that a new pattern might develop solely because it is valuable as a species identification. When two species met, Mayr said, they would benefit if their species identity were clearly obvious because the harmful effects of hybridisation (loss of reproductive potential because most hybrids are sterile) would be averted. There is support for this notion from the observation that when two related species do meet or overlap they differ more than when they do not. Mayr, and Darwin, calls this "character divergence". But two species, almost by definition, occupy different ecological niches, each of which requires different adaptations, and I think it is reasonable to assume that these different adaptations will call for different decorations to advertise them. Initially these would only be used for assessing quality within a species—later they may be taken over and used as species identifying signals to reduce hybridisation between two species.

Decoration in isolation

The theories that say that species evolved decor to keep them isolated from related species have other problems. They do not explain the many cases of decorations that have evolved in species that have never been in contact with closely related species. They also require that the pattern stop evolving as soon as reproductive isolation has been achieved, as there will no longer be any selective pressure to change the pattern.

The theory of optimal decorative patterns predicts that a new pattern can be advantageous even if only one mutant possesses it, if it makes that mutant's qualities easier to judge. In this way new patterns *could* spread through the population. The spread of a new form through the population would then be a simple consequence of a change in the adaptations of that population, and there is no need to invoke any other restrictive conditions such as relatedness or genetic drift to account for the spread of the new pattern. The new common pattern spreads, like any other signal, on the basis of individual selection. These arguments are not restricted to the evolution of signals within a species. They apply equally well to signals shared by predators and their prey, or parasites and their hosts.

In essence I am saying that if it competes with others it will be to an animal's advantage to invest in advertising its quality with a particular decorative pattern. It will also be to its advantage to understand the way that patterns are being used to transmit messages of quality. These are the principles that underly all the examples I have discussed.

What of man? To the best of my knowledge there is as yet no ultimate explanation that suggests an advantage in certain artistic patterns rather than others. Human society is competitive, so people might be expected to use decorative patterns to advertise quality. I believe that a particular artistic investment by an artist to decorate a product may be understood as a consequence of his attempts to advertise the quality of his product. It may also be an advertisement of the artist's own artistic qualities. And the ability we have to understand art may have evolved as a consequence of our striving to assess differences in quality using biologically important signals. The theory of optimal decorative patterns may thus form a biological basis for the ultimate "advantage" of art, the evolutionary function of art.

The philosophical difficulty in explaining art is to understand why an individual should invest in art—either to produce it, or to own it, or to understand it—when that individual could instead invest in real assets that would directly make it a better competitor in society. The theory of optimal decorative patterns provides a model that attempts to explain the real gain inherent in the use of certain patterns, in terms of advertising and understanding advertisements. In so doing I believe it not only allows us to understand the basis of animal signals, but also provides clues about the use of certain art styles to advertise material quality. □