

# Adaptation and Self-Organization in Primate Societies

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The primary method by which science endeavors to order the world is the analytic approach, consistent with Cartesian principles of dividing the problem in as many sections as required for an optimal solution, and progressing from the simplest to the most complex reasoning. When the interactions among the various elements of the system being studied are minimal, such a procedure indeed makes it possible to formulate laws that describe chains of causality. However, when the variables are interdependent and linked by non-linear equations, the atomistic method cannot account for the phenomenon in its entirety. Spurred by this inadequacy, scientists sought to discover synthetic methods which, early in the twentieth century, led to the conceptualization of holistic theories in a number of disciplines. The most highly developed fields are the psychology of form, structural anthropology (1)\*, and the various systems theories (2). More recently, the development of epigenetic concepts in biology has corresponded to the appearance of different theories of pattern in physics and mathematics (3, 4) and to the progressive emergence of the concept of self-organization (5, 6, 7). The objective is to explain the production of complex structures on the basis of interacting elements, none of which contains a guiding scheme that dictates these structures. In biology, the challenge is to locate the constraints that are expressed in a space of possibilities (8) in order to develop a theory of organization that is capable of predicting the finite number of forms that living creatures can assume (9). This school of thought can be described as structuralist, emergentist, self-organizational, or epigeneticist, depending on the theoretical version that is emphasized.

\* Numbers in parentheses refer to bibliographic citations at the end of the article.

## Form and Function in the Theory of Evolution

Even though considerations on the opposition between form and function can be found in Aristotle, the true debate on the subject is tied to the beginnings of biology: the debate arises at the inception of biology and persists throughout the development of the field. When biology was established in the sixteenth and seventeenth centuries, the goal of natural history was to define and classify forms. When the terms “system” and “structure” appear, they are being used to describe the order of nature rather than its functioning (10). The nineteenth century saw the emergence of the notion of organization and the twin concepts of structure and function. Cuvier wrote that “All the organs of a particular animal form a unique system, all the parts of which support, act upon, and react to one another; and any modification of one of these parts must bring about analogous modifications in all of them” (11). Thus the scientists involved in comparative anatomy or embryology tried to understand the interdependence of the different parts of the organism (12, 130). The advent of the theory of evolution shifted the emphasis to the organism’s external relations, relegating all the preceding problems to secondary importance and “nipping in the bud a nascent theory of pattern” (14). Darwinism represents an “ecological theory of evolution” in which the organism is conceived essentially as a set of atomic parts, each of which is subject only to the constraints of adaptation to the environment. This is an exclusively functionalist view, which considers the forms as dependent on unique events (15). Neo-Darwinism pursued this line by defining evolution as the natural selection of stochastic variations (16). Though the existence of “correlated variations” among traits was recognized by both Darwin and the neo-Darwinians, it was deemed insignificant (17).

Historically, because of the evidence of material forms, the domain of morphogenesis has been the favored meeting ground for proponents of functionalism and those of structuralism. The force of Haeckel’s theory of recapitulation (“Phylogenesis is the mechanical cause of ontogenesis”) won the day for the functionalists, and the study of immediate causes was for a long time rejected as being unimportant compared to the studies under-

taken in the service of phylogeny (18). In spite of the dominance of functionalist views for nearly a century, the structuralist minority survived from the time of Darwin's contemporaries to our own time (13, 19, 20). Affirming that internal constraints channel the evolutionary process and influence the direction it takes, this line of thought has recently undergone a vigorous resurgence. At the turn of the century, more and more scientists, preoccupied with morphology, came to develop concepts that made it possible to account for the structural constraints encountered by organisms: *homologous series* in genetics (21), *forced correlations* in the study of shape (22), *epigenetic landscape* in the study of development (23), *architectural constraints* in paleontology (24). Finally, a modification of conceptions relating to the processes of evolution (25) provoked renewed interest in structures, with an emphasis on the developmental constraints that represent the basis upon which selection acts (14, 16, 17, 26). Such ideas have extended to various disciplines, and developmental constraints are now taken into account not only in macroscopic studies but also at the cellular and molecular level (12, 26, 27, 28). There is general agreement that a theory of evolution would be complete only if it included a group of epigenetic laws (17, 29).

In comparison with progress in these areas, the disciplines that deal with the study of animal societies have evolved slowly. Disciplines such as sociobiology and behavioral ecology remained anchored in a strict neo-Darwinism (30). Ethology has principally constructed itself as a neo-Darwinian interpretation of behavior. Its founders, Lorenz (31) and Tinbergen (32, 33), influenced by the psychology of form, emphasized the necessity of studying the living creature in its entirety, a departure from the atomism previously espoused by behaviorists and reflexologists. But their interest focused above all on the interactions between the subject and its environment, and therefore on the problems of survival. Though undeniably fertile, this approach resulted in a failure to consider the constraints of development, with attention instead to the function of behaviors. Sociobiological theory further refined this Darwinian conception, integrating the concepts of population genetics with the study of behavior and social organizations; but here again, in spite of its real heuristic value, this theory added

nothing to the understanding of forms, leaving aside the question of the relation between gene and behavioral phenotype (34).

Even though epigeneticist views have regularly been expressed in studies of the development of individual behaviors (35, 36, 37, 38), the general opinion in ethology remains that behavior is determined by the interaction of genotype and environment. However, as Ho and Saunders emphasize, "Although it is often said that the genotype interacts with the environment during development, this statement reflects a certain degree of sloppy thinking. It is rather the epigenetic system which interacts with the environment and ultimately generates those variations on which selection can act. The epigenetic system belongs, strictly speaking, to the phenotype rather than the genotype" (16). As Oyama remarks, "When behavioral scientists say that the behavior is plastic, there remained the implicit assumption that the form of the body was predetermined. Even if we admit that behavior is more sensible to environmental variations than morphology, it is a phenotype and, as such, subject to internal constraints" (39). Behavior is not infinitely flexible; we must admit that the epigenetic systems of transformation confine it to a limited number of possible solutions.

Whereas the first attempts to integrate epigenetic effects with the evolutionist perspective have remained isolated (40), analysis of the immediate causes of behavior has attracted renewed interest. With the debate reopened, the number of contributions to this approach is growing (37, 38, 41, 42, 43, 44, 45, 46, 47), and the concepts of self-organization are gaining ground in the study of animal societies (48, 49, 50). The domain of primatology, while relatively isolated from this evolution of ideas, has undergone a parallel development of its own. The study of primate behavior has brought to light an increasing number of facts indicating that the internal constraints of organizations play a major role in the form and functioning of their societies. What follows aims to demonstrate the coherence and the heuristic power of epigeneticist thought as applied to social organizations that are by nature self-organizations.

## **Adaptation and the Null Hypothesis**

By incorporating research on the survival value of behaviors into the program of ethology, Tinbergen (51) implicitly asserted that every behavioral trait must have a function. In Tinbergen's successors, the functional consequences of which he spoke became the adaptive value of behavior, in keeping with the classical neo-Darwinian schema (52, 53). But adaptation represents an onerous concept in theoretical terms: in order to conclude that natural selection intervenes, a mechanism for action must still be proposed (54). In spite of the reservations expressed by several authors (55, 56, 57, 58, 59, 60), the hypothesis of the adaptive function of all social behaviors remains the norm in the study of non-human primates. The utilitarian argument is often the only justification for this (61), the present consequences of a biological trait indicating the reasons for its existence. The null hypothesis, that is, the possibility that the behavioral trait under consideration is not an adaptation, is generally not taken into account. Trivial though it may often appear, it nevertheless represents a parsimonious theoretical response, which in many cases is capable of accounting for the emergence of a behavior simply by examining the constraints that are imposed on the individual, whether these constraints are morphological, physiological, cognitive, or social. This will be demonstrated by the following series of examples.

The occasional occurrence of genital swelling typical of estrus in pregnant females has given rise to a number of functionalist interpretations: estrus after conception could be seen as a tactic whereby the female attracts males, conceals the ovulation phase, or deceives them as to their possible paternity, in order to obtain the protection of males for herself or her offspring (62, 63). However, males rarely show an interest in females in such reproductive periods. Post-conception estrus is a quite widespread phenomenon among primates and other mammals, and is not limited to certain social organizations. It results from variations in steroid levels (64). This phenomenon can be seen as the accidental consequence of the complex endocrine mechanisms that control gestation, without requiring recourse to a supplementary hypothesis.

Sociobiological theory predicts that individuals ought to recognize conspecifics engendered by the same father. This presumes rigid recognition mechanisms that would be incompatible with the behavioral flexibility and broad learning capacities that are known to exist in primates. In fact, the existence of such an effect has never been irrefutably demonstrated (65). The grooming of wounds in the Sri Lankan macaque (*Macaca sinica*) has been interpreted as an example of reciprocal altruism: an individual tends the wounds of a conspecific in order to secure the latter's active support in future conflicts (66). But non-human primates do not appear to have anticipatory faculties that are sophisticated enough to allow them to develop exchanges over long periods of time. The study of coalitions formed by male baboons (*Papio cynocephalus*) in order to overcome females in estrus indicates that their acts are not guided by a common goal. When two allies repel a third male, it appears that each one is pursuing an immediate personal goal: only one of them mates with the female, while the second probably gains nothing other than the upper hand over the repelled rival (67, 68). Even in the chimpanzee (*Pan troglodytes*), quantitative analysis shows that we have no proof of intentional reciprocity in social exchanges (69).

If constraints can prohibit certain behaviors or tactics, conversely the removal of constraints can authorize or even foster the emergence of behaviors. Forced copulation is known to exist in the orangutan (*Pongo pygmaeus*): a male mates with a female despite her resistance. This behavior has been interpreted as a reproductive strategy, either as an effort on the part of the female to select a partner or to choose the time to reproduce (70), or as a tactic employed by young males who, unlike fully grown males, cannot follow females in estrus for long periods of time (71). This is not convincing, for immature males have access to females only outside their fertile periods, and the females' resistance is ineffectual. On the other hand, the species is distinguished by an essentially solitary life and a high degree of sexual dimorphism. Such a state of fact implies that the female does not have the necessary allies to stop a male that weighs twice as much as she does. Given the sexual motivations of males, forced copulations occur when the physical and social context permits it (72). No other explana-

tion is needed. The situation observed in the chimpanzee and the gorilla (*Gorilla gorilla*) bears out this interpretation. "Rapes" are the exception in the natural populations of these two species, whereas in captivity forced copulations occur regularly when a female is isolated with a male (73).

Other examples show that a particular context allows a potential to be expressed. In normal situations, the males of certain species show little interest in infants. However, in the squirrel monkey (*Saimiri sciureus*), they may spontaneously interact with young individuals if the females are experimentally removed from the group (74). In the rhesus macaque (*Macaca mulatta*), an isolated male exhibits maternal behaviors if an infant is placed with it (75).

In order to explain the mounts that regularly occur between adult females, it has been suggested that these are reproductive tactics intended to signal their receptive state to the males, or else to reduce the chances that the rival females will be inseminated. But these sociobiological hypotheses are not borne out by an examination of the facts (76). In the Japanese macaque (*Macaca fuscata*), the frequency of mounts between females increases in the reproductive season and during the early stages of gestation; this effect is particularly marked in groups with a limited number of males (77). The fortuitous combination of unusual demographic and hormonal circumstances is sufficient to explain the phenomenon. Mounts involving partners of the same sex are also the norm in groups composed exclusively of males (76).

In the rhesus macaque, it happens that certain females may carry two infants at once, their own and another mother's, often of a higher social status. It has been suggested that the female is thus fostering the development of special ties between her offspring and partners belonging to dominant matriline (78). It is possible that the young of dominant mothers are more attractive. These mothers are also more permissive: often at some distance from them, their infants can easily be taken up by other females. It is not necessary to invoke the direct action of natural selection in order to explain this phenomenon. In the same species, it is known that males that change troops often join a troop to which a brother has already immigrated. Given that the group structure

is based on matriline, individuals tend to mate with partners belonging to the same matriline (79). These results can be interpreted in sociobiological terms – theories of parental investment and kinship selection. A father is supposed to protect his own offspring or nephews if they remain associated. But such an explanation is gratuitous. Immediate causes such as familiarity and preference for the companions that the individual has grown up with are sufficient to induce the observed structural effects.

In macaques and baboons, species in which adult males establish special ties with certain females, it is observed that these males offer protection to the offspring of their female “friends.” It has long been assumed that this is a form of parental investment: the males mate with the female and aid their offspring. Now that paternity analyses have established that quite often males are not the fathers of the infants they take care of, another functionalist explanation is put forth: caring for the young increases the male’s chances of being chosen as a sexual partner by the female (72, 80). It is simpler to think that the infant that remains near the mother becomes familiar to the males (83), that is, that social relations channel the behavior of individuals. In the small species, which share the rearing of infants, carrying the infant can increase their chances of survival. There again, however, it appears that this is not a mating tactic (84), and the decisive parameter is not paternity (44, 85, 86, 87).

The fact that conflicts are often more frequent among subjects belonging to the same matriline in macaques (*Macaca fuscata*, *Macaca mulatta*) does not gibe with the theory of kinship selection which holds that competition must decrease in inverse relation to the number of genes in common. It has been proposed that aggression towards immature kin serves a teaching and socialization function for the young (88). However, as the members of a single matriline are generally found in proximity with one another, it is inevitable that conflicts will regularly break out among them. What is operative is group structure, rather than the function of individual acts.

Not infrequently, behaviors resulting in negative consequences can be interpreted as adaptive. In groups of lemurs (*Lemur*), in periods of reproduction, certain individuals are persistently



attacked by their conspecifics to the point of expulsion or death (89). In fact, this is an artifact of captivity; the phenomenon does not exist in natural populations and it appears to correspond to an increased rate of migration in the period in question (90, 91).

It is also possible to offer a functionalist interpretation of depression in primate infants separated from their mothers. I myself have in the past proposed seeing depressed behavior as a waiting response, adapted to a temporarily unsolved problem (92). Disengagement and passivity are responses that are observed in a restricted situation from which subjects cannot escape. But it is not at all necessary to resort to natural selection to explain this. It is probable that depression signifies that the subject's ability to respond has been overtaxed to the point where certain individuals even end up dying (93).

### **The Interdependence of the Parties**

For the proponents of functionalism, the above account of behaviors is inadequate because it makes reference only to immediate reasons, without considering ultimate causes. However, epigeneticist thought in no way denies the existence of adaptive behaviors. Quite the contrary, it inserts the hypothesis of non-selection in an evolutionary schema that integrates both the intervention of developmental constraints and selection processes. A behavioral trait can be neutral or even lead to harmful consequences, but nevertheless be maintained in a population because it is the result of another trait that is subjected to positive selection (17).

In insect societies, individual behaviors are strongly determined by genetics. As a first approximation, some errors notwithstanding, it may be granted that their collective accomplishments are the result of a self-organization based on the operation of behavioral algorithms retained by natural selection (49, 94). In mammals such as primates, this conservative Hamiltonian fiction of a universe without friction is no longer tenable. Individual plasticity is such, and the number of factors exerting contradictory influences is so great, that we must expect the emergence of numerous secondary effects, static and other by-products brought

about by organizations that could be seen either as relative orders or relative disorders – that is, in fact, fluctuating orders (96).

A spectacular illustration of the noise that can be generated by a social organization can be found in the cases of infanticide reported in groups of non-human primates. For the functionalists, the killing of rivals' offspring constitutes an extreme result of sexual selection (95). If a male assumes dominance of a group and causes the death of an infant, his behavior is supposed to represent an adaptive tactic: he eliminates the offspring of a rival and accelerates the mother's return to estrus so as to inseminate her sooner (96, 97). The possibility of a selection leading to such behavior is problematical. There is no evidence that the male gains any advantage by eliminating the genes of his conspecifics; moreover, infanticide represents only a secondary factor among the numerous causes of mortality to which an infant can fall victim (98). But there is more. If we examine the facts, we find that males may kill the young even after the female's ovulation period, that the onset of estrus is not noticeably hastened, that juvenile individuals can be killed, that many infants are not attacked, and that a male can kill his own offspring – to say nothing of intra-community cannibalism that is known to exist in the chimpanzee (99). The infants are most often hurt when they are on the mother; the attacks are not actually targeted against the infants specifically, but rather against all the individuals in the group (60, 98, 100). Finally, infanticides can occur outside the context of a take-over ousting a dominant male, but they are always associated with periods of extremely high tension. The most parsimonious hypothesis consists of seeing infanticide as a by-product of aggressive behavior and, more precisely, as the secondary consequence of a generalized situation of conflict in which the infants are killed by accident (98, 101). Whereas a bite only wounds an adult female, it leads to the death of an infant. Under these conditions, it is not necessary to explain why infanticide is rarer when several adult males are present in the group: each one of them represents a powerful defender for females in search of allies.

Adoption, which saves an infant, and kidnapping, which on the contrary can bring about its death by starvation, are two behaviors that occur fairly regularly in primates if the circumstances are

conducive (102, 103). These behaviors may occur among kin as well as non-kin. The same is true more generally of what is called allomaternal behavior, that is, caring for young born of other mothers: the infants are carried, protected, groomed, and handled, sometimes roughly (104). There is no shortage of mutually contradictory adaptationist hypotheses proposed to explain these behaviors, which are seen as a form of socialization, a learning process for the young female, assistance to the mother, or on the contrary as abusive treatment intended to reduce the offspring of a rival female (102, 105). It is more likely that allomaternal behavior, whether adroit or clumsy, whether it involves kidnapping or adoption, results from one and the same tendency: the attraction of females to infants (57). This is the trait that is selected; it is a vital one in species with extended periods of growth and development. Newborns have distinctive morphological signs. It would seem difficult to understand why females, who must pay considerable attention to their own offspring would show no interest in other mothers' infants. For that to be possible, one would have to postulate the intervention of brief, selective attachment processes, such as imprinting, which are incompatible with what we know about primates' learning abilities: these abilities are independent of context, that is, something learned in one situation can be generalized to another situation. It should be added that the hypothesis of non-selection in no way forbids that allomaternal behavior has repercussions for nutrition and reproduction. In fact, it allows the mother to devote more time to searching for food (106) and, by reducing the time spent with the infant at her breast, it can decrease the interval between births (107).

Interference by the young in adult matings represents another examples of the covariation phenomenon. Immature individuals come into contact with copulating partners and emit affiliative, or sometimes ambivalent, expressions (108). The functionalist hypothesis suggests that the young individual is trying to prevent the fertilization of its mother in order to delay the birth of a rival that would monopolize the female's attention. However, the harassment in no way prevents insemination; the female involved is not always the mother of the interfering individual; and finally the sociobiological version is powerless to account for the fact that

such interference is frequent in certain species and rare or nonexistent in many other species. In terms of psychological causes, the young exhibit intense reactions to matings that involve a partner with whom they have developed strong affective ties. It appears that they are attempting to participate in the interaction or to protect their social relationship (108, 109). In anthropomorphic terms, it might be said that they are exhibiting misplaced jealousy. But, above all, such harassment occurs only in the species where the male is sufficiently tolerant to accept exuberant manifestations by immature subjects (109). Similar variations are observed in the case of allomaternal behavior. The transfer of infants is commonly observed in the species in which conspecifics are not separated by major differences in social status (110, 111). It may be concluded from this that minimal asymmetry in dominance relationships facilitates social exchanges including care-giving to infants and interference in mating.

A special role has sometimes been attributed to elderly individuals (112). These subjects are relatively inactive and tend to be less socially involved. They nevertheless remain full members of the group and they often provide valuable support for their partners. Studies of the vervet (*Cercopithecus aethiops*) have observed that the presence of a grandmother increases the chances of survival for the young (113). Longevity exhibits an allometric relation with other traits such as body or brain size; there is reason to believe that natural selection operates upon these traits collectively. That does not mean, however, that every effect of longevity can be chalked up to selection. Aging affects every aspect of the organism and its activity. The behavioral particularities of elderly subjects are most likely secondary consequences of age-related alterations in physical performance (114, 115).

Learning capacities are also apt to induce a slew of secondary effects, in particular in the social domain. Whenever individuals with elaborate cognitive abilities form social groups with overlapping generations, it is inevitable that acquired behaviors will be socially transmitted. Thus it is that traditions observed in non-human primates arise. Many of these traditions have to do with useful innovations and concern the acquisition and processing of food, care for the body, or communicative signals; in contrast,

others appear to be gratuitous (116). Whatever the case may be, in the absence of verbalized norms, ape traditions remain fragile and fleeting phenomena on the evolutionary level. Their populations are always vulnerable to losing what they have acquired and reverting to their initial conditions (117, 118). As a consequence, the traditions do not last long enough for a cultural milieu to be permanently established. Natural selection cannot come into play and bring about genetic changes. If learning abilities are indeed a selected trait, on the contrary traditions are only an epiphenomenon perceived by the observer at the level of the group.

### **The Unpredictability of Solutions**

To the preceding arguments, functionalists will reply that they do not disregard the way the various elements of an organization interact to produce a large number of effects. It is to take this interaction into account that they construct models explaining the subject's behavior as resulting from a compromise among the various forces exerted upon it, as for any phenotype (34, 119, 120). This method is productive when it serves to guide research. By calculating the costs and benefits attached to different strategies, one is able to evaluate the variables that are likely to play a role in a well-defined problem (121). But this approach often leads researchers astray. In many cases, they claim to embrace complex situations in which many factors intervene and they assume to boot that selection mechanisms inevitably bring the animal to choose the best strategy. This leads to models that cannot be proved and that lead to failure (17, 59, 122). The real world does not evolve as predicted by game theory. The subject's ignorance with regard to many environmental variables, and the existence of non-linear effects that place the subject in unstable systems, combine to make it impossible to optimize the subject's behavior. Adaptation is an imperfect and imprecise process. In order to survive and reproduce in the face of fluctuating situations, the individual can only try to be better than his rivals by adopting "adequate," "necessary," "sufficient," or "tolerable" tactics (55, 123, 124).

Theories that attempt to explain social relations and modes of grouping patterns in non-human primates take into account only two independent factors, the risk of predation and the distribution of food resources (120, 125, 126, 127). This gives rise to models whose predictions are extremely difficult to test, as their own authors acknowledge (127). The past and present action of the environment can never be separated; any flaw in the models is immediately attributed to a modification in the pressures of selection that prevailed during the evolution of the species. What would become of their status as falsifiable theories if they incorporated other determinants that, though previously neglected, exert a major influence on animal groupings? The action of pathogenic agents constitutes one such forgotten parameter. It is known that parasite infestation of subjects can vary as a function of the subjects' habitat, group size, and rank (128, 129, 130, 131, 132), and the same is probably true for microbial infections (133).

Another variable that is ignored by socio-ecological models is the transfer of information. Yet communications are constantly occurring in the context of foraging, finding the best paths, and avoiding danger. Primates learn from each other and are continuously paying attention to their companions' behavior (134, 135, 136, 137). The value of information varies according to the diversity of the habitat or the cognitive abilities of the species being studied. The level to which these abilities themselves have developed exerts a profound influence on the functioning of social groups. It affects the number of conspecifics liable to be known and remembered, the mechanisms by which group members are coordinated, or the ability to read social relations, which are crucial information when an individual immigrates to another group, for example (138, 139). It is reasonable to think that the hostility that prevails between chimpanzee groups is a consequence of their capacity to form mental representations relating to the group they belong to as a whole (139); this consequence has important repercussions for the demography and social organization of chimpanzees, since it can even lead to the extermination of one community by another (140, 141).

The intervention of numerous parameters means that it is often difficult to distinguish between causes and effects (59). Attempts

have been made to show that the presence of several adult males in a group serves to detect predators (142). The sentinel role had drawn criticism earlier since it invoked selection at the level of the group (54, 56). The current hypothesis involves sexual selection, with the females choosing the males that are able to offer protection (142). But predators are not the only reason for vigilance, and conspecifics are kept under constant surveillance (143, 144). If adult males spend a large part of their time on the periphery of the group, observing the surrounding, it is first of all out of personal interest, which requires monitoring the presence of other adult males (145). Their attitude can be advantageous to the group, and we must take this into account in our understanding of social organization as a whole, but it is not necessary to believe that this is a male function that is specifically selected in order to serve females. Likewise, whereas the theory predicts that the members of a group foraging for food must spread out spatially so as to optimize the risks of predation and the nutritional gains, it appears that the position of subordinated individuals results first of all from the social constraints to which they are subject (146).

When the action of ecological factors is channeled by social organization, there are no simple causes. The same is true of life-history traits. When the frequency of aggressive behavior directed against a female is correlated to her reproductive state (147), we should not seek determinism in distant causes and a competitive strategy that would be mysteriously linked to her cycle. The state of a female's endocrine functions has direct and indirect effects on behavior, and moreover it is associated with the presence of offspring, whose age influences the nature of the conflicts in which their mother is led to intervene. These variables must be taken into account together if we are to understand the variations in the female's behavior (148).

Certain effects predicted by sociobiological theory are highly unlikely to be demonstrated owing to the multiplicity of variables involved. According to Trivers and Willard's hypothesis (149), when conditions of parental health are liable to influence their offspring's chances of reproduction, dominant mothers must give birth to a higher proportion of males, since males can have numerous offspring; conversely, subordinate mothers are better off pro-

ducing more daughters: if the number of offspring a female can have is limited, on the other hand it remains relatively stable. The hypothesis of competition for resources makes the opposite prediction in certain circumstances: when females remain with their native group for their entire lives, higher-ranking mothers must invest in daughters, whom they are able to protect, whereas subordinate mothers find it advantageous to produce sons who will emigrate upon reaching maturity (150). At the present, despite efforts undertaken to verify these hypotheses, the results remain contradictory. It appears overall that the sex ratio in primate populations hovers around 50 per cent. In certain groups, the proportion varies from the mean value, either higher or lower. If there are still grounds for wondering whether these fluctuations are directional or rather purely stochastic (151), it can in any case be affirmed that there is little fluctuation in baboons, macaques, and vervets, a fact that discounts the action of selection mechanisms (60). To rescue these hypotheses, van Schaik and Hardy (152) have proposed that the mechanism described by Trivers and Willard prevails when food is abundant, while competition for resources dominates when food is scarce. However clever this model may be, it presupposes two adaptive phenomena, each one adjusted to a different level of competition. It is difficult to imagine an optimization mechanism, operating on a physiological level, that would be capable of anticipating the best tactic to pursue through the sum of events and variables that impinge on the life of the mother and her offspring.

### **Morphogenetic Effects**

The intervention of mechanisms of positive feedback induces autocatalytic processes that generate powerful morphogenetic effects. If the resulting social forms do not bring about truly harmful effects on adaptation to the environment, then these forms can be conserved and individuals will be obliged to adjust their behavior in turn. That a social organization is structured on the basis of interactions that occur among its members is a well-established fact in the study of non-human primates (153, 154, 155). But



the observer is the one who recognizes the structures. As Ashby expresses it (8), the organization exists in part in the eye of the beholder. If we attempt to reduce the perceived forms to strategies, without regard for the epigenetic constraints that produced them (120, 156, 157), this amounts to attributing a selected function to reified structures, in other words, to endowing appearances with an adaptive value (139, 158).

The emergence of social structures can be simulated on a computer by using methods and concepts that have been developed in the field of distributed artificial intelligence (139, 159, 160). These approaches make it possible to show that complex structures can emerge from the interaction of artificial agents that react solely to local conditions in their environment. Forms of cooperation among agents devoid of intentionality can be seen to appear; this calls for caution in interpreting the motivations involved in cases of reciprocity reported in primates (69, 160). Patterns of grouping and traveling in male chimpanzees have been reproduced without recourse to other motivations than seeking food or sexual partners (159).

By creating close interdependence among individuals, coalitions represent a fundamental structural force among certain groups of primates. The same models cannot account for organizations in which alliances in conflicts are frequent, and for others in which alliances are rare or absent. This is demonstrated by a comparison of two contrasting systems of dominance and kinship. In a species such as the Indian langur (*Presbytis entellus*), the dominance of females depends mainly upon age: high-ranking as young adults, they lose status as they grow old. In the rhesus macaque and the Japanese macaque, on the other hand, aged females often occupy a high social position. These differences have been interpreted as expressions of opposing reproductive strategies (112). In species that form cohesive matrilineal groups, females would thus have the advantage of supporting their kin. In the langur, in contrast, females change groups when they reach adulthood, so that the members of a troop thus have few kinship ties; it would thus be more advantageous for the females to be dominant as adults, when they must raise their offspring; they could then become more altruistic when they are no longer of

reproductive age. Such an interpretation can be conceived only by ignoring the effects necessarily entailed by the existence of a constraint such as the alliance of related partners. While the lack of strong coalitions in the langur obliges the female to rely mainly on her own physical strength, the frequency of coalitions among macaques confers great power upon their genealogical structures. Using demographic simulations, Datta (161) has shown that if females have few allies, they generally lose rank as they grow old. Conversely, when sub-groups of kin are strong in number, the play of coalitions produces the dominance structures that are typical of rhesus and Japanese macaques, with the mother dominating her daughters and younger sisters holding sway over older sisters.

It should be observed that the existence of frequent coalitions can lead to the same result as the lack of alliances, if the preference for partners related by blood is not too marked: in both cases, in the absence of unconditional support, older females cannot maintain a position of dominance. I have elsewhere proposed that coalitions among kin increase the asymmetry of dominance among the members of a group, this asymmetry reinforcing the cohesion of kinship ties by a feedback loop (110). This can explain both rigid genealogical systems that are found in species with strong hierarchies, such as the rhesus macaque and Japanese macaque, and more loosely structured organizations such as those found in other species of macaques (*Macaca arctoides*, *Macaca sylvanus*, *Macaca tonkeana*, *Macaca radiata*); the latter are characterized by the lesser importance of kinship ties and a weaker influence of dominance structure (110, 162, 163, 164). The hypothesis of a covariation of the degree of nepotism and the asymmetry of power has recently been confirmed through comparison of a large number of macaque groups (165, 166). More generally, it is observed that individuals are not separated by major differences in rank in the species in which kinship ties are unimportant (167, 168, 169).

With regard to linking the degree of nepotism to that of asymmetry of dominance in macaques, it is impossible not to take issue with socio-ecological models that presume the existence of selective pressures acting independently upon each of the two param-

ters. It is still possible to suggest that the equilibrium threshold between the two parameters represents the variable to be optimized (163, 165). However, at this time, no correlation has been observed between the system of relations that is particular to each species of macaque and the habitats that gave rise to them (164). Taken together, the organizations of the macaques can be interpreted as a single system of transformations in which the variation of one element modifies the others in turn and shifts the system from one state of equilibrium to another. From this point of view, dominance and kinship relations, degree of tolerance and reconciliation, the mother's permissiveness, the development of allomaternal behavior, or the frequency with which the young intervene in matings, for example, are covariant traits. Macaques can be classified on a four-point scale, from species strictly structured according to genealogy to those characterized by looser structures (164). As on a periodic table of the elements, it is possible to predict where a species fits in on the basis of a single known behavioral trait: the absence of interference by the young in matings indicates a low level of interindividual tolerance, which would place a species at one extreme of the scale; in contrast, extensive allomaternal behaviors would signal looser social relations, placing the species in question at the other end of the scale.

To assert that the type of organization is in part determined by internal forces of attraction by no means suggests that the external environment exerts no influence. But it does affirm that the action of ecological constraints is channeled by social organization. And above all, it means accepting all the consequences of this social channeling, in particular the appearance of unforeseen effects that the functionalist theories are powerless to explain. Studies over the past decade have revealed that the seasonal aspect of reproduction plays a pre-eminent role in determining mating tactics that are available to males. In species living in temperate climates, most females enter estrus in the fall, no male makes exclusive claims on them, and it follows that rank and paternity rate exhibit only a slight correlation. In contrast, in tropical species, reproduction takes place year round, there is generally no more than one female in estrus in a group, the dominant male is in a position to control her during the fertile period, and as a consequence, the probability of a

male's paternity is closely correlated with his social rank (170, 171, 172, 173). This entails the following paradox: in non-seasonal species with minor dominance differentials (*Macaca tonkeana*, *Macaca arctoides*), social rank has more influence on the reproductive success of males than in species in which hierarchical differences are marked but where fertility is synchronous (*Macaca mulatta*, *Macaca fuscata*). This separation of the asymmetry of dominance structures from the consequences of sexual competition is in flagrant contradiction of current socio-ecological models that explain the level of competition with reference to the distribution of food resources in the habitat where the species has evolved.

The consequences of dominance structures on reproductive success are difficult to demonstrate in primates because of the diversity of tactics that they are capable of employing (174, 175). Achieving high social rank entails not only advantages but also disadvantages in the form of wounds, stress, or pathology (129, 176, 177). To appreciate the individual's adaptation to its environment, the consequences of social organization in all its aspects must be considered. In animals with an extensive life span, only longitudinal studies lasting several decades are capable of evaluating the impact of a given factor on the reproductive success of individuals (177, 178, 179). Rather than considering a few behaviors that are presumed to be adaptive, such studies thus take into account all the effects of variables such as kinship ties or dominance structure, both in short-term competition and in their interference with fertility or life expectancy, maturation, or aging, or again in their potential repercussions such as kidnaping, adoption, or infanticide. Such a perspective approaches relations of causality with caution, giving contingency its due and avoiding the isolation of the various elements of the system. Appearances notwithstanding, this perspective is in every way opposed to Dunbar's puristic formulation of the functionalist vision, which assumes a single causal arrow: "Whatever an animal is and does is part and parcel of its reproductive strategy, for every action necessarily has consequences for the extent to which it can contribute genes to future generations" (180).

\* \* \*

The discovery of the structure of the genome was such a dramatic that it provoked unqualified support for the notion of a genetic program. The gene has been made into a homunculus of the phenotype, and the fact that the genetic code serves only to fabricate the primary structure of proteins (181) has been thoroughly lost from view. It is typical that the pioneering students of primatology (I. S. Bernstein, H. Kummer, T. E. Rowell), educated before the discovery of DNA, have repeatedly expressed reservations as to the omnipotence of natural selection. The study of behavior has profited greatly from the functionalist program, but we are now in danger of being dragged by the excesses of this program towards an impasse, if our theoretical constructions, however admirable they may be, cannot be regularly tested. The accumulation of unproven hypotheses, such as the strategy of infanticide or the existence of sperm competition (182), produces countless epicycles that threaten to change our theories into a Ptolemaic system. Too many articles end in discussions whose only *raison d'être* is to evaluate the respective merits of individual advantage, reciprocity, or kinship selection. Since any behavior can be explained by a clever combination of these different mechanisms, the postulate of adaptive function becomes unfalsifiable (30, 60, 183).

It can be stated as a rule that the role of epigenetic constraints becomes all the more important as the distance from the level of expression of the genome increases. It is thus at the level of the social phenotype that we must expect to encounter the most powerful effects of self-organizational forces that are not directly adaptive (55, 58). The mechanisms that explain that certain traits are the covariant product of other traits picked out by selection have not yet been given the attention they deserve. Two mechanisms originate in the constitution of the individual: these are *the link between individual traits and their pleiotropic effect on social organization*. It is known that different morphological and physiological traits of the individual covary because of interrelations at the level of the genome (e.g., pleiotropy of genes, gene linkage) or at that of development (e.g., allometric relations, physiological constraints). We must expect to find similar effects at the level of the individual's behavior because of the links between psychological, emotional, cognitive, or communicative abilities, whether the con-

straint that links them is genotypic or phenotypic. Because the psychological traits are linked to each other and to physical and psychological variables, aging or the female's endocrine state entails multiple effects upon behavior and social organization. In the same way, the faculties that make it possible to protect a social relationship can produce interference by the young in matings. The pleiotropic effect of individual traits is itself related to the fact that a single trait is capable of causing multiple effects on social organization. Thus it is that females' interest in their infant leads them to take care of their companions' offspring, or that the cognitive abilities necessary to solve a given problem are brought to bear in an entirely different domain. The notion of species-specific temperament (184, 185) allows us to understand that the individual's attributes produce a disposition to enter into one or another type of relationship. Temperament and other traits of group members are not independent of one another. The sum of behaviors of similarly constituted individuals engenders social forms by a simple iterative effect (139, 186). We know that life-history traits limit the number of possible social organizations (120, 187). Still, our knowledge is a long way from allowing us to appreciate to what degree the various individual traits generate or reinforce one another, or on the contrary, are mutually exclusive.

The long list of behaviors discussed above illustrates abundantly the *structural constraints* brought about by the interaction of individuals. These constraints play a major role in the social channeling of individual behaviors, and it is the action of these constraints that, through the interplay of kin-based coalitions, gives rise to a forced correlation between asymmetry of power and the degree of nepotism. Pleiotropy and the linkage of individual traits can be coupled with the intervention of structural constraints. To return to the example of allomaternal behavior, generalized interest in infants results from the phenotypic incompatibility between the possession of learning capacities separated from context and the selective attraction of females to their own offspring. The pleiotropic effects brought about by this trait can be expressed only in social organizations in which asymmetrical dominance structure is sufficiently weak enough for the mother to allow her companions to carry her infant.

Another mechanism that is largely ignored is *social inheritance*. We know that the parents' behavior is capable of affecting the phenotypic characteristics of their offspring and of influencing evolutionary processes (188, 189, 190). This is particularly true in species in which social learning is important and in which generations overlap broadly. In the rhesus macaque, mothers transmit their social rank and their alliance network to their offspring (161, 191). It has been shown that behaviors are correlated from one generation to the next: sociable mothers have sociable daughters (192), and restrictive mothers have restrictive daughters (193); still, in the absence of cross-fostering experiments such as those conducted on mice in laboratories, it is impossible to evaluate the respective roles that genetic inheritance and social inheritance play in these correlations. The action of the social milieu is not limited to parental influence, but involves all the members of a group. If young macaques belonging to two different species are gathered in a single group, it is observed that the rate of post-conflict reconciliation is multiplied threefold in one species (*Macaca mulatta*), stabilizing at a level comparable to the rate in the other species (*Macaca arctoides*); this effect persists for several weeks after the two species are separated (194). The socialization of the individual by its conspecifics contributes to the reproduction of the social milieu by influencing its temperament and the type of relations it will establish.

The processes of genetic assimilation and the action of an environment modified by preceding generations are the focus of recent theoretical developments (20, 195). If a subject inherits not only from the parental genome but also from the milieu created by its conspecifics, it can be said that there is a transmission of phenotype from one generation to the next. Compounding the direct influence of environmental factors on the subject is the additional action of the genome expressed through the demographic and behavioral traits of the social milieu; these traits in effect represent a phenotypic realization of the genotype of the individuals that make up the group (187). This action includes the influence of social forms and of characteristics that are not directly selected, and it can accelerate or slow down the process of evolution (188, 189). It is not yet possible to measure all the consequences of such

effects. Nevertheless, the social milieu that is thus created determines the conditions of selection and chooses a phenotype on the basis of the norm of reaction of the genotype.

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