The Handicap Principle

SELECTION AND RELIABILITY OF SIGNALS

BY AMOTZ AND AVISHAG ZAHAVI

The gazelle tries to convince the wolf that i is not an easy prey and that the wolf would be wasting time and energy by chasing it.

Even when a predator is staring you in the face, it may be possible to signal that the chase is not worth his while. But you had better make sure the predator understands the signal with all its implications or it could be the worse for you! Amotz and Avishag Zahavi of Tel Aviv University shed light on the bizarre world of biological signaling.

A gazelle resting or grazing in the desert is nearly invisible; the color of its coat blends well with the desert landscape. A wolf appears. One would expect the gazelle to freeze or crouch and do its utmost to avoid being seen. But no: it rises, barks and thumps the ground with its forefeet, all the while watching the wolf. The thumps of the gazelle's hooves carry through the desert ground over long distances; its curved horns and dark-and-light pattern on its face make it easy to see that the gazelle is, in fact, looking at its enemy.

If the wolf comes nearer, one would expect the gazelle to flee as fast as it can. But it does not: often the gazelle repeatedly jumps high on all four legs and only then begins to run, wagging its short black tail against its conspicuous white rump with black border. These high jumps are very clearly linked to the approach of the wolf: a gazelle escaping immediate, urgent danger (such as hunters in a jeep) flees in an entirely different manner — it runs away silently at great speed, making good use of the topography to conceal its escape.

WHAT IS THE GAZELLE SIGNALING?

Why does the gazelle reveal itself to a predator that might not otherwise spot it? Why does it waste time and energy jumping up and down ("stotting") instead of escaping as fast as it can? Because the gazelle is signaling to the predator that it has seen it; by "wasting" time and by jumping high in the air rather than bounding away, it demonstrates in a reliable fashion that it is able to outrun the wolf. The wolf, upon learning that it has lost its chance to surprise its prey and that this gazelle is in tip-top physical shape, may decide to look for more promising prey.

Even parties in the most adversarial relationships, such as prey and predator, may communicate provided that they have a common interest in doing so. In the case of the gazelle and the wolf, they do; both want to avoid a pointless chase. The gazelle tries to convince the wolf that it is not an easy prey and that the wolf would be wasting time and energy by chasing it. Even if the gazelle is sure that it can outrun the wolf it, too, would prefer to avoid an exhausting chase. In order to convince the wolf not to give chase, the gazelle has to expend precious time and energy that it will need, should the wolf ignore its signals and decide to chase it anyway.

There is a logical relationship between the signal and the message it conveys. The gazelle displays its confidence in its ability to outrun the predator by drawing attention to itself and by showing off its ability. The investment that animals make in signals is similar to the "handicaps" imposed on the stronger contestants in a game or a sporting event: the removal of the superior player's queen in a chess match, the extra weight the swifter race horse must carry, or the score of several strokes with which the more accomplished golfer starts. A handicap proves beyond a doubt that the victor's win is due to mastery, not chance. The peacock's tail and the stag's antlers are handicaps in this very special sense: they allow an individual animal to demonstrate its quality.

Are animal signals always reliable? We believe that most of

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If by stotting a gazelle that
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t is easy prey. Such a gazelle
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hope for the best. So, to
e the reliability of a signal, one has to consider the invest-
it entails. The cost – the handicap that the signaler takes on
rantees that the signal is reliable.

The boxer in the ring keeps his chin down, close to his chest, and holds his body coiled like a spring. Boxers have already committed themselves to fight. By contrast, the defiant posture of someone like Mussolini (right), with his straight back, chest thrown out, shoulders back and chin up, is designed to intimidate an opponent, making an actual fight unnecessary.

HANDICAPS AS KEYS FOR RELIABLE THREATS

Rivals rarely attack each other without first signaling their
ntions. Most of the time, they do not attack at all and the
lict between them is resolved by an exchange of threats.
Mammals, birds, reptiles, fish, insects – in fact, all living
tures that communicate in any way – use threats. Resolving a
flict by threats alone prevents the loss of time and energy, and
risk of injury or death that attend an actual battle. It is easy to
lerstand that the winner gains by using threats rather than
ting, but why should threats make the other party back down?
at is it that convinces one of the opponents to give up a bit of
d, a potential mate, a territory, without even trying to fight?
viously, if one is going to lose anyway, it is better to lose
hout going through a fight. But can one be sure one is going to
e? What is it that convinces one of the two rivals that its defeat
inevitable or that what it would gain by winning is not worth
cost it would incur by fighting?

We suggest that the threats themselves are reliable indicators
each rival's chances in a fight. By definition, reliable threats are
gnals enabling one rival, the one likelier to win a fight, to threat-
more effectively than the one most likely to lose. How can a signal work that way? The threat itself must increase the risk that the threatener will be attacked or will be at a disadvantage if the attack takes place; an animal genuinely willing to fight, and confident of its ability to win, may find such a risk reasonable but one lacking strength or motivation will perceive the risk as excessive and thus be unable to threaten to the same degree. Hence, for a threat to be reliable, the signal must increase the danger to the threatener – and an escalation of the threat must increase the danger even further.

A quick look at known threat signals illustrates this point. Threatening by approaching a rival is very common indeed. Approaching is a reliable threat because, by coming close to its rival, the signaler opens itself to attack. If such signals were pure convention, any movement would be as likely as any other to take the meaning of threat. If the most clearly visible movement were the aim, then a movement sideways would have been better than a movement forward or backward. But a movement sideways is less risky and thus, though clearer, is less reliable as a signal. Likewise, if signals were arbitrary conventions, a movement backward would be just as likely to become a threat as a movement forward. We know of no case, however, in which a movement away from one's rival has become such a threat signal.

Furthermore, everybody knows the stance of the defiant human: straight back, chest thrown out, shoulders back, chin up.

This is a very inefficient and risky posture in which to enter hand-to-hand combat. The uptilted chin is exposed to blows; the erect body makes it difficult for the threatener to launch a surprise attack or to change position at all. It is the exact opposite of a boxer's or wrestler's stance in the ring. Ready to attack or avoid an attack, the boxer keeps his chin down, close to his chest, and holds his body coiled like a spring; he is on the alert, balanced on the balls of his feet and ready to seize any opportunity. But, of course, boxers cannot resolve the match by threats; they have already committed themselves to fight.

By contrast, the threatener uses precisely this vulnerability to enhance his threat. By standing up straight, he gives up the benefit of a good defensive stance and the option of a surprise attack. In the days before razors, a man's thrown-out chin presented another risk: it brought the threatener's beard nearer to his rival and easier to grab.

CONFLICT AND COMMUNICATION IN COURTSHIP

Sexual displays often attain gigantic dimensions and take bizarre forms. Peacocks presenting themselves to peahens spend time and energy holding their enormous tails spread open and upright, and vibrating them rapidly. Males of many other bird species grow long tail feathers for sexual displays. For their sizes, some male pheasants and birds of paradise have tails almost as large as the peacock's, while the males of certain songbirds, like the widow birds of Africa, have tails that proportionally are even longer.

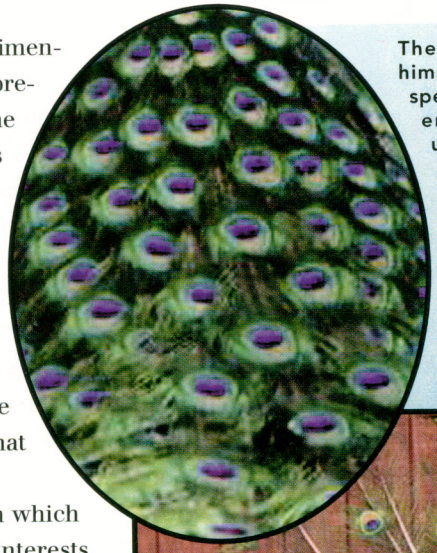
Courtship is a competitive matter in which males and females have conflicting interests. Each wants the highest-quality mate it can get — the best one to improve its offspring's genes and, depending on the gender and species, the best to raise those young. The male, like a good salesman, does whatever he can to impress females; the female, like a shrewd customer, checks the merchandise and accepts only proven quality.

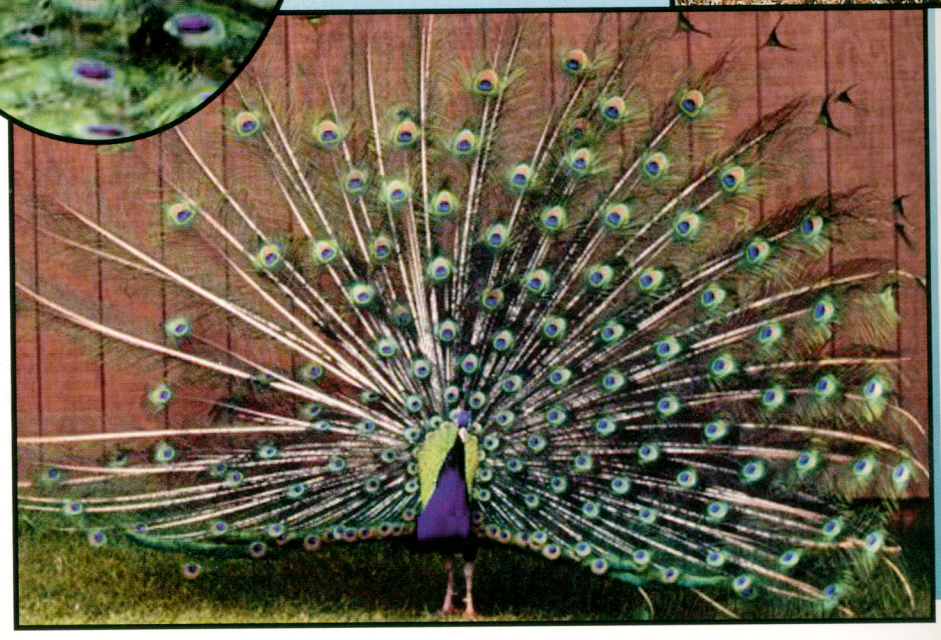
MALES AND FEMALES

Of course, females also advertise themselves to males with the same ensuing conflict of interests but their opportunities are different. The number of a female's offspring is limited by her own capacity to produce eggs or undergo pregnancies; a male's breeding success depends more on the number as well as the quality of the females he can persuade to breed with him. For the sake of convenience, and since males as a rule invest more in advertising than females, the issue will be discussed here mostly in terms of males as presenters and females as choosers.

How can one prove oneself to be superior? In most cases, several signals of different kinds are used in courtship. In birds, special feathers, bright colors, singing and calling, dancing and gift-giving – the last three of which all demand time and energy – play their part. Each modality brings out a particular quality of the male; the female can then use several criteria with which to assess him.

Take the display of the peacock. The male holds his tail upright and spread out (which demands considerable effort). From time to time he shakes his tail vigorously; this produces a remarkable rattle, requiring yet more effort. In order to put on such shows, peacocks have to drag massive tails around most of





The peacock (below) presenting himself to the peahen (right) must spend time and energy holding his enormous tail spread open and upright, vibrating it rapidly in the presence of potential predators. This proves to the peahen that he is strong and brave. Furthermore, since any distortion would readily be apparent in a pattern made up of concentric circles, the "eye" pattern of the peacock's tail feathers (left) shows that there was no flaw in the growth process, nor any missing feathers.

e year, proving they can manage to find food and avoid edators despite such a burden. Furthermore, since y distortion would readily be apparent in a pattern made up of ncentric circles, the "eye" patterns of the peacock's tail feathers ow that there was no flaw in their growth process, and any ssing feather would clearly distort the perfect order of the eyes. ıe dancing, the glisten of the peacock's feathers, the crown on s head all add up to a symphony of shape, color, pattern, ovement and sound – a performance that is announced with riodic roars.

Singing can also demonstrate the ability to provide. Time vested in singing cannot be used for foraging. A courting male ıo handicaps himself by singing continuously provides evidence at he needs less time to forage, either because he is very ficient or because his territory is very rich. Experimentally, ale yellow-bellied sunbirds that had ıt been given insects did not sing ıile those supplied with insects and gar water sang often and at length.

COMMON MARKINGS EVOLVING THROUGH COMPETITION

Are there signals that evolve without the element of competition or enmi- ? What about those structures and arkings that allow one to tell a given species from another, or stinguish the male of a species from the female and the juvenile ɔm the adult? Most scientists assume that common interest, ther than competition among individuals explains the evolution these traits. In our view, they evolve just as all other signals do hrough the competition among individuals to demonstrate their ıality.

Did these markings evolve in order to enable animals to entify members of their species? Not necessarily. We identify a ıngaroo by its special shape and gait, and it is very likely that ıngaroos themselves do the same. Yet no one suggests that the ıape and gait of kangaroos evolved in order to help kangaroos cognize one another. The fact that features are used by animals identify the species, age or gender of other animals does not ove that the features evolved for that purpose.

In most species of babblers, the group-living desert bird in our vn studies, males and females look alike. Luckily for us, in the ırticular species found at Hatzeva in the Israeli Negev desert, ere is a minute difference: females have dark brown irises, hile males have lighter, yellow-tan irises. These birds treat range babblers according to their gender: males attack males

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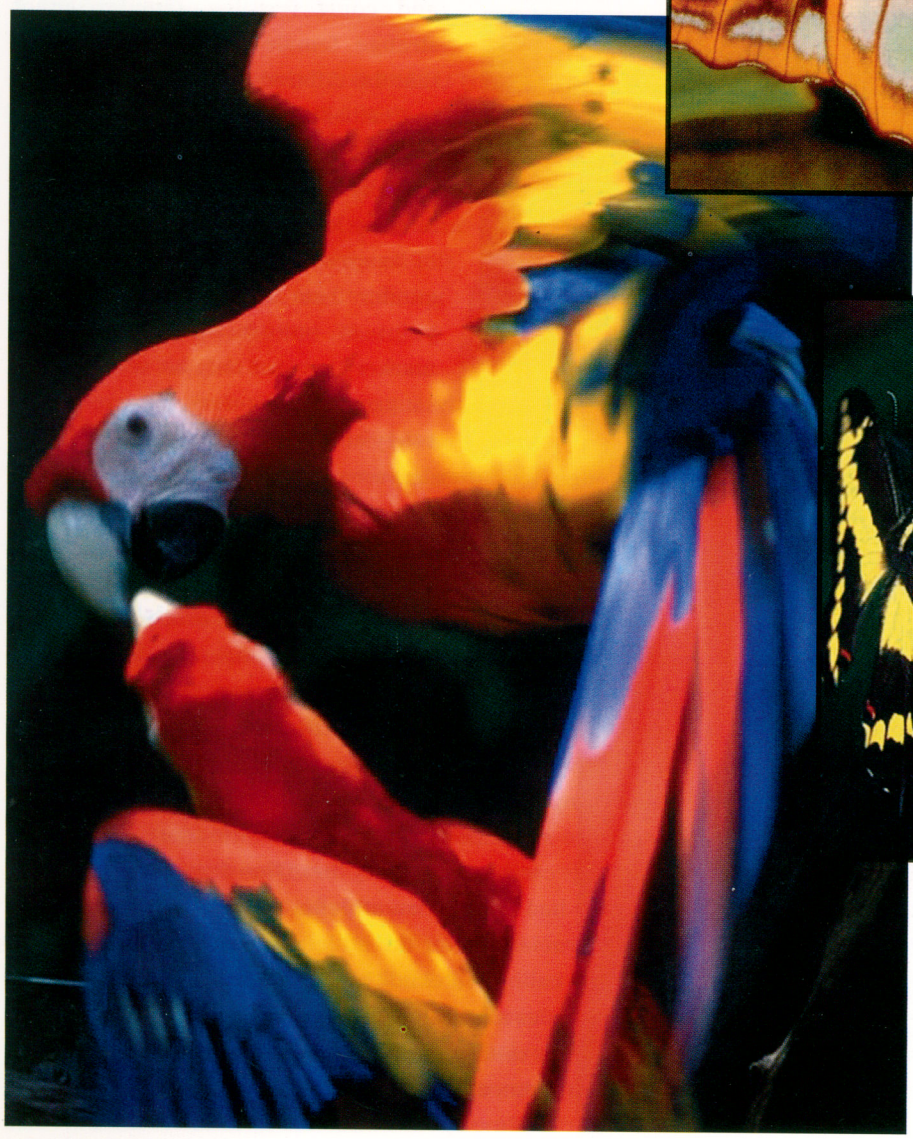
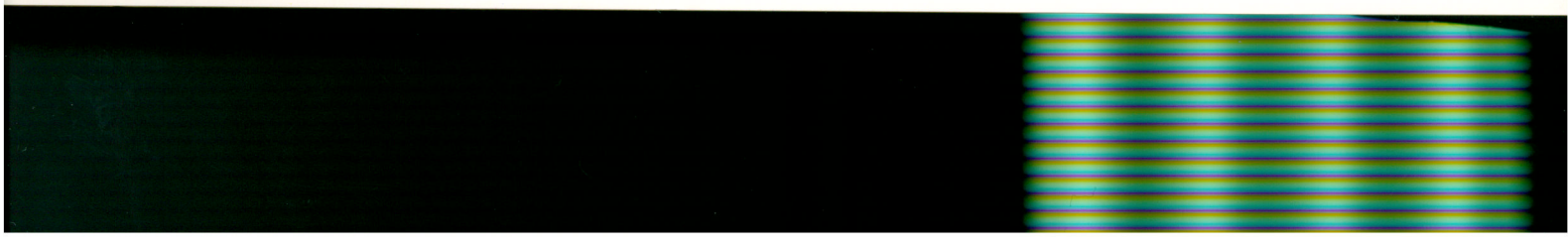
and court females, females attack strange females. One could assume that the difference in eye color evolved so that babblers could tell the gender of other babblers. Not so: these birds can actually tell the gender of a strange babbler long before they see the color of its eyes. If they can tell a stranger's gender from a distance, what is the point of one small gender-specific marker that can only be seen at close quarters? Would anybody suggest that women use eyeliner in order to let men know that they are women? Men can figure that much out long before they see a woman's face, let alone her eyes. We were led to the conclusion that the different colors of the male and female babbler's eyes evolved not to indicate gender but for some other reason.

It is likely that so-called specific markings evolve through the competition that members of the species engage in to determine their relative quality. The markings which appear uniform are the very ones to show most clearly the fine differences among individuals with respect to the attributes most important to them. The closer the competition – the more evenly matched individuals are with regard to some desirable attribute – the more helpful uniform markings can be in exposing these fine distinctions. Anybody who has ever had to judge an athletic, musical or beauty contest knows how crucial it is for the athletes to compete under highly regulated and calibrated conditions: the musicians must play the same music under similar conditions and the beauty contestants appear in similar clothing, precisely in order to tell the fine differences between them and select the best of the best.

It is important to emphasize that the issue of choice is crucial:



Butterfly wings with color bands; bird's feathers with contrasting colors. The wings of birds and butterflies are often outlined with a narrow band of color. This makes it easier to spot individuals who are clumsy and injure their wings or feathers, or ones who were malformed.



or a signal to evolve, the receiver of the signal must have at least ne other alternative, otherwise there is no chance of affecting the eceiver's actions and no point in signaling to it. A gazelle can tell a olf reliably that it is an excellent runner and that the wolf has lit- e chance of catching it, but if the wolf has no alternative of find- g other prey, it nevertheless has to try to catch that gazelle even ough the gazelle has just proven that the chase will be a hard one.

THE SIGNIFICANCE OF DECORATIONS

If animals' markings evolved in order to bring out small fferences between competing individuals within a species, they nnot be arbitrary. Any markings could ve to identify species, gender or age t, if specific markings in fact are to ow off certain important traits in mbers of the group who compete to ve their quality, those markings have be the best for highlighting the ical differences.

Which body parts are emphasized n animal's decoration and what is r importance to that animal? Many cies of hoofed animals have kings that outline their rumps: hes of color, as in most antelopes, or stripes like the zebra's. patterns make it easy to tell from behind which animals are od shape and which are thinner than they should be. In species, the hind leg muscles are of immense importance. A ator looking for easy prey, a rival evaluating chances in a st, a female looking for the best father for her offspring – all benefit from evaluating the muscles of the rump. And the als' patterns make it easier to conduct just such an ation.

ecorative markings can also advertise social status. The tit's black band, the white patch on a magpie's wing, the patch under the beak of a Harris's sparrow, an eye-like spot ish's fin and the bulbul's prominent white eye ring all serve claim their owners' prestige (social status) and, in fact, are d "badges of status." How can a purely decorative marking eliable indication of anything? Evolutionarily speaking, is there to prevent a young or low-quality bird from ping a high-status decorative pattern and gaining an age over its more capable rivals?

tus badges, like other markings, amplify differences y demonstrating an individual's quality. The status badge sizes the excellence of an individual of higher quality, the adge bringing out the inferiority of a lesser individual; for instance, eye stripes emphasize head movement and so accentuate both the steady gaze of a confident individual and the shiftiness of the insecure. The confident animal gains by drawing attention to its gaze; the insecure one loses.

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THE SELECTION OF SIGNALS

It seems that natural selection encompasses two different, often opposing, processes. One kind of selection favors straightforward efficiency and operates in all areas except signaling. It makes features other than signals more effective and less costly; "utilitarian selection" is a good description. The other kind, "signal selection," results in costly features and traits which look like "waste." It is precisely this cost, the signaler's investment in the signals, that makes those signals reliable. They are traits whose value to the signaler is to convey information to those who receive them. There is a difference between traits that evolved for other reasons, such as body size or a kangaroo's gait, and those which evolved solely to convey information. One can judge the direction of another's gaze by watching its eyes, yet eye movement is not primarily a signal. On the other hand, eye rings and small tufts of hair or feathers are signals; their function is to show an observer more clearly, or from a greater distance, the direction of an individual's gaze.

Thus signals are not arbitrary; rather, each signal is the one best suited reliably to convey the specific message it carries. It follows that there must be a logical connection between the message and the signal. The Handicap Principle enables us to make predictions and makes it possible to figure out from the nature of a signal what message it conveys and, likewise, what might logically serve as a signal for a given message.

SUGGESTED READING

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