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Evolution and Modification of Behavior

The Waning of Humaneness

Here Am I — Where Are You?:
The Behavior of the Greylag Goose

On Life and Living

Konrad Lorenz

On Aggression

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fish of the butterfly fish genera. The only peaceful one I know is the four-eyed butterfly, and this is the only one whose characteristic design is broken up into such small details that it can be recognized only at very close quarters.

The most remarkable thing of all is that coral fish which are poster-colored in youth and plain-colored at sexual maturity show the same correlation between coloring and aggression: as babies they are furious defenders of their territory but as adults they are far more peaceable; in some, one has the impression that they are obliged to divest themselves of their fight-eliciting colors in order to make friendly contact between the sexes possible. This certainly applies to the demoiselle group; several times I saw a brilliantly black and white species spawning in the aquarium, for this purpose changing their striking color for a monotonous dull gray, only to hoist the flag again as soon as spawning was over.

Chapter Three

What Aggression Is Good For

What is the value of all this fighting? In nature, fighting is such an ever-present process, its behavior mechanisms and weapons are so highly developed and have so obviously arisen under the selection pressure of a species-preserving function, that it is our duty to ask this Darwinian question.

The layman, misguided by sensationalism in press and film, imagines the relationship between the various "wild beasts of the jungle" to be a bloodthirsty struggle, all against all. In a widely shown film, a Bengal tiger was seen fighting with a python, and immediately afterward the python with a crocodile. With a clear conscience I can assert that such things never occur under natural conditions. What advantage would one of these animals gain from exterminating the other? Neither of them interferes with the other's vital interests.

Darwin's expression, "the struggle for existence," is sometimes erroneously interpreted as the struggle between different species. In reality, the struggle Darwin was thinking of and which drives evolution forward is the competition between near relations. What causes a species to disappear or become transformed into a different species is the profitable "invention" that falls by chance to one or a few of its members in the ever-

lasting gamble of hereditary change. The descendants of these lucky ones gradually outstrip all others until the particular species consists only of individuals who possess the new "invention."

There are, however, fightlike contests between members of different species: at night an owl kills and eats even well-armed birds of prey, in spite of their vigorous defense, and when these birds meet the owl by day they attack it ferociously. Almost every animal capable of self-defense, from the smallest rodent upward, fights furiously when it is cornered and has no means of escape. Besides these three particular types of inter-specific fighting, there are other, less typical cases; for instance, two cave-nesting birds of different species may fight for a nesting cavity. Something must be said here about these three types of inter-specific fighting in order to explain their peculiarity and to ~~distin~~guish ~~them from~~ the *intra*-specific aggression which is really the subject of this book.

The survival value of inter-specific fights is much more evident than that of intra-specific contests. The way in which a predatory animal and its prey influence each other's evolution is a classical example of how the selection pressure of a certain function causes corresponding adaptations. The swiftness of the hunted ungulate forces its feline pursuers to evolve enormous leaping power and sharply armed toes. Paleontological discoveries have shown impressive examples of such evolutionary competition between weapons of attack and those of defense. The teeth of grazing animals have achieved better and better grinding power, while, in their parallel evolution, nutritional plants have devised means of protecting themselves against being eaten, as by the storage of silicates and the development of hard, wooden thorns. This kind of "fight" between the eater and the eaten never goes so far that the predator causes extinction of the prey: a state of equilibrium is always established between them, endurable by both species.

The last lions would have died of hunger long before they had killed the last pair of antelopes or zebras; or, in terms of human commercialism, the whaling industry would go bankrupt before the last whales became extinct. What directly threatens the existence of an animal species is never the "eating enemy" but the competitor. In prehistoric times man took the Dingo, a primitive domestic dog, to Australia. It ran wild there, but it did not exterminate a single species of its quarry; instead, it destroyed the large marsupial beasts of prey which ate the same animals as it did itself. The large marsupial predators, the Tasmanian Devil and the Marsupial Wolf, were far superior to the Dingo in strength, but the hunting methods of these "old-fashioned," relatively stupid and slow creatures were inferior to those of the "modern" mammal. The Dingo reduced the marsupial population to such a degree that their methods no longer "paid," and today they exist only in Tasmania, where the Dingo has never penetrated.

In yet another respect the fight between predator and prey is not a fight in the real sense of the word: the stroke of the paw with which a lion kills his prey may resemble the movements that he makes when he strikes his rival, just as a shotgun and a rifle resemble each other outwardly; but the inner motives of the hunter are basically different from those of the fighter. The buffalo which the lion fells provokes his aggression as little as the appetizing turkey which I have just seen hanging in the larder provokes mine. The differences in these inner drives can clearly be seen in the expression movements of the animal: a dog about to catch a hunted rabbit has the same kind of excitedly happy expression as he has when he greets his master or awaits some longed-for treat. From many excellent photographs it can be seen that the lion, in the dramatic moment before he springs, is in no way angry. Growling, laying the ears back, and other well-known expression movements of fighting behavior are seen in predatory

animals only when they are very afraid of a wildly resisting prey, and even then the expressions are only suggested.

The opposite process, the "counteroffensive" of the prey against the predator, is more nearly related to genuine aggression. Social animals in particular take every possible chance to attack the "eating enemy" that threatens their safety. This process is called "mobbing." Crows or other birds "mob" a cat or any other nocturnal predator, if they catch sight of it by day.

The survival value of this attack on the eating enemy is self-evident. Even if the attacker is small and defenseless, he may do his enemy considerable harm. All animals which hunt singly have a chance of success only if they take their prey by surprise. If a fox is followed through the wood by a loudly screaming jay, or a sparrow hawk is pursued by a flock of warning wagtails, his hunting is spoiled for the time being. Many birds will mob an owl, if they find one in the daytime, and drive it so far away that it will hunt somewhere else the next night. In some social animals such as jackdaws and many kinds of geese, the function of mobbing is particularly interesting. In jackdaws, its most important survival value is to teach the young, inexperienced birds what a dangerous eating enemy looks like, which they do not know instinctively. Among birds, this is a unique case of traditionally acquired knowledge.

Geese and ducks "know" by very selective, innate releasing mechanisms that anything furry, red-brown, long-shaped, and slinking is extremely dangerous, but nonetheless mobbing, with its intense excitement and the gathering together of geese from far and wide, has an essentially educational character as well as a survival value; anyone who did not know it already learns: foxes may be found *here!* At a time when only part of the shore of our lake was protected by a foxproof fence, the geese kept ten or fifteen yards clear of all unfenced cover

likely to conceal a fox, but in the fenced-in area they penetrated fearlessly into the thickets of young fir trees. Besides this didactic function, mobbing of predators by jackdaws and geese still has the basic, original one of making the enemy's life a burden. Jackdaws actively attack their enemy, and geese apparently intimidate it with their cries, their thronging, and their fearless advance. The great Canada geese will even follow a fox over land in a close phalanx, and I have never known a fox in this situation try to catch one of his tormentors. With ears laid back and a disgusted expression on his face, he glances back over his shoulder at the trumpeting flock and trots slowly—so as not to lose face—away from them.

Among the larger, more defense-minded herbivores which, en masse, are a match for even the biggest predators, mobbing is particularly effective; according to reliable reports, zebras will molest even a leopard if they catch him on a veldt where cover is sparse. The reaction of social attack against the wolf is still so ingrained in domestic cattle and pigs that one can sometimes land oneself in danger by going through a field of cows with a nervous dog which, instead of barking at them or at least fleeing independently, seeks refuge between the legs of its owner. Once, when I was out with my bitch Stasi, I was obliged to jump into a lake and swim for safety when a herd of young cattle half encircled us and advanced threateningly; and when he was in southern Hungary during the First World War my brother spent a pleasant afternoon up a tree with his Scotch terrier under his arm, because a herd of half-wild Hungarian swine, disturbed while grazing in the wood, encircled them, and with bared tusks and unmistakable intentions began to close in on them.

Much more could be said about these effective attacks on the real or supposed enemy. In some birds and fishes, to serve this special purpose brightly colored "aposematic" or warning colors have evolved, which predators notice and associate with

unpleasant experiences with the particular species. Poisonous, evil-tasting, or otherwise specially protected animals have, in many cases, "chosen" for these warning signals the combination of red, white, and black; and it is remarkable that the Common Sheldrake and the Sumatra Barb, two creatures which have nothing in common either with each other or the above-named groups, should have done the same thing. It has long been known that Common Sheldrake mob predatory animals and that they so disgust the fox with the sight of their brightly colored plumage that they can nest safely in inhabited foxholes. I bought some Sumatra Barbs because I had asked myself why these fishes looked so poisonous; in a large communal aquarium, they immediately answered my question by mobbing big Cichlids so persistently that I had to save the giant predators from the only apparently harmless dwarfs.

There is a third form of fighting behavior, and its survival value is as easily demonstrated as that of the predator's attack on its prey or the mobbing by the prey of the eating enemy. With H. Hediger, we call this third behavior pattern the *critical reaction*. The expression "fighting like a cornered rat" has become symbolic of the desperate struggle in which the fighter stakes his all, because he cannot escape and can expect no mercy. This most violent form of fighting behavior is motivated by fear, by the most intense flight impulses whose natural outlet is prevented by the fact that the danger is too near; so the animal, not daring to turn its back on it, fights with the proverbial courage of desperation. Such a contingency may also occur when, as with the cornered rat, flight is prevented by lack of space, or by strong social ties, like those which forbid an animal to desert its brood or family. The attack which a hen or goose makes on everything that goes too near her chicks or goslings can also be classified as a critical reaction. Many animals will attack desperately when surprised by an enemy at less than a certain critical distance, whereas they would have

fled if they had noticed his coming from farther away. As Hediger has described, lion tamers maneuver their great beasts of prey into their positions in the arena by playing a dangerous game with the margin between flight distance and critical distance; and thousands of big game hunting stories testify to the dangerousness of large beasts of prey in dense cover. The reason is that in such circumstances the flight distance is particularly small, because the animal feels safe, imagining that it will not be noticed by a man even if he should penetrate the cover and get quite close; but if in so doing the man oversteps the animal's critical distance, a so-called hunting accident happens quickly and disastrously.

All the cases described above, in which animals of different species fight against each other, have one thing in common: every one of the fighters gains an obvious advantage by its behavior or, at least, in the interests of preserving the species it "ought to" gain one. But intra-specific aggression, aggression in the proper and narrower sense of the word, also fulfills a species-preserving function. Here, too, the Darwinian question "What for?" may and must be asked. Many people will not see the obvious justification for this question, and those accustomed to the classical psychoanalytical way of thinking will probably regard it as a frivolous attempt to vindicate the life-destroying principle or, purely and simply, evil. The average normal civilized human being witnesses aggression only when two of his fellow citizens or two of his domestic animals fight, and therefore sees only its evil effects. In addition there is the alarming progression of aggressive actions ranging from cocks fighting in the barnyard to dogs biting each other, boys thrashing each other, young men throwing beer mugs at each other's heads, and so on to bar-room brawls about politics, and finally to wars and atom bombs.

With humanity in its present cultural and technological situation, we have good reason to consider intra-specific ag-

gression the greatest of all dangers. We shall not improve our chances of counteracting it if we accept it as something metaphysical and inevitable, but on the other hand, we shall perhaps succeed in finding remedies if we investigate the chain of its natural causation. Wherever man has achieved the power of voluntarily guiding a natural phenomenon in a certain direction, he has owed it to his understanding of the chain of causes which formed it. Physiology, the science concerned with the normal life processes and how they fulfill their species-preserving function, forms the essential foundation for pathology, the science investigating their disturbances. Let us forget for a moment that the aggression drive has become derailed under conditions of civilization, and let us inquire impartially into its natural causes. For the reasons already given, as good Darwinians we must inquire into the species-preserving function which, under natural—or rather precultural—conditions, is fulfilled by fights within the species, and which by the process of selection has caused the advanced development of intra-specific fighting behavior in so many higher animals. It is not only fishes that fight their own species: the majority of vertebrates do so too, man included.

Darwin had already raised the question of the survival value of fighting, and he has given us an enlightening answer: It is always favorable to the future of a species if the stronger of two rivals takes possession either of the territory or of the desired female. As so often, this truth of yesterday is not the untruth of today but only a special case; ecologists have recently demonstrated a much more essential function of aggression. Ecology—derived from the Greek *oikos*, the house—is the branch of biology that deals with the manifold reciprocal relations of the organism to its natural surroundings—its "household"—which of course includes all other animals and plants native to the environment. Unless the special interests of a social organization demand close aggregation of its mem-

bers, it is obviously most expedient to spread the individuals of an animal species as evenly as possible over the available habitat. To use a human analogy: if, in a certain area, a larger number of doctors, builders, and mechanics want to exist, the representatives of these professions will do well to settle as far away from each other as possible.

The danger of too dense a population of an animal species settling in one part of the available biotope and exhausting all its sources of nutrition and so starving can be obviated by a mutual repulsion acting on the animals of the same species, effecting their regular spacing out, in much the same manner as electrical charges are regularly distributed all over the surface of a spherical conductor. This, in plain terms, is the most important survival value of intra-specific aggression.

Now we can understand why the sedentary coral fish in particular are so crazily colored. There are few biotopes on earth that provide so much and such varied nutrition as a coral reef. Here fish species can, in an evolutionary sense, take up very different professions: one can support itself as an "unskilled laborer," doing what any average fish can do, hunting creatures that are neither poisonous nor armor-plated nor prickly, in other words hunting all the defenseless organisms approaching the reef from the open sea, some as "plankton," others as active swimmers "intending" to settle on the reef, as millions of free-swimming larvae of all coral-dwelling organisms do. On the other hand, another fish species may specialize in eating forms of life that live on the reef itself and are therefore equipped with some sort of protective mechanism which the hunting fish must render harmless. Corals themselves provide many different kinds of nourishment for a whole series of fish species. Pointed-jawed butterfly fish get their food parasitically from corals and other stinging animals. They search continuously in the coral stems for small prey caught in the stinging tentacles of coral polyps. As soon as they see these, they pro-

duce, by fanning with their pectoral fins, a current so directly aimed at the prey that at the required point a "parting" is made between the polyps, pressing their tentacles flat on all sides and thus enabling the fish to seize the prey almost without getting its nose stung. It always gets it just a little stung and can be seen "sneezing" and shaking its nose, but, like pepper, the sting seems to act as an agreeable stimulant. My beautiful yellow and brown butterfly fishes prefer a prey, such as a piece of fish, stuck in the tentacles of a stinging sea anemone, to the same prey swimming free in the water. Other related species have developed a stronger immunity to stings and they devour the prey together with the coral animal that has caught it. Yet other species disregard the stinging capsules of coelenterates altogether, and eat coral animals, hydroid polyps, and even big, strong, stinging sea anemones, as placidly as a cow eats grass. As well as this immunity to poison, parrot fish have evolved a strong chisellike dentition and they eat whole branches of coral including their calcareous skeleton. If you dive near a grazing herd of these beautiful, rainbow-colored fish, you can hear a cracking and crunching as though a little gravel mill were at work—and this actually corresponds with the facts, for when such a fish excretes, it rains a little shower of white sand, and the observer realizes with astonishment that most of the snow-clean coral sand covering the glades of the coral forest has obviously passed through parrot fish.

Other fish, plectognaths, to which the comical puffers, trunk, and porcupine fish belong, have specialized in cracking hard-shelled mollusks, crabs, and sea urchins; and others again, such as angelfish, specialize in snatching the lovely feather crowns that certain feather worms thrust out of their hard, calcareous tubes. Their capacity for quick retraction acts as a protection against slower predators, but some angelfish have a way of sidling up and, with a lightning sideways jerk of the mouth, seizing the worm's head at a speed surpass-

ing its capacity for withdrawal. Even in the aquarium, where they seize prey which has no such quick reactions, these fish cannot do otherwise than snap like this.

The reef offers many other "openings" for specialized fish. There are some which remove parasites from others and which are therefore left unharmed by the fiercest predators, even when they penetrate right into the mouth cavities of their hosts to perform their hygienic work. There are others which live as parasites on large fish, punching pieces from their epidermis, and among these are the oddest fish of all: they resemble the cleaner fish so closely in color, form, and movement that, under false pretenses, they can safely approach their victims.

It is essential to consider the fact that all these opportunities for special careers, known as ecological niches, are often provided by the same cubic yard of ocean water. Because of the enormous nutritional possibilities, every fish, whatever its specialty, requires only a few square yards of sea bottom for its support, so in this small area there can be as many fish as there are ecological niches, and anyone who has watched with amazement the thronging traffic on a coral reef knows that these are legion. However, every one of this crowd is determined that no other fish of his species should settle in his territory. Specialists of other "professions" harm his livelihood as little as, to use our analogy again, the practice of a doctor harms the trade of a mechanic living in the same village.

In less densely populated biotopes where the same unit of space can support three or four species only, a resident fish or bird can "afford" to drive away all living beings, even members of species that are no real threat to his existence; but if a sedentary coral fish tried to do the same thing, it would be utterly exhausted and, moreover, would never manage to keep its territory free from the swarms of noncompetitors of different "professions." It is in the occupational interests of all sedentary species that each should determine the spatial dis-

tribution that will benefit its own individuals, entirely without consideration for other species. The colorful "poster" patterns, described in Chapter One, and the fighting reactions elicited by them, have the effect that the fish of each species keep a measured distance only from nutritional competitors of the same species. This is the very simple answer to the much discussed question of the function of the colors of coral fish.

As I have already mentioned, the species-typical song of birds has a very similar survival value to that of the visual signals of fishes. From the song of a certain bird, other birds not yet in possession of a territory recognize that in this particular place a male is proclaiming territorial rights. It is remarkable that in many species the song indicates how strong and possibly how old the singer is, in other words, how much the listener has to fear him. Among several species of birds that mark their territory acoustically, there is great individual difference of sound expression, and some observers are of the opinion that, in such species, the personal visiting card is of special significance. While Heinroth interpreted the crowing of the cock with the words, "Here is a cock!" Baeumer, the most knowledgeable of all domestic-fowl experts, heard in it the far more special announcement, "Here is the cock Balthazar!"

Among mammals, which mostly "think through their noses," it is not surprising that marking of the territory by scent plays a big role. Many methods have been tried; various scent glands have been evolved, and the most remarkable ceremonies developed around the depositing of urine and feces; of these the leg-lifting of the domestic dog is the most familiar. The objection has been raised by some students of mammals that such scent marks cannot have anything to do with territorial ownership because they are found not only in socially living mammals which do not defend single territories, but also in animals that wander far and wide; but this opinion is only partly correct. First, it has been proved that dogs and

other pack-living animals recognize each other by the scent of the marks, and it would at once be apparent to the members of a pack if a nonmember presumed to lift its leg in their hunting grounds. Secondly, Leyhausen and Wolf have demonstrated the very interesting possibility that the distribution of animals of a certain species over the available biotope can be effected not only by a space plan but also by a time plan. They found that, in domestic cats living free in open country, several individuals could make use of the same hunting ground without ever coming into conflict, by using it according to a definite timetable, in the same way as our Seewiesen housewives use our communal washhouse. An additional safeguard against undesirable encounters is the scent marks which these animals—the cats, not the housewives—deposit at regular intervals wherever they go. These act like railway signals whose aim is to prevent collision between two trains. A cat finding another cat's signal on its hunting path assesses its age, and if it is very fresh it hesitates, or chooses another path; if it is a few hours old it proceeds calmly on its way.

Even in the case of animals whose territory is governed by space only, the hunting ground must not be imagined as a property determined by geographical confines; it is determined by the fact that in every individual the readiness to fight is greatest in the most familiar place, that is, in the middle of its territory. In other words, the threshold value of fight-eliciting stimuli is at its lowest where the animal feels safest, that is, where its readiness to fight is least diminished by its readiness to escape. As the distance from this "headquarters" increases, the readiness to fight decreases proportionately as the surroundings become stranger and more intimidating to the animal. If one plotted the graph of this decrease the curve would not be equally steep for all directions in space. In fish, the center of whose territory is nearly always on the bottom, the decline in readiness to fight is most marked in the vertical direc-

tion because the fish is threatened by special dangers from above.

The territory which an animal apparently possesses is thus only a matter of variations in readiness to fight, depending on the place and on various local factors inhibiting the fighting urge. In nearing the center of the territory the aggressive urge increases in geometrical ratio to the decrease in distance from this center. This increase in aggression is so great that it compensates for all differences ever to be found in adult, sexually mature animals of a species. If we know the territorial centers of two conflicting animals, such as two garden redstarts or two aquarium sticklebacks, all other things being equal, we can predict, from the place of encounter, which one will win: the one that is nearer home.

When the loser flees, the inertia of reaction of both animals leads to that phenomenon which always occurs when a time lag enters into a self-regulating process—to an oscillation. The courage of the fugitive returns as he nears his own headquarters, while that of the pursuer sinks in proportion to the distance covered in enemy territory. Finally the fugitive turns and attacks the former pursuer vigorously and unexpectedly and, as was predictable, he in his turn is beaten and driven away. The whole performance is repeated several times till both fighters come to a standstill at a certain point of balance where they threaten each other without fighting.

The position, the territorial "border," is in no way marked on the ground but is determined exclusively by a balance of power and may, if this alters in the least, for instance if one fish is replete and lazy, come to lie in a new position somewhat nearer the headquarters of the lazy one. An old record of our observations on the territorial behavior of two pairs of cichlids demonstrates this oscillation of the territorial borders. Four fish of this species were put into a large tank and at once the strongest male, A, occupied the left, back, lower corner and

chased the other three mercilessly around the whole tank; in other words, he claimed the whole tank as his territory. After a few days, male B took possession of a tiny space immediately below the surface in the diagonally opposite right, front, upper corner. There he bravely resisted the attacks of the first male. This occupation of an area near the surface is in a way an act of desperation for one of these fish, because it is risking great danger from aerial predators in order to hold its own against an enemy of its own species, which, as already explained, will attack less resolutely in such a locality. In other words, the owner of such a dangerous area has, as an ally, the fear which the surface inspires in its bad neighbor. During succeeding days, the space defended by B grew visibly, expanding downward until he finally took his station in the right, front, lower corner, so gaining a much more satisfactory headquarters. Now at last he had the same chances as A, whom he quickly pressed so far back that their territories divided the tank into two almost equal parts. It was interesting to see how both fishes patrolled the border continuously, maintaining a threatening attitude. Then one morning they were doing this on the extreme right of the tank, again around the original headquarters of B, who could now scarcely call a few square inches his own. I knew at once what had happened: A had paired, and since it is characteristic of all large cichlids that both partners take part in territorial defense, B was subjected to double pressure and his territory had decreased accordingly. Next day the fish were again in the middle of the tank, threatening each other across the "border," but now there were four, because B had also taken a mate, and thus the balance of power with the A family was restored. A week later I found the border far toward the left lower area, and encroaching on A's former territory. The reason for this was that the A couple had spawned and since one of the partners was busy looking after the eggs, only one at a time was able to at-

tend to frontier defense. As soon as the B couple had also spawned, the previous equal division of space was re-established. Julian Huxley once used a good metaphor to describe this behavior: he compared the territories to air-balloons in a closed container, pressing against each other and expanding or contracting with the slightest change of pressure in each individual one. This territorial aggression, really a very simple mechanism of behavior-physiology, gives an ideal solution to the problem of the distribution of animals of any one species over the available area in such a way that it is favorable to the species as a whole. Even the weaker specimens can exist and reproduce, if only in a very small space. This has special significance in creatures which reach sexual maturity long before they are fully grown. What a peaceful issue of the "evil principle"!

In many animals the same result is achieved without aggressive behavior. Theoretically it suffices that animals of the same species "cannot bear the smell of each other" and avoid each other accordingly. To a certain extent this applies to the smell signals deposited by cats, though behind these lies a hidden threat of active aggression. There are some vertebrates which entirely lack intra-specific aggression but which nevertheless avoid their own species meticulously. Some frogs, in particular tree frogs, live solitary lives except at mating time, and they are obviously distributed very evenly over the available habitat. As American scientists have recently discovered, this distribution is effected quite simply by the fact that every frog avoids the quacking sound of his own species. This explanation, however, does not account for the distribution of the females, for these, in most frogs, are dumb.

We can safely assume that the most important function of intra-specific aggression is the even distribution of the animals of a particular species over an inhabitable area, but it is certainly not its only one. Charles Darwin had already observed

that sexual selection, the selection of the best and strongest animals for reproduction, was furthered by the fighting of rival animals, particularly males. The strength of the father directly affects the welfare of the children in those species in which he plays an active part in their care and defense. The correlation between male parental care and rival fighting is clear, particularly in those animals which are not territorial in the sense which the Cichlids demonstrate but which wander more or less nomadically, as, for example, large ungulates, ground apes, and many others. In such animals, intra-specific aggression plays no essential part in the "spacing out" of the species. Bisons, antelopes, horses, etc., form large herds, and territorial borders and territorial jealousy are unknown to them since there is enough food for all. Nevertheless the males of these species fight each other violently and dramatically, and there is no doubt that the selection resulting from this aggressive behavior leads to the evolution of particularly strong and courageous defenders of family and herd; conversely, there is just as little doubt that the survival value of herd defense has resulted in selective breeding for hard rival fights. This interaction has produced impressive fighters such as bull bison or the males of the large baboon species; at every threat to the community, these valiantly surround and protect the weaker members of the herd.

In connection with rival fights attention must be drawn to a fact which, though it seems paradoxical to the nonbiologist, is, as we shall show later on in this book, of the very greatest importance: purely intra-specific selective breeding can lead to the development of forms and behavior patterns which are not only nonadaptive but can even have adverse effects on species preservation. This is why, in the last paragraph, I emphasized the fact that family defense, a form of strife with the extra-specific environment, has evolved the rival fight, and this in its turn has developed the powerful males. If sexual rivalry, or

any other form of intra-specific competition, exerts selection pressure uninfluenced by any environmental exigencies, it may develop in a direction which is quite unadaptive to environment, and irrelevant, if not positively detrimental, to survival. This process may give rise to bizarre physical forms of no use to the species. The antlers of stags, for example, were developed in the service of rival fights, and a stag without them has little hope of producing progeny. Otherwise antlers are useless, for male stags defend themselves against beasts of prey with their fore-hoofs only and never with their antlers. Only the reindeer has based an invention on this necessity and "learned" to shovel snow with a widened point of its antlers.

Sexual selection by the female often has the same results as the rival fights. Wherever we find exaggerated development of colorful feathers, bizarre forms, etc., in the male, we may suspect that the males no longer fight but that the last word in the choice of a mate is spoken by the female, and that the male has no means of contesting this decision. Birds of Paradise, the Ruff, the Mandarin Duck, and the Argus Pheasant show examples of such behavior. The Argus hen pheasant reacts to the large secondary wing feathers of the cock; they are decorated with beautiful eye spots and the cock spreads them before her during courtship. They are so huge that the cock can scarcely fly, and the bigger they are the more they stimulate the hen. The number of progeny produced by a cock in a certain period of time is in direct proportion to the length of these feathers, and, even if their extreme development is unfavorable in other ways—his unwieldiness may cause him to be eaten by a predator while a rival with less absurdly exaggerated wings may escape—he will nevertheless leave more descendants than will a plainer cock. So the predisposition to huge wing feathers is preserved, quite against the interests of the species. One could well imagine an Argus hen that reacted to a small

red spot on the wings of the male, which would disappear when he folded his wings and interfere neither with his flying capacity nor with his protective color, but the evolution of the Argus pheasant has run itself into a blind alley. The males continue to compete in producing the largest possible wing feathers, and these birds will never reach a sensible solution and "decide" to stop this nonsense at once.

Here for the first time we are up against a strange and almost uncanny phenomenon. We know that the techniques of trial and error used by the great master builders sometimes lead inevitably to plans that fall short of perfect efficiency. In the plant and animal worlds there are, besides the efficient, quantities of characteristics which only just avoid leading the particular species to destruction. But in the case of the Argus pheasant we have something quite different: it is not only like the strict efficiency expert "closing an eye" and letting second-rate construction pass in the interests of experiment, but it is selection itself that has here run into a blind alley which may easily result in destruction. This always happens when competition between members of a species causes selective breeding without any relation to the extra-specific environment.

My teacher, Oskar Heinroth, used to say jokingly, "Next to the wings of the Argus pheasant, the hectic life of Western civilized man is the most stupid product of intra-specific selection!" The rushed existence into which industrialized, commercialized man has precipitated himself is actually a good example of an inexpedient development caused entirely by competition between members of the same species. Human beings of today are attacked by so-called manager diseases, high blood pressure, renal atrophy, gastric ulcers, and torturing neuroses; they succumb to barbarism because they have no more time for cultural interests. And all this is unnecessary, for they could easily agree to take things more easily; theoreti-

cally they could, but in practice it is just as impossible for them as it is for the Argus pheasant to grow shorter wing feathers.

There are still worse consequences of intra-specific selection, and for obvious reasons man is particularly exposed to them: unlike any creature before him, he has mastered all hostile powers in his environment, he has exterminated the bear and the wolf and now, as the Latin proverb says, *"Homo homini lupus."* Striking support for this view comes from the work of modern American sociologists, and in his book *The Hidden Persuaders* Vance Packard gives an impressive picture of the grotesque state of affairs to which commercial competition can lead. Reading this book, one is tempted to believe that intra-specific competition is the "root of all evil" in a more direct sense than aggression can ever be.

In this chapter on the survival value of aggression, I have laid special stress on the potentially destructive effects of intra-specific selection: because of them, aggressive behavior can, more than other qualities and functions, become exaggerated to the point of the grotesque and inexpedient. In later chapters we shall see what effects it has had in several animals, for example, in the Egyptian Goose and the Brown Rat. Above all, it is more than probable that the destructive intensity of the aggression drive, still a hereditary evil of mankind, is the consequence of a process of intra-specific selection which worked on our forefathers for roughly forty thousand years, that is, throughout the Early Stone Age. When man had reached the stage of having weapons, clothing, and social organization, so overcoming the dangers of starving, freezing, and being eaten by wild animals, and these dangers ceased to be the essential factors influencing selection, an evil intra-specific selection must have set in. The factor influencing selection was now the wars waged between hostile neighboring tribes. These must have evolved in an extreme form of all those so-called "warrior virtues" which unfortunately many people still regard as desirable ideals. We shall come back to this in the last chapter of this book.

I return to the theme of the survival value of the rival fight, with the statement that this only leads to useful selection where it breeds fighters fitted for combat with extra-specific enemies as well as for intra-specific duels. The most important function of rival fighting is the selection of an aggressive family defender, and this presupposes a further function of intra-specific aggression: brood defense. This is so obvious that it requires no further comment. If it should be doubted, its truth can be demonstrated by the fact that in many animals, where only one sex cares for the brood, only that sex is really aggressive toward fellow members of the species. Among sticklebacks it is the male, in several dwarf cichlids the female. In many gallinaceous birds, only the females tend the brood, and these are often far more aggressive than the males. The same thing is said to be true of human beings.

It would be wrong to believe that the three functions of aggressive behavior dealt with in the last three chapters—namely, balanced distribution of animals of the same species over the available environment, selection of the strongest by rival fights, and defense of the young—are its only important functions in the preservation of the species. We shall see later what an indispensable part in the great complex of drives is played by aggression; it is one of those driving powers which students of behavior call "motivation"; it lies behind behavior patterns that outwardly have nothing to do with aggression, and even appear to be its very opposite. It is hard to say whether it is a paradox or a commonplace that, in the most intimate bonds between living creatures, there is a certain measure of aggression. Much more remains to be said before discussing this central problem in our natural history of aggression. The important part played by aggression in the inter-

action of drives within the organism is not easy to understand and still less easy to expound.

We can, however, here describe the part played by aggression in the structure of society among highly developed animals. Though many individuals interact in a social system, its inner workings are often easier to understand than the interaction of drives within the individual. A principle of organization without which a more advanced social life cannot develop in higher vertebrates is the so-called ranking order. Under this rule every individual in the society knows which one is stronger and which weaker than itself, so that everyone can retreat from the stronger and expect submission from the weaker, if they should get in each other's way. Schjelderup-Ebbe was the first to examine the ranking order in the domestic fowl and to speak of the "pecking order," an expression used to this day by writers. It seems a little odd though, to me, to speak of a pecking order even for large animals which certainly do not peck, but bite or ram. However, its wide distribution speaks for its great survival value, and therefore we must ask wherein this lies.

The most obvious answer is that it limits fighting between the members of a society, but here in contrast one may ask: Would it not have been better if aggression among members of a society were utterly inhibited? To this, a whole series of answers can be given. First, as we shall discuss very thoroughly in a later chapter (Ten, "The Bond"), the case may arise that a society, for example, a wolf pack or monkey herd, urgently needs aggression against other societies of the same species, therefore aggression should be inhibited only *inside* the horde. Secondly, a society may derive a beneficial firmness of structure from the state of tension arising inside the community from the aggression drive and its result, ranking order. In jackdaws, and in many other very social birds, ranking order leads directly to protection of the weaker ones. All social animals are "status seekers," hence there is always particularly high tension between individuals who hold immediately adjoining positions in the ranking order; conversely, this tension diminishes the further apart the two animals are in rank. Since high-ranking jackdaws, particularly males, interfere in every quarrel between two inferiors, this graduation of social tension has the desirable effect that the higher-ranking birds always intervene in favor of the losing party.

In jackdaws, another form of "authority" is already linked with the ranking position which the individual has acquired by its aggressive drive. The expression movements of a high-ranking jackdaw, particularly of an old male, are given much more attention by the colony members than those of a lower-ranking, young bird. For example, if a young bird shows fright at some meaningless stimulus, the others, especially the older ones, pay almost no attention to his expressions of fear. But if the same sort of alarm proceeds from one of the old males, all the jackdaws within sight and earshot immediately take flight. Since, in jackdaws, recognition of predatory enemies is not innate but is learned by every individual from the behavior of experienced old birds, it is probably of considerable importance that great store is set by the "opinion" of old, high-ranking, and experienced birds.

With the higher evolution of an animal species, the significance of the role played by individual experience and learning generally increases, while innate behavior, though not losing importance, becomes reduced to simpler though not less numerous elements. With this general trend in evolution, the significance attached to the experienced old animal becomes greater all the time, and it may even be said that the social coexistence of intelligent mammals has achieved a new survival value by the use it makes of the handing down of individually acquired information. Conversely, it may be said that social coexistence exerts selection pressure in the direction of better

learning capacity, because in social animals this faculty benefits not only the individual but also the community. Thus longevity far beyond the age of reproductive capacity has considerable species-preserving value. We know from Fraser Darling and Margaret Altmann that in many species of deer the herd is led by an aged female, no longer hampered in her social duties by the obligations of motherhood.

All other conditions being equal, the age of an animal is, very consistently, in direct proportion to the position it holds in the ranking order of its society. It is thus advantageous if the "constructors" of behavior rely upon this consistency and if the members of the community—who cannot read the age of the experienced leader animal in its birth certificate—rate its reliability by its rank. Some time ago, collaborators of Robert M. Yerkes made the extraordinarily interesting observation that chimpanzees, animals well known to be capable of learning by imitation, copy only higher-ranking members of their species. From a group of these apes, a low-ranking individual was taken and taught to remove bananas from a specially constructed feeding apparatus by very complicated manipulations. When this ape, together with his feeding apparatus, was brought back to the group, the higher-ranking animals tried to take away the bananas which he had acquired for himself, but none of them thought of watching their inferior at work and learning something from him. Then the highest-ranking chimpanzee was removed and taught to use the apparatus in the same way, and when he was put back in the group the other members watched him with great interest and soon learned to imitate him.

S. L. Washburn and Irven de Vore observed that among free-living baboons the band was led not by a single animal but by a "senate" of several old males who maintained their superiority over the younger and physically stronger members by firmly sticking together and proving, as a united force,

stronger than any single young male. In a more exactly observed case, one of the three "senators" was seen to be an almost toothless old creature while the other two were well past their prime. On one occasion when the band was in a treeless area and in danger of encountering a lion, the animals stopped and the young, strong males formed a defensive circle around the weaker animals. But the oldest male went forward alone, performed the dangerous task of finding out exactly where the lion was lying, without being seen by him, and then returned to the horde and led them, by a wide detour around the lion, to the safety of their sleeping trees. All followed him blindly, no one doubting his authority.

Let us look back on all that we have learned in this chapter from the objective observation of animals, and consider in what ways intra-specific aggression assists the preservation of an animal species. The environment is divided between the members of the species in such a way that, within the potentialities offered, everyone can exist. The best father, the best mother are chosen for the benefit of the progeny. The children are protected. The community is so organized that a few wise males, the "senate," acquire the authority essential for making and carrying out decisions for the good of the community. Though occasionally, in territorial or rival fights, by some mishap a horn may penetrate an eye or a tooth an artery, we have never found that the aim of aggression was the extermination of fellow members of the species concerned. This of course does not negate the fact that under unnatural circumstances, for example confinement, unforeseen by the "constructors" of evolution, aggressive behavior may have a destructive effect.

Let us now examine ourselves and try, without self-conceit but also without regarding ourselves as miserable sinners, to find out what we would like to do, in a state of highest violent aggressive feeling, to the person who elicited that emotion. I do not think I am claiming to be better than I am when I say

that the final, drive-assuaging act, Wallace Craig's consummatory act, is not the killing of my enemy. The satisfying experience consists, in such cases, in administering a good beating, but certainly not in shooting or disemboweling; and the desired objective is not that my opponent should lie dead but that he should be soundly thrashed and humbly accept my physical and, if I am to be considered as good as a baboon, my mental superiority. And since, on principle, I only wish to thrash such fellows as deserve these humiliations, I cannot entirely condemn my instincts in this connection. However, it must be admitted that a slight deviation from nature, a coincidence that put a knife into one's hand at the critical moment, might turn an intended thrashing into manslaughter.

Summing up what has been said in this chapter, we find that aggression, far from being the diabolical, destructive principle that classical psychoanalysis makes it out to be, is really an essential part of the life-preserving organizaton of instincts. Though by accident it may function in the wrong way and cause destruction, the same is true of practically any functional part of any system. Moreover, we have not yet considered an all-important fact which we shall hear about in Chapter Ten. Mutation and selection, the great "constructors" which make genealogical trees grow upward, have chosen, of all unlikely things, the rough and spiny shoot of intra-specific aggression to bear the blossoms of personal friendship and love.

Chapter Four

The Spontaneity of Aggression

In the previous chapter, I think it has been adequately shown that the aggression of so many animals toward members of their own species is in no way detrimental to the species but, on the contrary, is essential for its preservation. However, this must not raise false hopes about the present situation of mankind. Innate behavior mechanisms can be thrown completely out of balance by small, apparently insignificant changes of environmental conditions. Inability to adapt quickly to such changes may bring about the destruction of a species, and the changes which man has wrought in his environment are by no means insignificant. An unprejudiced observer from another planet, looking upon man as he is today, in his hand the atom bomb, the product of his intelligence, in his heart the aggression drive inherited from his anthropoid ancestors, which this same intelligence cannot control, would not prophesy long life for the species. Looking at the situation as a human being whom it personally concerns, it seems like a bad dream, and it is hard to believe that aggression is anything but the pathological product of our disjointed cultural and social life.

And one could only wish it were no more than that! Knowledge of the fact that the aggression drive is a true, primarily

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